# THE ECOLOGY OF SOUTH-EAST TASMANIAN PHYTAL ANIMAL COMMUNITIES. III. PATTERNS OF SPECIES DIVERSITY

# G.J. EDGAR

Department of Zoology, University of Tasmania, Box 252C, G.P.O. Hobart, Tasmania 7001, Australia

Abstract: Diversity indices which have been widely used in ecological studies were calculated for each of 135 samples of phytal macrofauna. A comparison of the properties of these indices indicated that they could be grouped into those primarily influenced by dominance (such as Simpson's Index, McIntosh's Index and  $E(S_2)$ ), those primarily influenced by the number of species (such as Menhinick's Index, Margalef's Index and Q), and those intermediate between the other two groups (such as the Shannon–Wiener Index and Brillouin's Index). Evenness indices were also calculated but were found to be highly dependent on sample size and consequently difficult to interpret.

Environmental correlates of dominance and the number of species per plant indicated that these two community parameters were relatively independent. Dominance and animal density were related as both appeared to be monotonically increasing functions of the level of food resources. The number of species was dependent on the weight of sampled algae but was also strongly influenced by wave exposure and habitat complexity (sensu number of microhabitats rather than rugosity). The wave exposure effects were interrelated to habitat structure; elongate plants having the greatest animal species densities at the sheltered site and compact plants having the greatest species densities at the exposed site.

#### INTRODUCTION

Phytal animal assemblages are useful for testing differing diversity hypotheses because samples are replicable, easily sorted, potentially rich in species (up to 100 macrofaunal species per plant) and the habitat complexity can be maintained as a constant by collecting algae of only one species. In fully marine regions free from pollution the environmental parameters are also readily defined by reference to depth, wave exposure, water temperature, and the structure of the algal community.

The initial aim of the present study was to determine the factors influencing the diversity of phytal animals at the semi-exposed and sheltered sites described earlier (Edgar, 1983a,b). To do this it was necessary to calculate diversity indices, rather than relying solely on the number of species per plant, because of the considerable variation in the size of algae sampled and consequently the number of animals associated with each plant. After calculating different indices, however, it became evident that the data could be interpreted to show that (1) diversity increased with depth, (2) diversity decreased with depth, (3) diversity was positively correlated with epiphytic biomass, and (4) diversity was negatively correlated with epiphytic biomass. The aim of this study was, therefore, extended from an investigation into the factors influencing the diversity of phytal animals at Bruny Is., Tasmania, to include an analysis of the more common

0022-0981/83/\$03.00 © 1983 Elsevier Science Publishers B.V.

diversity indices and to determine their usefulness in situations involving highly variable sample sizes.

During the past twenty years studies of diversity have evolved into distinct mathematical and biological streams with very few investigations during that time dealing with both of these aspects (one exception being the study of Sanders, 1968). The mathematically orientated approach has tended to involve the analysis of the properties of diversity indices, and the proposal of new ones. Field ecologists have been more interested in the causes of diversity, and generally rely on a few standard indices to describe a community of organisms and reduce it to one or two variables. The mathematical aspects are usually ignored in these studies on the basis that different diversity indices are highly correlated (e.g. Hicks, 1980).

The most widely used indices of diversity are the total number of species S (also known as the species richness, or as the species density if it relates to a physical variable, such as area; see Hurlbert, 1971), the Shannon-Wiener Information Index H' (MacArthur, 1965), Simpson's Dominance Index SI (Simpson, 1949) and Pielou's Evenness J (Pielou, 1966a). Hill (1973) found that these four measures were mathematically related and he proposed that the transformed indices  $N_1 = \exp(H')$  and  $N_2 = 1/SI$  were preferable to H' and SI because they follow Renyi's definition of a generalized entropy (which also includes the number of species  $S(=N_0)$ ), and  $N_1$  can be thought of as the number of abundant species and  $N_2$  as the number of very abundant species. He further recommended that  $N_1/N_0$  and  $N_2/N_1$  be used as evenness indices in preference to  $J(= \ln[N_1]/\ln[N_0])$ . Modifications to Hill's evenness indices, which were shown to be superior in situations with a low number of species, were proposed by Heip (1974)  $(N_1 - 1/N_0 - 1)$  and Alatalo (1981)  $(N_2 - 1/N_1 - 1)$ . Pielou (1966b) had previously demonstrated that H' cannot be used in situations where every member of the community has been counted, and in this situation Brillouin's Index H is appropriate. In a critical study of diversity, Hurlbert (1971) also suggested alternative indices to H'; viz. HE = the proportion of inter-individual encounters which is interspecific, and  $E(S_n)$  = the expected number of species in a random subsample of n individuals.

Other diversity indices which are occasionally used in ecological studies are Margalef's Index Ma (Margalef, 1967), Menhinick's Index Me (Menhinick, 1964), McIntosh's Index Mc (McIntosh, 1967) and the Species Dominance Index D (Berger & Parker, 1970). Recently, Kempton & Taylor (1976) proposed a further index, Q, based on the slope of the cumulative species curve in the mid-range of abundances, and it has been claimed that this index is better than others for discriminating between different communities (Kempton & Wedderburn, 1978).

A graphical procedure has also been used for comparing the diversities of communities. This involves the calculation of "rarefaction" curves to depict the number of species expected for any given number of individuals (Sanders, 1968; Simberloff, 1979). The original method used to calculate these curves has been shown to be incorrect and the appropriate methods are given by Hurlbert (1971) and Heck *et al.* (1975).

Since diversity trends on a localized scale have not always been found to be reflected

within a larger area (Jumars, 1976), the scale from which community information has been obtained is also of considerable importance. For convenience, diversity has been partitioned into different scales depending on how the investigator defines a habitat. The diversity within a habitat has been called the alpha diversity, differences between habitats the beta diversity and the total diversity of the system the gamma diversity (Whittaker, 1972). The present study has primarily been restricted to alpha diversity (the diversity of animal assemblages on individual plants).

Theories on the causes of diversity, particularly in reference to latitudinal gradients, are reviewed by Pianka (1966, 1974) and Rohde (1978) and invoke either physical or biological factors. The biological hypotheses are not discussed in the present study as they involve mechanisms such as predation (Paine, 1966) and competition (Dobzhansky, 1950) which have not been investigated but ultimately depend on physical factors within the environment. The major physical factors suggested to contribute to the diversity of communities are habitat heterogeneity, environmental stability, and the level of food resources (related to nutrients, light, and productivity).

The number of species within a habitat is now widely accepted to be closely related to the complexity of both physical and biological structures within the habitat (e.g. MacArthur, 1964; Abele, 1974; Luckhurst & Luckhurst, 1978). The effects of stability on diversity are much less clear because they are closely related to biogeographic processes, such as the dispersal of organisms, and need to be assessed on several different time scales. Pianka (1974) divided the stability hypotheses into three: (1) the evolutionary time hypothesis which assumes diversity increases with the age of the community by the speciation of organisms to fill available niches, (2) the ecological time hypothesis whereby niches in disturbed habitats are not completely occupied because plants and animals do not have sufficient time to re-invade the habitat fully, and (3) the climatic stability hypothesis which considers that few organisms can live in unstable environments where species need to have broad tolerance limits and consequently occupy broad niches. The contribution of nutrients to the diversity of systems is also problematical, with some authors claiming that productivity increases diversity (Connell & Orias, 1964) and others that it decreases diversity (Margalef, 1969). On the basis of computer simulations of simple non-equilibrium systems, Huston (1979) predicted that the greatest diversities would be found in areas of low productivity.

