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Lissarca notorcadensis (Bivalvia: Philobryidae) living on Notocidaris sp. (Echinoidea: Cidaridae): Population dynamics in limited space*

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Summary. Population dynamics of the epizoic bivalve *Lissarca notorcadensis* living on spines of cidaroid sea urchins in the Weddell Sea were investigated. Total production (somatic & gonad) of the suspension feeding bivalve ranged between 16.5 and 487.4 mg AFDM y^{-1} per sea urchin. Annual sedimentation rates are not sufficient to maintain the production of the Lissarca sub-populations carried by the sea urchins, and resuspension of organic matter is most likely to be an important food source. The ratio of the number of freshly settled juveniles to the number of embryos brooded is between 0.054 and 0.207 and seems negatively related to the biomass already present, indicating intraspecific competition for space. Interspecific competition for space is caused by the strong preference of *L. notorcadensis* as well as other epizoa (colonial anthozoans and bryozoans) for the spines located on the aboral hemispere of the sea urchins.

Introduction

The philobryid bivalve *Lissarca notorcadensis* MEVILL and STANDEN, 1907 is endemic to the Antarctic and exhibits a circum-Antarctic distribution in depths of 18–1120 m (Dell 1990). On the Weddell Sea shelf and slope it is the most common bivalve and has been subject of a recent analysis of its ecology (Brey and Hain 1992; Prezant 1989). The suspension feeding bivalve attaches itself by byssus threads to the long primary spines of cidaroid sea urchins (see e.g. plates 1 & 2 in Mortensen 1920) and occasionally to bryozoan colonies and hydrozoan colonies. Fertilization is most likely to take place by spermatophores directly transferred to the female (Janssen 1990), and the young develop inside the parental mantle cavity. Fully developed juveniles are released during austral spring (December–January). This behaviour allows for the investigation of the dynamics of semi-isolated sub-populations of *L. notorcadensis*, e.g. those inhabiting cidaroid sea urchins with special reference to inter- and intraspecific competition for the limited space available.

Methods

During cruises of RV "Polarstern" in austral summer (January–February) of the years 1987, 1989 and 1991, nine specimens of the genus *Notocidaris* carrying *Lissarca notorcadensis* were handpicked from Agassiz trawl samples at five different stations (Fig. 1) and stored separately in 70% ethanol.

In the laboratory, all specimens of *L. notorcadensis* were removed from the sea urchin spines, counted and measured. Biomass was calculated from the size (i.e. maximum shell length) frequency distribution and the length (L) - mass (AFDM, ash free dry mass) relation taken from Brey and Hain (1992):

$$\text{mg AFDM} = 0.018 \cdot \text{mm } L^{2.567};\ N = 26 \text{ size classes, 232 specimens}$$

Somatic production was calculated by the mass specific growth rate method (see Crisp 1984) using von Bertalanffy growth curves of *L. notorcadensis* referring to the northern and southeastern Weddell Sea shelf (Brey & Hain 1992):

$$\text{North: } L_t = 12.140 \cdot [1 - e^{-0.085 \cdot (t - 1.477)}]$$
$$\text{North: } L_t = 9.802 \cdot [1 - e^{-0.112 \cdot (t - 1.247)}]$$

Female gonad production was calculated by the relation between the number of embryos brooded in the mantle cavity (N_{emb}) and female body mass M (mg),

$$\text{North: } N_{emb} = -8.414 + 17.655 \cdot M;\ r = 0.687,\ N = 38$$
$$\text{South: } N_{emb} = -2.923 + 12.477 \cdot M;\ r = 0.682,\ N = 94$$

and the average embryo mass at release, 0.031 mgAFDM. For further details of production calculations see Brey and Hain (1992). *L. notorcadensis* settles on the long primary spines of the cidaroids. Each interambulacral plate carries one of these spines (Fig. 2). The last two, three or four primary spines adjacent to the peristome are lance-shaped and are used to protect the juveniles which are carried in the peristome region (Mortensen 1909; 1946). In six of the nine cidaroids factors affecting the distribution of *L. notorcadensis* among the primary spines were analyzed. The number of bivalves per spine was determined and the spine length was measured. The amount of other epizoa, mainly anthozoan colonies and bryozoan colonies, was measured in mm spine length. The position of the spines on the test surface was determined by two axes, the peripherial axis (i.e. five

