

The consequences of broadcasting, brooding, and asexual reproduction in echinoderm metapopulations

Life-cycle
Demography
Asteroidea
Transition matrix

Cycle de vie
Démographie
Asteroidea
Matrices de transition

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ABSTRACT

Different modes of reproduction were examined in the context of entire life cycles for seven starfish species so that adult survival could be compared with reproductive output and first year survival. Data were assembled from the literature and included two asexual species, *Linckia multifora* and *Nepanthia belcheri*; two brooders, *Asterina phylactica* and *Leptasterias hexactis*; one species with benthic eggs that does not brood, *Asterina gibbosa*; one species with lecithotrophic development in the plankton, *Patiriella pseudoexigua*; and one planktotrophic species, *Pisaster ochraceus*. A negative correlation was found between first-year survival and adult survival rates which also correlated with mode of reproduction: highest adult survival and lowest first-year survival was found for *P. ochraceus*, the planktotrophic species, and lowest adult survival was coupled with highest first-year survival in asexual species.

A matrix model was developed to explore the metapopulation consequences of different modes of reproduction. Asexual species are similar to species with planktonic larvae that also have long-lived adults in that both are well insulated from the vagaries of planktonic life, one by avoiding the plankton all together and the other by having very low transition probabilities for the first year of life but high transition probabilities for retention of adults in the population. Species with short-lived adults and planktonic development of larvae are more closely tied to changes in first-year survival rates with respect to over-all dynamics of metapopulations.

RÉSUMÉ

Les conséquences de divers modes de reproduction, production de larves pélagiques, incubation et reproduction asexuée chez les métapopulations d'échinodermes.

Différents modes de reproduction sont examinés à travers les cycles vitaux de sept espèces d'étoiles de mer ; le taux de survie des adultes est comparé à la production gonadique et au taux de survie durant la première année. Les données, extraites de la littérature, se rapportent à 1) deux espèces asexuées, *Linckia multifora* et *Nepanthia belcheri*, 2) deux espèces incubantes, *Asterina phylactica* et *Leptasterias hexactis*, 3) une espèce à développement benthique qui ne protège pas ses œufs, *Asterina gibbosa*, 4) une espèce à développement planctonique lécithotrophique, *Patiriella pseudoexigua*, et 5) une espèce planctotrophique, *Pisaster ochraceus*.

Une corrélation négative est observée entre le taux de survie durant la première année et le taux de survie des adultes, lui-même corrélé au mode de reproduction. Le plus fort taux de survie des adultes et le plus faible taux de survie durant la première année sont observés chez *P. ochraceus*, l'espèce planctotrophique,

tandis que le plus faible taux de survie des adultes est associé au plus fort taux de survie durant la première année chez les espèces asexuées.

Un modèle matriciel a été développé pour analyser les conséquences des différents modes de reproduction chez les métapopulations. Les espèces asexuées sont similaires aux espèces à larves planctoniques et longue durée de vie, dans la mesure où toutes deux échappent aux caprices de la vie pélagique, les unes ne dépendant pas du plancton en général, les autres ayant peu de chances de survie au-delà de la première année mais une forte probabilité de maintien des adultes dans la population. Les espèces à courte durée de vie et à développement larvaire planctonique ont un taux de survie nettement plus variable durant leur première année, en rapport avec la dynamique des métapopulations.

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INTRODUCTION

Life cycles of organisms represent a long history of selective tinkering and, in general, the life cycle that is observed is expected to show adjustments in all parts of the cycle in response to changes in one part. Schedules of survival and reproduction are at the core of all theoretical discussions of life cycles dating back to Fisher (1930), Birch (1948), and Cole (1954) and implicit or explicit in all life-history discussions is that trade-offs exist such that if resources are used for one activity they can not be used for something else. Analysis of tradeoffs has focused on relationships among numbers and sizes of offspring, adult size and growth, and survival (*e.g.* Stearns, 1992).

Population growth rate or fitness is determined by mean values for schedules of survival and fecundity as well as variability of these traits (*e.g.* Tuljapurkar, 1982 *a, b*; Orzack, 1985; Caswell, 1989) and so changes in morphology, physiology, or behavior that change means and variances of life-cycle transitions will change fitness. Changes in mean values for offspring number are correlated with mode of reproduction in marine invertebrates, as well as other groups of organisms, and these changes in mode of reproduction are perceived as changes that should modify early survivorship (*e.g.* Menge, 1975).

There is general agreement concerning the ranking of reproductive modes that should improve the chances of first year survival: the form of reproduction with the lowest first-year survival is planktotrophy, followed by planktonic lecithotrophy, attached benthic lecithotrophic eggs with no planktonic stage, brooding, and, finally, asexual reproduction, such as autotomy of body parts that regenerate, and fission of a body into two or more pieces of approximately equal size. Asexual reproduction should have the highest first year survival rate.

Changes that increase the mean and reduce variation in survival from spawning or asexual reproduction to an age of one year should improve fitness and as a consequence free resources that had been used for maintenance to increase fitness in other ways, such as more offspring. This scenario has been presented by Stearns (1976) and continues to be an attractive explanation (*e.g.* Grant, 1990).