All three major physical factors suggested to influence diversity varied in a predictable manner within the phytal environment and were investigated in this study.

# SAMPLING METHODS

The sampling and sorting methods used to collect algae and extract the motile macrofaunal animals have already been described (Edgar, 1983a,b) and characteristics of the phytal assemblages at the two sites at Fancy Point given. These sites were both quite sheltered, but one locality at the end of a point (Edgar, 1983a) had greater wave

exposure and will be referred to as semi-exposed. Similar sampling and sorting procedures were also used to collect a further 15 algae from the exposed eastern coast of Bruny Island at One Tree Point (12 km NNE of Fancy Point, 43°6'S: 147°24'E) on 10 November, 1981. These samples comprised five plants of the elongate species Cystophora moniliformis<sup>1</sup> from 1 m below low water mark and a further five replicates each of Cystophora and the comparatively small-sized Zonaria sp. from 6 m depth.

# **RESULTS AND DISCUSSION**

# COMPARISON OF INDICES

The diversity and evenness indices investigated in this study are listed in Table I. These indices were calculated for each of the 135 faunal samples at the semi-exposed site. Pearson correlation coefficients, which indicate the degree of association between these indices, are shown below the diagonals in the correlation matrices of Tables II and III. Correlations relating the index O to the other indices have not been included as this index cannot be calculated when the number of species is low.

The number of species (S) was closely related to the number of individuals (N) as both were strongly influenced by algal weight. N was also positively correlated with Ma, and negatively correlated with Me, because species accumulated with sample size faster

Diversity and evenness indices investigated in the original	is study: $Mc$ is the widely used modification of McIntosh's index $(1-\sum n_i^2)$ .
	Diversity
S = number of species	$H = (1/N) \ln \frac{N}{n_1! n_2! \dots n_s!}$
$Ma = (S-1)/\ln N$	$E(S_n) = S - {\binom{N}{n}}^{-1} \sum_{i=1}^{S} {\binom{N-n_i}{n}}$
$SI = \sum p_i^2$	$N_1 = \exp(H')$
$H' = -\sum p_i \ln p_i$	$N_2 = 1/SI$
$Me = S/\sqrt{N}$	$Mc = 1 - \sum p_i^2$
$D = p_{\max}$ HE = $(N/N - 1)(1 - \sum p_i^2)$	$Q = (S/2)\overline{\log}(R_2/R_1)$
]	Evenness
$J = H' / \ln S$	$E_{21} = N_2 / N_1$
$E_{10} = N_1/S$ $E'_{10} = (N_1 - 1)/(S - 1)$	$E'_{21} = (N_2 - 1)/(N_1 - 1)$

s

TABLE I

N = total number of individuals;  $n_i$  = number of individuals of the *i*th species; n = number of individuals within the subsample;  $p_i$  = proportional abundance of the *i*th species;  $p_{max}$  = the maximum proportional abundance of any species;  $R_1$  = lower quartile of the species-abundance distribution;  $R_2$  = upper quartile of the species-abundance distribution;  $S_n$  = number of species in a subsample of n individuals.

<sup>&</sup>lt;sup>1</sup> See Table VII for taxonomic authorities.

TABLE II

Pearson correlation coefficients relating diversity indices, the number of individuals and the number of species: correlations below the diagonal were calculated from 135 samples with variable abundances; correlations above the diagonal were calculated from 60 samples with between 50 and 200 individuals.

Index	N	S	H'	$N_1$	SI	$N_2$	Н	Ma	Me	Mc	HE	Q	6
N	-	0.51	0.17	0.18	-0.15	0.11	0.31	0.27	-0.13	0.14	0.11	-0.12	0.00
S	0.72	I	0.84	0.84	- 0.69	0.72	0.86	0.96	0.77	0.72	0.68	-0.61	0.74
H'	0.03	0.58		0.94	-0.95	0.89	0.99	06.0	0.86	0.97	0.95	- 0.90	0.70
N,	-0.02	0.55	0.94	Ţ	-0.82	0.97	0.93	0.90	0.86	0.89	0.82	-0.82	0.72
SI	0.04	-0.40	-0.93	-0.81		-0.79	-0.95	-0.75	-0.73	-0.99	- 1.00	0.96	-0.54
$N_2$	-0.13	0.37	0.87	0.96	-0.80	-	0.87	0.79	0.77	0.88	0.79	-0.85	0.59
Н	0.19	0.73	0.97	0.91	-0.87	0.80		0.89	0.79	0.96	0.94	- 0.89	0.65
Ma	0.42	0.89	0.83	0.81	- 0.66	0.65	0.88	1	0.91	0.78	0.74	-0.66	0.83
Me	- 0.44	0.02	0.70	0.69	0.68	0.73	0.51	0.46	1	0.76	0.74	-0.66	0.86
$M_{C}$	- 0.07	0.40	0.96	0.88	-0.99	0.88	0.88	0.68	0.72	1	0.98	-0.97	0.57
НЕ	-0.13	0.23	0.85	0.71	- 0.90	0.74	0.67	0.51	0.69	0.89	1	-0.96	0.54
D	0.11	-0.27	-0.78	- 0.78	0.94	-0.84	-0.75	-0.53	-0.66	-0.95	-0.92		-0.43

# DIVERSITY OF PHYTAL ASSEMBLAGES

than ln N but slower than  $\sqrt{N}$ . All of the evenness indices were negatively correlated with animal abundance (N) at a highly significant level (P < 0.001).

In order to reduce the variability caused by sample size, the correlation coefficients above the diagonal of the matrices given in Tables II and III were calculated using the 60 samples having between 50 and 200 individuals.

The diversity indices can be divided into those sensitive to the species richness of the phytal assemblage (S, Ma, Me, Q), those sensitive to the dominance of the assemblage  $(SI, N_2, Mc, HE, D)$ , and those falling between the other two groups  $(H', N_1, H)$ . These three groupings are more clearly seen by relating the different indices to the  $E(S_n)$  series of Hurlbert (1971) (Table IV). The expected number of species in a random subsample of two individuals  $E(S_2)$  is directly related to SI and consequently, but with differing degrees of linearity, to  $N_2$ , HE (Peet, 1974) and Mc (Heip & Engels, 1974). The curvilinear relationship between SI and  $N_2(=1/SI)$  resulted in a greater correlation

#### TABLE III

Pearson correlation coefficients relating evenness indices, the number of individuals and the number of species: correlations below the diagonal were calculated from 135 samples with variable abundances; correlations above the diagonal were calculated from 60 samples with between 50 and 200 individuals.

	N	S	J	$E_{10}$	$E_{21}$	$E'_{10}$	$E'_{21}$
N	1	0.51	-0.09	-0.32	- 0.11	-0.28	-0.05
S	0.72	1	0.50	0.18	-0.12	0.28	0.06
J	-0.55	-0.34	1	0.89	0.47	0.94	0.65
$E_{10}$	-0.64	-0.62	0.91	1	0.72	0.99	0.81
$E_{21}$	-0.41	-0.58	0.66	0.82	1	0.66	0.97
$E'_{10}$	-0.61	-0.55	0.95	0.99	0.80	1	0.78
$E'_{21}$	-0.38	-0.46	0.78	0.85	0.97	0.86	1

#### TABLE IV

Pearson correlation coefficients relating diversity indices and indices in the  $E(S_n)$  series: correlations were calculated from 60 samples with abundances between 50 and 200 individuals.

