Effects of temporary food limitation on survival and development of brachyuran crab larvae

LUIS GIMENEZ[1,2]*† AND KLAUS ANGER[1]

[1]BIOLOGISCHE ANSTALT HELGOLAND, STIFTUNG ALFRED-WEGENER-INSTITUT FÜR POLAR- UND MEERESFORSCHUNG, 27498 HELGOLAND, GERMANY AND [2]SECCIÓN OCEANOLOGÍA, FACULTAD DE CIENCIAS, IGUÁ 4225, 11400 MONTEVIDEO, URUGUAY

†PRESENT ADDRESS: BIOLOGISCHE ANSTALT HELGOLAND, STIFTUNG ALFRED-WEGENER-INSTITUT FÜR POLAR- UND MEERESFORSCHUNG, 27498 HELGOLAND, GERMANY

*CORRESPONDING AUTHOR: lgimenez@awi-bremerhaven.de

As a consequence of the combined effects of prey patchiness and diel or tidal vertical migrations in the water column, decapod crustacean larvae may experience temporal or spatial variability in the availability of planktonic food. In a laboratory study, we evaluated effects of temporarily limited access to prey on the larvae of three species of brachyuran crabs, Chasmagnathus granulata, Cancer pagurus and Carcinus maenas. Stage-I zoeae were fed ad libitum for 4 or 6 h per day (20 or 25% treatments; 6 h tested in C. pagurus only), and rates of larval survival and development were compared with those observed in continuously fed control groups (24 h, 100%). In C. granulata, we also tested if intraspecific variability in initial biomass of freshly hatched larvae originating from different broods has an influence on early larval tolerance of food limitation. Moreover, we exposed embryos and larvae of this estuarine species to moderately decreased salinities to identify possible interactions of osmotic and nutritional stress. Finally, we evaluated in this species the effect of food limitation on survival from hatching through all larval instars to metamorphosis. In all three species, limited access to prey had only weak or insignificant negative effects on survival through the Zoea-I stage. The strength of the effects of temporary food limitation varied in C. granulata significantly among broods. However, no significant relationships were found between initial larval biomass (C content) and either survival or development duration. Strongly decreased survival to metamorphosis was found when food limitation continued throughout larval development. Thus, early brachyuran crab larvae are well adapted to transitory lack of planktonic food. The capability of the Zoea-I stage of C. granulata to withstand nutritional stress also under conditions of concomitant salinity stress allows them to exploit various brackish environments within estuarine gradients. However, continued exposure to limited access to planktonic prey may exceed the nutritional flexibility of C. granulata larvae.

INTRODUCTION

Natural variability in the availability of planktonic food organisms has been considered as one of the principal factors affecting survival in the pelagic environment. Experiments with copepods (Tiselius, 1992) or with larvae of fish (Lasker, 1975) and invertebrates (Barnes, 1956; Paulay *et al.*, 1985; Harms *et al.*, 1994; Sulkin *et al.*, 1998) showed that food densities allowing for moderate survival, growth and successful development in the laboratory are usually higher than average concentrations of suitable prey in the sea. This paradox may be solved if consumers of plankton show a more generalistic feeding behaviour than previously assumed. Crab larvae, for example, are generally considered as carnivorous, but their survival and growth may depend also on the additional utilization of alternative prey including phytoplankton, protists and detritus (Sulkin and van Heukelem, 1980; Harms *et al.*, 1991, 1994; Sulkin and McKeen, 1999; Anger, 2001; Hinz *et al.*, 2001; Perez and Sulkin, 2005)., Transitorily optimum food concentrations due to plankton patchiness may be an

alternative or additional explanation for successful growth and development of carnivorous plankton organisms in a nutritionally dilute environment. This phenomenon occurs, as a consequence of both oceanographic and biological processes, at various spatial and temporal scales (Barry and Dayton, 1991; Andersen and Nielsen, 2002). On long-term temporal scales (weeks to months), low levels of food availability occur typically at high latitudes, where strong seasonality of plankton production selects for abbreviated and/or lecitotrophic modes of development (Anger et al., 2004; Thatje et al., 2005).