Few studies on life-history traits of echinoderm species with different modes of reproduction have been conducted in sufficient detail that complete life-cycles can be drawn

with transition probabilities, and there are none that supply such information so spatial and temporal variability can be evaluated. Yet it is clear that such information is needed not only to understand the evolution of life histories but also for applied purposes such as management of natural resources and the design of marine reserve systems.

This paper examines data on echinoderms, and in particular starfishes, to evaluate the effects of different reproductive modes on transitions in the life cycle, specifically first-year and adult survival rates. Also, after making estimates of these transitions for a selection of echinoderm species, I will present a model for combining populations into metapopulations that provides some insights into the importance of dispersal with respect to fitness and probable stability characteristics of metapopulations of species with different modes of reproduction.

METHODS

Life-cycle information in the form of age- or size-specific rates of survival and reproduction was obtained from a number of published studies. To reanalyze data, I had to make a number of assumptions. The two most important assumptions are: 1) populations have seasonally stable structure; that is, at the same time each year they have the same proportions in ages or sizes; and, 2) populations are seasonally stationary, which means that from year to year the population growth rate, λ , is equal to 1.0.

Two different, though related, forms of the life cycle were used for analysis (Figs. 1, 2). In the first (Fig. 1), an age-structured matrix was created with a terminal age, ω , and with the possibility of age-specific changes in reproduction and survival for adults. This is the standard Leslie matrix. Data that were used included all information but one transition; namely, first year survival P_0 . The characteristic equation for Figure 1 was obtained by following the outline provided by Caswell (1985, 1989). A Z-transformation was performed, which is just multiplying all transitions by λ^{-1} . All possible loops through node 1 were determined and then all transitions in a loop were multiplied together. Products from all individual loops were then added together and set equal to 1.0. A bit of additional algebra was all that was needed to form the characteristic equation of the graph:

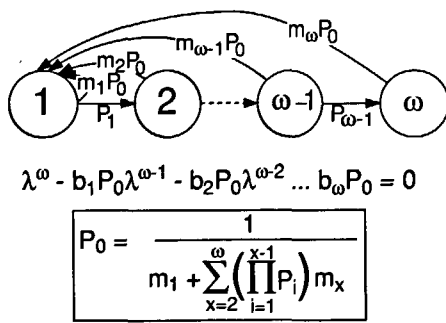


Figure 1

Life-cycle with age-structure that is the equivalent of the Leslie matrix; P_0 = first year survival; P_x = age-specific survival for age classes from 1 to ω ; m_x = age-specific fecundity; formula for estimating P_0 is for population growth rate λ set equal to 1.

$$\lambda^\omega - b_1 P_0 \lambda^{\omega-1} - b_2 P_0 \lambda^{\omega-2} \dots - b_\omega P_0 = 0 \quad (1)$$

where b_1 is m_1 , b_2 is $P_1 m_2$, b_3 is $P_1 P_2 m_3$, etc. After setting $\lambda = 1.0$, it is a simple matter to solve for P_0 . Obviously, however, because it is assumed that $\lambda = 1.0$, it is possible to skip the Z-transform and obtain the products of all of the loops, sum them together, set them equal to 1.0 and solve for P_0 .

A second, though related, approach was to assume fixed rates of reproduction and adult survival with no terminal age; i.e. survival does not change with age (Fig. 2). The characteristic equation of this graph is substantially simpler than for Figure 1:

$$\lambda^a - P_A \lambda^{a-1} - P_j^{a-1} m_A P_0 = 0 \quad (2)$$

where,

λ = the population growth rate, which is the largest real root of Eq. 2.

a = age at first reproduction.

P_j = annual survival rates of juveniles from age 1 to age at first reproduction, a .

P_A = annual adult survival rate.

m_A = annual production of (female offspring)/(adult female).

P_0 = first year survival rate.

Once again, λ is set equal to 1.0 and, for some published data sets, I have also set $P_j = P_A$, which reduces Eq. 2 to:

$$P_0 = \frac{1 - P_A}{P_A^{a-1} m_A} \quad (3)$$

Eq. 2 also was used to estimate adult survival, P_A , in two cases (Menge, 1975) where estimates of P_0 were provided:

$$P_A^{a-1} + \frac{1}{m_A P_0} P_A - \frac{1}{m_A P_0} = 0 \quad (4)$$

In several other data sets, I estimated P_A by using the relationship between the mean of a size-frequency distribution, \bar{S}_t , and the growth and survival functions that determine the mean (Ebert, 1973; Ebert and Russell, 1993):

$$\bar{S}_t = S_\infty (1 - e^{-Z}) \sum_{i=0}^{\infty} e^{-Zi} (1 - b.e^{-K((t+i))})^{-n} \quad (5)$$

With the Richards function for modeling growth and constant adult survival the parameters in Eq. 5 are:

S_∞ = asymptotic size

K = the growth-rate constant with units of time⁻¹

n = a shape parameter; e.g. $n = -1$ for the Brody-Bertalanffy equation and $+1$ for logistic growth

$$b = \frac{S_\infty^{-1/n} - S_R^{-1/n}}{S_\infty^{-1/n}} \quad (6)$$

t = time since recruitment of animals that are size S_R ; t generally is set equal to 0.