Index	$E(S_2)$	$E(S_3)$	$E(S_5)$	$E(S_7)$	$E(S_{10})$	$E(S_{15})$	$E(S_{25})$	$E(S_{50})$
N	0.109	0.101	0.082	0.066	0.049	0.031	0.003	-0.026
S	0.675	0.689	0.710	0.726	0.743	0.763	0.786	0.808
H'	0.947	0.960	0.976	0.983	0.986	0.984	0.971	0.933
$N_1$	0.819	0.845	0.882	0.905	0.925	0.940	0.946	0.926
Sİ	- 0.999	- 0.997	-0.985	-0.970	-0.950	-0.921	-0.877	-0.808
$N_2$	0.790	0.818	0.856	0.878	0.894	0.901	0.892	0.850
H	0.938	0.949	0.959	0.962	0.960	0.951	0.929	0.881
Ма	0.744	0.761	0.789	0.811	0.834	0.862	0.895	0.927
Me	0.741	0.761	0.797	0.825	0.855	0.890	0.933	0.976
Мс	0.984	0.991	0.994	0.989	0.978	0.955	0.916	0.847
Q	0.545	0.561	0.594	0.624	0.661	0.709	0.774	0.843
HE	1.000	0.998	0.987	0.973	0.953	0.925	0.883	0.814
D	-0.955	-0.958	-0.950	-0.936	-0.913	-0.877	-0.821	-0.739

coefficient between  $N_2$  and  $E(S_{15})$  than  $E(S_2)$ . Non-parametric correlation coefficients, however, would obviously relate  $N_2$  and  $E(S_2)$  at the maximum level. D was also closely associated with the lower end of the  $E(S_n)$  series. Ma, Me and Q were much more significantly correlated with  $E(S_n)$  indices in the upper end of the series and hence are measures of species richness  $(E(S_N) = S)$ . H' showed an almost 1:1 correspondence with the intermediate index  $E(S_{10})$ . This relationship, found and discussed previously by Smith et al. (1979), was surprisingly independent of the number of individuals within the sample (Table V).

Pearson corre	elation	coefficients	s relating <i>I</i> from sam	H' and ind ples with	ices in the differing a	$E(S_n)$ series.	es: correlati	ons were c	alculated
Abundance range	n	$E(S_2)$	$E(S_3)$	$E(S_5)$	$E(S_7)$	$E(S_{10})$	$E(S_{15})$	$E(S_{25})$	E(S <sub>50</sub> )
10-25	16	0.965	0.978	0.988	0.985	0.972			4
26-50	25	0.946	0.973	0.991	0.993	0.991	0.985	0.970	
51-100	36	0.948	0.963	0.981	0.990	0.995	0.993	0.978	0.935
101-200	23	0.953	0.966	0.980	0.987	0.992	0.994	0.991	0.965
201 +	31	0.932	0.953	0.978	0.989	0.994	0.994	0.984	0.964

TABLE V

The evenness indices, particularly J, tended to be positively correlated with S when samples with approximately the same number of individuals were compared. Sheldon (1969) and De Benedictis (1973) showed that this correlation follows directly from the theoretical properties of evenness indices.

Evenness and species richness are generally considered to be end points of a continuum, with the different measures of diversity being influenced by these two components in varying proportions (Peet, 1974). This assumption is unjustified as both the  $N_2 \rightarrow N_1 \rightarrow N_0$  series of Hill and the  $E(S_2) \rightarrow E(S_{10}) \rightarrow E(S_N)$  series indicate that the commonly used diversity indices fall between Simpson's Index, or a directly related function, and the number of species. Evenness indices are best visualized as functions of the gradients of these diversity series. It should be evident that even though  $N_2$  is often considered to be an evenness term (e.g. Birch, 1981) it differs considerably by being a number rather than a ratio. For the example of a community composed of two species in equal numbers,  $N_2$  is very low (= 2, the number of very abundant species) while all evenness indices are maximal (= 1).

The implication of the extremely strong correlation between the evenness indices and animal abundance is that evenness indices should be used with great caution to characterize communities. In samples of a community where all species have not been counted, evenness indices will necessarily decrease with increasing sample size because the denominator of the evenness ratio increases at a faster rate than the numerator as species are added to the collection. This effect is clearly seen in the example given in

Table VI and is most characteristic of indices which incorporate S. Although J has been widely employed to describe sampled communities, it generally has been incorrectly used because the total number of species has not been known (see Pielou, 1975).

### TABLE VI

Diversity and evenness indices calculated for an assemblage of phytal animals collected from Acrocarpia paniculata and several derived subsamples: the distribution of abundances of the species in Collection 1 (with frequencies in parentheses) was 928, 784, 765, 234, 194, 149, 57, 52, 43, 24, 22, 20, 18, 17, 16, 15, 13, 11, 9, 8(2), 7, 5(2), 4(4), 3(3), 2(9), 1(19); Collection 2 represented the expected abundances of species in a subsample of 10% of Collection 1 (a species-abundance distribution of 93, 78, 77, 23, 19, 15, 6, 5, 4, 2(7), 1(8)); Collection 3 represented a 99% reduction of Collection 1 (a species-abundance distribution of 9, 8(2), 2(2), 1(3)); Collection 4 was similar to Collection 3 but expanded 100 times (a species-abundance distribution of 900, 800(2), 200(2), 100(3)).

-		Colle	ection		
Index	1	2	3	4	
N	3466	342	32	3200	
S	59	24	8	8	
H'	2.13	2.04	1.72	1.72	
SI	0.182	0.187	0.215	0.215	
$N_1$	8.43	7.67	5.59	5.59	
$N_2$	5.49	5.35	4.65	4.65	
J	0.52	0.64	0.83	0.83	
$E_{10}$	0.143	0.32	0.70	0.70	
$E_{10}^{\prime}$	0.128	0.29	0.66	0.66	
$E_{21}^{10}$	0.65	0.70	0.83	0.83	
$E_{21}^{'}$	0.60	0.65	0.80	0.80	

Evenness indices based on the ratio of  $N_2$  to  $N_1$  are more robust because they become relatively independent of sample size whenever animal abundances exceed a threshold level. Despite the theoretically unbounded nature of H', Margalef (1972) has shown that this index is bounded in practical situations (see also May, 1975), and Sanders (1968) found that it remained constant with sample sizes > 200 individuals. Thus, changes in sample sizes above 200 individuals will probably not greatly affect H',  $N_1(=\exp(H'))$ or  $N_2$  (which varies only in a relatively minor way with animal abundance), and the index  $N_2/N_1$  can be reliably used. Alatalo's (1981) correction should be used in these situations, however, to prevent the anomaly of  $N_2/N_1$  going to 1 in situations of extreme dominance.

For each of the phytal samples discussed in the following sections, the number of individuals (N), the number of species (S) and the inverse of Simpson's Index  $(N_2)$  have been used to describe the samples because they encompass the range of diversity indices. S was chosen in preference to the other three species richness indices because the relationships between S and  $\ln N$  and  $\sqrt{N}$  were not linear, and Q becomes unreliable with low species number (Kempton & Wedderburn, 1978). If all samples in this study had been rich in species Q could have been usefully used to reduce the variability caused

by differing sample size. All dominance related indices  $(SI, N_2, HE, E(S_2), Mc, D)$  could equally well have been used as parameters of phytal samples.  $N_2$  was chosen because it is expressed in the same units as S and hence is directly comparable. Moreover, the other dominance-related indices are bounded on both sides (by 0, 1 or 2) and as they approach the asymptote show relatively minor changes with marked changes in the species-abundance distribution. The inverse of dominance, which is measured by  $N_2$ , will be referred to as heterogeneity (see Peet, 1974).