At a scale of one or a few days, regional or local patches of food are often associated with water stratification occurring during calm weather conditions, but they may soon be destroyed by wind-generated turbulent mixing (Lasker, 1975). Effects of food limitation on this scale were in previous studies mostly evaluated by means of point-of-reserve-saturation and point-of-no-return experiments (Anger, 2001; Giménez, 2002; Paschke et al., 2004). These investigations revealed that short initial periods of feeding during the postmoult phase (mostly restricted to 1–2 days) suffice to allow for subsequent successful development through the remaining time (several days) of the moulting cycle, even in complete absence of food.

One of the most important sources of variability in the availability of planktonic food is associated with the occurrence of diel or tidal cycles of vertical migration in both predators and prey, balancing optimal food intake against predation risk (Liu et al., 2003). These migrations take place at a yet smaller scale, implying significant changes in food concentrations within a few hours (Queiroga et al., 1997; Garrison, 1999; Forward and Tankersley, 2001; Rawlinson et al., 2004). Due to such behavioural patterns, crab larvae may pass several times per day through water bodies with highly variable prey densities. This scenario was experimentally examined by Sulkin et al. (Sulkin et al., 1998), who observed that the survival of the Zoea-I larvae of two brachyuran species was only little affected when the access to prey was limited to only 4 or 6 h per day. This experimental study explores potential effects of prey patchiness exclusively on this short-term scale, testing if brachyuran crab larvae are able to effectively exploit temporarily available patches of suitable food, and if a rapid accumulation of nutritional energy allows them to tolerate subsequent periods of food shortage.

As a primary focus of this study, we addressed the question if the tolerance to limited access to prey varies interspecifically in planktotrophic larvae, as previously observed in holoplanktonic organisms (Dagg, 1977; Tiselius, 1992). We chose an approach of daily food limitation (food availability limited to 4 or 6 h per day) to compare the 'nutritional vulnerability' (Sulkin, 1978)

between first-stage larvae of three species of brachyuran crabs originating from diverse geographic-climatic regions and habitats, Cancer pagurus, Carcinus maenas and Chasmagnathus granulata. Cancer pagurus and C. maenas are common in the eastern North Atlantic; the latter species has been introduced also in several other regions of the world (Anger et al., 1998). While C. granulata lives in the intertidal and supratidal zones of brackish salt marshes along the coasts of southeastern South America (Boschi et al., 1992; Giménez, 2003), C. maenas is a marine-estuarine species occurring in the intertidal and shallow subtidal zones, and C. pagurus is a subtidal marine crab.

As another focus of this study, we were interested to know if the tolerance of food limitation varies between different broods or changes under additional stress conditions. Since the early larvae of C. granulata are in their natural habitat exposed to decreased salinities (Anger et al., 1994), we tested in this species if the tolerance of nutritional stress in the Zoea-I stage is affected by this potentially interacting physical stress factor. If larvae are evolutionarily adapted to food limitation, this adaptation should operate not only at the optimal but also in suboptimal salinities. Additionally, the amount of larval energy reserves, which may be utilised during periods of scarcity of food, is also influenced by maternal factors and by environmental conditions experienced during the preceding embryonic phase (Giménez, 2002; Giménez and Anger, 2003; Paschke et al., 2004). We thus compared in this species also the tolerance of food limitation among larvae originating from different females, whose eggs were incubated at different salinities.

We also evaluated if the tolerance of food limitation changed in later larval stages of C. granulata reared from hatching to metamorphosis under continued conditions of daily limited access to prey. The purpose of this experiment was to evaluate the long-term effect of daily access to prey and identify possible ontogenetic changes in the nutritional vulnerability of successive developmental stages or cumulative effects of continued nutritional stress, which should be indicated by a gradually increasing mortality in later stages.

