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Experimental study of growth in the echinoid *Paracentrotus lividus* (Lamarck, 1816) (*Echinodermata*)

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Abstract

Multimodal size frequency distribution (i.e., a few individuals growing very fast and a few individuals growing very slowly) among an originally homogeneous cohort of juveniles *Paracentrotus lividus* is observed in reared conditions when they are 6–24 months old. The splitting of this cohort into homogeneous size-classed subgroups results in an increased growth of the smaller animals that catch up with the bigger ones in 4 months time. This indicates that the smaller animals are not genetically less productive and suggests they were inhibited in their growth due to the presence of larger ones. Supposing such growth inhibition also occurs in the natural environment, the observed mechanism could be very efficient in stabilizing field populations of aggregative echinoid species by maintaining a protected pool of small individuals with high growth potential but inhibited by the density of larger ones.

Keywords: Echinoid; Growth; Population dynamics; Size-frequency distribution

1. Introduction

Echinoid surveys in the field are often based on size frequency distribution studies which theoretically allow the separation of different cohorts (Ebert, 1973; Kenner, 1992; Guillou and Michel, 1993). When proceeding so, authors necessarily assume that the size frequency distribution in a single cohort is normal or at least unimodal (Ebert, 1981; Ebert et al., 1993; Botsford et al., 1994). When animals can be aged, the assumption of normality can be tested because the different cohorts are unambiguously separated. Since

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size is not a reliable indication of the age of echinoids (Ebert, 1967; Levitan, 1988) and since the possibility to age them with growth lines remains disputed (Ebert, 1986; Gage, 1992; Ebert and Russel, 1993; Gebauer and Moreno, 1995), the interpretations of size frequency distributions among natural populations of echinoids remain rather speculative unless the assumption of normality can be verified. The difficulty may be bypassed by rearing animals under controlled conditions without the pressure of predators which should allow a good follow-up of their growth and enable the observation of a cohort's distribution. Indeed, parameters like recruitment, mortality and age of the individuals can be known precisely. Small scale cultivation of echinoids under artificial conditions has been successfully performed for several years (e.g., Hinegardner, 1969; Fridberger et al., 1979; Le Gall, 1989) and among the various aspects tackled by different authors, growth seems to be a privileged one (Ebert, 1975; Fridberger et al., 1979; Frantzis and Grémare, 1992). Yet, data remain rather limited and little interpretation of the size distribution itself has been performed. Cellario and Fenaux (1990) observed that there was a "wide size dispersion pattern with age progress" in *P. lividus* rearing. They also observed that the relative spreading of size (standard deviation of test diameters/average test diameter ratio) increases rapidly in early postmetamorphic life, reaches a constant level at 2–3 mm of mean test diameter (the distribution is then at its widest) and begins to decrease when the animals become larger than 10 mm in diameter. As far as we know, no study treated more precisely the size distribution shape of a cohort of reared echinoids.

The present paper focuses on how size distribution of reared *P. lividus* changes with time. It aims at testing if this distribution is normal and attempts to determine the factors that lead to its spreading.

2. Materials and methods

All the echinoids used in this work were produced in laboratory. They were cultivated with a method adapted from Le Gall (1989). The original strain comes from the rocky shore of Morgat (Brittany, France).

2.1. Rearing procedure

Spawning was induced by injecting 0.5 M KCl in the body cavity of adult individuals. Eggs of one female were transferred in a small plastic jar containing 800 ml of sea water. A quantity of sperm equivalent to 0.5 ml of milt was added to the eggs. The fertilization was controlled after 4 h and the number of fertilized eggs was evaluated. The embryos (in the gastrula stage) were then transferred in a 200 l larval rearing tank to a concentration of 250 embryos per liter. Larvae were fed daily with *Phaeodactylum tricornutum* from the third day on. The water remained unchanged for the whole larval period.

About twenty days later, competent larvae were transferred in clean sieves with a 250 μm mesh. Sieves with larvae were placed in toboggans (see Le Gall, 1989) with 10 cm depth of recirculating water providing a gentle uniform current around them. Metamor-

phosis was induced by introducing coralline algae in the sieves. Larval fixation and metamorphosis took less than 24 h.

The day before juveniles become exotrophic, 5 g (fresh weight) of green alga *Enteromorpha linza* per 100 cm^2 sieve surface were distributed. From this moment on, the same food quantity was given every 15 days. The treatment remained identical during the first year, except that the sieve diameter and mesh size were progressively increased according to the growing diameter of the individuals. After one year, when the smallest echinoids reached more than 5 mm in test diameter, all the individuals were put in a basket with a 5 mm mesh and transferred in another toboggan where stronger water current and higher echinoid biomass occurred. From this moment on, and twice a week, individuals were fed ad libitum with fresh kelp *Laminaria digitata*.

