

Original papers

Competition among the pioneers in a seasonal soft-bottom benthic succession: field experiments and analysis of the Gilpin-Ayala competition model

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Summary. Controlled experiments, designed to assess the effects of pioneers on succession on an intertidal sandflat, provided evidence for interspecific competition between juvenile *Hobsonia florida* (Polychaeta, Ampharetidae) and oligochaetes. The field data were fitted to both the linear Volterra and non-linear Gilpin-Ayala competition equations. With its greater number of parameters, the Gilpin-Ayala model must provide a better fit to observed population abundances. The Gilpin-Ayala model is flawed as an explanation of the population trajectories of the *H. florida* and oligochaetes, because its non-linearity parameter affects only intraspecific competition. With either model our field data demonstrate a solution to Hutchinson's paradox. With competition coefficients near unity and similar carrying capacities, the predicted population trajectories are heavily dependent on initial conditions. The predicted times to competitive exclusion are long and can easily exceed the typical period of environmental constancy. Our study offers evidence for Neill's competitive bottleneck: competition acts primarily on the developmental stages of one of a pair of competing species. The permanent meiofauna may act as a competitive bottleneck for the population growth of benthic macrofauna. The mechanism of this competitive interaction probably involves exploitative interspecific competition for benthic diatoms.

Key words: Succession – Benthic – Non-linear – Competition – Model

There are only a few demonstrations of competition in the marine soft-bottom benthic literature. Connell (1983) and Schoener (1983) cite only seven field experiments which documented competition in the soft-bottom benthos: Bertness (1981), Kastendiek (1982), Peterson (1979, 1982), Peterson and Andre (1980), Race (1982), and Woo-

din (1974). Reise (1985:155) concluded, "There is no evidence for reciprocal competition ("... an increase in either one harms the other", MacArthur) from tidal flats". Perhaps the most famous demonstration of competition in the soft-bottom benthos is Fenchel's (1975) study of character displacement in hydrobiid gastropods, which Fenchel and Kofoed (1976) showed could be competing for benthic diatoms. But even this classic study has been criticized (Levinton 1982; Hylleberg 1986; Cherrill and James 1987) and provides only indirect evidence for past competition.

Our field experiments were not designed to study competition. We wanted to test mechanisms of succession (Connell and Slatyer 1977) by decreasing and increasing the abundances of pioneers at the onset of seasonal succession. These field experiments, which we call 'removal' and 'enhancement' experiments respectively, were established at the onset of the seasonal succession of the benthic infauna of an intertidal sandflat at the mouth of the Skagit River on northern Puget Sound (Washington State, USA). After the initial experimental manipulation of infaunal densities, we sampled to observe changes in population abundances between replicated "treatment" and "control" areas through time. Gallagher et al. (1983) used enhancement experiments on the same sandflat and found little evidence of negative biological interactions. Here we describe an additional enhancement experiment and a removal experiment that demonstrate intense negative interactions due to competition among the pioneers of the seasonal Skagit succession.

Our removal experiment was inspired by Neill's (1975) study of competition among aquatic microcrustaceans in laboratory cultures. He added a predatory fish intermittently to reduce selectively the equilibrium abundance of a competitively dominant cladoceran and documented a sharp increase in the equilibrium abundance of the other competing species. Our design differs from Neill's in that we added the predators in a single, short-term pulse to obtain a selective reduction of a key spe-

cies. Using terms from Bender et al. (1984), Neill's and our designs are 'press' and 'pulse' designs, respectively. We tested three different predator treatments to increase the odds of obtaining a selective removal of a key species. A short-term (3 day) addition of the epifaunal predator *Eogammarus confervicolus*, an epifaunal gammarid amphipod, reduced selectively the abundances of *Hobsonia florida*, a pioneer in the seasonal Skagit succession (Fig. 1a)

The pulsed reduction of *H. florida* densities led to a large increase in oligochaete abundance. The joint abundances of *H. florida* and oligochaetes were analyzed using both the Volterra (1926) and Gilpin-Ayala competition models (Ayala et al. 1973; Gilpin and Ayala 1973). Our initial modeling goal was to estimate the models' parameters, especially the interspecific competition coefficients. A second goal was to predict the equilibrium

abundances of the competing species and to determine whether stable coexistence was possible. A final goal was to compare the Volterra and Gilpin-Ayala models as explanations of the population dynamics of these species.

Materials and methods

We performed the experiments on the northern section of the Skagit flats, an intertidal sandflat (median grain size = 120 µm) near the mouth of the North Fork of the Skagit River on Northern Puget Sound (Washington State, USA). The community inhabiting this area and some processes affecting larval recruitment are described in Gallagher et al. (1983) and Eckman (1979, 1983).

We designed two concurrent experiments, called the removal and enhancement experiments, 100 m seaward of the fringing bulrush marsh at approximately +2 m (above MLLW) tidal height.

Table 1. Experimental designs

a The field layout. The treatment designations correspond to those in Table 1 b. Treatment blocks are marked with brackets

East										West											
1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10-12
[(]				(
900	50	25	AMB		AZ	C/T	COR.	T			50	25	AMB	900		C/T	T	COR.	AC		
Eo.	Eo.	Cr.									Eo.	Cr.		Eo.							

b The operations performed on each sampling date are indicated:

Experiment name Treatment level	Sampling day									
	Day -3	Day 0 8 May 1981	Day 3	Day 9	Day 12	Day 19	Day 26	Day 34	Day 55	
<i>Enhancement experiment:</i>										
Azoic control (AZ)	A, B, D	E, I (8, 8)		I (3, 4)	I (8, 8)	I (4, 4)	I (4,4)	I (8, 8)	I (4, 4)	
Tube array (T)	A, B, D	E, F, I (8, 8)			I (8, 8)					
<i>Corophium</i> /Tube (C/T)	A, B, C, D	E, F, I (8, 8)		I (3, 4)	I (8, 8)	I (4, 4)	I (4, 4)	I (8, 8)	I (4, 4)	
<i>Corophium</i> (COR.)	A, B, C, D	E, I (8, 8)			I (8, 8)					
<i>Removal experiment:</i>										
Ambient control (AC)		A, D	E, I (8, 8)	I (2, 4)	I (4, 4)	I (4, 4)	I (4, 4)	I (4, 4)	I (4, 4)	
900- <i>Eogammarus</i> (900 Eo)		A, D, G	E, H, I (8, 8)	I (3, 4)	I (4, 4)	I (4, 4)	I (4, 4)	I (4, 4)	I (4, 4)	
100- <i>Eogammarus</i>		A, D, G	E, H, I (8, 8)							
25- <i>Crangon</i>		A, D, G	E, H, I (8, 8)							

A Sleeves inserted; B Natural sediment replaced; C *Corophium* added; D 250-µm mesh added; E Sleeves removed; F Tube array planted; G Predators added within sleeves; H Predators removed; I Random sampling and number of samples sorted (East patch, West patch)

c Statistical Model for day 3 abundance data $k=4$ =number of treatments; $n=2$ =number of replicate patches/treatment; $r=8$ =number of replicate subsamples/Patch; α_i =effect of the i 'th treatment; σ^2 =sample variance; σ^2_β =patch within treatment variance

Source of variation	Degrees of freedom	Mean square	Expected mean square	Test statistic
Between treatments	$k-1$	S^2_1	$\sigma^2 + r\sigma^2_\beta + nr(\sum \alpha_i^2 / (k-1))$	$S^2_1 / S^2_2 \tilde{F}_{(k-1, k(n-1), 1-\alpha)}$
Experimental error (Patches within treatment)	$k(n-1)$	S^2_2	$\sigma^2 + r\sigma^2_\beta$	$S^2_2 / S^2_3 \tilde{F}_{(k(n-1), k n(r-1), 1-\alpha)}$
Sampling error	$kn(r-1)$	S^2_3	σ^2	
Total	$knr-1$			

We first marked out a 24-m long transect parallel to the bulrush marsh and to the incoming tide. We used two 26-cm diameter patches (530 cm² area) for each treatment level in an experiment and assigned one replicate patch randomly to the 4-m long eastern and western blocks in the transect. The positions of each patch in the 24-m array are shown in Table 1a. We did not spatially intersperse replicates of the removal and enhancement experiment because no between-experiment statistical tests were planned. Each experimental patch was enclosed for the first 3 days by a 25 cm high cylindrical plastic sleeve (i.e., a 5-gal bottomless bucket) that protruded 5 cm above the sediment surface.

The removal experiment

There were four levels of predator treatment, designated by the number and genus of predator added: Ambient-control (no predators), 900-*Eogammarus*, 100-*Eogammarus*, and 25-*Crangon* treatments. These predator densities far exceed those found naturally. Our goal was not to test the importance of predation to community structure but merely to reduce infaunal abundances quickly and selectively. We collected *Eogammarus confervicolus* from the interstices of mussel clumps and collected the epifaunal shrimp *Crangon franciscorum* by seine from a tidal channel within the fringing bulrush marsh. *Eogammarus confervicolus* is a small (5–10 mg dry weight) epifaunal gammaridean amphipod which is omnivorous in the laboratory, feeding on macroalgae, meiofauna, or macrofauna. We kept the predators without food for 3 days before adding them within the sleeves enclosing patches of the natural community. The two ambient-control patches were enclosed in plastic sleeves for 3 days, but no predators were added. We placed a 250 μ m Nitex[®]-mesh screen over all of the sleeves to retain the added predators and exclude larger animals from the patches. The sleeves retained a 5-cm deep pool of water during low tide, which prevented the desiccation of the epifaunal predators. At the end of 3 days we removed both predators and sleeves.