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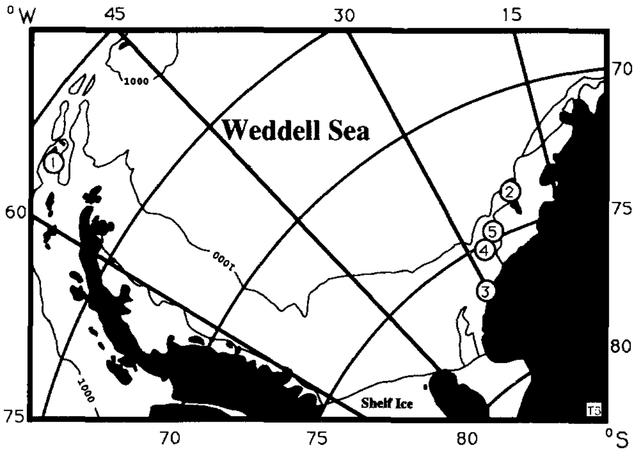

Fig. 1. Distribution of sampling stations in the Weddell Sea. 1: 15. Jan. 1989; 2: 12. Feb. 1989; 3: 12. Jan. 1987; 4: 17. Jan. 1990; 5: 9. Feb. 1990

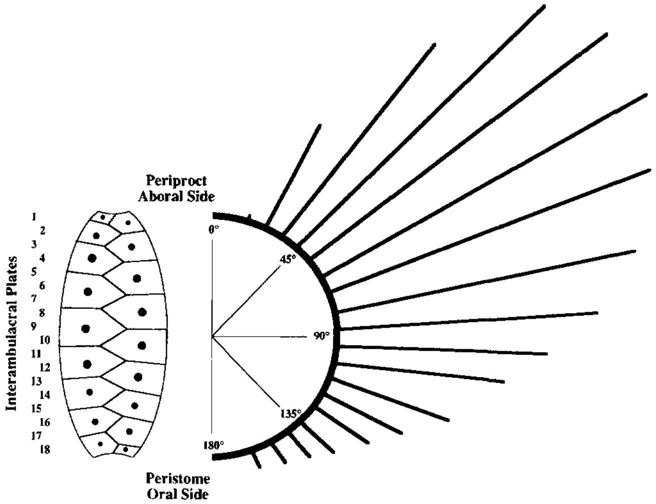

Fig. 2. Schematic drawing (front view and sectional view) of an interambulacral sector of a cidaroid with 18 interambulacral plates. The relation of spine length to test diameter is true to scale

interambulacral sectors) and the aboral-oral axis (i.e. number of interambulacral plate). Since the number of interambulacral plates increases with increasing diameter of the test, the position on the aboral-oral axis was converted from spine number to degrees (0–180°) to make different sized sea urchins comparable (Fig. 2). The data of the six specimens were pooled for the analysis of the distribution of *L. notorcadensis* on the spines, assuming that the inert nature of the spines makes interspecific differences in spine colonization unlikely.

Results

Abundance and biomass

The nine specimens of *Notocidaris* sp. ranged from 30 to 63 mm diameter and should have carried between 65 and 95 primary spines. Between 41 and 72 of these were still present, 1 to 31 spines were completely lost, most likely during trawling. Abundance and biomass values of *Lissarca notorcadensis* ranged from 65 ind. & 31.0 mg AFDM to 1241 ind. & 942.7 mg AFDM per sea urchin (Table 1). Figure 3 shows the length-frequency distributions of *L. notorcadensis* inhabiting the nine cidaroids.

Production

Somatic (P_s) and gonad production (P_g) of *L. notorcadensis* ranged between 13.1 & 342.0 mg AFDM y^{-1} and 3.4 & 145.4 mg AFDM y^{-1} per sea urchin, respectively. Annual production/biomass (P/B) ratios were between 0.309 and 0.424 (somatic) and 0.109 and 0.154 (gonad), respectively. Total production (P_t) ranged from 16.5 mg AFDM y^{-1} to 487.4 mg AFDM y^{-1}, and the total P/B ratio was in the range of 0.432 y^{-1} to 0.552 y^{-1} (Table 1).