The entire rearing was carried out in natural dim light and at a constant temperature of 18±2°C all year long. The water was renewed continuously at a rate of 200–300% of the total volume per day with fresh natural sea water allowed to settle for at least 30 h beforehand.

2.2. Size frequency distribution just after the metamorphosis

All the larvae issued from a single fertilization (Fa) and reared as described above in the same tank were induced to metamorphosis the same day. Postmetamorphics were not fed. They were fixed (3% glutaraldehyde) and photographed 7 days after metamorphosis. Pictures were transferred on a Kodak photoCD and the test diameter of every individual computed by image analysis software. Actual size was determined by using a graduated background. The frequencies of observed sizes were tested against a normal and a log-normal distribution with a Kolmogorov–Smirnov test adapted by Lilliefors for intrinsic comparison (Sokal and Rohlf, 1981).

2.3. Follow up of a single reared strain of juveniles during 30 months

A whole strain issued from a single fertilization (Fb) was cultivated over 30 months. The test diameter of each individual was measured every 6 months with a sliding calliper. The first set of measurements was performed when echinoids were 6 months old (no measurements were done just after metamorphosis because of the extreme fragility of early post-metamorphics). The total number of individuals was 536 at 6 months old and dropped progressively to 280 at 30 months old. The mean mortality was thus 48% in a 2-year period.

Size frequency data obtained were then tested against a normal and a log-normal distribution. Possible multimodality was checked by the graphical method of Bhattacharya (1967). Since the number of individuals is low, data need to be smoothed before applying the method:

$$Y_i = \frac{1}{4}Y_{o,(i-1)} + \frac{1}{2}Y_{o,i} + \frac{1}{4}Y_{o,(i+1)}$$

where $Y_{o,i}$ = frequency observed in the size class i, and Y_i = smoothed frequency for the class i.

The minimal number of modes that match the observed size frequency distribution (i.e., when a χ^2 test gives a probability higher than 0.05) was determined by the technique of maximum-likelihood estimator using NORMSEP (Hasselblad, 1966, modified by Mac Donald and Pitcher, 1979).

2.4. Effect of size sorting on the growth of juveniles and interactions among them

Three additional fertilizations (Fc, Fd and Fe) were done at different times with parents not genetically related. Produced individuals were sorted twice before the beginning of the experiment so as to have several homogeneous batches in terms of size. The experiment started with populations of Fc, Fd and Fe being respectively 4, 6 and 8 months old. Four batches (Fc1 to Fc4) and six batches (Fd1 to Fd6) of 50 size-sorted echinoids were set up for Fc and Fd, respectively. Mean-sized individuals of Fe were separated into nine batches of 20 echinoids (Fe1 to Fe8 plus a control batch randomly chosen).

Each Fc to Fe batch was cultivated in a sieve of 20×15 cm of surface with a 2 mm mesh except the control batch of Fe whose 20 individuals were reared separately in 20 different sieves. Individuals were fed ad libitum with *Enteromorpha linza* exclusively. The seaweeds covered the entire surface of the sieve so there was no competition for food. Experiments lasted for 4 months and the final test diameter of all echinoids from each batch was measured with a sliding calliper.

3. Results

3.1. Size distribution among early post-metamorphics and change through time

Statistics on the distribution of the test diameters among early post-metamorphics (Fa) is presented in Table 1. Temporal evolution in the size frequency of all the individuals of the cohort followed during 30 months (Fb) is presented in Table 1 and Fig. 1. The test diameter of early post-metamorphics distribute along a normal curve characterized by a mean of 497 μm and a standard deviation of 56 μm (Kolmogorov–Smirnov/Lilliefors test, $P \geq 0.05$).

At 6 months old, distribution is neither normal, nor log-normal ($P \leq 0.001$, Kolmogorov-Smirnov/Lilliefors test); multimodality appears, although not clearly yet. Two modes can be identified by both graphical and numerical analysis. However, this kind of graph might also be obtained with an unimodal distribution very skewed to the right (skewness = 0.748).

After 12 months, the distribution does not match a normal nor log-normal one. This time, a "head" portion is clearly distinguishable. It concerns 18 individuals, that is 5.1% of the total. At least two other classes could be separated although not clearly isolated from each other. The distribution is widely spread. The ratio between the 10% larger and the 10% smaller is 3.2 in test diameter and 30.9 in wet weight.