The enhancement experiment

This experiment was designed to test the effects of animal tubes and the tube-building gammaridean amphipod *Corophium salmonis* on the recruitment of infaunal populations to initially abiotic sediments. Samples of the natural community in the previous 2 years indicated that *C. salmonis* may be responsible for the decline of the pioneers in the Skagit succession (cf. Fig. 1c and 1d). This experiment was designed to test whether *C. salmonis* would inhibit the recruitment of oligochaetes and *H. florida*. We used commercial foundry sand (well sorted with 125 μ m median grain size) to replace the natural sediment in foundry-sand patches. The simulated tubes (2 mm in diameter \times 2 cm long) were made from wooden applicator sticks and were reasonable mimics of natural *H. florida* tubes in size.

To create the twice replicated abiotic patches on 5 May, 1981 (day 3) we inserted plastic sleeves over randomly chosen patches within the 24-m long study area. One replicate for each treatment was chosen for a 4-m long array in the western and eastern blocks (Table 1a). We removed the natural sediment from each patch to a depth of 20 cm and replaced it with foundry sand. *Corophium salmonis* can be collected in large numbers from the bulrush marsh area. *C. salmonis* does not recruit onto the flat before the first week of July (Fig. 1d). Several thousand swimming and positively phototactic amphipods were collected by decanting a quickly stirred slurry of surface sediments through a 500- μ m mesh sieve. After separating the *C. salmonis* from other animals and debris in the laboratory, we added 10 g (wet weight) of *C. salmonis* to each of four patches. Two patches served as a *C. salmonis* treatment and two as a *C. salmonis*/Tube treatment. We placed 250- μ m

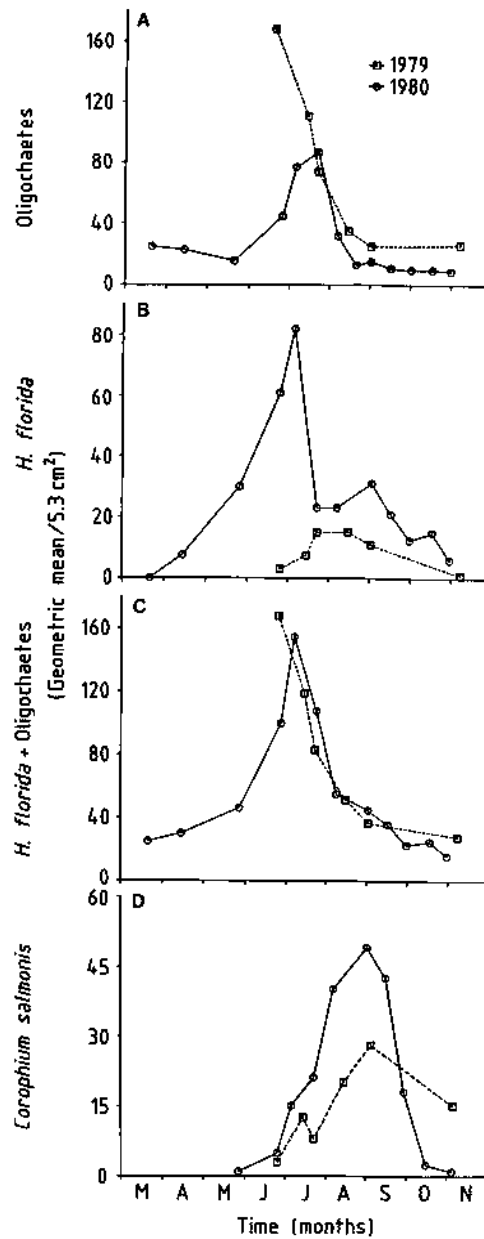


Fig. 1A–D. Geometric mean abundances per 5.3 cm² core of Skagit populations in 1979 (dotted lines) and 1980 (solid lines), the 2 years preceding this study at a site 200 m seaward of the present study site. Means are based on 5–15 replicate samples, processed as described in Gallagher et al. (1983). Abundances are plotted for A *H. florida*, B Oligochaetes, C Oligochaetes + *H. florida* and D *Corophium salmonis*.

screens over the sleeves and left the sleeves in place for 3 days. During this period the *C. salmonis* individuals built tubes and a fine layer of dark sediment covered the foundry sand. After 3 days, we removed the sleeves and placed a 40 \times 40-cm regular array of simulated tubes (tube density approximately 2.5 per 10 cm²) over four of the 26-cm diameter patches (the "Tube-array" and "*Corophium*/Tube" patches, Table 1b); tubes were not added to the two foundry sand patches (Foundry-sand controls). Three days after planting the tube arrays, we added several hundred more simulated tubes to replace those lost near the areas disturbed by the removal of the sleeves; we noted little loss of tubes during the remainder of the experiment.

Sample analysis

We subsampled all patches with an 11-mm diameter (0.95 cm² area) corer inserted to a depth of 5 cm. Metal stakes, positioned 50 cm from the center of the patches, allowed us to position a circular frame for sampling. We took samples within each patch from positions chosen randomly with the restriction that no samples were taken within 2 cm of either the edges of a patch or positions sampled during the two previous sampling periods.

Four or eight samples were taken from each patch approximately every 3–4 days over a 55-day period (Table 1b). We sorted those samples taken on days 3, 9, 12, 19, 26, 34, and 55. A few replicate samples were lost in transit.

We preserved the samples with 10% buffered formalin, stained with Rose Bengal. In the laboratory, we sieved each sample with a 250- μ m mesh sieve nested over a 63- μ m mesh sieve. Most of the juvenile macrofauna and meiofauna passed readily through the 250- μ m mesh sieve.

We sorted and counted all of the infaunal taxa, including the meiofaunal-sized (less than 500 μ m) polychaete larvae and juveniles, and all meiofauna on the early sampling dates. To save processing time, we did not sort harpacticoid copepods and nematodes on later sampling dates (nematode abundances sometimes exceed 200 per 0.95-cm² core).

Hobsonia florida settles at the four-setiger stage and can grow to greater than 2 cm length. We distinguished the recently settled juveniles from the older *H. florida* by the presence of branchiae, acquired at the six-setiger developmental stage (Zottoli 1974). Most of these six-setiger *H. florida* juveniles and their mucous tubes pass readily through a 250- μ m mesh sieve.

Statistical analysis

This experiment used a randomized block design, but the statistical model for the ANOVA used the mixed-model nested ANOVA,

with patch variance nested within variance due to treatment level (Table 1c). Three classes of factors could affect our dependent variables, the population abundances of the infaunal taxa. First are those factors incorporated into the structure of the two experimental designs: predation (4 levels in the removal experiment) and presence of *Corophium* or tubes (4 levels in the enhancement experiment). The second are those factors "randomized out" of the experiment: (1) spatial variability over a 16-m transect (see Table 1a), and (2) spatial variability within each 26-cm patch. The final class is the group of innumerable factors neither incorporated in the design nor randomized out. Every experimenter necessarily neglects some conceivably causal factors, and the choice of factors to be randomized out is essentially a matter of judgment (Kendall et al. 1983). We could not test directly for 'sampling period' or 'sampling period \times predator-treatment' interaction effects (e.g., using two-factor ANOVA) since our experimental design involved subsampling the same patches through time. A two-factor ANOVA with 'sampling period' as a factor would have serially correlated errors between times within patches, an error Hurlbert (1984:204) refers to as temporal pseudoreplication. As a final caveat on our statistical design, our "statistical population" and inferences based on our statistical tests are restricted to only one 16-m long transect during a 55-day period in the spring and early summer of 1981.

We used the logarithmic transform [$\log(x+1)$] on the population abundance data to meet assumptions of homoscedasticity in the parametric nested ANOVA (using the F_{max} test as our test statistic). Mean abundances are reported as the back-transformed ($10^x - 1$) or geometric means. These geometric means and standard deviations of transformed variates were used in our application of the Levenberg-Marquardt non-linear regression algorithm described below.

We tested for predation effects on day 3 using a mixed-model, nested ANOVA (Sokal and Rohlf 1981:274). The ANOVA tables corresponding to this design (Table 1c) allow two hypotheses to be tested: (1) Is there significant variance between patches within treatments, and (2) are there significant differences among treatments? Using a blocked ANOVA design, we could detect no differ-

Table 2. Infaunal abundances in the ambient-control and predator-treated patches on 11 May 1981, 3 days after the predators were added. All taxa with abundances greater than 0.1 per 0.95 cm² shown. Abundances are geometric means; 8 replicate 0.95-cm² samples were analyzed for each of the twice replicated patches for each treatment. Treatment differences were tested using 'Between Treatment MS'/'Experimental MS' (Table 1c). The significance of patch within treatment variance was tested using 'Experimental Error'/'Sampling Error' (Table 1c). The experimental error is often less than the sampling error. Pooling of experimental and sampling error does not change the outcome of the tests

Taxon	Ambient control	Treatment			Treatment effect $F_{(3,4)}$	Patch within treatment effect $F_{(4,56)}$
		900- <i>Eogammarus</i>	100- <i>Eogammarus</i>	25- <i>Crangon</i>		
Total <i>Hobsonia florida</i>	9.6	2.4	10.6	9.2	26.8**	0.6
juveniles (no branchiae)	9.5	2.0	10.3	8.9	26.7**	0.7
Oligochaetes	3.7	5.8	4.1	3.3	1.3 (ns)	1.6 (ns)
Harpacticoid copepods:						
copepodites only	24.4	10.4	23.9	22.7	7.0*	1.1
nauplii (incl. <i>H. jadensis</i>)	14.4	6.4	19.8	17.4	6.8*	0.8
<i>Huntemannia jadensis</i>	4.6	2.1	3.3	3.5	2.8	0.7
Nematodes	36.8	41.9	40.8	34.2	0.7	0.2
Foraminifera	9.3	7.7	9.8	11.6	0.6	0.7
Ostracods	0.8	1.0	0.9	0.6	0.1	3.3*
<i>Manayunkia aestuarina</i>	0.1	0.2	0.3	0.1	not tested	
<i>Macoma balthica</i>	0.1	0	0.1	0.1	not tested	

* Probability <0.05

** Probability <0.01

ences between eastern and western blocks. The variance between patches within treatments (tested with [patch within treatment MS]/[Error MS], Table 1c) was significant ($P < 0.05$, Table 2) only for ostracods on day 3 in the removal experiment.