S_R = size of new recruits, generally set as equal to the mode of the smallest component of a size-frequency distribution or series of size-frequency distributions.

Z = the instantaneous rate of mortality when $N_x = N_0 e^{-Zx}$ with x the age of individuals in a cohort that began with N_0 individuals

Finally, Z is related to survival, P_A :

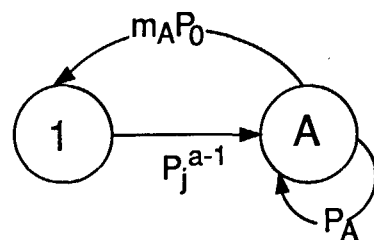
$$P_A = e^{-Z} \quad (7)$$

A final complication arises with fissiparous species. The value of Z that is determined from growth and size structure includes both death and fission; however, if fission is the only means of reproduction, annual fission rate, F , and annual mortality are related (Ebert, 1983):

$$M = \frac{F}{1 + F} \quad (8)$$

and

$$P_A = 1 - M = \frac{1}{1 + F} \quad (9)$$



$$\lambda^a - P_A \lambda^{a-1} - P_j^{a-1} P_0 m_A = 0$$

$$P_0 = \frac{1 - P_A}{P_j^{a-1} m_A}$$

Figure 2

Simplified life-cycle graph with age-structure; a = age at first reproduction, P_0 = first year survival, P_A is annual adult survival rate and m_A = fecundity; formula for estimating P_0 is for population growth rate λ set equal to 1.

RESULTS

Studies of asteroids have spanned reproductive modes from asexual forms that have arm autotomy or are fissiparous to planktotrophic species. Two species that have attracted substantial attention and have the greatest degree of detail for their life-cycles are *Asterina gibbosa* and *A. phylactica* (Crump, 1978; Emson and Crump, 1979, 1984; Strathmann *et al.*, 1984). *Asterina gibbosa* lays egg masses and abandons them whereas *A. phylactica* lays egg masses that are brooded.

A transition matrix was created in which all transitions were known except P_0 , which was solved by creating the characteristic equation, setting $\lambda = 1.0$ and solving for P_0 . The survival, or P_x , values in the transition matrix were based on a Weibull distribution (Weibull, 1951; Pinder *et al.*, 1978):

$$P_x = e^{[(x/b)^c - ((x+1)/b)^c]} \tag{10}$$

in which

$$b = \omega e^{-v/c} \tag{11}$$

If a cohort begins with 1000 individuals then the last individual is alive when $I_x = 0.001$, which defines the parameter v in Eq. 11:

$$v = \ln(-\ln(0.001)) \tag{12}$$

and

$c = a$ shape parameter; $c = 1$ for Deevey type II, $c > 1$ for Deevey type I and $c < 1$ for Deevey III

$\omega =$ age at which the last individual of a cohort is alive.

I used $c = 3$ for both *Asterina* species in order to have survival rates decrease as animals increased in size, which is what Emson and Crump contend. I selected $\omega = 7$ years for *A. phylactica* and $\omega = 12$ years for *A. gibbosa* based on the likely growth curves and age to 95 % of maximum size.

To estimate age-specific fecundity, m_x , I used size of newly released animals as 0.75 mm for both species, estimates of size at age, and estimated maximum size from data in Emson and Crump (1979). If 4.5 mm is age at 1 year for *A. phylactica* and maximum size is 13 mm, then

$$4.5 = 13 - (13 - 0.75)e^{-K} \tag{13}$$

and $K = 0.40 \text{ yr}^{-1}$.

For *A. gibbosa*, size at 3 years was used in order to make the estimated sizes fit the estimates of Emson and Crump (1979). Maximum size seems to be about 30 mm. Consequently,

$$15.6 = 30 - (30 - 0.75)e^{-3K} \tag{14}$$

which gives $K = 0.24 \text{ yr}^{-1}$.

The relationship between size at age x (S_x) and numbers of eggs in a brood (m_x) is:

$$m_x = 8.68 S_x - 14 \tag{15}$$

for *Asterina phylactica* and

$$m_x = 41 S_x - 327.7 \tag{16}$$

for *Asterina gibbosa*.

Age-specific size, fecundity and survival (Tab. 1) were assembled as life-cycle graphs to estimate P_0 using Eq. 1.

Table 1

Age-specific size in millimeters, fecundity (m_x), and annual survival rate (P_x) for the starfishes *Asterina phylactica* and *A. gibbosa* based on data presented by Emson and Crump (1979, 1984).