After 18 months, the general shape remains the same with a head clearly detached, except that the two other classes seem to have merged. The head is represented by 26

Table 1
Statistical analysis of the size frequency distribution of single cohorts of *P. lividus* at different ages

Age (months):	1	6	12	18	24	30
Fertilization treatment:	Fa Killed 7 days after metamorphosis	Fb Same cohort of reared echinoids followed in controlled conditions				
General descriptive statistics on size frequencies (individual horizontal test diameter in mm)						
Number of individuals	296	536	361	296	285	280
Median	0.501	4	15	23	31	36
Mean	0.497	4.81	17.1	24.6	32.3	36.9
Standard deviation	0.056	2.28	5.51	6.98	6.12	5.56
Skewness	−0.275	0.748	0.851	0.599	0.136	0.042
Kurtosis	0.226	−0.044	0.373	0.094	−0.024	0.139
Intrinsic goodness of fit test to a normal curve (Kolmogorov–Smirnov/Lilliefors)						
Maximum difference	0.046	0.172	0.125	0.097	0.077	0.064
Probability	0.127**	0.000	0.000	0.000	0.000	0.011*
Intrinsic goodness of fit to a log-normal curve (Kolmogorov–Smirnov/Lilliefors)						
Maximum difference	0.068	0.130	0.075	0.064	0.059	0.095
Probability	0.002	0.000	0.000	0.005	0.018*	0.000
Component analysis by the graphical Bhattacharya's method						
Number of modes	1	2	3 or 4	2	3 or 4	1 or 2
Groups clearly separated	–	–	2	2	2	–
Characterization of the groups (maximum-likelihood estimator method, NORMSEP) (minimal number of groups giving a χ^2 probability >0.05)						
Number of groups	–	2	3	2	3	1
χ^2 value	–	8.41	14.50	21.44	24.48	26.71
Probability	–	0.077**	0.488**	0.554**	0.140**	0.181**
Mean of group 1		3.43	13.3	23.1	18.4	36.9
SD group 1		1.15	2.49	5.39	1.82	5.56
Percentage in 1		58.2	53.2	91.3	2.3	100
No. of ind. in 1		312	192	269	7	280
Mean of group 2		6.73	20.2	39.6	27.7	
SD group 2		2.07	3.61	1.97	2.54	
Percentage in 2		41.8	41.7	8.7	34.4	
No. of ind. in 2		224	151	26	98	
Mean of group 3			31.2		35.3	
SD group 3			1.34		5.00	
Percentage in 3			5.1		63.3	
No. of ind. in 3			18		179	

* Fitting is significant ($P \geq 0.01$); ** Fitting is very significant ($P \geq 0.05$).

animals (8.7% of the total number) which means there are newcomers. The distribution is always widely spread. The mean size of the heading class is 39.6 mm, which is already more than the mean size (36.9 mm) of all the individuals one year later, when they will be 30 months old.

After 24 months, the individuals forming the head seem to be caught up by the mean sized ones. However, some individuals do not follow this general movement, and a tail

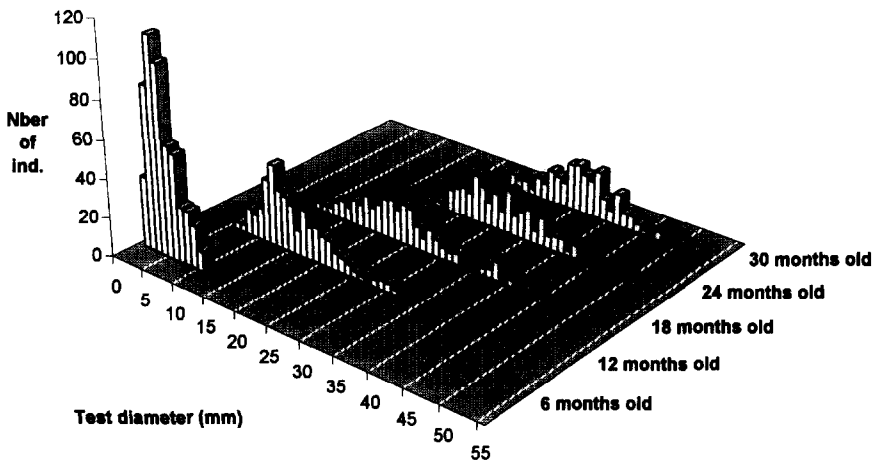


Fig. 1. Evolution of a single cohort of *P. lividus* (Fb) reared in stable environmental conditions according to time.

remains, amounting to 2.7% of the total population. The shape of the distribution is completely changed: skewness decreases (0.136) and the whole distribution matches possibly a log-normal one (Kolmogorov–Smirnov/Lilliefors, $P \geq 0.01$).