METHOD

All experiments were performed under controlled conditions of temperature (constant 18°C for C. maenas and C. granulata; 15°C for C. pagurus) and an artificial 12:12 h light:dark photoperiod (daytime from 8.00 to 20.00 h), with filtered natural seawater from the North Sea (salinity of 32); lower salinities were obtained by diluting seawater with tap water. Ovigerous females of C. granulata were obtained from juveniles sampled in Mar Chiquita lagoon, Argentina and cultured since 1991 in the laboratory of the

Helgoland Marine Biological Station (Germany). Following Sulkin *et al.* (Sulkin *et al.*, 1998), we compared larval survival and development of *C. pagurus*, *C. maenas* and *C. granulata* in two experimental treatments with limited access to prey (restricted to 4 and 6 h per day) and in one control group with permanent (24 h) access to prey. In *C. maenas* and *C. granulata*, we had only one treatment with limited access to prey (4 h), while two treatments (4 and 6 h) were tested in *C. pagurus*. Since previous studies had shown that the Zoea-I larvae of these species are unable to survive to the second zoeal stage under conditions of complete food deprivation (Dawirs, 1984, 1986; Anger, 1987; Giménez, 2002), we did not include a starvation treatment without any access to prey.

In *C. pagurus* and *C. maenas*, the experiments were carried out with larvae originating from one female each, while in total 12 different hatches were used in the experiments with *C. granulata* (see below). Freshly hatched zoeae were reared in eight replicate bowls (80 ml for *C. maenas* and *C. granulata*, 100 ml for the larger zoeae of *C. pagurus*), with 10 individuals per replicate. In daily intervals, the culture water was changed, crab larvae were checked microscopically for mortality or moulting, and freshly hatched *Artemia* sp. nauplii were added *ad libitum* (~10–15 nauplii per ml) as food. In the two treatments, food was offered exclusively during the period 10:00–14:00 or 10:00–16:00 h; thereafter, the larvae were transferred to filtered water without food. All experiments were run until the larvae had either died or moulted to the second zoeal stage. The response variables were the percentage survival (number of individuals moulted to Zoea II) and mean duration of development from hatching to the Zoea-II stage.

For each species, the data of percentage survival and duration of development were analysed with one-way ANOVA (Zar, 1996), with access to prey as factor. Homogeneity of variance was checked with Cochran tests, normality with plots of residual errors. Both data sets met normality and variance homogeneity, allowing to use untransformed data. Significantly different treatments were identified with Student-Newman-Keuls (SNK) test.

For the experiments with *C. granulata*, we obtained larvae from 12 different ovigerous females, which had been maintained individually from the day of egg laying to larval hatching in aquaria with 15, 20 and 32 salinity (i.e. 4 females per salinity). The incubation period varied between 25 and 35 days and was not significantly affected by these salinities (Giménez and Anger, 2001). Freshly hatched Zoea-I larvae were used for experiments and for measurements of initial biomass (dry weight; carbon, C; nitrogen, N). Potential relationships between initial larval biomass and survival or duration of development were explored using the Pearson correlation coefficient.

Effects of salinity and among-brood variability were analysed with ANOVA, with factors defined as follows: (i) access to prey (fixed, two levels: control and 4 h); (ii) salinity condition during egg or embryonic development (referred to as 'embryonic salinity'; fixed, three levels: 15, 20 and 32 salinity); (iii) brood (random, nested in embryonic salinity, four broods within each salinity); and (iv) salinity condition during larval development (or 'larval salinity'; fixed, two levels: 20 and 32 salinity). There were five groups (replicates) with 10 individuals per treatment combination, maintained in vials with 80 ml. Raw data of survival and duration of development were highly heterogeneous. Arcsine transformation of percentage survival and logarithmic transformation of development times led to variance homogeneity and normality of residuals. Significantly different treatments were identified by SNK test.