Recruitment

Recruitment success of each *L. notorcadensis* sub-population inhabiting one sea urchin was estimated from the relation between the number of embryos brooded by the population (N_{emb}) and the number of recently recruited juveniles ≤ 1.7 mm in the population (N_{juv}, first peak of size-frequency distribution in Fig. 3). Recruitment success, i.e. N_{juv} as fraction of N_{emb}, is 0.110 on the average, ranging from 0.054 to 0.207. There is a weak negative

Table 1. The investigated sea urchins and their populations of *L. notorcadensis*. Units of mass are mg AFDM

			Notocidaris sp.			*Lissarca notorcadensis*								
No	Depth m	Area	Diam. mm	Spines	Spines lost	N	B mg	M mg	P_s mg y^{-1}	P_g mg y^{-1}	P_t mg y^{-1}	P_s/B y^{-1}	P_g/B y^{-1}	P_t/B y^{-1}
1a	414	North	59	75	24	438	269.6	0.62	93.7	38.5	132.2	0.348	0.143	0.490
1b	414	North	56	95	34	1241	942.7	0.76	342.0	145.4	487.4	0.363	0.154	0.517
1c	414	North	63	95	21	421	242.7	0.58	84.1	35.4	119.5	0.347	0.146	0.492
2a	294	South	30	65	1	148	52.0	0.35	23.0	5.7	28.7	0.442	0.110	0.552
2b	294	South	55	80	18	73	44.8	0.61	13.9	5.5	19.4	0.309	0.123	0.432
2c	294	South	50	80	21	84	45.8	0.54	15.9	5.9	21.8	0.348	0.129	0.477
3	358	South	54	65	24	65	31.0	0.48	13.1	3.4	16.5	0.424	0.109	0.532
4	427	South	37	65	10	149	92.9	0.62	29.4	12.1	41.5	0.317	0.130	0.447
5	475	South	42	70	4	289	169.2	0.59	57.7	21.3	79.0	0.341	0.126	0.467

N: Number of bivalves per sea urchin; B, M: Biomass, mean individual body mass; P_s, P_g, P_t: Somatic, gonadal, total production