Age	<i>Asterina phylactica</i>			<i>Asterina gibbosa</i>		
	Size	m_x	P_x	Size	m_x	P_x
0	0.75	0	?	0.75	0	?
1	4.79	0	0.868		0	0.972
2	7.50	51	0.682		0	0.927
3	9.31	66.8	0.475	15.76	0	0.862
4	10.53	77.4	0.293	18.8	443.0	0.784
5	11.34	84.4	0.160	21.19	541.0	0.695
6	11.89	89.2	0.077	23.07	618.2	0.601
7	12.50	92.4	0.033	24.55	678.8	0.509
8				25.71	726.4	0.420
9				26.63	764.2	0.338
10				27.34	792.2	0.266
11				27.91	816.6	0.205
12				28.36	835.0	0.153

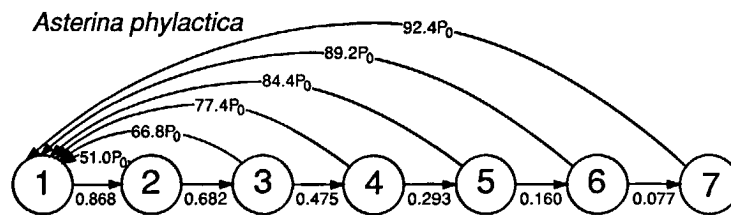


Figure 3

Life-cycle graph for *Asterina phylactica* using data from Table 1; based on work by Emson and Crump (1984).

The life-cycle graph for *Asterina phylactica* is shown in Figure 3, which has a characteristic equation:

$$\lambda^7 - 44.2680P_0\lambda^5 - 36.4129P_0\lambda^4 - 20.041P_0\lambda^3 - 6.4030P_0\lambda^2 - 1.0827P_0\lambda - 0.0864P_0 = 0 \quad (17)$$

After setting $\lambda = 1.0$, P_0 in Eq. 17 is 0.0088 yr^{-1} . A similar procedure was followed for *Asterina gibbosa* using m_x and P_x data in Table 1 and P_0 was estimated to be 0.0008 yr^{-1} . First year survival is about one order of magnitude better for *A. phylactica*. In order to compare the two *Asterina* spp with other starfish, I simplified the life cycle by using the estimate of P_0 for each species together with Eq. 4 to obtain estimates of the average adult survival for each species (Tab. 2).

Menge (1975) provides estimates of m_A , P_0 and age at first reproduction for *Leptasterias hexactis*, a brooder, and *Pisaster ochraceus*, which has planktotrophic larvae. Adult survival was estimated using Eq. 4 (Tab. 2). *Pisaster* is very long lived; at equilibrium, the average age of starfishes in a population, $-\frac{1}{\ln P_x}$, would be 20 years, compared with an average age of 8 years for *Leptasterias*.

Chen and Chen (1992) have published life history information for *Patriella pseudoexigua*, which has lecithotrophic development in the plankton. They include estimates of age at first reproduction (a), fecundity (m_A), and sufficient detail concerning growth so parameters of the Richards function could be estimated (Ebert, 1980). The Richards function shape parameter is $n = -1.50$, the growth rate constant K is 1.06 yr^{-1} and asymptotic size, $S_\infty = 15.7 \text{ mm}$. The size distribution from April 1988 was used to estimate Z . Mean size was about 11 mm and S_R was 2.5 mm and so, applying Eq. 5, $Z = 0.291 \text{ yr}^{-1}$. Chen and Chen give an

estimate of 1500 eggs produced by an average female so the number of females/female, m_A , would be 750. First year survival, P_0 , is unknown but after one year, $P_A = 0.747$; i.e. $\exp(-Z)$. Age at first reproduction seems to be 2 years for *P. pseudoexigua* and so by using Eq. 3, $P_0 = 0.00045$ (Tab. 2).

Finally, two asexual asteroid species, *Nepanthia belcheri* (Ottesen and Lucas, 1982) and *Linckia multifora* (Rideout, 1978) were analyzed to produce estimates of P_0 and P_A . The *Linckia multifora* population studied by Rideout consisted entirely of individuals in various stages of regeneration following arm autotomy. Rideout presents monthly data (his Tab. 1) for numbers of individuals in various stages of regeneration. Because autotomized arms take roughly one month to become comets, the monthly rate of autotomy is the number of new individuals per individual, m_A , and can be calculated from the monthly number of autotomized arms (A) and the total number of starfish (T) in the samples. Because the total, T , in Rideout's table includes autotomized arms (A), I first subtracted A from T to get an estimate of the number of individuals that produced the autotomized arms:

$$m_A = \frac{A}{T - A} \text{ month}^{-1} \quad (18)$$

For example, in April 1974 there were 27 animals in the sample, 6 of which were autotomized arms (A) and so m_A is 6 divided by 21, not 27; the autotomy rate for April 1974 was 0.286 month^{-1} . The mean monthly autotomy rate for 12 months was 0.096 month^{-1} , which can be used to estimate monthly survival rate and then annual survival rate.

Table 2

First year and adult survival rates for starfishes with different modes of reproduction; F = fissiparous; A = arm autotomy; B = benthic egg masses; BR = brooding; L = lecithotrophic; P = planktotrophic; a is the age at first reproduction.