In order to discern any differences among the Ambient-control, 25-Crango, and 100-Eogammarus treatments on day 3, the logarithmically transformed abundances for all taxa for these treatments were analyzed by linear discriminant analysis (Morrison 1976; Nie et al. 1975).

Stepwise multiple regressions of the Ambient-control and 900-Eogammarus treatment data were performed using SPSS (Nie et al. 1975) to test whether interspecific competition coefficients between oligochaetes and *H. florida* could be estimated using regression (Schoener 1974; Crowell and Pimm 1976). Either oligochaete or *H. florida* abundance was used as the dependent variable, and sampling time and treatment designation, coded as binary dummy variables (Draper and Smith 1981:241), were forced as independent variables in the regression analysis. After the covariation due to these habitat variables was accounted for, we inspected the partial correlation of the dependent variable with the abundance of other taxa in the community. The sign and magnitude of these partial correlations should be related to the interspecific competition coefficient if all relevant independent variables, especially resource supply, are assessed (Schoener 1985; Carnes and Slade 1988). Unfortunately, we did not have estimates of the probable key resource, benthic diatoms.

Fitting the Volterra and Gilpin-Ayala models

The Gilpin-Ayala model can produce two types of non-linear population dynamics not found in Volterra's model. First, the zero-growth isoclines can be non-linear in the Gilpin-Ayala model, whereas they are linear in the Volterra model. Second, per capita growth ($1/N \, dN/dt$) can be a non-linear function of population abundance (N) in the Gilpin-Ayala model but not in Volterra's. The Gilpin-Ayala and Volterra models can be described with the same differential equation:

$$\frac{1}{N_1} \frac{dN_1}{dt} = r_1 \left(1 - \left(\frac{N_1}{K_1} \right)^{\theta_1} - \alpha_{12} \frac{N_2}{K_1} \right) \quad (1)$$

where r_1 , K_1 , and α_{12} have their conventional meanings as per capita population growth in the absence of competition (in units of time⁻¹), carrying capacity, and apparent interspecific competition coefficient (Emlen 1984:138). θ_1 is a non-linearity parameter ranging from -1 to positive infinity (Pomerantz et al. 1980).

An analogous equation can be written for the competing species. Volterra's model is a special case of the Gilpin-Ayala model when $\theta = 1$.

Leslie (1957) and Vandermeer (1969) fitted Volterra's model by first estimating r and K from single-species cultures. They then used these parameter estimates as parameters in least-squares regressions using population abundance data from two-species cultures to estimate the interspecific competition coefficients. Ayala et al. (1973) estimated r , K , α_{ij} and θ simultaneously from two-species population data from 19 cultures, begun with different initial abundances of two competing *Drosophila* species. Typically, Leslie's (1957) finite difference form of the Volterra model or discrete-time transformations of the non-linear equations (Pomerantz et al. 1980, Gilpin et al. 1986) are used in least-squares regression. Unfortunately, fitting the discrete-time transformation of the Gilpin-Ayala model produces a consistent underestimate of the value of θ , called the pseudo- θ problem by Pomerantz et al. (1980). We developed a new approach, based on numerical integration of the differential equations, to fit the Volterra and Gilpin-Ayala models to field data. Tests with simulated data indicate that this fitting method does not suffer from the pseudo- θ problem.

Our approach fit eight parameters simultaneously to the popu-

lation abundance data from four different patches, sampled over seven time periods. The population abundances on the first of the dates were used to initialize the model. Our new technique solves the differential equations by integrating the initial value problem using standard numerical techniques. This approach, described more fully in the Appendix, is only summarized here. The non-linear competition equations were integrated with an adaptive Runge-Kutta algorithm, described by Press et al. (1986). We used the initial abundances observed in each of the four patches on day 3 to generate predicted population trajectories through the 55-day experiment. We used the Levenberg-Marquardt non-linear regression algorithm (Press et al. 1986) to find the set of parameter estimates that best fit the population trajectories of both *H. florida* and oligochaetes in each of the four patches through six time periods. We thus estimated 8 parameters (r , K , α , and θ for each species) using 48 population abundances (2 taxa \times 2 treatments \times 2 patches per treatment \times 6 dates). We fit Volterra's model by setting θ equal to 1.0 in Eq. 1. Our goodness-of-fit criterion for most analyses was the residual sum of squares between predicted and observed geometric mean abundance divided by the variance of the logarithmically transformed data. The mean and variance of the untransformed abundances were positively correlated, making the use of these variances problematic in fitting data. We also compared the results obtained using two additional goodness-of-fit criteria: the residual sum of squares (unscaled by variance) and the residual sum of squares divided by the untransformed variances. The parameter estimates using these two criteria were similar to those reported here with one notable exception. Our estimate of θ for *H. florida* often greatly exceeded 1, and the magnitude of the estimate was very sensitive to the choice of denominator in the goodness-of-fit criterion.

We could not statistically test whether the Gilpin-Ayala model was significantly better than Volterra's since the underlying distribution of our goodness-of-fit statistic is unknown. Following Draper and Smith (1981:484), a potential statistic for testing whether one model was better than another is:

$$F = \frac{[SSQR_i/(n-p_i)]}{[SSQR_j/(n-p_j)]} \quad (2)$$

where i, j denote two different models, $SSQR_i$ is the sum of squares of residuals of the fit of model i , n is the number of observations (=48 in this study), and p_i represents the number of estimated parameters in the i th model (=8 for Volterra's and 10 for Gilpin-Ayala's; the initial abundance estimates account for 2 of the parameters).

This statistic should be distributed approximately as $F(n-p_i, n-p_j, 1-\alpha)$ under the null hypothesis of no difference between model fits; the value of this test statistic should exceed 1.7 to reject the null hypothesis at an alpha level of 0.05. Since our observed mean abundances at different times within a patch are not independent, this critical value is only approximate. Incidentally, Leslie (1957) faced the same problem of serial correlation in fitting Gause's (1934) original data on competition among protozoa with Volterra's model.

To estimate the precision of the parameter estimates, we fit the parameters using our non-linear regression algorithm to four jackknifed data sets formed by deleting one patch from each set. Our jackknife approach was inspired by Meyer et al. (1986), who used the jackknife and bootstrap to estimate the precision of r in the Euler-Lotka equation. We calculated Tukey's pseudovalue for each of the parameters for each jackknifed data set using formulae in Efron (1982). The mean of these pseudovalue provides a jackknifed estimate of the parameters. We calculated the standard deviation of the jackknifed estimate, again using Tukey's equation (Efron 1982:14). Meyer et al. (1986) and Heltshe and Forrester (1985) used Tukey's jackknife estimation procedure, as described in Efron (1982), for growth rate in the Euler equation and species diversity, respectively.

Results and Discussion

The removal experiment

No significant differences among the replicated 100-*Eogammarus*, 25-*Crangon* and ambient-control treatments

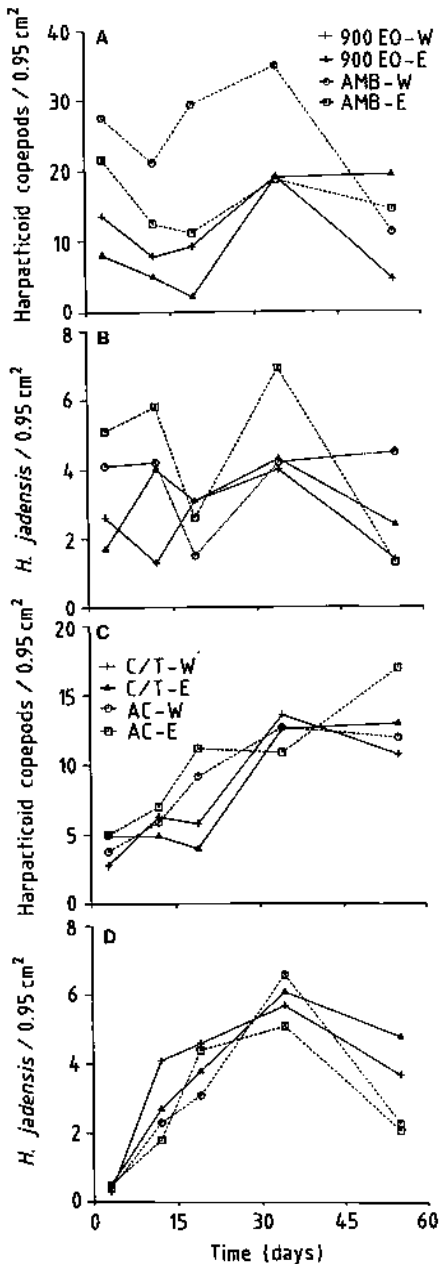


Fig. 2A-D. Geometric mean abundances per 0.95 cm² of A harpacticoid copepodites (other than *Huntemannia jadenensis*) and B *H. jadenensis* in the replicated patches of the removal experiment. 900 *Eo*-W and 900 *Eo*-E are the western and eastern replicates of the 900-*Eogammarus* treatment; AMB-W and AMB-E are the replicates of the ambient-control treatment (see Table 1a). Geometric mean abundances per 0.95 cm² of C harpacticoid copepodites (other than *H. jadenensis*) and D *H. jadenensis* in the replicated patches of the enhancement experiment. AC-W and AC-E are the western and eastern replicate patches for the azoic control treatment; C/T-W and C/T-E are the replicate patches for the *Corophium*/Tube treatment (Table 1a)

were detected using either nested ANOVA or linear discriminant analysis on day 3. Because of the absence of a treatment effect, samples from the 100-*Eogammarus* and 25-*Crangon* patches were not sorted on later dates. The 900-*Eogammarus* treatment, however, caused reductions in the abundances of *H. florida* juveniles and harpacticoid copepods relative to the ambient-control and other treatments (Table 2). The addition of *E. confervicolus* could have produced effects other than direct predation (e.g., nutrient enrichment or disturbance), but such effects would be quickly dissipated after day 3 by the action of wind and tides.

