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The effect of source pool maturity on the process of island colonization: an experimental approach with protozoan communities

Michael S. Henebry and John Cairns, Jr.

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Artificial substrate islands were exposed to source pool protozoan communities of differing maturities (i.e., some stage of development between pioneer and mature) in a series of laboratory microecosystem experiments. The process of species accrual on the islands was analyzed with the MacArthur-Wilson noninteractive colonization model. Exposure of initially barren islands to source pools which were in an early stage of development resulted in significantly ($\alpha = 0.05$) more rapid initial colonization rates and faster attainment of equilibrium species numbers than exposure to the most mature source pools. The results supported the hypothesis that colonization rates onto the islands were influenced by the maturity of source pools and the proportion of pioneer species in the source pool communities.

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Искусственные островки субстрата оставляли для заселения простейшими из исходных источников, в которых были сообщества простейших на разных стадиях формирования (т.е. от пионерных стадий до зрелых), в условиях лабораторного эксперимента с микроэкосистемами. Процесс увеличения числа видов на островках анализировали с помощью неинтерактивной модели колонизации Мак Артура – Уилсона. При контакте исходно незаселенных островков с пулами, где сообщества простейших находились на равных стадиях развития, начальная колонизация протекала очень быстро, и в количестве видов быстрее достигалось равновесие, чем при контакте с пулами, содержащими зрелые сообщества. Результаты подтверждают гипотезу о том, что скорость заселения островков зависит от степени зрелости сообществ в исходных пулах и доли пионерных видов в сообществах пулов.

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Introduction

Our previous microecosystem experiments (Henebry and Cairns in press) have shown that the accumulation of protozoans on small artificial laboratory islands mimicked the colonization of oceanic islands by insects (Simberloff and Wilson 1969, 1970) and by birds (Diamond 1969) which conformed to the general model of island colonization proposed by MacArthur and Wilson (1967). There was also some evidence that species composition and stage of development of source pool communities influenced the rate of species accumulation on small islands exposed to them. Protozoan species pools which had not yet reached stable equilibrium numbers on artificial substrates anchored in a lake resulted in higher rates of species accumulation on the initially barren islands in the laboratory systems (Henebry and Cairns in press). However, those experiments were not run long enough for equilibria to become established on islands in the test systems, which led to inaccurate estimates of equilibrium numbers and colonization rates when the MacArthur-Wilson noninteractive model was fitted to the data.

The goals of this study were to (a) follow the colonization process of islands in the laboratory systems until relatively stable equilibrium numbers of species were reached; (b) more carefully regulate the invasion of the systems by protozoan contaminants (a minor problem in the earlier study); and (c) develop a system for designating particular species of protozoa as "pioneer species" whenever evidence to support this view became available. The hypothesis was that islands exposed to source communities which themselves were at early stages of the colonization process would be colonized at a faster rate than islands exposed to mature communities (those at or near equilibrium) because of a greater proportion of pioneer species in the developing communities. The influence of the species composition of a source pool community on the colonization of nearby islands has not heretofore been tested as rigorously as the effects of island size and distance from a source pool on colonization rate. Yet a consideration of the species composition of a source pool may be as important as distance from the source and size of the target area in predicting the rate of colonization of an island or the rate of recovery of a damaged ecosystem.

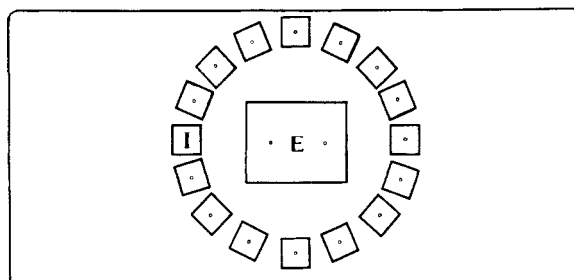


Fig. 1. Placement of island and epicenter (source pool) substrates in the microecosystems. Distance between epicenter (E) and island (I) PFU's is approximately 9.5 cm.

Materials and methods

Source communities for the laboratory systems were collected on 76 × 64 × 25 mm polyurethane foam units (PFU's) which had been anchored in Pandapas Pond, Montgomery County, Virginia, for 3 d, 1, 3, or 13 wk during autumn and winter 1976–1977. In order to accurately census species comprising the source pools used in the experiments, each PFU from the pond was bisected; one half was placed into a microecosystem, the other half was "harvested" immediately and the protozoan species identified. At the end of each experiment, each PFU which had served as a source in a laboratory system was harvested and the protozoa identified.