In order to evaluate effects of continually limited access to prey on survival from hatching to metamorphosis to the first juvenile instar, we used larvae of *C. granulata* obtained from two additional broods. For each brood, the larvae were reared in three groups with 50 individuals each and kept under control conditions (continuous food availability; 24 h) or with access to prey limited to 4 h or 6 h per day. From hatching to the moult to the third zoeal stage, the larvae were reared in groups in glass vials with 500-ml seawater (32 salinity). Thereafter, they were reared individually in glass vials to avoid potential cannibalistic effects. The number of survivors (S) was described as a function of age since hatching following the model $S = A + B \cdot \log(Age)$, where A is a fitted constant and B is mortality rate. The effect of food treatments on mortality rate was evaluated with a general linear model and Tukey tests.

RESULTS

Zoea I of *C. pagurus* and *C. maenas*

Limited access to prey did not significantly reduce the survival of Zoea-I larvae of *C. maenas* or *C. pagurus* (Fig. 1, Table I). In *C. pagurus*, however, there was a significant increase in the duration of development to the Zoea-II stage compared with the control group. In *C. maenas*, the difference in development time was marginally significant ($P = 0.052$; Fig. 1 and Table I). In both species, the increment in the duration of development was >10%.

Zoea I of *C. granulata* under different salinities

Limited access to prey decreased significantly the rate of survival and increased the duration of development (Fig. 2a and b). The strength of these effects, however, varied among broods from different females (Tables II and III). In 8 out of 12 broods, the larvae with only 4 h access to prey showed only slightly or moderately
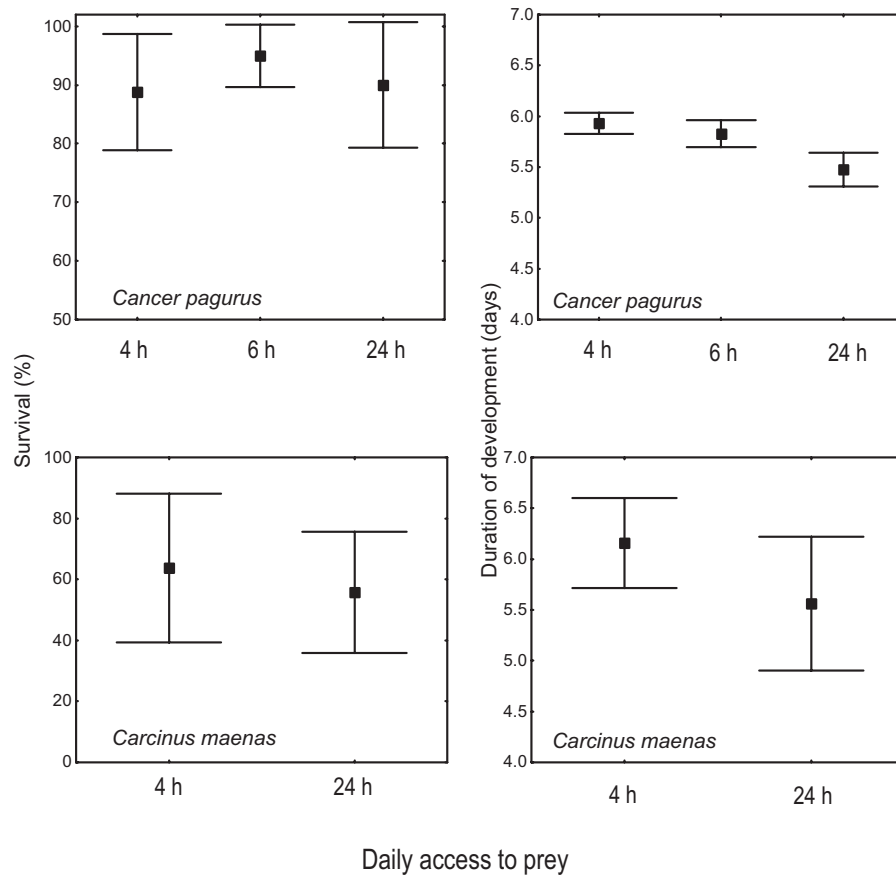
Fig. 1. Effects of limited access to prey on mean survival and duration of development of Zoea-I larvae from *Cancer pagurus* and *Carcinus maenas*. Error bars are standard deviations.