Alatalo's correction of Hill's Ratio  $(E'_{21})$  has also been calculated for each sample so that comparison can be made with evenness indices published in related studies. Significant correlations between this index and physical variables generally have not, however, been discussed because they were directly attributable to changes in the other community parameter.

# HABITAT COMPLEXITY

The mean values and the standard deviations of the diversity parameters for each algal species collected at the semi-exposed site are listed in Table VII. There is little evidence to support Hick's (1980) contention that algae with relatively large surface areas (such as Cladophora feredayi, Halopteris pseudospicata, Anotrichium sp., and Ulva sp.) possess greater habitat complexity than other algal species, and consequently greater diversity of animals. In fact, the opposite relationship seems to occur with the highly dissected algae having both fewer species and lower animal heterogeneity. The comparatively low diversity of animals among the fine-bladed algae was confirmed by the correlation coefficients relating the measured physical components of algal structure (see Edgar, 1983a) and  $N_2$  (Table VIII). Non-parametric Spearman rank correlations rather than Pearson correlations were calculated between the physical variables and the community parameters because many of these relationships were not linear. The highly significant correlation between the log final width of branches (LFW) and  $N_2$  was presumably a direct consequence of the size relationships described by Edgar (1983a). Filamentous algae have a preponderance of small animals with large population sizes, resulting in the considerable numerical dominance of a few species (Fig. 1). The degree of branching (DB) and  $N_2$  were also significantly correlated, largely because of the high intercorrelation between DB and LFW (r = -0.502). As well as the filamentous algal species, the wide-bladed algae Ulva sp. and Carpoglossum confluens were also characterized by very low animal heterogeneity. Carpoglossum possessed a slimy coating of chemical exudates and it is possible that few animal species survive for long periods on both this species and Ulva because of toxins such as those reported by Magre (1974).

The great variability in the weights and surface areas of the different algal species makes comparison of the number of species between plants difficult. Nevertheless, the species number against log abundance curve shown in Fig. 2 indicates that the algae with the relatively greater number of species (high species richness) were those such as Sargassum bracteolosum, Seirococcus axillaris, Caulerpa geminata, and Jeannerettia

Algal species	N	S	$N_2$	$E_{21}'$
Thamnoclonium clariferum J. Ag.	99.4 + 28.6	25.4 + 7.9	$10.6 \pm 3.4$	$0.66 \pm 0.13$
Anotrichium sp.	$28.2 \pm 19.3$	$8.4 \pm 3.0$	$3.8 \pm 1.2$	$0.67 \pm 0.08$
Hemineura frondosa Harv.	67.4 ± 32.8	$20.2 \pm 3.3$	$9.9 \pm 1.5$	$0.72 \pm 0.07$
Plocamium angustum Hook. & Harv.	$94.6 \pm 45.0$	$22.6 \pm 7.7$	$5.8 \pm 0.6$	$0.54 \pm 0.11$
Phacellocarpus labillardieri (Mert.) J. Ag.	$79 \pm 110$	$25.8 \pm 10.5$	$7.1 \pm 2.8$	$0.59 \pm 0.15$
Jeannerettia lobata Hook. & Harv.	$109 \pm 59.6$	$26.2 \pm 5.7$	$10.1 \pm 2.9$	$0.64 \pm 0.08$
Hormosira banksii (Turn.) Dec.	49.8 ± 34.8	$10.2 \pm 4.7$	$5.8 \pm 3.3$	$0.75 \pm 0.07$
Halopteris pseudospicata Sauv.	$740 \pm 517$	25.6 ± 6.8	$3.9 \pm 1.2$	$0.59 \pm 0.08$
Ecklonia radiata (C. Ag.) J.Ag. fronds	$16.0 \pm 14.7$	$9.0 \pm 5.0$	$6.2 \pm 2.6$	$0.86 \pm 0.14$
Ecklonia radiata holdfasts	114 ± 87.6	$24.2 \pm 8.6$	$8.7 \pm 3.6$	$0.62 \pm 0.15$
Acrocarpia paniculata (Turn.) Aresch.	$2032 \pm 1336$	$52.2 \pm 11.3$	$5.6 \pm 1.0$	$0.51 \pm 0.08$
Cystophora torulosa (R.Br. ex Turn.) J. Ag.	550 ± 475	$34.6 \pm 10.0$	$7.8 \pm 4.5$	$0.59 \pm 0.12$
Cystophora retroflexa (Labill.) J. Ag.	321 ± 528	$22.8 \pm 10.6$	$8.7 \pm 3.5$	$0.68 \pm 0.12$
Cystophora moniliformis (Esper) Wom. & Niz.	657 ± 596	$30.6 \pm 8.9$	$6.3 \pm 2.4$	$0.52 \pm 0.10$
Caulocystis cephalornithos (Labill.) Aresch.	$409 \pm 320$	$25.4 \pm 5.1$	$8.2 \pm 2.4$	$0.70 \pm 0.06$
Sargassum decipiens (R.Br. ex Turn.) J. Ag.	$607 \pm 536$	$31.2 \pm 13.5$	$8.7 \pm 2.2$	$0.63 \pm 0.12$
Sargassum bracteolosum J. Ag.	$210 \pm 97.6$	$33.2 \pm 8.0$	$13.2 \pm 3.9$	$0.68 \pm 0.08$
Sargassum verruculosum (Mert.) C. Ag.	$60.0 \pm 65.9$	$13.2 \pm 6.6$	$6.2 \pm 3.6$	$0.69 \pm 0.12$
Carpogiossum confluens (R.Br. ex Turn.) Kuetz.	$39.2 \pm 26.8$	$8.2 \pm 4.2$	$3.4 \pm 2.5$	$0.69 \pm 0.23$
Seirococcus axillaris (R.Br. ex Turn.) Grev.	$632 \pm 470$	38.0± 9.9	$9.7 \pm 6.8$	$0.56 \pm 0.20$
Zonaria turneriana J. Ag.	$47.8 \pm 19.3$	$20.4 \pm 8.9$	$12.3 \pm 6.3$	$0.76 \pm 0.09$
Zonaria sp.	73.6 ± 32.5	$18.8 \pm 5.8$	$7.4 \pm 4.1$	$0.59 \pm 0.13$
Caulerpa trifaria Harv.	36.6 ± 22.2	$17.2 \pm 7.2$	$10.3 \pm 4.1$	$0.78 \pm 0.13$
Caulerpa geminata Harv.	$63.8 \pm 18.6$	$24.6 \pm 7.0$	$13.5 \pm 6.0$	$0.72 \pm 0.11$
Ulva sp.	$21.8 \pm 16.8$	$4.8 \pm 2.3$	$2.4 \pm 1.1$	$0.72 \pm 0.24$
Cladophora feredayi Harv.	72.2 ± 34.1	$11.4 \pm 2.2$	$4.7 \pm 1.3$	$0.70 \pm 0.11$

TABLE VII

Mean values ( $\pm$  SD) of the community parameters for the algal species collected at Fancy Point.