The colonization trays used in these experiments were identical to those used in earlier experiments (Henebry and Cairns in press), but the procedure was modified so that each island was harvested only once. A L:D 16:8 light regime was maintained in the system's fluorescent lighting and temperature was allowed to fluctuate with the ambient (20–22°C).

Four replicate island PFU's were harvested from each system on days 1, 3, 5, 7, 9, 11, 13, and 21 after set-up (no 21-day harvest for island tested with the 3-wk source pools). Source pool and island PFU's were positioned as shown in Fig. 1. A control consisting of 10 island size PFU's in a partially covered tray of pasteurized pond water was monitored frequently before and during the course of the colonization experiments.

Each control and experimental island was harvested

Tab. 1. Numbers of protozoan species on source pool communities used in laboratory microecosystem experiments.

	Source pool colonization time							
	3 d		1 wk		3 wk		13 wk	
	A	B	A	B	A	B	A	B
No. species at start	13	10	31	—*	37	35	54	57
No. species at finish	13	11	15	—	14	15	26	27
% species survival	100	110	48	—	38	43	48	47
% species reaching islands	92	100	54	—	52	74	44	35

* No 'B' series with 1-wk source pool.

by fully squeezing its content into a wide-mouth glass jar. Four slides of living material were prepared from each sample, and all protozoan species in each were identified and recorded using standard keys (e.g., Leidy 1879, Pascher 1913–1927, Kahl 1930–1935, Kudo 1966). Four slides have been found to reveal over 85% of species actually present in a sample and were sufficient to establish species richness (Cairns and Yongue 1968).

Results

The number of protozoan species found on source PFU units of different maturities at the beginning and end of each experiment, the percent species survival, and the percent of their species reaching test islands is given in Tab. 1. Species numbers on source pools increased in proportion to the length of time allowed for colonization in Pandapas Pond. A recent colonization curve from Pandapas Pond, collected and analyzed by the method of Cairns et al. (1979) shows that an equilibrium number of species may be reached after approximately two weeks exposure (Fig. 2).

The percentage of species surviving on the source pools after 21 d in the colonization trays varied from greater than 100% for one of the 3-d sources to a low of 38% for one of the 3-wk source pools. In determining the percent of species reaching islands, a species was counted if it was found on any island at anytime during a particular experiment. The 3-d source pools contributed the highest percentage (96%) of their species to the surrounding islands, while only about 40% of species from the 13-wk source pools reached islands in the test systems.

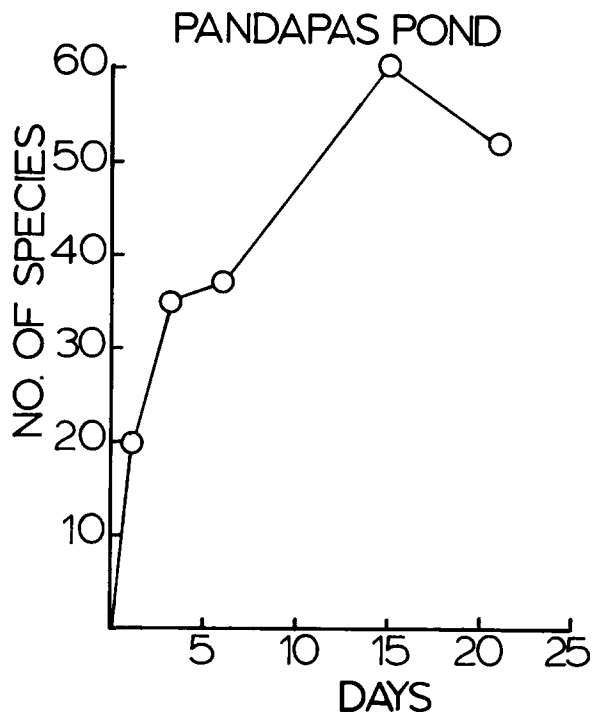


Fig. 2. Colonization curve for PFU substrates placed in Pandapas Pond, summer 1976.