Table I: ANOVA to evaluate the effect of access to prey, on survival of the Zoea I and duration of development to Zoea II of Carcinus maenas and Cancer pagurus

	df_f	MS_f	df_e	MS_e	F	P
Carcinus maenas						
Survival	1	0.025	14	0.063	0.403	0.536
Duration of development	1	1.425	14	0.316	4.514	0.052
Cancer pagurus						
Survival	2	87.5	21	80.4	1.089	0.355
Duration of development	2	0.456	21	0.018	25.27	$<1 \cdot 10^{-5}$

df_f, degrees of freedom of factor (access to prey); df_e, degrees of freedom of error; MS_f, mean squares of factor; MS_e, mean squares of error.

decreased survival (<34%) as compared with the controls, while a significant increase in the duration of development occurred in all broods (Table IV).

The salinity conditions during larval rearing affected in general the survival and duration of development through the Zoea-I stage. In survival, the effect of salinity was independent of the effect of access to prey (no significant interaction between feeding condition and larval salinity: Table II and Fig. 2a), but this effect occurred in duration of development in larvae kept under limited food conditions (Table III; Fig. 2b). Other effects of salinity varied among the broods of origin, but also among treatments with different embryonic salinities (Fig. 2c and d; Tables II and III). In four broods, larval survival was significantly decreased (by ∼20–30%) at a rearing salinity of 20, while no such effect occurred in larvae originating from the other eight females. In larvae obtained from eggs that had previously been incubated in brackish water (15 or 20 salinity), survival was slightly decreased in full-strength seawater (32 salinity; Fig. 2c); however, this effect was statistically not significant (Table II). The duration of development was in these larvae independent of rearing salinity (20–32 salinity; Fig. 2d). However, in Zoea-I larvae that hatched from broods incubated at 32 salinity, the
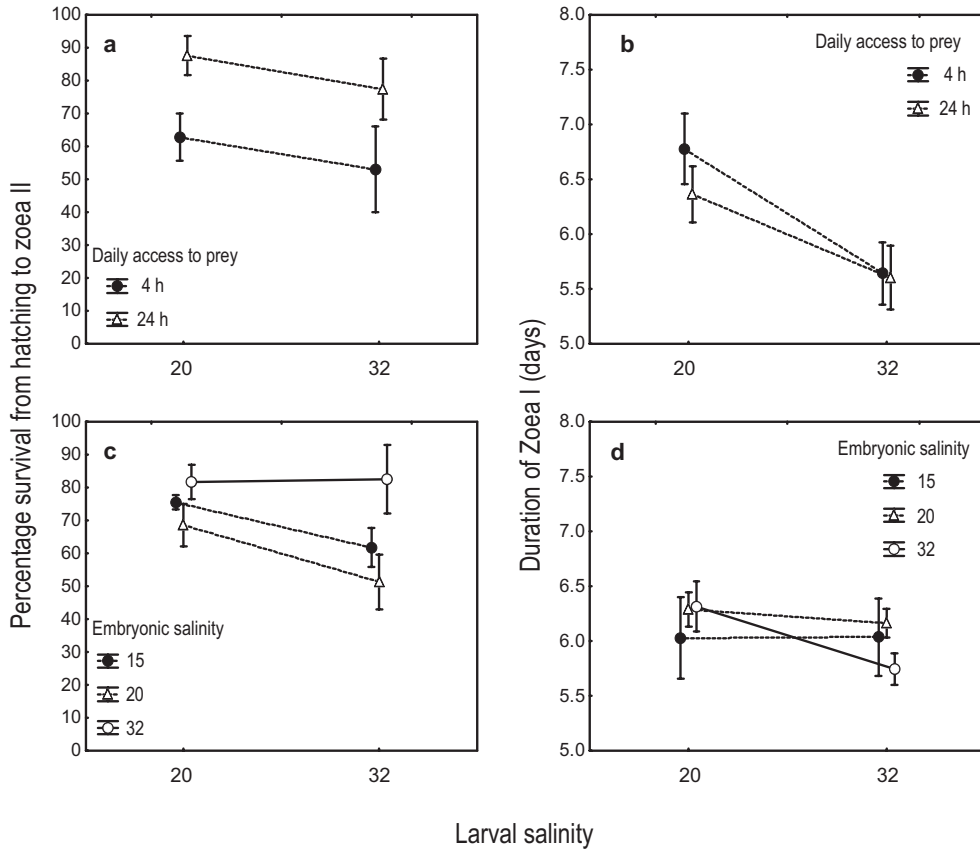
Fig. 2. *Chasmagnathus granulata*. Effects of limited access to prey, embryonic and larval salinity exposure on mean survival and duration of development of Zoea I. Combined effects of larval salinity and access to prey are given in (a) for survival and in (b) for duration of development; combined effects of larval and embryonic salinity are given in (c) for survival and in (d) for duration of development. Error bars are standard errors among broods.