190

G.J. EDGAR

#### DIVERSITY OF PHYTAL ASSEMBLAGES

#### TABLE VIII

Spearman rank correlation coefficients relating community parameters and the physical variables discussed in detail by Edgar (1983a): DE, depth; WW, wet wt; DW, dry wt; EW, epiphytic wt; SA, surface area; ML, maximum length; LMW, log maximum width of primary axis; DB, degree of branching; LFD, log depth of final branches; LFW, log width of final branches; \* 0.05 > P > 0.01; \*\* 0.01 > P > 0.001; \*\*\* P < 0.001.

Variable	N	S	N <sub>2</sub>	E' <sub>21</sub>
DE	-0.362***	-0.165	0.345***	0.284**
WW	0.589***	0.568***	-0.004	-0.196*
DW	0.462***	0.469***	0.006	-0.190*
EW	0.462***	0.423***	0.104	-0.038
SA	0.471***	0.265**	-0.281**	-0.244**
ML	0.405***	0.266**	0.148	-0.118
LMW	0.201*	0.269**	0.123	-0.062
DB	0.132	-0.075	-0.356***	-0.282**
LFD	0.112	0.235*	0.195*	0.118
LFW	-0.164	0.114	0.390***	0.192*



Fig. 1. Hypothetical example showing the greater expected heterogeneity of animals on wide-bladed algae (such as *Zonaria*) compared to finely-branched algae (such as *Halopteris*): A, the total size-abundance distribution of two amphipod species among all algae within the area studied, note that small species are generally more abundant than larger species; B, the relative proportions of the total animals of different sizes which are found on finely-branched and wide-bladed algae (cf. the size distributions of animals associated with *Halopteris* and *Zonaria* in Fig. 4, Edgar, 1983a); C, the expected size distributions of the two amphipod species on finely-branched and wide-bladed algae.

*lobata* with considerable variation in the widths of axes and branches. Algae growing close to the reef substratum such as *Caulerpa* spp., *Zonaria* spp., *Ecklonia radiata* holdfasts, and *Cystophora torulosa* were also rich in species, primarily because they have a component of benthic as well as phytal animals. One further alga with high species richness, *Thamnoclonium clariferum*, was heavily colonized by epiphytic sponges and bryozoans and had a number of animal species associated with this sessile fauna (e.g. the amphipods *Leucothoe* spp., *Colomastix* sp., and *Seba* sp.). The correlation



Fig. 2. Relationship between the number of species and the logarithm of the number of individuals for animals collected from different algae: the curve of best fit  $y = 1 + 4.55x^{1.974}$  has been plotted; algal abbreviations are as follows, T.c., Thamnoclonium clariferum; A.sp., Anotrichium sp.; H.f., Hemineura frondosa; P.a., Plocamium angustum; P.l., Phacellocarpus labillardieri; J.l., Jeanneretia lobata; H.b., Hormosira banksii; H.p., Halopteris pseudospicata; E.r.f., Ecklonia radiata fronds; E.r.h., Ecklonia radiata holdfasts; A.p., Acrocarpia paniculata; C.to., Cystophora torulosa; C.r., Cystophora retroflexa; C.m., Cystophora moniliformis; C.ce., Caulocystis cephalornithos; S.d., Sargassum decipiens; S.b., Sargassum bracteolosum; S.v., Sargassum verruculosum; C.co., Carpoglossum confluens; S.a., Seirococcus axillaris; Z.t., Zonaria turneriana; Z.sp., Zonaria sp.; Ca.t., Caulerpa trifaria; Ca.g., Caulerpa geminata; U.sp., Ulva sp.; C.fe., Cladophora feredayi.

coefficients shown in Table VIII indicate that the number of species and the number of individuals increased with the weight of algae and epiphytes at approximately the same level of significance. Surface area was much more highly correlated with N than with S. The large number of animal species associated with algae having both wide and thin axes probably caused the significant correlation between the log maximum width of primary axis (LMW) and S.

Perhaps the reason for the disagreement between the findings of this study and those of Hicks (1980) relates to the size of the organisms under investigation. Macrofauna possibly treat filamentous algae as a single habitat, but partition the wider algae into several habitats of differing branch widths, while meiofaunal harpacticoid copepods respond to the surface area of wide algae as a unit but subdivide the filamentous environment. In a related study on habitat complexity, Luckhurst & Luckhurst (1978) found that the number of large fish species was significantly correlated with the rugosity of coral reefs, but no significant relationship was found for the smaller species.

# DEPTH

The heterogeneity of the phytal assemblage increased significantly with depth but the number of individuals and the number of species decreased, the latter, however, at an insignificant level (Table VIII). In order to reduce the variability resulting from differences in size and shape of algae, the correlation coefficients were re-calculated using data from the elongate fucoid algae belonging to the genera *Cystophora, Acrocarpia, Caulocystis,* and *Sargassum* which had wet weights between 25 and 200 g. Animal abundance ( $r_s = -0.674$ , n = 28, P < 0.001) and number of species ( $r_s = -0.517$ , P = 0.002) were again negatively correlated with depth, while  $N_2$  ( $r_2 = 0.446$ , P = 0.009) and evenness ( $r_s = 0.614$ , P < 0.001) were positively correlated with depth.

The scatter diagram relating S to depth (Fig. 3) shows that the relationship between



Fig. 3. Scatter diagram showing the number of species versus depth for animals associated with elongate fucoid algae.

these variables was non-linear, with a pronounced increase in the number of species per plant (the species density) occurring in waters shallower than 2 m. This depth was similar to that at which considerable changes in both the algal and faunal assemblages occurred (Edgar, 1983a).

The decrease in the dominance of the phytal assemblage with depth was caused by several very abundant amphipods which were present only in shallow water and were probably responding to the increased food resources in regions of considerable water flow (Edgar, 1983a). When the species-abundance distributions of animals among the five *Sargassum verruculosum* and *Caulocystis cephalornithos* collected in shallow water are compared with the faunas on five similar plants from deeper water (Fig. 4) it is clearly evident that very abundant phytal species were absent from deep water. *Caulo* 



Fig. 4. Species-abundance distributions of the faunas collected from *Sargassum veruculosum* and *Caulocystis* cephalornithos from shallow (A, < 2.2 m) and deep (B, > 2.3 m) water depths.

*cystis* and *Sargassum verruculosum* were grouped together in this analysis because the faunas on these species were previously found to be indistinguishable (Edgar, 1983b) and the mean dry weight of these algae collected in deep water (4.20 g) was similar to that of plants from shallow water (4.46 g). The abundance histograms of the faunas associated with these algae also indicate that the "shallow" algae had a greater component of rare animals (those occurring on a single occasion) than the "deeper" plants. This may be related to the species richness of the algal assemblage which was greatest at 1 m depth (Edgar, 1983a) and possibly allowed a comparatively large species pool of phytal animals to coexist.

# SEASON

Despite the peaks of abundance shown by most animal species occurring in late summer or early autumn (Edgar, 1983b), the heterogeneities of the phytal assemblages



Fig. 5. Seasonal variation in the mean number of animal species per plant ( $\bigcirc$ ) and  $N_2$  ( $\bigcirc$ ) for phytal assemblages collected from different algae.

on all erect algae were low at this time (Fig. 5) because the plants were dominated by a few rapidly growing amphipod species capable of responding quickly to the considerable epiphytic resources. The heterogeneity of animals was greater on *Zonaria* than on the erect algae during the summer, possibly due to the large proportion of benthic species in the *Zonaria* assemblage partly buffering the dramatic increases in the abundant phytal species.

Seasonal changes in S were opposite to changes in  $N_2$  with the greatest number of phytal species per plant occurring in March and April. This was caused by the collection of rare species on plants most frequently during autumn, the time when those species became most abundant, rather than the migration of additional species from other habitats. The total number of species collected from July to December (191 species) was almost identical to the number collected over the first six months of the year (187 species) when the species densities of animals associated with individual plants were greatest.