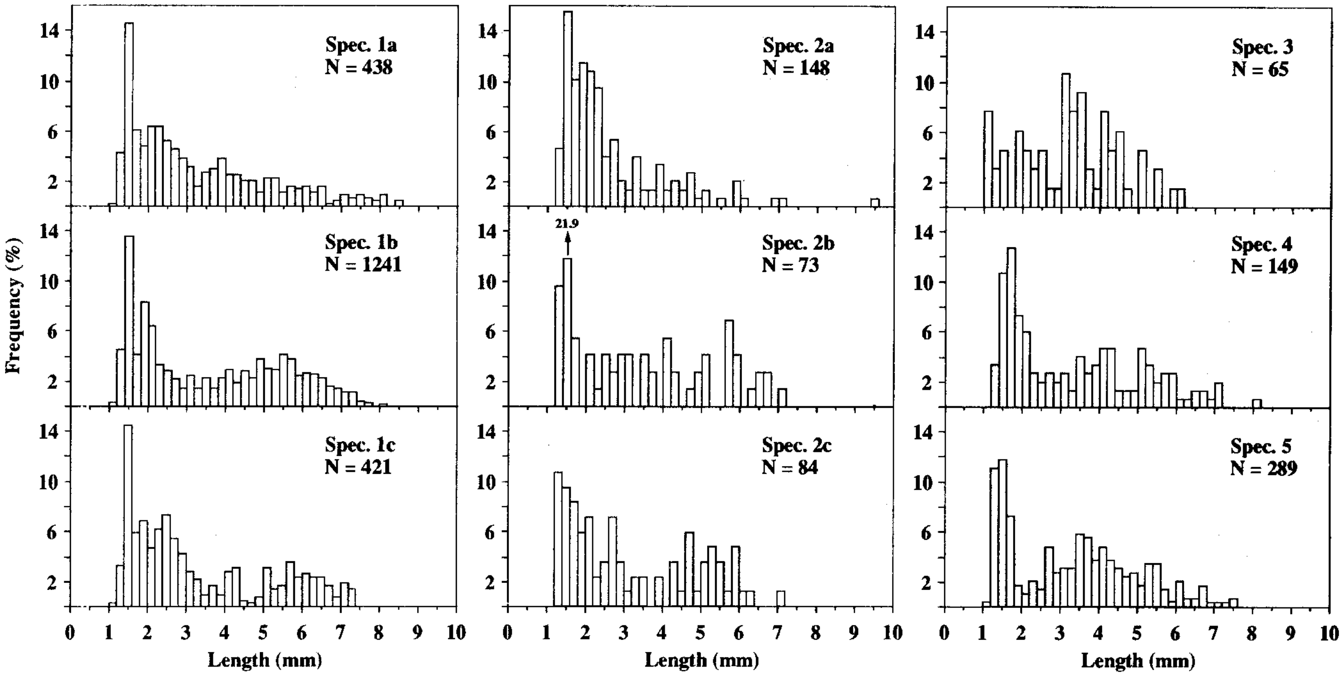

Fig. 3. Shell length-frequency distributions of *L. notorcadensis* inhabiting the nine sea urchins (spec. numbers refer to Table 1)

Table 2. Correlation among cidaroid diameter (mm), position of spine on the aboraloral axis (0°–180°), spine length (mm), amount of other epizoa per spine (mm spine length) and number of *L. notorcadensis* per spine (N). 342 Data sets, * indicates significant correlation at $\alpha = 0.05$

	Cidaroid diameter	Aboral-oral axis position	Spine length	Other epizoa
Cidaroid diameter	1			
A-O axis position	0.015	1		
Spine length	0.168*	−0.288*	1	
Other epizoa	0.022	−0.188*	0.655*	1
N/Spine	0.146*	−0.326*	0.379*	−0.144*

relation ($P = 0.064$) between recruitment success and the biomass already present (Fig. 4):

$$\log(N_{juv}/N_{emb}) = -0.542 - 0.218 \cdot \log(B_{adult});\quad N = 9;\ r = -0.640$$

Distribution on spines

342 spines of the six sea urchins were used for the analysis of the distribution of *L. notorcadensis*. Spines partially lost were included to improve statistical power, assuming a random distribution of single bivalves and of bivalve patches along the spines. A preliminary analysis of correlation among the parameters in question showed the number of *L. notorcadensis* per spine to be correlated positively to sea urchin diameter and spine length, and negatively to spine position on the aboral-oral axis and the amount of other epizoa (Table 2, Fig. 5). Spine length is related significantly to diameter and position on the aboral-oral axis (see Fig. 2), whereas the amount of other epizoa is related to spine length and position on the aboral-oral axis (Table 2).

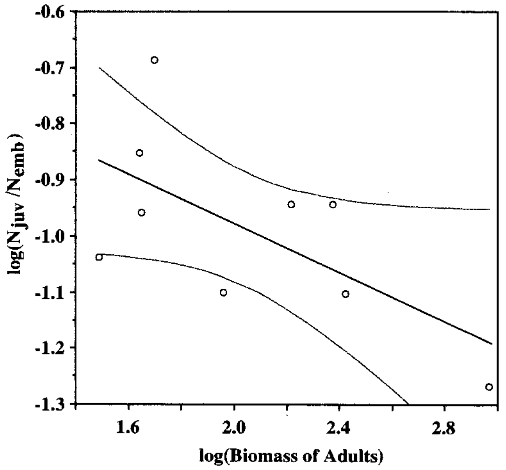

Fig. 4. Relation between the biomass of *L. notorcadensis* on a cidaroid (B, sum of all specimens > 1.7 mm length) and recruitment success (number of juveniles ≦ 1.7 mm as fraction of total number of embryos brooded by the population). $\log(N_{juv}/N_{emb}) = -0.542 - 0.218 \cdot \log(B_{adult})$; $N = 9$; $r = -0.640$; $P = 0.064$; Curved lines represent the 95% confidence bands for the true mean of $\log(N_{juv}/N_{emb})$