Table II: ANOVA to evaluate the effect access to prey (food), larval and embryonic salinity and brood on survival of the Zoea I of Chasmagnathus granulata

Factor	Df_f	MS_f	df_e	MS_e	F	P
Food	1	6.58	9	0.21	31.75	$<10^{-3}$
Brood	9	0.55	192	0.04	15.05	$<10^{-6}$
Larval salinity	1	0.83	9	0.24	3.48	0.096
Embryonic salinity	2	1.69	9	0.55	3.08	0.096
Food × brood	9	0.21	192	0.04	5.68	$<10^{-6}$
Food × embryonic salinity	2	0.48	9	0.21	2.30	0.154
Food × larval salinity	1	0.03	9	0.03	1.17	0.308
Brood × larval salinity	9	0.24	192	0.04	6.53	$<10^{-6}$
Embryonic salinity × larval salinity	2	0.44	9	0.24	1.85	0.212
Food × brood × larval salinity	9	0.03	192	0.04	0.79	0.624
Food × embryonic salinity × larval salinity	2	0.01	9	0.03	0.38	0.694

Table III: ANOVA to evaluate the effect access to prey (food), larval and embryonic salinity, and brood on duration of development to Zoea II of Chasmagnathus granulata

Factor	df_f	MF_S	df_e	MS_e	F	P
Food	1	54.14	9	1.42	37.99	$<10^{-3}$
Brood	9	4.84	191	0.08	61.87	$<10^{-6}$
Larval salinity	1	3.64	9	0.17	21.82	$<10^{-2}$
Embryonic salinity	2	1.09	9	4.84	0.23	0.80
Food × brood	9	1.42	191	0.08	18.21	$<10^{-6}$
Food × embryonic salinity	2	2.97	9	1.42	2.082	0.18
Food × larval salinity	1	1.11	9	0.13	8.772	<0.05
Brood × larval salinity	9	0.17	191	0.08	2.133	<0.05
Embryonic salinity × larval salinity	2	2.59	9	0.17	15.55	$<10^{-2}$
Food × brood × larval salinity	9	0.13	191	0.08	1.624	0.11
Food × embryonic salinity × larval salinity	2	0.23	9	0.13	1.799	0.22

df_e, degrees of freedom of factor (access to prey); df_e, degrees of freedom of error; MS_f, mean squares of factor; MS_e, mean squares of error.

df_f, degrees of freedom of factor (access to prey); df_e, degrees of freedom of error; MS_f, mean squares of factor; MS_e, mean squares of error.