After 30 months, the latecomers forming the tail catch up the mean sized ones, and the distribution loses its significant multimodal shape. The shape becomes symmetrical: low skewness of 0.042 and approach a normal curve ($0.01 \leq P \leq 0.05$, Kolmogorov–Smirnov/Lilliefors). The spreading decreases also: the ratio 10% larger/10% smaller drops to 1.8 in size and to 5.3 in wet weight.

3.2. Effect of size sorting on juveniles' growth

Fig. 2 and Table 2 show the initial and final size distributions of the four Fc size-sorted batches. A Kolmogorov–Smirnov/Lilliefors test applied on each distribution showed that 2 cases out of the 4 did not match a Gaussian curve ($P \leq 0.01$). Since extremes were eliminated before the experiment began (only mean-sized individuals were used), non normality in the distribution of the whole cohort is not due to the spreading of these extremes, producing 'head' and 'tail' classes, but could be the consequence of differential growth rates among all individuals, including mean-sized ones.

Fig. 3 shows the size distributions of the Fd batches at the beginning of the experiment (Fig. 3A) and after 4 months of controlled rearing (Fig. 3B). Table 3 presents the statistics on these data. The difference between the Fd batches after 4 months is only of slight significance (Kruskal–Wallis, $0.01 \leq P \leq 0.05$) although each batch of Fd was made up initially of individuals from a different size class, going from

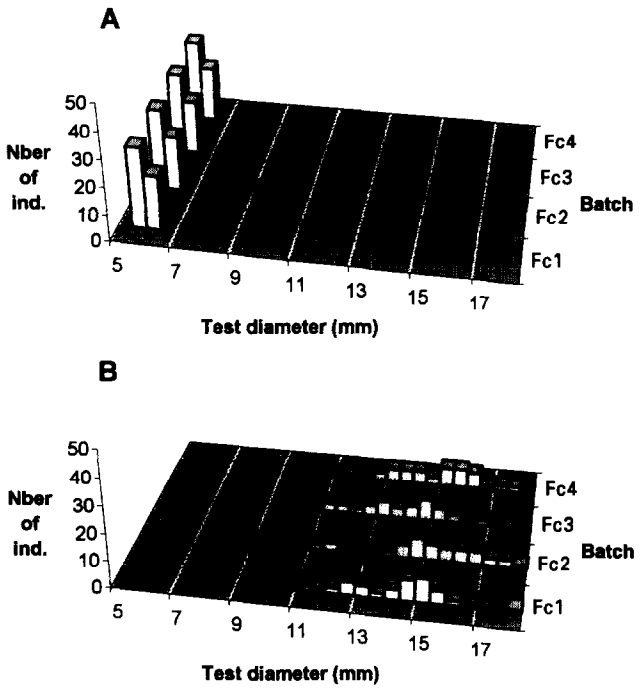


Fig. 2. Size distribution of Fc juveniles in each batch in the beginning of the experiment (A) (extreme individuals have been eliminated) and 4 months later (B).

10.5 mm in Fd1 ('head' individuals) to 6 mm in Fd5 and Fd6 (mean-sized individuals). Thus, it seems that size sorting eliminates the factor(s) that maintained the difference in sizes between the batches so that smaller individuals catch up rapidly to the larger ones.

Table 2
Statistics on the four batches of Fc in the beginning of the experiment (initial) and after 4 months (final)

Batch	Fc1	Fc2	Fc3	Fc4
Treatment	Size sorted batches of mean-sized individuals only (no 'head' already differentiated)			
Initial mean size (mm)	6.0	6.0	6.0	6.0
Final mean size (mm)	14.3	15.1	14.0	14.9
Increase in size (mm)	8.3	9.1	8.0	8.9
Kolmogorov–Smirnov/Lilliefors test on final sizes (mm)				
Maximum difference	0.161	0.148	0.106	0.124
Probability	0.003**	0.008**	0.175	0.061