Four taxa showed long-term differences in population abundances between the ambient-control patches and patches affected by the 900-*Eogammarus* treatment. The abundances of harpacticoid copepods (other than *Huntemannia jadenensis*), reduced by the 3-day addition of *E. confervicolus*, gradually converged on ambient densities by the end of the experiment (Fig. 2a). Treatment effects, detectable by nested ANOVA, disappeared by day 19. Abundances of *Huntemannia jadenensis*, a large harpacticoid copepod, were reduced in the 900-*Eogammarus* patches (Fig. 2b), but the differences were not significant even on day 3 (Table 2). Harpacticoid copepod nauplii were also reduced in the 900-*Eogammarus* treatment on day 3 (Table 2) but were not sorted on later sampling dates.

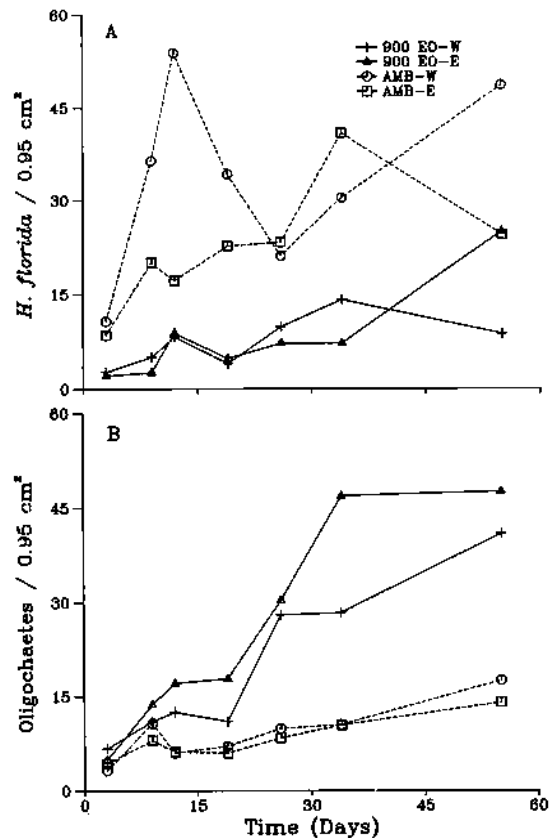


Fig. 3A, B. Geometric mean abundances per 0.95 cm² of A total *Hobsonia florida* and B oligochaetes in the replicated patches of the removal experiment. Symbols as in Fig. 2a and b

The absolute differences in abundances of *H. florida* in the 900-*Eogammarus* and ambient-control patches became greater with time (Fig. 3a). *Eogammarus confervicolus* did not significantly affect the initial abundances of oligochaetes, but we noted increasingly pronounced differences between the ambient-control and 900-*Eogammarus* patches on later sampling dates (Fig. 3b). By day 12, oligochaetes had higher densities in patches that had low abundances of *H. florida*.

The enhancement experiment

The *Corophium* manipulation was unsuccessful in maintaining higher abundances of *C. salmonis* relative to foundry-sand control patches. The 10 g (wet weight) of *C. salmonis* is roughly equivalent to roughly 900 individuals. The mean abundance of *C. salmonis* in thirty-two 0.95-cm² cores taken on day 0 was 1.6, which corresponds to a density per patch of roughly 900. Thus, virtually all of the animals added survived to the beginning of the experiment. On day 3, however, only two *C. salmonis* individuals were found in 64 samples, and one of those was in a foundry-sand control patch. For the remainder of the study, we sorted samples only from the *Corophium*/Tube and foundry-sand control patches. These will be called 'tube-array' and 'azoic-control' treatments.

Three taxa were affected by the presence of simulated tubes. *Hobsonia florida* abundances were lower in patches containing tubes by the end of the experiment (Fig. 4a). *Huntemannia jadensis* abundances (Fig. 2d) and tanaid abundances (not shown) were higher in the tube-array patches, but total harpacticoid abundances did not show a consistent increase in the tube-array treatment (Fig. 2c). These results generally confirm Eckman (1983) and Gallagher et al. (1983), who noted higher abundances of harpacticoid copepods and tanaids around tubes. The present results apparently contradict Eckman's (1983) finding of higher recruitment of *H. florida* into tube arrays, but the differences could be due to differences in experimental design. Eckman (1983) used plastic drinking straws to simulate tubes, his treatment patches were not replicated, and his experiments were performed in mid-April 1980, a period of very low *H. florida* recruitment rates and abundances (abundance data in Eckman 1982).

The foundry-sand patches provide important information about population growth rates in azoic patches on the flat. The peak of larval recruitment of *H. florida* to the foundry-sand patches occurred only after day 19 (Fig. 4a), whereas the peak of larval recruitment in the ambient-control patches in the removal experiment occurred between days 3 and 12 (Fig. 3a). The sharp drop in population growth in the 900-*Eogammarus* and ambient-control patches in the latter half of the 55-day period (Fig. 3a) suggest density-dependent limitation since larvae were still recruiting to the foundry-sand patches. From day 9 on, *Hobsonia florida* recruited to the foundry-sand patches at rates faster than to the 900-

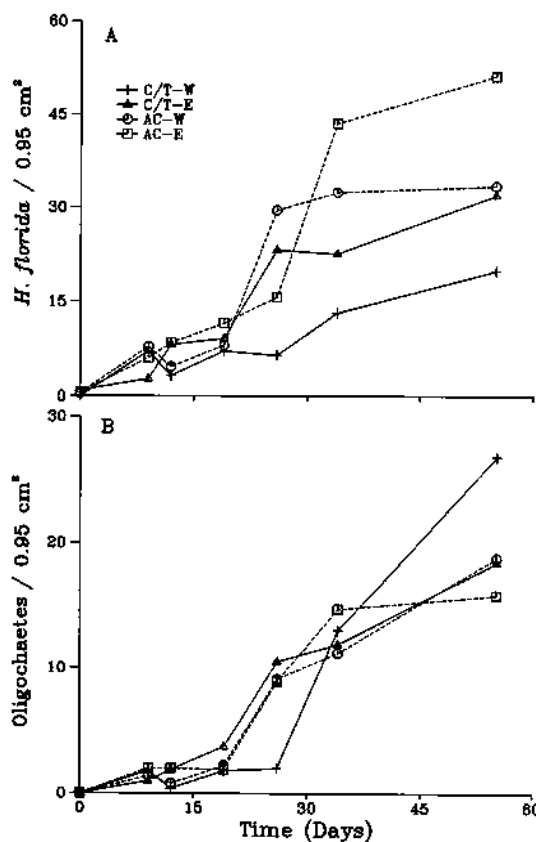


Fig. 4A, B. Geometric mean abundances per 0.95 cm² of A total *Hobsonia florida* and B oligochaetes in the replicated patches of the enhancement experiment. Symbols as in Fig. 2c and d

Eogammarus patches (cf. Figs. 3a, 4a). Population abundances of oligochaetes were low in these foundry-sand patches (Fig. 4b) relative to the 900-*Eogammarus* patches (Fig. 3b). Thus, these results are consistent with competition between *H. florida* juveniles and oligochaetes.

The inferred negative effects of oligochaetes on *H. florida* are reciprocated. Oligochaete population abundance remained low in the ambient-control patches throughout the experiment (Fig. 3b). *Hobsonia florida* is the only taxon that had a consistently higher abundance in these ambient-control patches relative to the 900-*Eogammarus* patches. Also, the abundances of oligochaetes remained relatively low in the enhancement experiment (Fig. 4b), whereas *H. florida* abundances in the enhancement experiment after day 34 (Fig. 4a) reached the high abundances observed in the ambient control cores (Fig. 3a). Harpacticoid copepods were also reduced initially in the 900-*Eogammarus* patches (Fig. 2a, b) and quickly recolonized the azoic sand patches (Fig. 2c, d). Since harpacticoid copepod abundances covary positively with *H. florida* abundance, they might have played a secondary role in depressing oligochaete population growth rate. The secondary role is due to the differential population growth of oligochaetes after day 19 in ambient and 900-*Eogammarus* patches (Fig. 3b) even though differences in harpacticoid copepod abundances had largely disappeared by this date (Fig. 2a, b).

The autecology of Hobsonia florida and oligochaetes

The mechanism underlying our results is probably exploitative or consumptive (Schoener 1983) competition among juvenile *H. florida* and oligochaetes for benthic diatoms. *Hobsonia florida* juveniles and oligochaetes are approximately the same size and may eat the same sized epipsammic diatoms. Benthic diatoms have been identified as a limiting resource for some intertidal benthic species in both laboratory and field studies (Admiraal et al. 1983; Admiraal 1984; Bianchi and Levinton 1984; Fenchel and Kofoed 1976; Gruia and Manoleli 1974).