Table IV: Response to limited access to prey in Zoea-I larvae of Chasmagnathus granulata hatched from 12 broods: mean survival, duration of development, and initial carbon (C) content

Brood	Mean survival (%)			Duration of development (days)			C content (µg ind⁻¹)
	24 h	4 h	% reduction	24 h	4 h	% delay	
1	85	64	24.7	5.19	6.07	16.88	2.97
2	87	46	47.1	5.00	6.20	23.89	3.92
3	73	54	26.0	5.19	6.36	22.37	2.27
4	75	65	13.3	6.93	7.29	5.12	2.99
5	60	40	33.3	5.81	6.72	15.72	2.17
6	99	40	59.6	5.72	5.95	4.19	2.16
7	69	37	46.4	6.05	6.77	11.86	2.37
8	88	46	47.7	6.18	6.65	7.52	2.59
9	100	88	12.0	5.24	6.15	17.44	2.54
10	95	71	25.3	5.23	7.78	48.84	2.27
11	92	91	1.1	5.43	6.65	2.33	1.99
12	67	53	20.9	5.46	6.29	15.05	3.01

% decrease and % delay: difference in survival and development, respectively, in relation to the control (24 food); embryonic salinity conditions: broods, 1–4, 15‰; broods 5–8, 20‰; broods 9–12, 32‰; data from different larval salinity conditions were pooled.

Table V: Correlation table between initial carbon content of Zoea I of Chasmagnathus granulata and survival or duration of development to Zoea II of C. granulata at different access to prey and larval salinity conditions

F	L	Survival		Duration of development	
		r	P	r	P
4	20	–0.08	0.79	–0.39	0.20
4	32	–0.18	0.59	–0.05	0.87
24	20	0.04	0.89	–0.12	0.72
24	32	0.04	0.89	–0.29	0.39

duration of development was significantly shorter in comparison to lower salinities (Fig. 2d).

Initial larval biomass at hatching ranged from 6.7 to 9.0 µg dry mass, 2.0–3.9 µg C individual⁻¹ (Table IV) and from 0.4 to 0.7 µg N individual⁻¹. This brood-specific variation in larval biomass showed no significant relationship with the rates of larval survival or development (Table V).

Complete larval development of *C. granulata*

In both broods tested, the survival rate of larvae reared under conditions of limited access to prey was significantly lower than that in the control groups (Fig. 3). Differences between mortality rates (Table VI) were consistently significant when controls were compared with any treatment (Tukey tests all $P < 0.01$), but no significant differences were found between different treatments with food limitation (Tukey tests all $P > 0.05$). Differences in mortality rate appeared between the second and the fourth zoeal instar (Table VII). Most of the larvae which survived to the Zoea-IV stage were later also able to metamorphose successfully to the first juvenile crab instar. At the end of larval development, survival under conditions of limited access to prey was decreased to ~10–25% of that observed in the continually fed control groups.