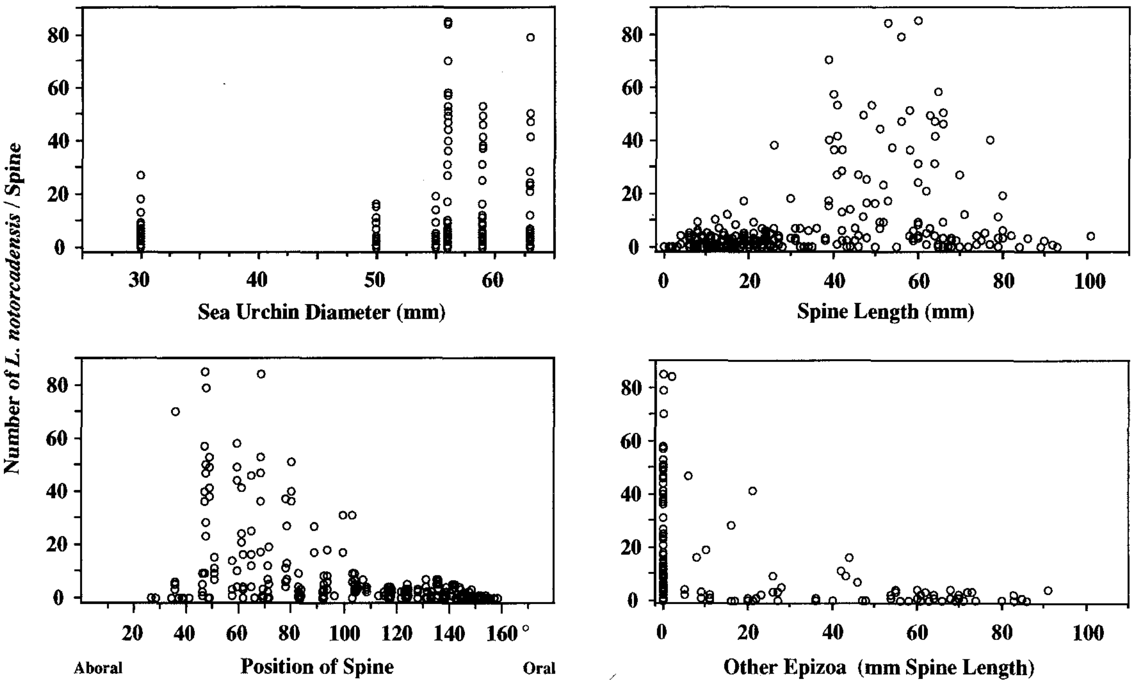

Fig. 5. The number of *L. notorcadensis* per sea urchin spine in relation to sea urchin diameter, spine length, position of spine on the aboral-oral axis, and amount of other epizoa ($N = 342$ spines from six sea urchins)

For the analysis of variance (ANOVA) the number of *L. notorcadensis* per spine was divided by spine length (24 spines of length $\leqslant$ 0.5 mm were excluded) to remove the effect of this parameter, and the variables "spine position on the aboral-oral axis" as well as "amount of other epizoa" were re-grouped into categories. The four-factor ANOVA found the number of bivalves per millimetre of spine to be significantly affected by the sea urchin specimen, by the position on the aboral-oral axis, and by the occupation of spines by other epizoa, whereas there is no effect of the interambulacral sector (Table 3A). Post-hoc tests showed the number of bivalves per millimetre of spine (N) to be significantly higher in the sea urchin specimens 1b (mean $N = 0.52$) and la (mean $N = 0.21$), in the range 40°–60° on the aboral-oral axis (mean $N = 0.50$), and on spines with no other epizoa (mean $N = 0.21$, Tables 3B and 3C).