Fig. 3 illustrates the accumulation of protozoan species with time on islands exposed to source pools of different maturities (each point on the graph is the mean of four observations). Those exposed to source pools of 3 d and 1 wk maturity reached peaks in species numbers by day 5. Peaks in species richness on islands tested with 3 and 13-wk source pools occurred on day 9

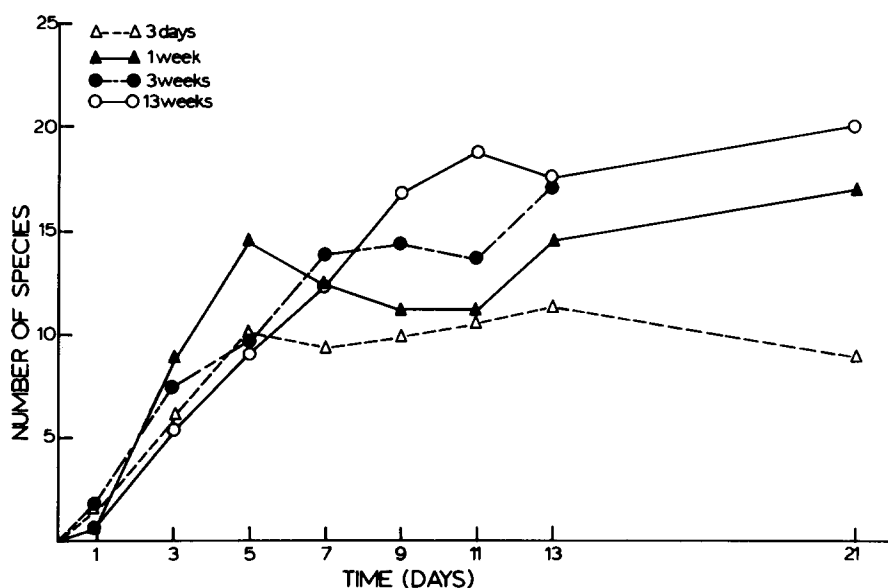


Fig. 3. Colonization curves for islands exposed to source pools of different maturities.

Tab. 2. Nonlinear regression analysis of model $S = \hat{S}_{eq} (1 - e^{-GT})$ for islands exposed to sources of different maturities. Lack of fit (L.O.F.) and α level attained are presented ($\alpha(F) > 0.01$ is required for decision level).

	Source pool maturity			
	3 d	1 wk	3 wk	13 wk
F	2.77	8.88 [3.33]*	0.54	3.59
α (F)	>0.025	<0.001 [>0.01]	>0.75	>0.01
\hat{S}_{eq}	10.77	L.O.F. [15.27]	17.87	23.83
	U=11.69** L= 9.85	U=17.93 L=12.62	U=22.15 L=13.60	U=28.72 L=18.94
G	0.323	[0.238]	0.171	0.105
	U=0.421 L=0.225	U=0.375 L=0.101	U=0.249 L=0.093	U=0.144 L=0.066
$t_{90\%}$	7.12	[9.6]	13.46	21.92

* Values without data for days 7, 9, and 11.

** Upper and lower asymptotic 95% confidence limits.

and 11, respectively. After these peaks, dynamic equilibria appeared to develop in all systems.

To determine if the process of species accumulation on the PFU islands could be adequately described by the MacArthur-Wilson noninteractive colonization model, $S(t) = \hat{S}_{eq} (1 - e^{-GT})$ with equilibrium species number \hat{S}_{eq} and constant G related to transition time, nonlinear regression procedures with Marquardt methods of estimation (Barr et al. 1976) were used to fit the model to the experimental data. Lack of fit tests were then used to test for any significant lack of fit (Cairns et al. 1979). The island colonization model adequately described the buildup of species on all islands except those tested with the 1-wk source pools. When numbers of species for day 7, 9, and 11 were left out of the data for islands tested with 1-wk source pools (explanation for this in discussion section), there was no significant lack of fit (L.O.F.) ($\alpha(F) > 0.01$).

Islands tested with 3-d source pools were estimated to equilibrate the most rapidly ($G = 0.323$, $t_{90\%} = 7.12$ d), with islands exposed to source pools of greater maturity taking progressively longer to reach equilibrium numbers of species (Tab. 2). The estimates of G and \hat{S}_{eq} for islands exposed to the 3-d (youngest) and 1-wk source pools were considered significantly different from estimates for islands exposed to the 13-wk (oldest) source pool because their asymptotic 95% confidence intervals did not overlap; this is equivalent to testing the hypothesis of equality at the $\alpha = 0.05$ level of significance. Sample sizes were moderately large ($n = 32$ for each experiment), so the use of the asymptotic confidence intervals provided in the output from the S.A.S. nonlinear regression program (Barr et al. 1976) in making statements regarding significance seemed justified.