Species	Reference	mode	a	P ₀	P _A
<i>Nepanthia belcheri</i>	Ottesen and Lucas 1982	F	1	0.135	0.135
<i>Linckia multifora</i>	Rideout 1978	A	1	0.331	0.331
<i>Asterina phylactica</i>	Emson and Crump 1984	BR	2	0.0088	0.636
<i>Leptasterias hexactis</i>	Menge 1975	BR	2	0.00040	0.886
<i>Asterina gibbosa</i>	Emson and Crump 1984	B	4	0.0008	0.759
<i>Patriella pseudoexigua</i>	Chen and Chen 1992	L	2	0.00045	0.747
<i>Pisaster ochraceus</i>	Menge 1975	P	5	1.46×10^{-9}	0.952

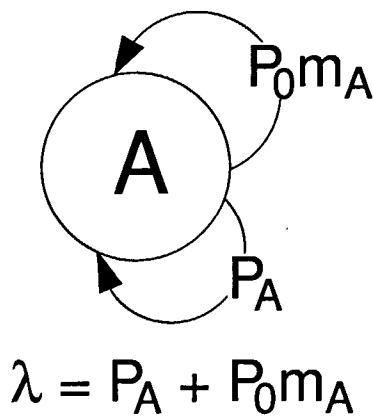


Figure 4

Life-cycle graph for species where reproduction begins at age 1 and all adults produce the same number of offspring.

The life-cycle graph for *Linckia multifora* is very simple (Fig. 4). All individuals are either adults or autotomized arms and based on the growth curve provided by Rideout, age at first autotomy of an autotomized arm is about one year. Monthly survival for autotomized arms held in aquaria was as good as survival of other regeneration stages and so P_0 was the same as P_A , which further simplifies the characteristic equation of Figure 4. With $\lambda = 1$, the equation is:

$$1 = P_A + P_A m_A \quad (19)$$

or

$$P_A = \frac{1}{1 + m_A} = \frac{1}{1 + 0.096} = 0.912 \text{ month}^{-1} \quad (20)$$

The annual survival rate is the product of the monthly survival rates or

$$P_A = 0.912^{12} = 0.33 \text{ yr}^{-1}$$

Using the annual survival rate of 0.33 in Eq. 19 shows that, on an annual basis, $m_A = 2$; each individual sheds two arms each year.

Nepanthia belcheri is a fissiparous species. Frequency of individuals showing evidence of recent fission is provided by Ottesen and Lucas (1982) in their Figure 3. The authors state that the rates of regeneration were sufficiently rapid that individuals would not be considered "recent" after one month following fission. Consequently, the frequency of fission products each month can be used to estimate monthly fission rates. The estimate involves correcting the frequency of regenerating animals, R , from their Figure 3, to account for the 3 for 1 split that is obtained by fission (Ottesen and Lucas, 1982, p. 226) and the fact that R was calculated by dividing fission products by total individuals which included fission products. I used the following formula to convert values (R) from their Figure 3 to monthly fission rates, F .

$$F = \frac{R}{3T - 2R} \quad (21)$$

I used data for just one year, from March 1976 through February 1977 and so did not include the March 1977

value from their Figure 3. The estimate for mean monthly fission rate is 0.0907, which means that the monthly rate of non-fission is 0.9093. Including the non-fission rate in calculations is necessary because an individual that undergoes fission is lost to the adult population. Substituting values into Equation 19 with the assumption that $P_0 = P_A$ yields:

$$1 = P_A(0.9093) + P_A(0.0907 \times 3)$$

so

$$P_A = 0.8464 \text{ month}^{-1} = 0.1352 \text{ yr}^{-1}$$

For the starfish data that were analyzed (Tab. 2), there is a clear pattern among modes of reproduction, first year survival, and adult survival (Fig. 5). The two species that reproduce asexually, *Linckia multifora* and *Nepanthia belcheri* have relatively low adult survival and relatively high survival of reproductive products. At the other extreme, *Pisaster ochraceus* has very low first-year survival and very high adult survival.

The different modes of reproduction are associated with changes in adult vs. first-year survival and, in general, the pattern fits expectations about the relationship between first-year survival and mode. I now want to examine the larger implications of this pattern with respect to the dynamics of populations that are linked together into metapopulations. To do this I will use values from Table 2 that are appropriate for starfishes in particular but which also would be appropriate for a wide range of species.

In order to simplify analysis, I will use Eq. 19 (Fig. 4) so that age at first reproduction will be at 1 year, which is the same as the model used by Schaffer (1974). In addition to age at first reproduction equal to 1 year and constant survival past 1 year, it also is assumed that reproductive output remains constant; that is, age 2 females have exactly the same number of female offspring as age 30 females.