** Does not fit a normal curve ($P \leq 0.01$).

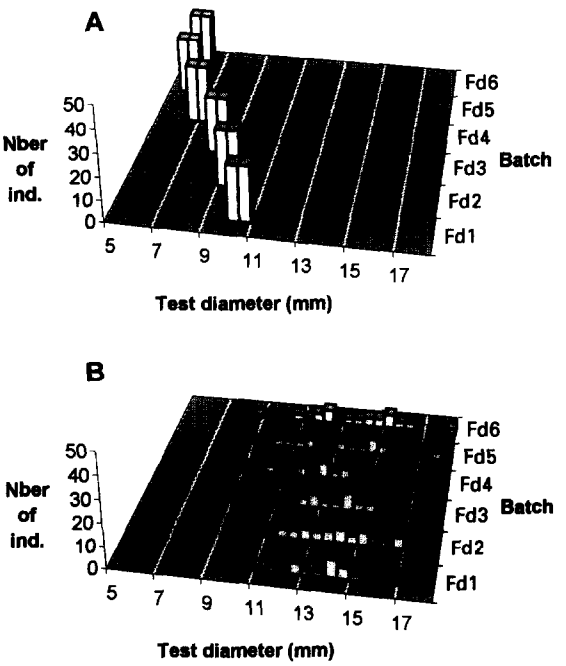


Fig. 3. Size distribution of Fd individuals in each batch (ranging from 'head' individuals, Fd1, to mean-sized ones, Fd5 and Fd6) at the beginning of the experiment (A) and 4 months later (B).

3.3. Interactions between individuals

Table 4 presents the size frequency distributions of Fe batches obtained after rearing them 4 months. The control shows the distribution of the sizes that can be expected without interactions between the individuals because each echinoid was cultivated independently. This distribution matches very well a normal curve (intrinsic Kolmogorov–Smirnov/Lilliefors test, $P>>0.05$) characterized by a mean of 18.5 mm (test diameter) and a standard deviation of 1.52 mm.

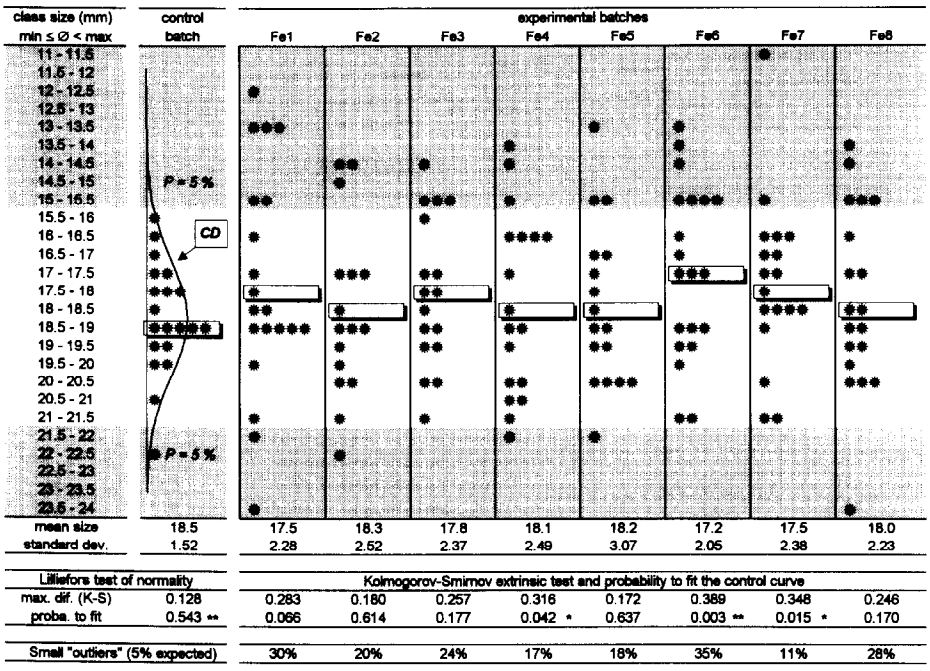
The distribution of the other eight experimental Fe batches is compared to the

Table 3
Statistics on the six batches of Fd in the beginning of the experiment (initial) and after 4 months (final)

Batch	Fd1	Fd2	Fd3	Fd4	Fd5	Fd6
Treatment	Size sorted batches ranging from 'head' to mean-sized individuals of a fertilization that already differentiated a heading group					
Initial mean size (mm)	10.5	9.5	8.5	7.0	6.0	6.0
Final mean size (mm)	14.0	14.0	13.2	12.7	13.5	13.6
Increase in size (mm)	3.5	4.5	4.7	5.7	7.5	7.6
Comparison of final mean sizes of the six batches (Kruskal–Wallis)						
Statistic value	11.85		associated probability			0.037*