Zottoli (1974) studied the life history of *H. florida* (= *Amphicteis floridus*, Banse 1979) and concluded that *H. florida* has a non-pelagic dispersal stage. At the time of recruitment at the 4-setiger stage, the smallest *H. florida* are approximately 200 μm long by 90 μm wide. During the first 3 days of the enhancement experiment approximately 300 *H. florida* recruited to each 530-cm² patch through a 250- μm mesh screen located 5 cm above the sediment. Thus, the non-planktonic *H. florida* larvae do not merely migrate laterally at the sediment-water interface; they are eminently transportable by currents. Zottoli (1974) found the development time from egg to the 6-setiger stage to be roughly 10 days at room temperature (20°–30° C). The effective field temperatures from May through June would be roughly 10° C less than that, leading to an approximate doubling of developmental time to 20 days (assuming a Q_{10} of 2). On day 55 of this study less than 20% of the *H. florida* population had reached the 6-setiger stage. One explanation for the low recruitment to the 6-setiger stage might be slower field development times, but the more likely explanation is a high mortality rate.

Our composite taxon "oligochaetes" is composed of at least three species. We did not identify the oligochaetes to species because there were no adequate keys for the Skagit oligochaetes when the samples were processed. We identified to species a subset of individuals from day-3 and day-55 samples from each of the treatments and found that an asexually reproducing naidid oligochaete, *Amphichaeta leydigii* Tauber 1879 (Brinkhurst and Kathman 1983) made up roughly 80% of the total oligochaete abundance. The next most abundant oligochaete was a morphologically similar but slightly larger asexually reproducing naidid, *Paranais birsteini* Sokolskaya (Brinkhurst and Coates 1985), which made up roughly 15% of the oligochaete numbers. The only other oligochaete observed was an unidentified tubificid. We were unable to detect any change in oligochaete species frequencies between treatments or through time (using chi-square tests). *Amphichaeta leydigii* was dominant on each sampling date in both the removal and enhancement experiments.

Naidid oligochaetes usually reproduce through paratomy, which results in the asexual production of a new individual from a bud formed from the posterior third of the worm. The size of an asexually produced *A. leydigii* bud is roughly the same as that of a recently settled *H. florida* juvenile: 100 μm diameter by 300 μm . Europe-

an populations of *Amphichaeta leydigii* bud in the spring and fall, coincidentally with blooms of benthic diatoms (Giere and Pfannkuche 1982). We can estimate approximate oligochaete birth rates using a modification of the equation for the frequency of dividing cells developed to estimate phytoplankton specific growth rates (McDuff and Chisholm 1982). The per capita birth rate should increase hyperbolically with budding frequency, according to the equation:

$$b = t_b^{-1} \ln(1 + f) \quad (3)$$

where b is the birth rate [d^{-1}], t_b is the duration [in days] during which oligochaete buds are visible, and f is the frequency of budding individuals observed in a sample.

Approximately 75% of the oligochaetes were budding at the start of the experiment. At the end of the experiment, 82% of the oligochaetes in the 900-*Eogammarus* patches and 67% in the ambient-control patches were budding. These differences in budding frequency were not significant by chi-square test, but such differences could be important demographically. We can estimate the importance of these differences in budding frequency if the value of t_b is known. If the initial population growth rate of 0.16 day^{-1} (estimated below using the Volterra model) is due to birth rate only, then the budding duration (t_b) corresponding to an initial budding frequency of 75% would be 3.5 days. If t_b is constant, the differences in birth rate corresponding to budding frequencies of 82% and 62% calculated using Eq. 3 would be 0.17 d^{-1} and 0.15 d^{-1} . Such differences in birth rate could produce nearly 3-fold differences in population abundances over 52 days. Hence, the differences in budding frequency observed might be associated with differences in specific birth rates sufficient to explain the changes in oligochaete abundance observed between treatments in this experiment, but differential mortality and migration could also account for these differences.

The Skagit oligochaetes are diatom grazers. The guts of *Amphichaeta leydigii* contain little else but pennate benthic diatoms. The guts of the larger *P. birsteini* contain some fine sand grains in addition to diatoms, but the guts of *A. leydigii* do not. The guts of juvenile *H. florida* contain silt and clay-sized particles in addition to pennate benthic diatoms. Giere and Pfannkuche (1982) review the now well documented preference of marine naidid oligochaetes for pennate benthic diatoms and the close coupling between naidid population growth rate and high benthic diatom standing stocks. More recently, Bagheri and McClusky (1982) found the population growth of *Amphichaeta sannio*, now believed to be synonymous with *A. leydigii* (Brinkhurst and Kathman 1983), is closely coupled to diatom standing stocks.

The competition models

We fit the competition models using the geometric mean abundances of *H. florida* and oligochaetes observed in

Table 3. The geometric abundances and variance of the logarithmically transformed abundances (in parentheses) are shown for each date in the removal experiment. These data were used in non-linear regression to fit the Volterra and Gilpin-Ayala models

Treatment	Taxon				Taxon			
	Day	Patch	<i>H. florida</i>	Oligochaetes	Patch	<i>H. florida</i>	Oligochaetes	
Amb. Control	3	E4	8.5 (0.07)	4.3 (0.04)	W3	10.7 (0.01)	3.2 (0.07)	
Amb. Control	9	E4	20.0 (0.08)	8.0 (-) ^a	W3	36.4 (0.01)	10.7 (0.02)	
Amb. Control	12	E4	17.1 (0.08)	6.2 (0.03)	W3	53.7 (0.03)	6.0 (0.06)	
Amb. Control	19	E4	22.6 (0.05)	6.0 (0.05)	W3	34.6 (0.06)	7.1 (0.02)	
Amb. Control	26	E4	23.2 (0.06)	8.4 (0.05)	W3	21.0 (0.01)	9.9 (0.03)	
Amb. Control	34	E4	40.8 (0.06)	10.4 (0.08)	W3	30.3 (0.04)	10.5 (0.02)	
Amb. Control	55	E4	24.4 (0.01)	14.0 (0.01)	W3	48.4 (0.002)	17.5 (0.01)	
900- <i>Eogammarus</i>	3	E1	2.0 (0.04)	4.9 (0.07)	W4	2.7 (0.04)	6.7 (0.02)	
900- <i>Eogammarus</i>	9	E1	2.6 (0.04)	13.7 (0.08)	W4	5.0 (0.09)	11.0 (0.01)	
900- <i>Eogammarus</i>	12	E1	8.8 (0.02)	17.1 (0.01)	W4	8.2 (0.01)	12.5 (0.01)	
900- <i>Eogammarus</i>	19	E1	4.8 (0.01)	17.8 (0.01)	W4	4.0 (0.06)	11.0 (0.10)	
900- <i>Eogammarus</i>	26	E1	7.2 (0.10)	30.3 (0.01)	W4	9.8 (0.09)	28.0 (0.03)	
900- <i>Eogammarus</i>	34	E1	7.2 (0.03)	46.9 (0.02)	W4	14.1 (0.03)	28.3 (0.02)	
900- <i>Eogammarus</i>	55	E1	24.9 (0.01)	47.6 (0.02)	W4	8.7 (0.001)	40.9 (0.01)	

^a Both replicates were identical. Because of the small sample size (2 replicate subsamples rather than the typical 4), we assigned the largest variance observed for the patch for the non-linear regression

the four patches (Table 3), and we also fit the models using four jackknifed data sets, each consisting of a different combination of three patches. The parameters for the Volterra model are shown in Table 4a, those for the Gilpin-Ayala model in Table 4b. The standard deviation of the four jackknifed parameter estimates indicate that precision of the estimates for the Volterra model is quite poor. The deletion of single patches in forming the four jackknifed data sets causes relatively large changes in the fitted parameter values.

Fitting competition models to field experimental data allows for few compromises in an experimental design. Replicate subsamples of each patch are needed to estimate the within-patch variance for the goodness-of-fit statistic; many sampling periods are needed to estimate changes in growth rate; and most importantly, many replicated patches are needed to increase the precision of the parameter estimates. Further constraining the design, in an intertidal community the experiment must be set up and all of the samples taken during a single low tide.

The chi-square goodness-of-fit for the non-linear Gilpin-Ayala model is slightly better than for the linear Volterra model. The observed population trajectories of the Volterra model (Fig. 5) and Gilpin-Ayala model (Fig. 6) do not differ appreciably, the zero-growth isoclines and equilibrium solutions of the two models do differ substantially. In the Volterra model (Fig. 5), oligochaetes competitively exclude *H. florida*, albeit at an exceedingly low rate. In the Gilpin-Ayala model, the best estimate of the non-linearity parameter, θ , for *H. florida* is 150 (Table 4b), and the zero-growth isocline is nearly rectilinear (Fig. 6). Two alternate equilibria are possible in the Gilpin-Ayala model. Oligochaetes can win or both species can coexist, depending on the initial population abundances (Fig. 6).

We computed the predicted trajectories for the combined replicates for the 900-*Eogammarus* and ambient-control treatments using both the Volterra and Gilpin-Ayala models (Figs. 5c, 6c). Although the equilibrium solutions differ drastically, the two models' predicted population trajectories are very similar and track the observed population trajectories from days 3 to 55.

The jackknifed estimates of the interspecific competition coefficients were close to 1, as were the estimates based on all four patches. We assessed the adequacy of a model in which *H. florida* and oligochaetes had interspecific competition coefficients equal to 1. We set the interspecific competition coefficients to 1 and fit the remaining parameters in the Gilpin-Ayala model. We found the trajectories to be virtually indistinguishable from the best Gilpin-Ayala fit (Fig. 7), and there was only a negligible 2% increase in the chi-square goodness-of-fit statistic (Table 4c). These data support the hypothesis that *H. florida* and oligochaetes can be regarded as nearly ecological equivalent species in their resource utilization patterns.