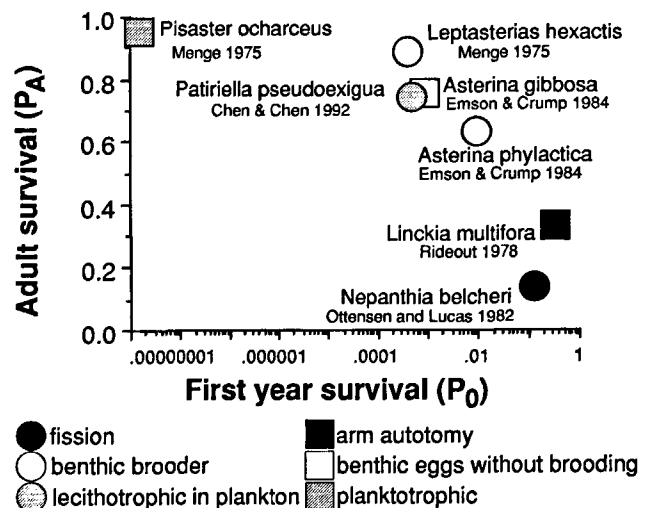


Figure 5

Summary of analysis of starfishes showing the correlation between adult survival and first year survival for species with different modes of reproduction.

Table 3

Stable-population distributions for extremes of reproductive modes, asexual reproduction and planktotrophy with long-lived adults; asexual mode represents data appropriate for *Linckia multifora* and the planktotrophy model used data appropriate for *Pisaster ochraceus*; population numbers refer to Figure 6 with 1 and 7 at the extremes of the distribution and 4 at the center.

Population	Asexual stable population	Planktotrophy stable population
1	1.00	1.00
2	1.85	1.46
3	2.41	1.89
4	2.61	2.00
5	2.41	1.89
6	1.85	1.46
7	1.00	1.00

Populations that have the characteristics of Figure 4 can be linked together to form a simple metapopulation with linkages determined by the mode of reproduction. For example, for asexual species or species that have benthic eggs, the loop for P_0m_x , that is offspring number times first year survival, is a self-loop back into the population; however, for species with planktonic larvae, the loop for P_0m_x , goes outside the population to some other population. I have constructed these two metapopulations (Fig. 6) to show these differences. In Figure 6 A populations 1 through 7 are weakly linked through the plankton so the probability of dispersal, P_d is much less than the combined probabilities of remaining as an adult and number of new one-year-old individuals added: $P_x + P_0m_x$. Because dispersal is very low, I also have included limited dispersal in the model by having each population (node) linked with a maximum of two other nodes. Nodes 1 and 7 have links with just one other node, which also would be reasonable for populations at the extreme of a range.

Figure 6 B is for species with planktonic larvae. I constructed the model so that spawning in a population (node) must go somewhere else to contribute to the metapopulation. I also increased the number of connections each node makes so the maximum is four. Populations 1 and 7 have links with just two other nodes: 5 and 6 for node 7 and 2 and 3 for node 1. Nodes 2 and 6 form connections with three other nodes and, finally, nodes 3, 4, and 5 have the maximum number of four connections each. For example, node 3 is connected with nodes 1, 2, 4, and 5.

I used data appropriate for *Linckia multifora* with model A in Figure 6, that is, $P_0 = P_A = 0.33$ and $m_x = 2$. There are no data that relate to the probability of dispersal but it probably is very low so I took $P_0 \times 10^{-4}$ or 0.000033 for P_d . In fact, this probably is too high but, as will be shown, I could be off by several orders of magnitude and the results would not be changed. I created a 7×7 matrix with the transitions. The diagonal of the matrix consisted of $P_A + P_0m_x$ and the supra- and sub-diagonals both were P_d . For illustration, if there would be just 4 nodes, the matrix A would be 4×4 :

$$A = \begin{bmatrix} P_A + P_0m_x & P_d & 0 & 0 \\ P_d & P_A + P_0m_x & P_d & 0 \\ 0 & P_d & P_A + P_0m_x & P_d \\ 0 & 0 & P_d & P_A + P_0m_x \end{bmatrix} \quad (22)$$

In analyzing the metapopulation of 7 populations with data appropriate for *Linckia multifora*, the dominant and subdominant roots of the characteristic equation were 1.00006 and 1.00005. The ratio of the dominant and subdominant roots is called ρ , the damping ratio (Caswell, 1989), and indicates how rapidly a system will return to its stable configuration, which in this case is the stable population distribution of the metapopulation. The larger the value of ρ , that is, the greater the difference between λ_1 and λ_2 , the more rapid the convergence. For the simulated *Linckia multifora* metapopulation, the ratio, ρ , is 1.00001, which means that if the metapopulation would be deformed away from the stable-population distribution in Table 2, convergence back to a stable configuration would take an exceedingly long time. In effect, populations of the metapopulation function independently, which is exactly what intuition tells us about populations consisting of asexually reproducing individuals. The stable-population distribution, which is the equivalent of the stable age distribution, is shown in Table 3. The shape of the distribution is caused by nodes at the end of the distribution, that is 1 and 7, being linked with just one other node whereas all other nodes are lined with 2; population 1 is linked just with population 2 but population 2 is linked with both population 1 and 3. The result is a symmetrical distribution with the largest population in the center of the metapopulation.