Discussion

At the end of the 21-d experiments using source pools which had been colonized by protozoa for a period of 3

d in Pandapas Pond, greater than 100% of the original species numbers survived. Probably the reason that more species were found after 21 d than at the initial harvest is that some species which were at densities too low to be detected by our sampling methods had proliferated in the laboratory systems. However, these pioneer source communities did exhibit higher degrees of stability (constancy of species numbers, Goodman 1975) than any of the more mature source communities. Less than 50% of the original species numbers of any of the more mature sources survived 21 d in the test systems. Goodman (1975) suggested that "some measures of instability, such as the fraction of species subsequently lost, may well increase with diversity," particularly when there were "drastic modifications of the entire landscape or in the creation of some experimental communities." Our results support Goodman's suggestion.

During the 21 d allowed for colonization in the laboratory experiments, the 3-d colonized source communities contributed 100% of their species numbers to islands in the test systems. The more mature source communities contributed only 39.5% (mean for 13-wk colonized sources) to 63% (mean for 3-wk sources) of their species to the experimental islands. It may be that the reason the 3-d colonized source communities had higher values as sources than the more mature communities is that they contained relatively more pioneer species.

Pioneer species are often those with r -selection strategies. These strategies include high reproductive rates, density independent mortality, and the ability to utilize variable or unpredictable resources in unsaturated, nonequilibrium communities (Pianka 1970). Another characteristic of pioneer species is their high degree of dispersibility, which is an adaptation to habitats that are temporary in space and time (Gadgil and Solbrig 1972).

Little information is available on the autecology of protozoa so it was necessary to adopt an operational

Tab. 3. The value of 53 common species of protozoa as "pioneers."

Taxa	Situation							Pioneer rating
	1 ^a	2 ^b	3 ^c	4 ^d	5 ^e	6 ^f	7 ^g	
Class Mastigophora								
Subclass Phytomastigia								
Order Chrysomonadida								
Family Chromulinidae								
<i>Chromulina pascheri</i> Hoefeneder				+	+			2
<i>Mallomonas caudata</i> Iwanoff				+				1
Family Ochromonadida								
<i>Monas</i> sp.	+	+	+		+			4
<i>Dinobryon sertularia</i> Ehrenberg					+			1
<i>Ochromonas</i> sp.			+		+			2
Order Cryptomonadidae								
Family Cryptomonadidae								
<i>Cryptochrysis commutata</i> Pascher						+		1
<i>Cryptomonas erosa</i> E.			+		+	+		3
<i>Chilomonas paramecium</i> E.			+		+			2
<i>Cyathomonas truncata</i> E.			+	+	+	+		4
<i>Rhodomonas lens</i> Pascher & Ruttner				+				1
Order Phytomonadida								
Family Chlamydomonadidae								
<i>Chlamydomonas</i> sp.			+	+	+	+	+	5
Family Phacotidae								
<i>Phachotus lenticularis</i> E.				+				1
Order Euglenoidida								
Family Anisonemidae								
<i>Anisonema acinus</i> Dujardin					+			1
<i>Anisonema pusillum</i> Stokes			+		+			2
<i>Entosiphon sulcatum</i> D.			+					1
<i>Peranema inflexum</i> skuja			+		+		+	3
Family Euglenidae								
<i>Phacus torta</i> Lemmermann						+		1
<i>Trachelomonas volvocina</i> Bernardi						+		1
Order Dinoflagellida								
Family Cystodiniidae								
<i>Glenodinium edax</i> Schilling				+	+			2
Subclass Zoomastigida								
Order Protomonadida								
Family Bodonidae								
<i>Bodo amoebinus</i> Gojdic	+						+	2
<i>B. caudatus</i> Dujardin	+	+			+	+	+	5
<i>B. edax</i> Klebs	+				+		+	3
<i>B. minimus</i> G.	+				+		+	3
<i>Pleuromonas jaculans</i> Perty	+	+			+	+		4
Class Sarcodina								
Subclass Rhizopoda								
Order Testacida								
Family Arcellidae								
<i>Arcella artocrea</i> Leidy						+		1
<i>A. vulgaris</i> E.						+		1
Subclass Actinopoda								
Order Heliozoida								
Family Acanthocystidae								
<i>Acanthocystis</i> sp.						+	+	2
Class Ciliata								
Subclass Holotricha								
Order Gymnostomatida								
Family Holophryidae								
<i>Holophrya simplex</i> Schewiakoff							+	1
<i>Urotricha agilis</i> (Stokes)			+			+		2
<i>Urotricha farcta</i> Claparede & Lachman						+		1