In both the Volterra and Gilpin-Ayala models of *H. florida* - oligochaete competition, the population trajectories and relative abundance of competitors on day 55 are determined by the initial population abundances. Even though the Volterra model predicts that oligochaetes should exclude *H. florida*, *H. florida* can be the numerical dominant for long periods of time if its initial abundances exceed those of oligochaetes. The time to competitive exclusion is long. With an initial abundance of 10.3 *H. florida* and 3.2 oligochaetes per 0.95 cm², 450 days are required before the *H. florida* abundances decline to less than 1.0. This period is equivalent to 80 times the shortest population doubling time for the competitive dominant.

There is an obvious reason for the long time to com-

Table 4. Fitted parameters for the Volterra and Gilpin-Ayala competition models. A jackknife procedure was used to estimate the variance of the parameters. For each model, 4 separate jackknifed data sets of the patches were analyzed. All four data sets were analyzed for the combined values. The jackknifed estimate of the parameters (Jack. Est.) and Tukey's standard deviation (SDEV) of the pseudovalue estimate were calculated using formulae in Efron (1982). The trajectories shown in Figs. 5-7 are based on the estimates from all patches a Volterra model ($\theta = 1.00$). The results of the combined fit are plotted in Fig. 5.

	<i>Hobsonia florida</i>				Oligochaetes				Chi-square ¹
	r_1	K_1	α_{12}	θ_1	r_2	K_2	α_{21}	θ_2	
No W4	0.128	55.9	0.859	1.00	0.138	55.9	0.924	1.00	327
No W3	0.131	49.1	0.975	1.00	0.129	58.7	1.352	1.00	245
No E4	0.112	68.7	1.444	1.00	0.123	51.1	0.728	1.00	326
No E1	0.174	66.9	1.788	1.00	0.114	47.9	0.641	1.00	231
All patches	0.135	64.2	1.408		0.124	50.7	0.754		409.6
Jackknife									
Estim.	0.136	76.3	1.832		0.118	42.8	0.282		
SDEV	0.040	13.9	0.645		0.015	12.5	0.475		

¹ Chi-square is lower in the jackknifed data sets than in the combined because there are fewer data being fit (36 vs 48)

b The full Gilpin-Ayala Model, Variable. The results of the combined fit are plotted in Fig. 6. We discovered after generating the jackknifed data sets that our regression algorithm was terminating while the values were increasing; θ for this taxon could increase to very high values with little change in chi-square. We could not perform Tukey's jackknife estimation on these data because of the uncertainty in estimates of θ

	<i>Hobsonia florida</i>				Oligochaetes				Chi-square
	r_1	K_1	α_{12}	θ_1	r_2	K_2	α_{21}	θ_2	
No W4	0.139	38.7	0.934	32.9	0.154	52.2	0.896	1.030	262
No W3	0.130	34.9	0.992	7.0	0.128	58.0	1.318	0.944	211
No E4	0.148	42.0	1.300	18.6	0.122	47.9	0.660	0.960	297
No E1	0.179	45.8	1.620	4.5	0.129	49.0	0.590	0.728	207
All patches	0.162	37.3	1.10	150.0	0.161	57.3	0.792	0.642	338

c Gilpin-Ayala model ($\alpha_{ij} = \alpha_{ji} = 1.00$). The predicted trajectories are plotted in Fig. 7

	<i>Hobsonia florida</i>				Oligochaetes				Chi-square
	r_1	K_1	α_{12}	θ_1	r_2	K_2	α_{21}	θ_2	
All patches	0.159	35.3	1.00	184.0	0.146	58.9	1.00	0.862	346.5

petitive exclusion. With parallel and closely spaced zero-growth isoclines, the model predicts the competitive dominant will have an exceptionally slow growth rate once the inferior competitor's zero-growth isocline has been reached. For such closely matched species, the outcome of competition can be likened to a race to the zero-growth isoclines; the species with a head start becomes the dominant. Hubbell and Foster (1986) reached a conclusion similar to ours without relying on mathematical formalism. Competitive exclusion of rain-forest trees was unlikely, they argued, because tree species have similar resource requirements and consequently long times to competitive exclusion.

The competitive interactions described here are best viewed from a non-equilibrium perspective (reviewed by Chesson and Case 1986). In nature, *H. florida* and oligochaetes are unlikely to ever achieve competitive equilibrium. These species compete in the context of a seasonal

succession driven by rapidly changing allogenic and autogenic processes, Diatom production and species composition change seasonally in response to light and temperature primarily (Admiraal 1984). The size-frequency distribution of the *H. florida* population shifts seasonally to larger size classes. Later succession species like *C. salmonis* recruit onto the flats (Fig. 1d) from their overwintering habitat in the high marsh (personal observations), drastically changing the population dynamics of these pioneer species and their resources. The time-invariant parameters of the Volterra model cannot model the seasonally changing sandflat habitat, and little credence should be attached to the equilibrium prediction based on the Volterra model (i.e. oligochaete dominance). Hutchinson (1967:480) provides a colorful metaphor for the type of competition observed on the Skagit flats, "The competitors of a given genus or other higher taxon are from time to time lined up, and sometimes the race be-

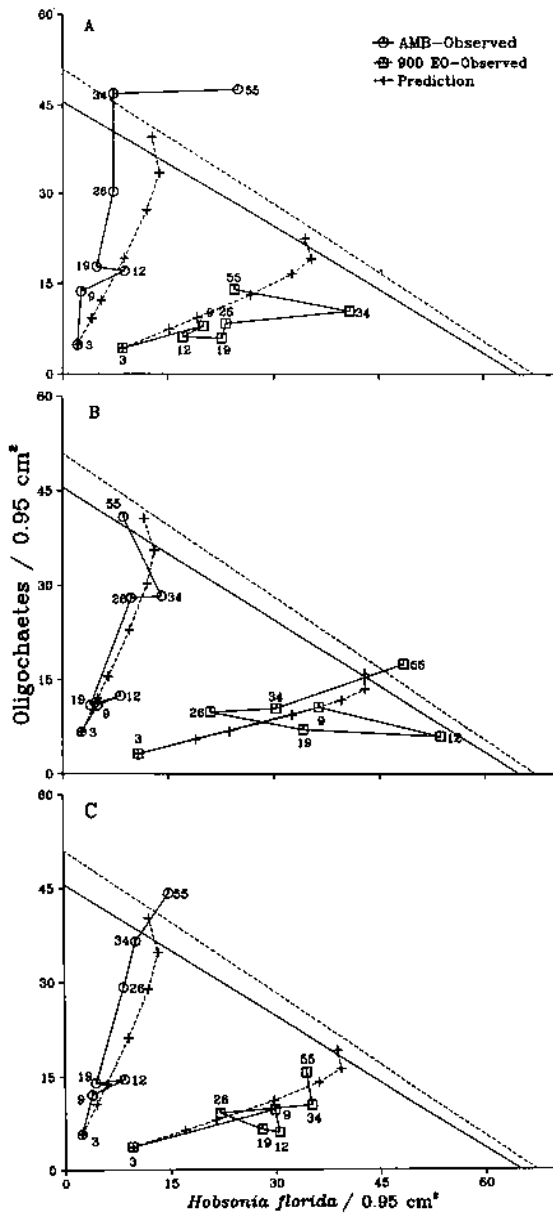


Fig. 5A-C. Using Volterra's model (see text) and the parameter estimates in Table 4a, predicted (+ symbols and dotted lines) and observed (open symbols and solid lines) trajectories for the *Hobsonia florida* and oligochaete populations are plotted for A the eastern and B the western patches of the removal experiment. The predicted fit was initialized with the mean abundances on day 3. C The observed trajectories for the means of the replicated patches and model predictions initiated with the overall day-3 mean abundances. Also plotted are the predicted linear zero-growth isoclines where the *H. florida* (solid line) and oligochaete (dotted line) population growth rates are zero

gins, but as it might be in the works of Lewis Carroll, the event is always called off before it is completed and something entirely different is arranged in its place."

Despite its success in fitting our data, we think that the Gilpin-Ayala model is seriously flawed and do not consider it as an adequate replacement for Volterra's model. The Gilpin-Ayala model is plagued by two prob-