* Difference slightly significant ($0.01 \leq P \leq 0.05$)

Table 4
Size distribution of Fe echinoids (♂) after having been reared individually (control) or together (experimental batches) for 4 months



Highlighted cells are the mean classes of each group. Grayed zones show 'outliers' (i.e., large and small sizes with $P \leq 0.05$ according to the control's fitted distribution CD). * Test significant; ** test highly significant.

theoretical normal curve fitted on the control with its estimated mean and standard deviation. In the absence of interactions, no more than 5% of the individuals should be smaller than 15.5 mm or greater than 21.5 mm (considered as potential outliers, grayed zones in Table 4). The number of small 'outliers' is much more important than this prediction in all eight batches, ranging from 11 to 35% of the total which indicates a consistent tendency: some of the individuals reared together were apparently inhibited in their growth. Moreover, whole batches Fe4, Fe6 and Fe7 do not match the control's distribution ($P \leq 0.05$, extrinsic Kolmogorov–Smirnov test). Consequent to this inhibition, the mean sizes in the experimental batches are systematically lower than the mean size of the control.

4. Discussion

Growth of the regular echinoid *P. lividus* was experimentally studied using homogeneous cohorts kept in controlled conditions. This homogeneity was obtained by using reared individuals from the same parental origin, induced to metamorphosis the same

day, fed ad libitum with the same food and kept in the same environment. Size frequencies observed among such a cohort distribute along an unimodal normal curve just after metamorphosis but present a multimodal shape with at least two, sometimes three, distinct subgroups (i.e., 'head', mean-sized and 'tail' individuals) when individuals were 6 to 24 months old. Multimodality disappeared around 30 months of age and size frequency distribution recovered a near-normal shape.

Such differences in growth between juveniles leading to non-normality in the size frequency distribution could be probably attributed to every individual, not only to extreme ones, as shown with mean-sized individuals of Fc batches. Moreover, the difference in speed of growth between heading and mean-sized echinoids cannot be attributed to their respective genetic potentials, for size sorting eliminates rapidly the differences in size between these subgroups (Fd). Hence, this difference is the consequence of an intraspecific competition between echinoids having different sizes. Furthermore, evidence of inhibition in the growth of smaller individuals is provided by the comparison of the size distribution of echinoids reared together (Fe1 to Fe8) or individually (Fe, control).

We observed that when echinoids of different sizes are reared together, the smaller ones tend to insert themselves between the larger ones along the walls and corners of the rearing baskets. In those aggregates, the water is relatively stagnant and the pH there is lower than the one measured in the running water of the tanks due to CO_2 accumulation (pH NBS 7.1–7.7 and 7.8–8.0, respectively). Poor water quality could then contribute to the slower growth rate of smaller juveniles. The difference in sizes between large 'inhibitor' and small 'inhibited' individuals does not need to be very important to engage the process of differential growth. Indeed, the spreading in sizes that occurs from originally homogeneous batches seems to be sufficient to trigger this intraspecific competition, as observed in the eight experimental Fe batches reared together.

Whether a multimodal size distribution inside a single cohort of juvenile echinoids could be possible in the field is worth questioning. If it is the case, then all studies using analysis of size frequency distributions and based on the separation of presumed unimodal cohorts from a whole population could be biased. Aggregative behavior is currently observed among various species of echinoids (Ebert, 1977: *Strongylocentrotus purpuratus*; Dafni and Tobol, 1987: *Tripneustes gratilla elatensis*; Levitan and Genovese, 1989: *Diadema antillarum*). In those cases, small juveniles are often found under larger conspecifics or between their spines where their rate of survival has proven to be higher thanks to the protection provided against predators (Tegner and Levin, 1983; Levitan and Genovese, 1989). Yet, the chemical conditions in this environment could vary a lot, as observed in our rearing devices, and growth could be greatly reduced for some individuals, causing the spreading of the size distribution of the cohort or transforming it into a multimodal one. The extension of the critical period when the echinoid is small and thus vulnerable to predators limits somewhat the benefits gained by the protection provided by the adult's spine canopy. However, if the adults' density decreases, the inhibition of a juvenile's growth is then removed. Some of them can grow very fast if food is available (as 'head' ones in the currently studied cohort) and rapidly replace missing adults. This mechanism could be very efficient in stabilizing field populations of aggregative species of echinoids by maintaining a protected pool of small individuals with high growth potential but inhibited by the density of larger ones.

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