Family Colepidae									
<i>Coleps bicuspis</i> Noland							+		1
<i>Coleps octospinatus</i> N.							+		1
Family Amphileptidae									
<i>Amphileptus clapedi</i> Stein								+	1
<i>Hemiophrys</i> sp.						+			1
Order Hymenostomatida									
Family Tetrahymenidae									
<i>Tetrahymena vorax</i> (Kidder, Lilly & Claff)							+		1
<i>Dichilum cuneiforme</i> Schewiakoff								+	1
<i>Glaucoma scintillans</i> E.						+	+		2
Family Parameciidae									
<i>Paramecium bursaria</i> E.							+	+	3
Family Frontonidae									
<i>Cinetochilum margaritaceum</i> Perty						+	+		2
<i>Cyrtolophosis mucicola</i> Stokes			+	+			+	+	4
Family Pleuronematidae									
<i>Cyclidium musicola</i> Kahl						+	+	+	3
<i>C. litomesum</i> Stokes						+		+	3
Subclass Spirotricha									
Order Heterotricha									
Family Stentoridae									
<i>Stentor igneus</i> Ehrenberg							+		1
Order Oligotricha									
Family Halteriidae									
<i>Halteria grandinella</i> Müller							+		1
Order Tintinnida									
<i>Codonella cratera</i> Leidy							+		1
Order Hypotrichida									
Family Oxytrichidae									
<i>Opistotricha similis</i> Engelmann							+	+	2
<i>Oxytricha fallax</i> Stein							+		1
<i>Pleurotricha lanceolata</i> Ehrenberg							+		1
<i>Uroleptus longicaudatus</i> Stokes								+	1
<i>Urostyla grandis</i> E.							+		1
Family Aspidiscidae									
<i>Aspidisca costata</i> Dujardin								+	1
Subclass Peritricha									
Order Peritrichida									
Family Vorticellidae									
<i>Vorticella convallaria</i> Linnaeus								+	2
<i>V. microstoma</i> E.								+	2

^a Protozoa found in control microecosystems (Henebry and Cairns in press).

^b Protozoa found in control microecosystems in our experiments.

^c Protozoa which colonized PFU's in Pandapas Pond by day 3.

^d Protozoa which colonized PFU's in Douglas Lake, Michigan, by day 1 (Henebry and Cairns in press).

^e Protozoa which reached microecosystems islands by day 3 in our experiments.

^f A list of "pioneer species" from a pond in North Carolina (Yongue and Cairns 1971).

^g Protozoa with a rating of > 1.5 on Maguire's (1963) dispersal index.

definition of pioneer species based on data from previous colonization studies. Tab. 3 contains lists of species which (a) were found in control systems in our microecosystem studies, (b) colonized artificial PFU islands by the third day of exposure in field or laboratory studies of the colonization process, or (c) had a dispersal index of 1.5 or higher in Maguire's (1963) beaker experiments. The last column contains the number of times a species was listed; this number was its rating as a pioneer species. If a species received a rating of two (2)

or above, it was considered to have relatively high value as a pioneer. The requirement that a species be listed at least two times was chosen because a species could have appeared once in the table by chance. Of the 53 species in the table, 26 were considered to have high values as pioneers and were designated "pioneer species."

Tab. 4 summarizes the occurrence of these pioneers on source pools of different maturities used in our experiments. Ninety-three percent of species seen in the 3-d colonized source communities were pioneers. For

Tab. 4. Occurrence of protozoan species with high pioneer ratings on source pools used in microecosystem experiments.

Species	Pioneer Rating	High Pioneer Value	Age of source pool			
			3 d	1 wk	3 wk	13 wk
<i>Monas</i> sp.	4	×	×	×	×	×
<i>Cyathomonas truncata</i>	4	×	×	×	×	×
<i>Chlamydomonas</i> sp.	5	×	×	×		
<i>Peranema inflexum</i>	3	×	×		×	×
<i>Ochromonas</i> sp.	2	×	×			
<i>Chilomonas paramecium</i>	2	×	×			
<i>Anisonema pusillum</i>	2	×	×	×		
<i>Cryptomonas erosa</i>	3	×	×	×		×
<i>Urotricha agilis</i>	2	×	×	×	×	×
<i>Cinetochilum margaritaceum</i>	2	×	×	×		×
<i>Glaucoma scintillans</i>	2	×	×	×	×	
<i>Cyclidium musicola</i>	3	×	×	×	×	
<i>Cyclidium litomesum</i>	3	×	×			×
<i>Hemiophrys</i> sp.	1		×			
Mean no. of species on source pools			14	31	36	55.5
No. species with high pioneer value			13	9	6	7
Percent of species with high pioneer value			93	29	17	13

the other source communities, the percentage of pioneer species ranged from 13 to 29 %.