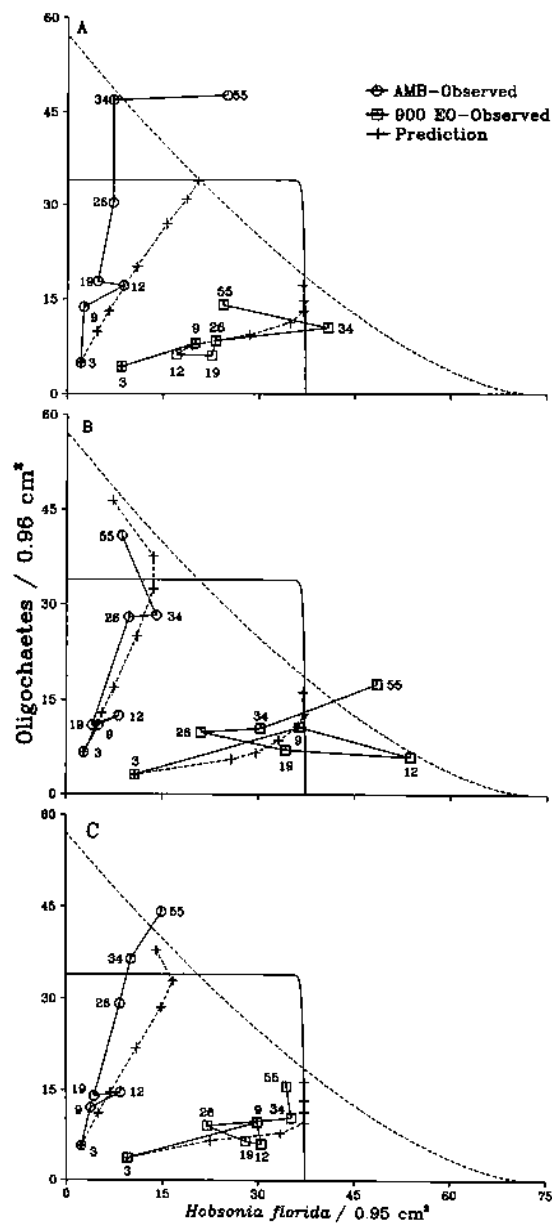


Fig. 6A-C. Using the Gilpin-Ayala model and parameter estimates of Table 4b (see text), predicted (+ symbols and dotted lines) and observed (open symbols and solid lines) trajectories for the *Hobsonia florida* and oligochaete populations are plotted for A the eastern and B the western patches of the removal experiment. The predicted fit was initialized with the mean abundances on day 3. C The predicted and observed trajectories for the means of the replicated patches. The predicted zero-growth isoclines where the *H. florida* (solid line) and oligochaete (dotted line) population growth rates are zero are shown in each figure

lems caused by the non-linearity parameter θ . First, the nonlinearity parameter affects only the intraspecific competition term in Eq. 1. As noted by Gilpin and Ayala (1973), the effects of interspecific competition are still assumed to be linearly dependent on population abundance of the competitor. Unfortunately at levels far greater than unity, the Gilpin-Ayala θ parameter acts

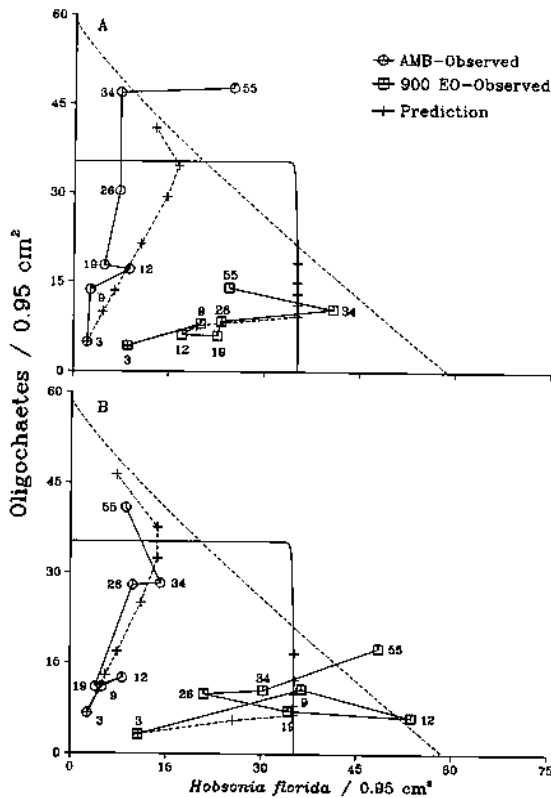


Fig. 7A, B. Using the Gilpin-Ayala model with $\alpha_{12} = \alpha_{21} = 1.0$ and the parameter estimates of Table 4c (see text) predicted (+ symbols and dotted lines) and observed (open symbols and solid lines) trajectories for the *Hobsonia florida* and oligochaete populations are plotted for A eastern and B western patches of the removal experiment. The predicted fit was initialized with the mean abundances in each patch on day 3. The predicted zero-growth isoclines where the *H. florida* (solid line) and oligochaete (dotted line) population growth rates are zero are shown in each figure. These differ only slightly from those in Fig. 6

not as a curvilinearity parameter but as an all-or-none weighting function. All density-dependent growth limitation is switched to the competing species, which acts in full accord with Volterra's linear assumption. This switching role at high θ can be seen when the interspecific competition coefficient is evaluated. Emlen (1984:138) observed that the apparent interspecific competition coefficient in the Gilpin-Ayala model, α'_{12} in Eq. 1 equals the conventional interspecific competition coefficient only if $\theta_1 = 1$:

$$\alpha_{12} \equiv \frac{\partial r_1 / \partial N_2}{\partial r_1 / \partial N_1} = \frac{\alpha'_{12}}{[\theta_1 (N_1 / K_1)^{\theta_1 - 1}]} \quad (4)$$

where $\partial r_1 / \partial N_2$ is the partial derivative of per capita growth in sp. 1 with respect to the change in sp. 2 abundance, $\partial r_1 / \partial N_1$ is the partial derivative of per capita growth in sp. 1 with respect to the change in species 1 abundance, α_{12} is the conventional interspecific competition coefficient, and α'_{12} and θ_1 are the Gilpin-Ayala parameters in Eq. 1.

With θ values much greater than 1, the conventional interspecific competition coefficient can reach extraordi-

narily high values, approaching infinity in the case of *H. florida* in this study. We regard this result as an unrealistic and unacceptable feature of the Gilpin-Ayala model. Nunney (1980) and Gardner and Gallagher (submitted) show that curvilinear zero growth isoclines are only possible because $\alpha_{12} \neq \alpha'_{12}$ in Eq. 4.

A second flaw affects the Gilpin-Ayala model if the estimated non-linearity parameter, θ , greatly exceeds 1. In that case the model can predict unrealistic population trajectories when abundances exceed the carrying capacity. In the present case, a 1% overshoot of the *H. florida* carrying capacity with θ equal to 150 results in a decline in per capita population growth at 3.4 times the maximal rate of population increase. Even a slight overshoot of carrying capacity results in a population crash. Gilpin et al. (1976) include analyses of expected population dynamics for θ values up to 1000 but do not discuss the strange and unrealistic population-dynamic consequences of large θ . Our simulation results showing a smooth approach to equilibrium (Fig. 6b) were attained only by integrating Eq. 1 four times daily as the carrying capacity of *H. florida* was approached. A daily integration time step resulted in population abundance trajectories that chaotically bounced off the *H. florida* zero-growth isocline like ping-pong balls.

There is a ready alternative to the Gilpin-Ayala model, which solves both of the aforementioned problems. This model, described by Gardner and Gallagher (in preparation), applies the non-linearity parameter to both the intra- and interspecific competition terms:

$$\frac{1}{N_1} \frac{dN_1}{dt} = r_1 \{1 - [(N_1 - \alpha'_{12} N_2) / K_1]^{\theta_1}\}. \quad (5)$$

The θ parameter in this model now can produce the curvilinearity of both intra- and interspecific density-dependent growth limitation. Equation 5 shares with the Volterra model the pedagogically appealing features that the interspecific competition coefficients are not dependent on competitor densities, and the zero-growth isoclines are linear. Although the best fit for θ for the *H. florida* population using Eq. 1 is 150, it is 0.1 in Eq. 5. Nunney (1980) and Gardner and Gallagher (submitted) discuss an alternative form of the Gilpin-Ayala model which can produce curvilinear zero-growth isoclines, but at the cost of producing density- and frequency-dependent interspecific competition coefficients.

The fit of both the Volterra and Gilpin-Ayala models to the population trajectories appears excellent. The Volterra and Gilpin-Ayala equations can be criticized on many grounds, but they do have an extraordinary flexibility in fitting field data. With only four patches though, the precision of our parameter estimates for the Volterra model is quite low. The Gilpin-Ayala model provides a better fit to our data, but its explanations of population dynamics with our parameters are not at all realistic. As a concise mathematical description and explanation for the observed population trajectories of *H. florida* and oligochaetes, we prefer the Volterra model.

Raymond Pearl viewed logistic growth as an irrefut-

able 'law of nature' (Kingsland 1985:75). We do not. The following assumptions, necessary to accept Volterra's model as a literal description of population dynamics, are not strictly met in the Skagit community:

1. The Skagit community must be spatially and temporally homogeneous with respect to the model's parameters.
2. Each population must respond to changes in its own abundance and that of its competitors instantly.
3. Age structure and phenotypic variation can be disregarded.
4. The interspecific competition coefficients are unaffected by changes in the species composition of the remainder of the community. That is, there are no higher-order interactions (e.g., see Neill 1974 and rebuttal by Pomerantz 1981).
5. The resource grows logistically at a time-scale rapid compared to the consumer populations.
6. Stochastic effects can be neglected.

Whether these models should be viewed as mere instruments for making projections and curve fitting is a matter of personal judgment and philosophy. We feel models should explain as well as predict. To serve as an explanation, either a model's assumptions should be met or the predictions of the model should be robust to violations of the assumptions. MacArthur (1972:33) observed that Volterra's model is never literally correct; its use should be based upon an understanding of the equations and upon field experience with the organisms. Although its assumptions are not met, the Volterra model's prediction of the fundamental importance of initial species composition and long times to competitive exclusion may be robust to violations of the assumptions.

The assumption of the Volterra model that differences in age structure are unimportant may be met during this 55-day period. Virtually all of the *H. florida* were in the 4-6 setiger size class during this period, and the asexually reproducing oligochaetes exhibit little change in species, age- or size structure. Obviously as the *H. florida* grow to larger sizes, our estimates of the interspecific competition coefficients and carrying capacity would change drastically. Frank (1957) was similarly constrained in his application of Volterra's competition model to competing species of *Daphnia*. His model fit one stage of the life cycle of these species (the asexual stage) but could not be used to predict the effects of ephippia production.