Model B in Figure 6 provides very similar results to model A when a species such as *Pisaster ochraceus* is used. The diagonal of the matrix is P_A and P_0m_x is moved to the supra- and sub-diagonals which means that recruits into a particular population never come from spawning from that population but were spawned by some other population of the metapopulation. A 5×5 version of this matrix is:

$$B = \begin{bmatrix} P_A & \frac{P_0m_x}{n} & \frac{P_0m_x}{n} & 0 & 0 \\ \frac{P_0m_x}{n} & P_A & \frac{P_0m_x}{n} & \frac{P_0m_x}{n} & 0 \\ \frac{P_0m_x}{n} & \frac{P_0m_x}{n} & P_A & \frac{P_0m_x}{n} & \frac{P_0m_x}{n} \\ 0 & \frac{P_0m_x}{n} & \frac{P_0m_x}{n} & P_A & \frac{P_0m_x}{n} \\ 0 & 0 & \frac{P_0m_x}{n} & \frac{P_0m_x}{n} & P_A \end{bmatrix} \quad (23)$$

where P_A is adult survival and n is the maximum number of connections that can be formed with other populations. I have made $n = 4$ for model B in Figure 6 which is also shown in matrix B above; population 3 has connections with 4 other populations whereas population 1 is connected with just 2 other populations.

For model B, I used $P_A = 0.96$ and $P_0m_x = 0.01$. The dominant and sub-dominant roots, λ_1 and λ_2 , are 0.9935 and 0.9773 so the damping ratio, ρ , is 1.017 which means that

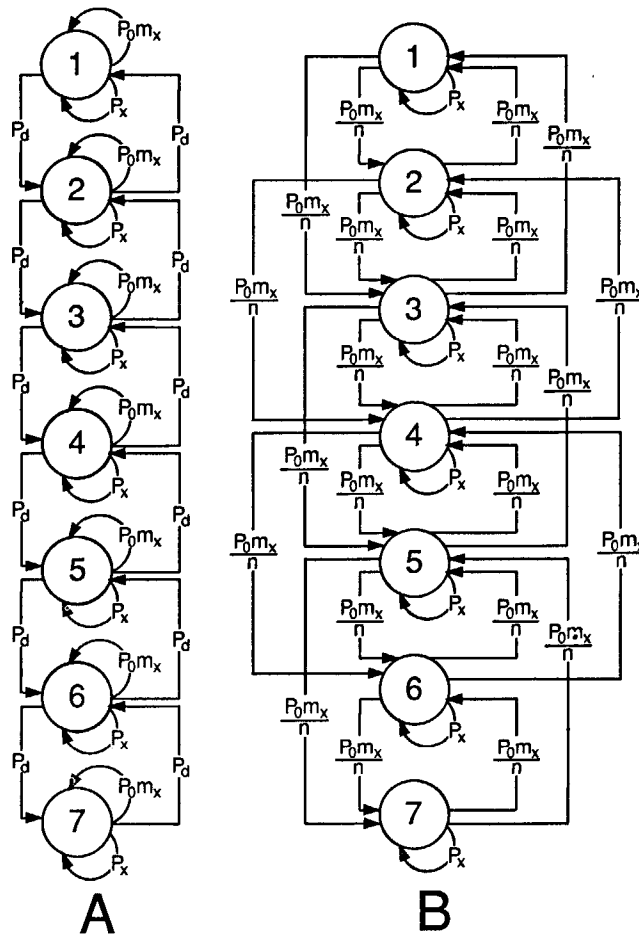


Figure 6

Metapopulations constructed using populations shown in Figure 4 A: life history appropriate for species that lack a planktonic stage; B: life history appropriate for species with a planktonic stage.

following deformation of the metapopulation, return to a stable configuration would be very slow; how long it would take would depend on how great the disturbance was. The stable population distribution (Tab. 3) again shows that the largest population would be the one farthest from the edges of the range.

A final analysis was made using data values appropriate for a lecithotrophic development similar to *Patiriella pseudoexigua* with $P_A = 0.76$ and $\frac{P_0 m_x}{n} = 0.07$. With these values in model B, the dominant and sub-dominant roots, λ_1 and λ_2 , were 0.9948 and 0.8812 so the damping ratio, ρ , is 1.129. This still is a rather small value; however it does indicate that convergence to a stable-population distribution in the metapopulation would be more rapid than for species such as *Pisaster ochraceus*.

A final aspect of the analysis was to examine elasticity values (Caswell, 1989) for the metapopulations, which measure the proportional effect of changes in transitions on metapopulation growth rate, λ_1 . Elasticity of a matrix element, a_{ij} is defined as:

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} \quad (24)$$

The sum of the elasticity values for the diagonal of the matrix is a measure of the importance of retention within a population and one minus this value measures the relative importance of dispersal with respect to metapopulation growth. For *Linckia multifora*, the sum of the elasticities of the diagonal elements was 0.99995 and so the elasticity for dispersal is just 0.00005, which means that changes in dispersal rate will have very little influence on overall growth-rate of the metapopulation. A 1000 % change in dispersal rate would change λ by only 0.05 %. Another way of viewing this is to see that a 10 % change in factors that retain individuals within a population would lead to a 9.99995 % change in λ and in order to equal this change through dispersal would require that dispersal success change by nearly 20,000 %. I could change the value for dispersal over several orders of magnitude without substantially changing the conclusions based on the analysis.