The very high percentage of pioneer species in the 3-d source communities was probably a major factor in the rapid colonization of islands exposed to them. The islands exposed to 3-d and 1-wk source pools had high colonization rates (G-values) and quickly reached equilibrium species numbers (Fig. 3). In the former case, this may reflect mostly the high dispersal capacity of the pioneer species which comprised nearly the entire species pool in the 3-d source community. The 1-wk source did have the second highest proportion of pioneers (29%), but, more important, pioneer species may have made up a much larger proportion of the total organisms than the 29% figure would indicate. The abundances of most species were higher in the sample from the 1-wk source community than in the sample from the source exposed for only 3 d. The high content of pioneer species in their source communities may explain the high G-values (a reflection of colonization rate) of the colonization curve for islands exposed to the 3-d and 1-wk source communities.

Patrick (1967) has shown that source pool (epicenter) species diversity can affect the number of diatoms found at equilibrium on experimentally placed glass slide islands. She found that species numbers on the slides equilibrated at 14–29 species with a source pool of 60 species and at 160 species when exposed to a pool of 250 species. In our experiments, islands exposed to increasingly mature source communities (with increasingly greater species diversities) accumulated significantly greater numbers of species.

In our experiments, unlike Patrick's (1967) studies, the colonization process was followed through time. This allowed observation of the effect of source pool community size and composition on colonization rate,

as well as the effect of source pool size on ultimate species richness on islands. The parameters ($t_{90\%}$, G, and \hat{S}_{eq}) estimated as a result of fitting the noninteractive model $S(t) = \hat{S}_{eq}(1 - e^{-Gt})$ lent support to the hypothesis that islands exposed to source communities of increasing maturity (increasing species diversity) take progressively longer to reach eventually higher equilibrium species numbers. These estimates also lend support to a similar hypothesis proposed by Cairns et al. (1979) as a reason to expect the attainment of equilibrium number of species to be more rapid for PFU islands drawing colonists from a stressed species pool in a lake situation. They suggested that a stressed community is commonly dominated by r-selected opportunistic species (analogous to pioneer species in our laboratory experiments) which are well adapted to the pioneer episodes of colonization and that barren islands drawing propagules from this type of pool would be expected to accumulate species more rapidly than islands drawing from a more complex source (such as the more mature source communities in our laboratory experiments).

Opler et al. (1977) observed that the recolonization of clearcut plots in tropical lowland forests which drew propagules from severely perturbed source areas was extremely rapid. This was attributed to the relatively large numbers of pioneer species within those immature source pools. Plots surrounded by more mature forest communities exhibited much slower increases in species richness within an equivalent time period.

The noninteractive colonization model adequately described the buildup of species on all islands except those tested with the 1-wk source community. The ciliate *Dileptus anser* Müller was very abundant from day 7 through day 11 in the 1-wk source test system. This predaceous protozoan is known to feed on other

ciliated protozoa, rotifers, and other small organisms (Bick 1972) and may have reduced populations of some species to levels where they were not detected by the sampling methods used, thus lowering the number of species counted on those days. In view of this, we tried fitting the model to the 1-wk colonization data without the points for days 7, 9, and 11. When these data were eliminated, there was no significant L.O.F. ($\alpha(F) > 0.01$).

The hypothesis that immature source communities result in both more rapid initial colonization rates and faster attainment of equilibrium species numbers on islands exposed to them was confirmed by the results of our laboratory experiments. The results also supported the hypothesis that colonization rates on islands were influenced by the proportion of pioneer species in source communities. The proportion of pioneer species decreased with the increasing maturity of source communities. Finally, these controlled laboratory experiments extended and clarified the results of field work on the colonization process by Patrick (1967), Opler et al. (1977), and Cairns et al. (1979), and quantitatively confirmed that kinds as well as numbers of species in source pools could be very important in determining the rate of colonization of islands. Species composition of source pools may also be of as much or greater importance than size or distance of a nearby source pool in determining the rate of recovery of a damaged ecosystem.

Hairston et al. (1968) have pointed out that there is a growing use of experimental manipulation in the testing of hypotheses in ecology. Important work has been accomplished in field experiments such as those of Simberloff and Wilson (1969, 1970). The use of model laboratory systems, with their inherent ease of manipulation, may prove an even more valuable tool in the formulation and testing of ecological principles.

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