The hypothesis that juvenile *H. florida* and oligochaetes are nearly perfect competitors (i.e., competition coefficients close to 1 and similar carrying capacities) helps explain a curious feature of the synecology of these species. We sampled the natural community in the 2 years prior to this study (1979 and 1980). The abundances of oligochaetes and *H. florida* change seasonally in a "boom-and-crash" cycle, with oligochaetes dominant in 1979 (Fig. 1a) and *H. florida* dominant in 1980 (Fig. 1b). The combined abundances of these pioneers were virtually the same on similar Julian calendar dates (Fig. 1c). Both populations may be tracking benthic diatom production, which is known to exhibit an annual

cycle, controlled by seasonal changes in temperature and light intensity (Admiraal 1984). In accordance with the predictions of our Volterra model, the pioneer species with a head start dominates in a given year, but the combined abundances are similar on the same date each year. Both populations crash after the first week of July when *Corophium salmonis* recruits onto the mudflat (Fig. 1d). *Corophium salmonis*, a gammaridean amphipod, is much larger than either of these species and also feeds on benthic diatoms. *Corophium salmonis* can also prey on both juvenile *H. florida* and oligochaetes. Thus, predation, competition, or both in concert could explain the successional sequence from *H. florida* and oligochaetes to *C. salmonis*. Experimental manipulation of *C. salmonis* densities, attempted unsuccessfully in this study, could rule out the possibility that the timing of the crash of the pioneer species and the recruitment of *C. salmonis* is merely a coincidence.

Regression of census data (Schoener 1974; Crowell and Pimm 1976) is an increasingly popular alternative to controlled field manipulations for estimating interspecific competition coefficients. Our application of regression was not successful in estimating the magnitude or even the sign of the competition coefficient between *H. florida* and oligochaetes. The seasonal abundances of these two species are positively correlated (Figs. 1, 3, 4). Even after the time effect was assessed using stepwise multiple regression with time coded for as a dummy variable (Draper and Smith 1981), the partial correlations between oligochaete and *H. florida* abundances were positive not negative (+0.23 in the ambient-control patches and +0.18 in the 900-*Eogammarus* patches). We suspect that both species' abundances were positively correlated with that of patchily distributed benthic diatom standing stocks within the 26-cm diameter patches. A regression analysis of the patch means, rather than the individual 0.95-cm² cores, would be more likely to yield negative partial correlations. A proper sample survey design for estimating the interspecific competition coefficients between these groups would require an assessment of the covariance of competitor abundances with their shared resource (Schoener 1985; Carnes and Slade 1988). Schwingamer (1983) estimated benthic diatom, meiofaunal, and juvenile macrofaunal standing stocks, and his path analysis revealed a negative but nonsignificant partial correlation between total macrofauna and total meiofauna.

The competitive bottleneck hypothesis

Neill (1975:824) described the competitive bottleneck as an age-specific competition for limited resources which ramifies throughout subsequent age classes and sets an upper limit on the number of individuals at those stages. The effects of competition on later age classes may be trivial and the growth rate of those later age classes may be independent of resource supply. Bell and Coull (1980) predicted the existence of a competitive bottleneck for the meiofaunal-sized recruits of the benthic macrofauna.

Our data are consistent with this bottleneck hypothesis. Oligochaetes and juvenile *H. florida* are probably members of a diatom-grazing guild (a guild is defined as a group of species that exploit the same class of environmental resources in a similar way [Root 1967]). The competitive bottleneck, faced by the meiofaunal-sized recruits of *H. florida* and caused by oligochaetes, does not result in exclusion of the *H. florida* but does affect their abundances. There have been few clear-cut confirmations of Bell and Coull's (1980) hypothesis. Weinberg et al. (1986) showed through life-table analyses that variations in juvenile growth rate had great importance to the population growth of *Gemma gemma*, a suspension-feeding marine bivalve, whereas variations in adult growth and survival were relatively unimportant. The study of Armonies and Hellwig-Armonies (1987) appears to contradict the meiofaunal bottleneck hypothesis. They found positive correlations between meiofaunal and macrofaunal abundance, as we did in this study. However, positive correlations even among competitors could occur if both competitor populations were positively correlated with a patchily distributed diatom resource. Manipulative field experiments or sample surveys which assess the covariance among meiofauna, macrofauna and their shared diatom resource are needed to test the generality of Bell and Coull's (1980) meiofaunal bottleneck hypothesis.

Hutchinson (1961) posed the paradox of the plankton: "How can a number of phytoplankton species coexist when all must compete for a few essential nutrients which are demonstrably in short supply?" He solved the paradox by proposing that environmental variations occur sufficiently frequently to prevent competitive exclusion. The long times to competitive exclusion predicted by our Volterra model may explain a similar paradox for the benthic-diatom grazers on the Skagit flats. For grazers that have very similar or identical patterns of resource utilization and similar carrying capacities, the times to competitive exclusion will be long, and even minor environmental variation can lead to long-term coexistence. Thus, the assumption that resource or habitat partitioning is required for the coexistence of sympatric populations of deposit feeders may not be valid.

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Appendix

The Gilpin-Ayala equations are non-linear in both K and θ , which limits the use of linear regression tech-

niques. Ayala et al. (1973) used non-linear regression to fit Eq. 1, but did not specify how the non-linear differential equation was integrated. Pomerantz et al. (1981) and Gilpin et al. (1986) used a finite-difference approximation of the Gilpin-Ayala model to fit laboratory data. Pomerantz et al. (1981) note that their method tends to underestimate the value of θ . Therefore, numerical integration of the non-linear Gilpin-Ayala equations combined with the Levenberg-Marquardt non-linear regression algorithm (Press et al. 1986) were used to fit the model parameters to the field data. An initial estimate of the parameters is improved, as indicated by the reduction of a chi-squared statistic, by means of formulae involving the derivatives of chi-square with respect to each parameter. In order to minimize the effects of outliers, the back-transformed geometric abundances were used as the observed data in estimating chi-square, and squared deviations were normalized by the variance of the log-transformed variates (Eq. A1)

$$X^2(\vec{a}) = \sum_{i=1}^2 \sum_{j=1}^6 \sum_{k=1}^4 \frac{[N_{ijk} - N_{ik}(t_j; \vec{a})]^2}{s_{ijk}^2} \quad (\text{A } 1)$$

where:

i \Leftrightarrow species

j \Leftrightarrow sample time

k \Leftrightarrow patches

N_{ijk} \Leftrightarrow observed geometric mean abundance

s_{ijk}^2 \Leftrightarrow sample variance

N_{ik} \Leftrightarrow model prediction

\vec{a} \Leftrightarrow parameter vector

$$= (r_1, K_1, a_{12}, \theta_1, r_2, \alpha_{21}, \theta_2)$$

We also used untransformed means and variances and obtained similar results for all parameters but θ , which is difficult to fit since it can greatly exceed 1 when fitting the *H. florida* trajectories.

The Levenberg-Marquardt algorithm requires the model values at each sample point as well as the derivatives of the model values with respect to the model parameters. Since the competition equations are expressed in differential form, they must be integrated to yield the predicted values. In the present study, we used an adaptive Runge-Kutta scheme described in Press et al. (1986). This technique allows for step sizes greater than 1 day when population abundance predictions are not needed for each day. The increased computational speed thus gained was important due to the number of iterations required to fit the parameters to the field data. The derivatives for the fitting procedure were also obtained by integration. The competition equations were differentiated with respect to the model parameters, and the order of differentiation reversed to obtain differential equations

which were integrated with the Runge-Kutta procedure. For example,

$$\begin{aligned} \frac{\partial}{\partial t} \left[\frac{\partial N_1}{\partial \theta_1} \right] = & r_1 \frac{\partial N_1}{\partial \theta_1} \left\{ 1 - \left(\frac{N_1}{K_1} \right)^{\theta_1} - \alpha_{12} \frac{N_2}{K_1} \right\} \\ & - r_1 N_1 \left\{ \left(\frac{N_1}{K_1} \right)^{\theta_1} \left[\ln \left(\frac{N_1}{K_1} \right) + \frac{\theta_1}{N_1} \frac{\partial N_1}{\partial \theta_1} \right] \right. \\ & \left. + \frac{\alpha_{12}}{K_1} \frac{\partial N_2}{\partial \theta_1} \right\} \end{aligned} \quad (\text{A2})$$

A total of 16 such equations is required (derivatives of N for each of 2 populations with respect to each of 8 parameters). The computational effort is less than implied, since many terms appear in several equations. The initial values of all the derivatives are 0, since the initial values of N_1 and N_2 are specified.

Data from all four patches were analyzed simultaneously to obtain the 'combined' values given in Table 4. The program was run on a personal computer, and convergence monitored as the program executed. Execution was halted when chi-square did not change by more than 0.001–0.003 at each iteration, and the values of the parameters did not change by more than 0.1%. Press et al. (1986) state that changes in chi-square of less than 0.1 are not likely to be related to significant changes in the parameters being fitted. The more stringent criteria were used here because it was found that convergence was quite slow. The cumulative effect of many iterations with changes in chi-square of 0.1 or less may be significant.

Care should be used in applying the Levenberg-Marquardt method to competition models. The initial estimates for the constant θ case were based on a "brute force" fitting of the model parameters to the Leslie (1957) finite difference forms of Volterra's equations. Thousands of systematically varied combinations of r , K and α_{ij} were used to generate trajectories using the Leslie equations, initialized with day-3 abundances from this experiment. The optimal combination of parameter estimates using this brute-force technique was found and chosen as the starting point for the constant θ simulations using our new algorithm. The results of the constant θ case were then used to initialize the varying θ simulations. In spite of this approach, we found that the fit could often be improved by perturbing the initial estimates. Our goal was to find the minimum of a chi-square statistic, which is distributed irregularly in an eight-dimensional parameter space. A certain amount of trial and error in exercising the fitting routine is required to gain confidence that a global minimum has been achieved.

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