Discussion

Sampling effects

Sampling by the Agassiz trawl caused damage to most of the sea urchins collected, spines were partially or completely lost (Table 1). This leads to an under-estimation of abundance, biomass and production estimates. Length-frequency distributions and parameters such as P/B ratio and recruitment success seem to be unbiased, since there are no clear hints for size-selective loss of bivalves during sampling. An exception may be sea urchin no. 3, where small ($\leq$ 2 mm) as well as large ($\geq$6.5 mm) *Lissarca* specimens seem to be under-represented (Fig. 3). However, beside sampling, station-specific effects, different stages of colonization and interspecific competition for space on the spines may be responsible for the high variability of abundance and biomass of *L. notorcadensis* among the nine specimens of *Notocidaris* sp. (Table 1).

Somatic and gonad production

The three cidaroids sampled on the northern shelf carry sub-populations of *L. notorcadensis* with distinctly higher abundance, biomass and production than those collected on the southeastern shelf (Table 1). These differences should be interpreted cautiously, since sample size is quite small, but they may be related to the better food supply in the north. Sedimentation on the northern Weddell Sea shelf may reach values well above 15 g $C_{org}\,m^{-2}\,y^{-1}$ (estimated from Bodungen et al. 1986), whereas sedimentation on the southeastern Weddell sea shelf is in the range of 5 g $C_{org}\,m^{-2}\,y^{-1}$ (Bodungen et al. 1988, Bathmann et al. 1991). However, the P/B ratios of the nine sub-populations do not differ very much (Table 1), indicating that the different food level mainly affects the carrying capacity but not productivity.

If growth efficiency (Production/Consumption) of *L. notorcadensis* is in the range of about 10% (see e.g. Hughes 1970, Hummel 1985, Rodhouse et al. 1981, Streit 1976), the nine sub-populations investigated require between 82 mg C_{org} (cidaroid no. 3) and 2437 mg C_{org} (cidaroid no. 1b) of food per year (1 mg AFDM = 0.5 mg C_{org}, Table 4). The amount of sedimenting matter theoretically available for a *Lissarca* sub-population can be calculated from the bottom area covered by the sea urchin, i.e. $[(\text{test diam.} + 2 \cdot \text{max spine length})/2]^2 \cdot \pi$. Only in the cidaroid specimens nos. 2b, 2c, and 3 do sedimentation rates meet

Table 3. Analysis of Variance (ANOVA) of the distribution of *L. notorcadensis* on cidaroid spines

A ANOVA

Source	Degrees of Freedom	Sum of Squares	Mean Square	F	*P*
Cidaroid Specimen	5	0.446	0.089	19.803	0.0001
Interambulacral Sector	4	0.013	0.003	0.707	0.5873
Aboral-Oral Axis Position	7	0.690	0.115	25.538	0.0001
Other Epizoa	3	0.104	0.052	11.539	0.0001
Residual	300	1.351	0.005		

B Means Table (mean number of *L. notorcadensis* per mm spine length and standard deviation)

Cidaroid Specimen

	Count	Mean	S.D.
1a	51	0.213	0.339
1b	51	0.522	0.468
1c	64	0.146	0.250
2a	56	0.137	0.213
2b	42	0.041	0.079
2c	54	0.043	0.080

Position of Spine (Deg)

	Count	Mean	SD
20–40	15	0.247	0.511
40–60	41	0.495	0.502
60–80	43	0.293	0.368
80–100	37	0.205	0.252
100–120	31	0.175	0.219
120–140	50	0.114	0.143
140–160	101	0.032	0.067

Other Epizoa

	Count	Mean	SD
<1/3	259	0.214	0.340
<2/3	12	0.124	0.177
>2/3	47	0.033	0.063

C Bonferroni/Dunn post-hoc test of differences between means (*: signif. difference at $\alpha = 0.05$)

Cidaroid Specimen

	1a	1b	1c	2a	2b
1a	/				
1b	*	/			
1c	–	*	/		
2a	–	*	–	/	
2b	*	*	–	–	/
2c	*	*	–	–	–

Position of Spine (Deg)

	20–40	40–60	6–80	–100	–120	–140
20–40	/					
40–60	–	/				
60–80	–	*	/			
–100	–	*	–	/		
–120	–	*	–	–	/	
–140	–	*	*	–	–	/
–160	*	*	*	*	*	–