For *Pisaster ochraceus*, the sum of elasticities for retention within a population P_A , is 0.9662 and so the elasticity for dispersal is 0.0338. A 10% change in adult survival would change λ by 9.6 % but to obtain a similar change in λ through dispersal would require a change of nearly 300 %.

Finally, for *Patiriella pseudoexigua*, the sum of the elasticities along the diagonal is 0.7640 and so the elasticity for

dispersal is 0.2360. A 10 % change in adult survival would lead to a 7.6 % change in λ which could be equaled by about a 30 % change in dispersal success.

The overall pattern is: the higher the retention of individuals within a population, the less important dispersal is with respect to metapopulation growth. It is important to see that retention can be due either to asexual reproduction with a high population turnover or due to a planktonic phase coupled with a long adult life span.

DISCUSSION

Although I have concentrated on analysis of asteroids, it is obvious that the analysis is applicable not only to other echinoderms but to organisms much more generally. Early survival of offspring and adult survival must be related and so, in general, the two will trade-off against each other simply because organisms tend to have average values of λ close to 1.0 when averaged over many populations and over many years. This does not mean that trends do not exist or that substantial errors can not be introduced when studies are conducted using just one population over a period of just a single year. The data sets that I used in this paper all suffer from problems of short time spans and limited geographic scope. Nevertheless, the general relationships among mode of reproduction and adult and first-year survival rates probably are correct.

The range of values for P_x , P_0 and m_x for a particular reproductive mode requires substantially more comparative work. For example, estimates of adult survival for a range of sea urchin species, all with planktotrophic larvae, ranged from 0.97 to 0.08 (Ebert, 1982). The value of 0.97 was for the large slate-pencil sea urchin *Heterocentrotus trigonarius* at Enewetak Atoll and 0.08 was for *Echinometra mathaei* at Eilat, Israel. At other locations, *E. mathaei* had estimated adult survival rates ranging from 0.97 at Anse à la Mouché, Mahé, Seychelles, to 0.42 at Enewetak Atoll. Average adult survival, P_A , for 9 *Echinometra mathaei* populations was 0.7.

For species with planktonic larvae, decreases in adult survival rate, P_A , mean that the sum of the elasticities along the diagonal of the transition matrix will decrease and the summed elasticities for life in the plankton will increase. Changes in first-year survival will have an increasing impact on λ until the extreme is reached for organisms that are annuals, where P_A is 0 and the dynamics of the metapopulation (Fig. 6 B) is determined entirely by m_A and first year survival. I know of no echinoderm species with planktonic larvae that are annuals but there are such examples from other phyla. For example, sea hares as a group have planktonic larvae and have just one reproductive season before dying.

Species with planktonic larvae appear to span the entire range of adult survival rates although data are insufficient to determine whether planktotrophy and lecithotrophy would occupy different regions of Figure 5 because available data indicate that at least some brooders may be as long lived as broadcasters. For example, *Leptasterias hexactis*, a brooder, seems to be at least as longevous as *Patiriella pseudoexigua*, which has planktonic development. A second example is supplied by two ophiuroid species studied in southern California (Medeiros-Bergen and Ebert, 1995) that differ in mode of reproduction. One species is a brooder (*Ophioplocus esmarki*) and the other has lecithotrophic planktonic larvae (*Ophionereis annulata*). Both species are long-lived with $P_x = 0.907$ for *O. annulata* and $P_x = 0.957$ for *O. esmarki*, which means that brooding does not have to imply that a trade-off will result in more resources devoted to reproduction as the expense of maintenance.

What was abundantly clear in assembling the data for this paper is that more detailed studies are needed of complete life cycles for marine organisms with different modes of reproduction over a number of years, in different habitats, and at different parts of geographic ranges. Such studies would contribute to three larger research goals. An important area for further work is the mapping of a model such as Figure 6 onto actual geographic regions; however, this will be difficult for species with a planktonic stage. The problem is to determine the boundaries of regions along a coast line, for example, that could be considered to be single nodes in Figure 6 or to define boundaries of metapopulations when more than one exists for a species.

A second area for further work must focus on determining the actual transitions from one node to another in Figure 6. Estimation of transitions will be extremely difficult because it will require knowing the number of fertilized eggs produced at each site together with the probabilities of reaching other sites.

Finally, there is a need to document temporal variability of transitions at different life-stages that could then be used to explore the life-history consequences of variability with different reproductive modes. The theoretical framework is in place (e.g. Tuljapurkar, 1982 a, b; Orzack, 1985; Caswell, 1989) but there are few good data sets to test theory. Because echinoderms span such a wide range of reproductive modes, they are excellent organisms for exploring the evolution of life histories in marine metapopulations.

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