Thus, seasonal changes in the heterogeneity and the number of phytal species per plant were almost certainly related to the level of epiphytes. Whether the primary response of phytal animals to epiphytes was due to the increased food resources or to the habitat complexity of filamentous algae remains to be determined, but it is likely that these factors were interrelated and both contributed to the species diversity patterns.

### EXPOSURE

The responses of the community parameters to exposure depended greatly on algal shape (Table IX). At the exposed site, the animal assemblage associated with elongate *Cystophora moniliformis* was characterized by very low species richness and the extreme abundance and dominance of two filter-feeding amphipod species. *Podocerus* sp. comprised 95% of all animals at 1 m depth while 84% of the total abundance at 6 m depth was contributed by *Caprella* sp. Animal abundance did not vary greatly with exposure at the sheltered and semi-exposed sites but remained considerably less than at the fully exposed site. The number of animal species also remained approximately constant at the Fancy Point sites while animal heterogeneity increased with the degree of shelter.

The number of species and heterogeneity of the faunal assemblages associated with *Zonaria* showed the opposite relationships to those deduced for the elongate algae. S and  $N_2$  both increased with the degree of wave exposure.

Few animal species probably survive the whiplash motion of *Cystophora* at the exposed site while *Zonaria* clumps buffer the effects of wave action and act as refuges. This is indicated by the greater number of animal species on *Cystophora* at 6 m depth, where wave action would have been considerably diminished, than at 1 m. Moreover, the two amphipod species which occurred abundantly on *Cystophora* were adapted to the motion of the environment by possessing strong, hook-like pereiopods.

The greater numbers of animal species on Zonaria at One Tree Point compared with the more sheltered, and hence stable, Fancy Point sites indicates that the number of

X	
Е	
ABI	
Ĥ.	

Mean values ( $\pm$  SD) of the dry weights of algae collected at sites with different wave exposure, and the community parameters associated with those algae: five replicates were collected in all cases other than at the sheltered site where data for 15 algae collected in September, October, and November have been grouped; S' indicates the total number of species collected in five samples; E, fully-exposed; M, semi-exposed; S, sheltered.

		Danth	Der ut					
Algal species	Exposure	m (m)	(g)	N	S	S	$N_2$	$E_{21}'$
Elongate algae						and the second		
Cystophora moniliformis	Ш	1	$4.9 \pm 6.6$	$1250 \pm 1920$	23	$9.4 \pm 2.7$	$1.4 \pm 3.9$	$0.35 \pm 0.21$
Cystophora moniliformis	ш	9	$9.3 \pm 9.2$	784 ± 462	34	$14.4 \pm 5.6$	$2.6 \pm 2.9$	$0.53 \pm 0.12$
Cystophora moniliformis	Μ	-	$14.2 \pm 11.7$	$657 \pm 596$	56	$30.6 \pm 8.9$	$6.3\pm2.4$	$0.52 \pm 0.10$
Sargassum decipiens	M	1	$4.4 \pm 3.9$	$607 \pm 536$	61	$31.2 \pm 13.5$	$8.7 \pm 2.2$	$0.63 \pm 0.12$
Sargassum verruculosum and Caulocystis cephalornithos	M	1	$4.5 \pm 2.8$	$344 \pm 377$	58	$21.4 \pm 9.0$	$6.8 \pm 3.4$	$0.65 \pm 0.09$
Sargassum verruculosum and Caulocystis cephalornithos	Μ	4	$4.2 \pm 3.2$	$125 \pm 103$	40	$17.2 \pm 8.4$	$7.7 \pm 3.0$	$0.73 \pm 0.06$
Sargassum verruculosum	S	ę	$8.2 \pm 3.6$	$374 \pm 147$	53 ± 12	$30.9 \pm 6.0$	$9.7 \pm 2.4$	$0.68 \pm 0.10$
Caulocystis cephalornithos	S	3	14.7 ± 9.1	$426 \pm 287$	<b>61</b> ± 17	$33.2 \pm 8.0$	$10.5 \pm 2.4$	$0.64 \pm 0.07$
Short algae								
Zonaria sp.	ц	9	$2.1 \pm 1.2$	$235 \pm 227$	16	$37.0 \pm 16.6$	$13.9 \pm 12.3$	$0.59 \pm 0.20$
Zonaria sp.	Σ	7	$3.8 \pm 2.0$	$73.6 \pm 32.5$	56	$18.8 \pm 5.8$	7.4 ± 4.1	$0.59 \pm 0.13$
Zonaria turneriana	M	7	$2.1 \pm 1.4$	$47.8 \pm 19.3$	69	$20.4\pm8.9$	$12.3 \pm 6.3$	$0.76 \pm 0.09$
Zonaria turneriana	S	ę	$1.2 \pm 1.0$	$98.5 \pm 117$	$40 \pm 10$	$17.3 \pm 6.4$	$7.2 \pm 2.2$	$0.71 \pm 0.12$

species gradually increases with exposure but sharply declines in conditions of extreme wave action (such as encountered by the *Cystophora* assemblage). A very similar relationship was found previously in New Zealand by Fenwick (1976). A reduction in species number in sheltered environments could account for the relatively low species density which was observed at the greatest depths at Fancy Point.

# COMPARISON OF MARINE AND TERRESTRIAL COMMUNITIES

A distinctive characteristic of macrofaunal phytal assemblages is the wide distributions among plants of almost all of the animal species (Edgar, 1983a). Although many animals associated with terrestrial plants are also generalists, specialists restricted to one or a few plant species comprise a sizeable proportion of communities (Eastop, 1972; Futuyma & Gould, 1979). The major reason for this contrast in community structure is probably the almost exclusive reliance of phytal animals on food resources external to the plant substratum (such as detritus, epiphytic algae, and particles in the water column). Animals residing on terrestrial plants, other than carnivores, generally feed directly on plant tissues or sap, and those animal species which specialize probably do so in order to breach particular chemical defenses (Janzen, 1973b). It is notable that the one abundant alga-boring animal at Fancy Point (the amphipod *Bircenna* sp.) was only collected from algae belonging to the order Fucales.

The sampling techniques used to collect fauna associated with terrestrial plants are varied but differ considerably from the methods used in this investigation. Consequently, published data which are directly comparable to the results of this study are not available. Nevertheless, a subjective comparison of related terrestrial data (e.g. the samples of Menhinick, 1967; Janzen, 1973a,b; Root, 1973) indicates that marine systems probably have greater alpha species density but much lower gamma species density. This is to be expected because of both the greater environmental stability of marine compared with terrestrial environments, and the increased animal densities resulting from the abundant external food resources. On the other hand, gamma species density is likely to be far greater in terrestrial systems because environmental gradients (temperature, humidity, rainfall, etc.) have considerable local ranges of variation and consequently can be partitioned into a relatively large number of distinct macro- and micro-habitats. The species richness of plants themselves, correlated with insect diversity by Murdoch *et al.* (1972), also contributes to the gamma diversity of plant-associated animals and is several orders of magnitude higher on the land than in the sea.