Other Epizoa

	<1/3	<2/3
<1/3	/	
<2/3	–	/
>2/3	*	–

Dependent variable: $\log(1 + N\ mm^{-1})$, $N\ mm^{-1}$ = Number per mm spine length. Independent variables: Sea urchin specimen; interambulacral sector; position of spine on aboral-oral axis (7 segments of 20° width); other epizoa (covering $<=1/3$, $<=2/3$, $>2/3$ of spine length)

Table 4. Production, food requirements and food availability

Cidaroid Specimen	P_t ($mgC_{org}y^{-1}$)	C ($mgC_{org}y^{-1}$)	Cidaroid area (cm^2)	S ($mgC_{org}y^{-1}$)	C/S
1a	66.1	661.1	377	565.5	1.2
1b	243.7	2437.2	346	519.0	4.7
1c	59.8	597.6	317	475.5	1.3
2a	14.4	143.5	133	66.5	2.2
2b	9.7	96.9	519	259.5	0.4
2c	10.9	109.2	394	197.0	0.6
3	8.3	82.6	360	180.0	0.5
4	20.8	207.7	104	52.0	4.0
5	39.5	395.0	216	108.0	3.7

P_t: total production of *L. notorcadensis* per sea urchin, C: Consumption of *L. notorcadensis* per sea urchin if $P_t/C = 10\%$, S: Sedimentation per sea urchin calculated from a rate of 15 g $C_{org}\ m^{-2}\ y^{-1}$ on the northern shelf and 5 g $C_{org}\ m^{-2}\ y^{-1}$ on the southeastern shelf

consumption of the *Lissarca* sub-populations, in the other six specimens, sedimentation is below consumption by a factor of 1.2 to 4.7 (Table 4). It is unlikely that underestimation of sedimentation and/or growth efficiency of *L. notorcadensis* can account completely for this discrepancy, so there must be additional food sources for the bivalve beside the direct input of organic matter from the pelagic system. These additional sources could be dissolved organic matter (DOM) and/or resuspended particulate organic matter (POM). Many marine invertebrates are able to aquisite DOM from seawater (Manahan et al. 1983; Manahan 1990), however, nothing is known about DOM uptake in *L. notorcadensis*. Sediment trap data from the southeastern Weddell Sea shelf indicate that resuspension of POM could provide additional food for suspension feeding species. At one station off Kapp Norvegia, a near-bottom sediment trap deployed at 600 m depth collected about 6 times more material (47 g DM y^{-1}) than a trap at 270 m depth (8 g DM y^{-1}, Arntz et al. 1992). The motility of the cidaroids could play a significant role too. The deposit feeding sea urchins may search actively for sediment patches rich in organic matter, which would in turn increase the amount of food provided for the epizoic bivalves by resuspension.

Reproductive effort, i.e. 100 · gonad production/total production, is 27% on the average, which is in the upper range of iteroparous (i.e. multiple breeding) mollusc species (see Browne and Russell-Hunter 1978). This may indicate that *L. notorcadensis* is forced by the harsh environmental conditions – scarce and oscillating food supply and low temperature (see Clarke 1988) – to invest comparatively more energy in reproduction to increase the probability of individual survival of the offspring (see e.g. Christiansen and Fenchel 1979).

Colonization and dispersal

Adult *L. notorcadensis* are hemisessile, therefore sea urchins usually will be colonized by freshly released juveniles, which may be able to drift with water currents using mucus threads, as described by Martel and Chia (1991) for several boreal mollusc species lacking planktonic larval stages. Occasional findings of juveniles distant from the adults in laboratory aquaria strengthen this assumption. Most of the larger (test diameter ≧20 mm) cidaroids found in trawl samples are colonized by at least some *L. notorcadensis*. Smaller specimens are either avoided actively, or they just did not live long enough to encounter a drifting *Lissarca* juvenile. However, taking into account that the average distance between adjacent specimens of cidaroids is about 6 m in the Weddell Sea area (mean abundance = 0.04 ind. m^{-2}, range: 0 - 0.36 ind. m^{-2}; unpubl. data of foto counts by J. Gutt, AWI), the near-bottom water currents on the Weddell Sea shelf (see above) seem to be strong enough for an effective dispersal of drifting juveniles. Exchange of juveniles among different specimens could be further enhanced by periodic feeding or breeding aggregations of the sea urchins, as observed in a bathyal cidaroid species (Young et al. in press *fide* Tyler et al. 1992).