Birch (1981) recently suggested that terrestrial and marine systems may be organized in different ways because species richness and evenness tended to be negatively correlated in marine communities but were presumed to be positively correlated in terrestrial communities. He found no similar correlation between S and SI. While these findings could be explained in terms of the differences in alpha and gamma diversity discussed above, a re-evaluation of the data used by Birch indicated that the significant correlation almost certainly resulted from nothing more than the mathematical property that evenness is negatively correlated with animal abundance. The two cited papers with data showing significant correlations between S and (1-J) (Gauld & Buchanan, 1959; McCloskey, 1970) also showed equally significant correlations between N and both S and (1-J).

## CONCLUSIONS

Animal abundance (N), the number of species (S) and animal heterogeneity  $(N_2)$  each provided useful information on the structure of phytal assemblages in this study. Animal abundance and  $N_2$  were closely related to each other as they appeared to be dependent on the level of food resources within the environment. The number of species and  $N_2$ proved to be relatively independent and presumably responded to different environmental conditions. S and  $N_2$  were positively correlated to each other in the studies of the exposure gradient and algal structure, but were negatively correlated in the studies of depth and seasonal variation.

Evenness indices did not contribute to the understanding of Bruny Island phytal assemblages. There is little doubt that evenness indices can efficiently discriminate between samples with different species-abundance distributions. Interpretation of these differences, however, is difficult because of the varied influences of animal abundances, species richness and dominance on evenness. The correlation found in this study between depth and  $E'_{21}(r_s = 0.614, n = 28, P < 0.001)$  was much more significant than those between depth and either S or  $N_2$ . Nevertheless, this predictable change in evenness could only be understood by reference to other indices and resulted from the synergistic effects of decreased animal abundance and increased heterogeneity with depth. Similar criticisms of evenness were originally made by Peet (1975) but have since attracted little attention.

Rarefaction curves were not investigated in this study due to the anticipated lack of additional information which they would provide. These curves are also sometimes difficult to interpret because they are greatly influenced by the number of individuals per sample. Species richness, as deduced from rarefaction curves, would have been found to increase with depth at Fancy Point because of the great abundance of filter-feeding caprellid and podocerid amphipods in shallow water. Species density was found, however, to decrease significantly.

The three environmental factors which have been proposed previously to contribute to diversity were each found to influence the diversity indices, but in different ways.

#### Habitat complexity

Simple, flat-thalloid algae and finely filamentous plants (both forms with great regularity in branch shape) were found to have very low species richness and heterogeneity. Both S and  $N_2$  were positively related to the "diversity" (sensu heterogeneity) of physical structures such as branch widths within the plant but not to the surface area/weight ratio (the degree of dissection). The well-known relationship between

diversity and structural complexity thus does not appear to be a simple function of rugosity but is probably dependent on an increase in the number of habitats as complexity increases and/or increasing animal abundance with increasing surface area. The size of structures within the habitat also seems to be of considerable importance, possibly because additional species may be able to survive within an environment if sufficient refuges within a given size range are available from predators.

# Environmental stability

A bell-shaped relationship similar to that predicted by Huston (1979), was deduced between environmental stability (as measured by wave exposure) and species density. Animal heterogeneity was also maximal at intermediate levels of wave exposure assuming that Zonaria plants at the sheltered site were the least disturbed of the phytal habitats studied. The reduced values of the diversity indices in conditions of extreme exposure almost certainly occurred because few phytal species were capable of surviving the disturbances which elongate algae underwent at the wave-swept site. The reasons for the reduced species richness in the calm habitats are more complex and possibly resulted from the aversion of many phytal species to the high detritus levels which were present on sheltered macroalgae (Dahl, 1948) and also the slightly greater seasonal variation in water temperatures. Alternatively, particular phytal species may have outcompeted others within the stable environment and excluded the poor competitors from plants. Such effects are well documented to occur on an ecological time scale in the rocky intertidal (Connell, 1961; Dayton, 1971) and are still consistent with the high diversity hypothesized to occur in stable environments such as the deep sea during an evolutionary time period. Species capable of controlling the abundances of the dominant competitor within a stable environment could presumably enter the system over a lengthy period of time, enriching the community and allowing a different species to become abundant until it is itself controlled.

# Food resources

Both the biomass of filamentous epiphytes and water depth (which was considered to be directly related to water movement and the flux of suspended food particles) were found to be strongly correlated with the abundance and dominance of the phytal assemblage. An increase in the abundance of rare species during the autumn period of maximum epiphytic biomass also resulted in an increase in the alpha species density. This effect, compounded by a concurrent increase in structural complexity, became difficult to detect with large sample size and would not occur on a gamma diversity scale. The contradictory results of previous productivity studies may have partly originated because H' has generally been used to estimate diversity and the two components of this index, species number and heterogeneity, respond in opposite fashion to productivity for small sample sizes. Furthermore, the relationship between species density and productivity is probably bell-shaped, despite its apparent lack of a turning point in this study, because the number of species generally declines when eutrophication occurs in situations of extreme enrichment (Riebesell, 1974; Bakelaar & Odum, 1978; Kondratieff & Simmons, 1982).

The non-linear relationships between environmental factors and diversity indices at Bruny Island indicate that a general theory of ecological diversity, which allows the diversity of habitats on a local scale to be predicted with accuracy, will probably never emerge. Nevertheless, more precision in the definition of diversity, and the separation of dominance from the alpha and gamma components of species density, might have prevented much of the confusion about the causes of diversity in past studies.

(Part IV of this series will be published in the next issue.)

### REFERENCES

- ABELE, L.G., 1974. Species diversity of decapod crustaceans in marine habitats. *Ecology*, Vol. 55, pp. 156-161.
- ALATALO, R.V., 1981. Problems in the measurement of evenness in ecology. Oikos, Vol. 37, pp. 199-204.
- BAKELAAR, R. G. & E. P. ODUM, 1978. Community and population level responses to fertilization in an old field ecosystem. *Ecology*, Vol. 59, pp. 660–665.
- BERGER, W. H. & F. L. PARKER, 1970. Diversity of planktonic Foraminifera in deep-sea sediments. Science, Vol. 168, pp. 1345–1347.
- BIRCH, D.W., 1981. Dominance in marine ecosystems. Am. Nat., Vol. 118, pp. 262-274.
- CONNELL, J. H., 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*, Vol. 42, pp. 710–723.
- CONNELL, J.H. & E. ORIAS, 1964. The ecological regulation of species diversity. Am. Nat., Vol. 98, pp. 399-441.
- DAHL, E., 1948. On the smaller Arthropoda of marine algae, especially in the polyhaline waters off the Swedish west coast. Lunds Univ. Arsskrift. N.F., Avd. 2, Undersök. över Öresund., No. 35, 193 pp.
- DAYTON, P. K., 1971. Competition, disturbance, and community organisation: the provision and subsequent organisation of space in a rocky intertidal community. *Ecol. Monogr.*, Vol. 41, pp. 351–389.
- DE BENEDICTIS, P.A., 1973. On the correlation between certain diversity indices. Am. Nat., Vol. 107, pp. 295-302.
- DOBZHANSKY, T., 1950. Evolution in the tropics. Am. Sci., Vol. 38, pp. 209-221.
- EASTOP, V.F., 1972. Deductions from the present day host plants of aphids and related insects. In, *Insect/plant relationships*, edited by H.F. van Emden, *Symp. Roy. Ent. Soc.*, No. 6, pp. 157-178.
- EDGAR, G.J., 1983a. The ecology of south-east Tasmanian phytal animal communities. I. Spatial organization on a local scale. J. Exp. Mar. Biol. Ecol., Vol. 70, pp. 129–157.
- EDGAR, G.J., 1983b. The ecology of south-east Tasmanian phytal animal communities. II. Seasonal change in plant and animal populations. J. Exp. Mar. Biol. Ecol., Vol. 70, pp. 159-179.
- FENWICK, G.D., 1976. The effect of wave exposure on the amphipod fauna of the alga *Caulerpa brownii*. J. Exp. Mar. Biol. Ecol., Vol. 25, pp. 1–18.
- FUTUYMA, D.J. & F. GOULD, 1979. Associations of plants and insects in a deciduous forest. *Ecol. Monogr.*, Vol. 49, pp. 33-50.
- GAULD, D.T. & J.B. BUCHANAN, 1956. The fauna of sandy beaches in the Gold Coast. Oikos, Vol. 7, pp. 293-303.
- HECK, K.L., G. VAN BELLE & D. SIMBERLOFF, 1975. Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. *Ecology*, Vol. 56, pp. 1459-1461.
- HEIP, C., 1974. A new index for measuring evenness. J. Mar. Biol. Assoc. U.K., Vol. 54, pp. 555-557.
- HEIP, C. & P. ENGELS, 1974. Comparing species diversity and evenness indices. J. Mar. Biol. Assoc. U.K., Vol. 54, pp. 559-563.
- HICKS, G. R. F., 1980. Structure of phytal harpacticoid copepod assemblages and the influence of habitat complexity and turbidity. J. Exp. Mar. Biol. Ecol., Vol. 44, pp. 157–192.