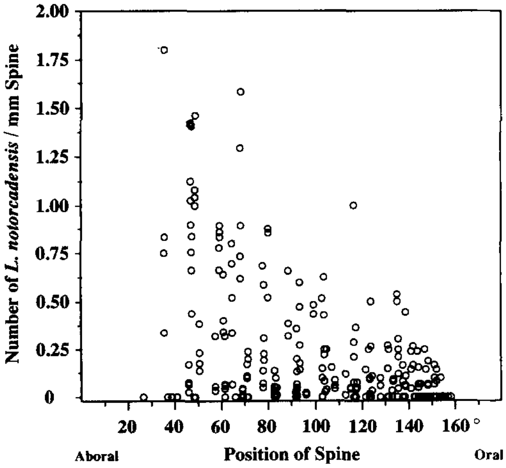

Fig. 6. The number of *L. notorcadensis* per millimeter of sea urchin spine in relation to the position of the spine on the aboral-oral axis ($N = 318$ spines from six sea urchins, the spines < 0.5 mm length present on most of the interambulacral plates No. 1 are excluded)

Distribution on spines

The inclusion of broken spines in the analysis may have affected the relation between *L. notorcadensis* number per spine and other parameters to a certain extend (Table 2, Fig 5), but the transformation to number per millimetre spine length should have eliminated this effect from the further analysis.

L. notorcadensis prefers to settle on those spines between 30°–60° on the aboral hemisphere of a cidaroid (Fig 6, Table 3), although the adjacent spines are not morphologically different. This particular distribution indicates that *L. notorcadensis* tries to settle at a position as high as possible above the sediment surface, most likely to improve its feeding conditions. In large cidaroids, the upper spines may reach well above the laminar boundary layer, which would provide a substantial advantage for *L. notorcadensis* with respect to the access to sedimenting matter (Jumars and Gallagher 1982).

In this context it is worth to note that *L. notorcadensis* is found very rarely on stones and boulders which may reach even higher into the water column, but almost exclusively on spines of cidaroids and occasionally on branches of hydrozoan and bryozoan colonies. These particular sites may either protect *L. notorcadensis* from crawling predators, e.g. amphipods, polychaetes or sea urchins, which may be not able to climb on thin branches or spines, or the hydrodynamic conditions around thin branches or spines are preferable to those along the surface of large objects.

The concentration of *L. notorcadensis* on the upper spines rises the question of intraspecific competition for space, because space is obviously limited. The negative relation between biomass already present and recruitment success (Fig. 4) gives evidence that there is competition for space. The higher the bivalve biomass already present on a particular cidaroid, the lower is the number of juvenile *Lissarca* settling on this sea urchin as fraction of the number of embryos produced. The importance of the proper position of the spines for *L. notorcadensis* is strengthened by the fact that the juveniles seem to drift away preferably than settle on the lower spines of their parent's sea urchin. However, the overall low recruitment success (mean = 0.11) indicates that a great part of the juveniles drifts away even if there is sufficient space available. This high dispersion rate (0.89, i.e. 1 − recruitment success) may counteract the problem of genetical isolation otherwise faced by spatially isolated sub-populations without pelagic larval stages.

The correlation matrix (Table 2) and the results of the ANOVA (Table 3) indicate strong negative interactions between *L. notorcadensis* and other epizoic taxa (mainly colonial anthozoans and bryozoans). *L. notorcadensis* as well as the colonial species prefer the same spines for settlement, but they do not co-exist in the same area of a cidaroid spine. *L. notorcadensis* juveniles seem to be unable to attach themselves on the surface of the colonial epizoa, whereas dense aggregations of *L. notorcadensis* seem to prevent the initial settlement of the colonial species (Fig. 5).

To sum up, food availability, intraspecific competition and interspecific competition are likely to be the main factors determining the distribution of *L. notorcadensis* among and along the sea urchin spines, whereas the significance of predation (Prezant 1989) remains uncertain.

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