- HILL, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology*, Vol. 54, pp. 427-432.
- HURLBERT, S. H., 1971. The nonconcept of diversity: a critique and alternative parameters. *Ecology*, Vol. 52, pp. 577-586.
- HUSTON, M., 1979. A general hypothesis of species diversity. Am. Nat., Vol. 113, pp. 81-101.
- JANZEN, D. H., 1973a. Sweep samples of tropical foliage insects: description of study sites, with data on species abundances and size distributions. *Ecology*, Vol. 54, pp. 659–686.
- JANZEN, D.H., 1973b. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology*, Vol. 54, pp. 687-708.
- JUMARS, P.A., 1976. Deep-sea diversity: does it have a characteristic scale. J. Mar. Res., Vol. 34, pp. 217-246.
- KONDRATIEFF, P.F. & G.M. SIMMONS, 1982. Nutrient retention and macroinvertebrate community structure in a small stream receiving sewage effluent. Arch. Hydrobiol., Vol. 94, pp. 83–98.
- KEMPTON, R.A. & C.R. TAYLOR, 1976. Models and statistics for species diversity. Nature (London), Vol. 262, pp. 818-820.
- KEMPTON, R.A. & R.W.M. WEDDERBURN, 1978. A comparison of three measures of species diversity. Biometrics, Vol. 34, pp. 25-37.
- LUCKHURST, B. E. & K. LUCKHURST, 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Mar. Biol.*, Vol. 49, pp. 317–323.
- MACARTHUR, R. H., 1964. Environmental factors affecting bird diversity. Am. Nat., Vol. 98, pp. 387-397.

MACARTHUR, R.H., 1965. Patterns of species diversity. Biol. Rev., Vol. 40, pp. 510-533.

- MAGRE, E.J., 1974. Ulva lactuca L. negatively affects Balanus balanoides (L.) (Cirripedia Thoracica) in tidepools. Crustaceana, Vol. 27, pp. 231–234.
- MARGALEF, R., 1967. Some concepts relative to the organization of plankton. Oceanogr. Mar. Biol. Annu. Rev., Vol. 5, pp. 257–289.
- MARGALEF, R., 1969. Diversity and stability: a practical proposal and model of interdependence. *Brookhaven Symp. Biol.*, Vol. 22, pp. 25-37.
- MARGALEF, R., 1972. Homage to Evelyn Hutchinson, or why there is an upper limit to diversity. Trans. Conn. Acad. Arts Sci., Vol. 44, pp. 211–235.
- MAY, R.M., 1975. Patterns of species abundance and diversity. In, *Ecology and evolution of communities*, edited by M.L. Cody & J.M. Diamond, Harvard University Press, pp. 81–120.
- MCCLOSKEY, L. R., 1970. The dynamics of the community associated with a marine scleractinian coral. Int. Rev. Gesamten Hydrobiol., Vol. 55, pp. 13–81.
- MCINTOSH, R.P., 1967. An index of diversity and the relation of certain concepts to diversity. *Ecology*, Vol. 48, pp. 392–404.
- MENHINICK, E. F., 1964. A comparison of some species-individuals diversity indices applied to samples of field insects. *Ecology*, Vol. 45, pp. 859–861.
- MENHINICK, E. F., 1967. Structure, stability and energy flow in plants and arthropods in a sericea lespedeza stand. *Ecol. Monogr.*, Vol. 37, pp. 255–272.
- MURDOCH, W.W., F.C. EVANS & C.H. PETERSON, 1972. Diversity and pattern in plants and insects. Ecology, Vol. 53, pp. 819-829.
- PAINE, R.T., 1966. Food web complexity and species diversity. Am. Nat., Vol. 100, pp. 65-75.
- PIANKA, E. R., 1966. Latitudinal gradients in species divesity; a review of concepts. Am. Nat., Vol. 100, pp. 33-46.
- PIANKA, E.R., 1974. Evolutionary ecology. Harper & Row, New York, 356 pp.
- PIELOU, E. C., 1966a. The measurement of diversity in different types of biological collections. J. Theor. Biol., Vol. 13, pp. 131–144.
- PIELOU, E.C., 1966b. Shannon's formula as a measure of specific diversity: its use and misuse. Am. Nat., Vol. 100, pp. 463-465.
- PIELOU, E.C., 1975. Ecological diversity. Wiley, New York, 165 pp.
- PEET, R.K., 1974. The measurement of species diversity. Annu. Rev. Ecol. Syst., Vol. 5, pp. 285-307.
- PEET, R.K., 1975. Relative diversity indices. Ecology, Vol. 56, pp. 496-498.
- RIEBESELL, J.F., 1974. Paradox of enrichment in competitive systems. Ecology, Vol. 55, pp. 183-187.
- ROHDE, K., 1978. Latitudinal gradients in species diversity and their causes. I. A review of the hypotheses explaining the gradients. Zbl. Biol., Vol. 97, pp. 393-403.
- ROOT, R. B., 1973. Organisation of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecol. Monogr., Vol. 43, pp. 95–124.

SANDERS, H.L., 1968. Marine benthic diversity: a comparative study. Am. Nat., Vol. 102, pp. 243-282.

SIMBERLOFF, D. S., 1979. Rarefaction as a distribution-free method of expressing and estimating diversity.

In, *Ecological diversity in theory and practice*, edited by J.F. Grassle, G.P. Patil, W. Smith & C. Taillie, International Publishing House, Fairland, Maryland, pp. 159–176.

SIMPSON, E.H., 1949. Measurement of diversity. Nature (London), Vol. 163, p. 688.

SHELDON, A.L., 1969. Equitability indices: dependence on the species count. Ecology, Vol. 50, pp. 466-467.

SMITH, W., J.F. GRASSLE & D. KRAVITZ, 1979. Measures of diversity with unbiased estimates. In, Ecological diversity in theory and practice, edited by J.F. Grassle, G.P. Patil, W. Smith & C. Taillie, International Publishing House, Fairland, Maryland, pp. 177-191.

WHFETAKER, R.H., 1972. Evolution and the measurement of diversity. Taxon, Vol. 21, pp. 213-251.