DISCUSSION

Our experiments showed that temporarily limited access to prey had either no significant effect at all on the rate of survival through the first zoeal stage of brachyuran crabs (*C. maenas* and *C. pagurus*) or it caused only a weakly enhanced mortality (*C. granulata*). The duration of Zoea-I development, by contrast, was generally prolonged in treatments where the access to prey was limited to 4 or 6 h per day. In *C. granulata*, the effects of limited access to prey varied among larvae produced by different females; while the effects on survival were largely independent of the salinity experienced during embryonic or zoeal development, the effects on duration of development depended on larval salinity. Larval survival to metamorphosis was in
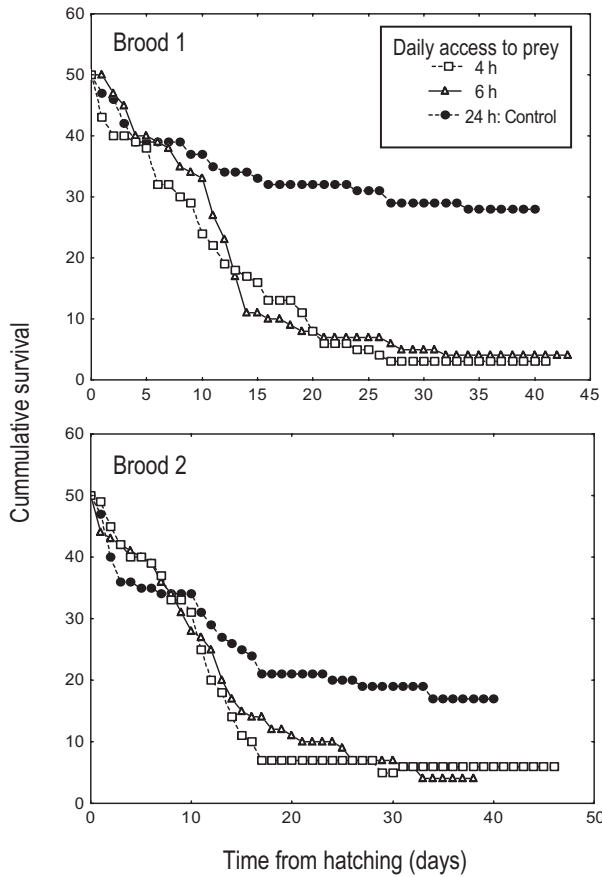
Fig. 3. *Chasmagnathus granulata.* Effects of limited access to prey on cummulative survival from hatching to metamorphosis to the first juvenile crab for larvae from two separate broods

Table VI: Statistics of the regression model: survival = A + B • log(Age), for larvae of Chasmagnathus granulata hatched from two broods and maintained under different levels of access to prey from hatching (day 0) to metamorphosis to the first juvenile

Treatment	A	B	R²
Brood 1			
Control	48.6040	−12.9856	0.973
6	60.7411	−37.1509	0.902
4	54.6553	−33.7382	0.927
Brood 2			
Control	48.7998	−20.1619	0.943
6	58.1222	−34.5191	0.912
4	56.7472	−33.4838	0.878

A, fitted constant. The mortality rate is represented by the paramenter 'B'; for all models $P < 10^{-6}$; for both hatches slopes differed significantly (general linear model test $P < 10^{-5}$).

Table VII: Number of individuals of Chasmagnathus granulata moulting to each instar for larvae hatched from two different broods and maintained under different levels of access to prey

Instar	Brood 1			Brood 2		
	24 h	6 h	4 h	24 h	6 h	4 h
Zoea I	50	50	50	50	50	50
Zoea II	39	36	30	35	32	34
Zoea III	34	15	17	28	22	15
Zoea IV	32	8	4	21	8	7
Megalopa	31	4	3	20	6	6
Juvenile	28	4	3	17	4	6

C. granulata increasingly affected by continued daily food limitation, suggesting a cumulative effect of long-term nutritional stress.

Limited access to prey in the Zoea-I stage: interspecific comparison

Our results are consistent with the findings by Sulkin *et al.* (Sulkin *et al.*, 1998), when the larval response to limited access to prey is compared among related species of crabs, independent of their geographic origin (Table VIII). For instance, both cancrid species, *C. pagurus* from the North

Table VIII: Percent increments (positive) or decrements (negative) in survival of Zoea I and growth (duration of development to Zoea II) for larvae of five brachyuran species reared under limited access to prey (4 and 6 h per day) as compared with the control group under permanent access

Species	Region	Survival		Growth	
		6 h	4 h	6 h	4 h
Cancer pagurus	**North Atlantic**	+7	−1	+6	+8
Cancer magister	North Pacific	+6		+4	
Carcinus maenas	**North Atlantic**		+14		+10
Chasmagnathus granulata	**South Atlantic**		−29		+18
Hemigrapsus oregoniensis	North Pacific		−21 to −9		+13 to +24

Data are from this paper (in bold) and from Sulkin *et al.* (Sulkin *et al.*, 1998). Data of *Chasmagnathus granulata* are mean values.

Sea and *Cancer magister* from the Pacific Ocean, showed a very weak influence of food limitation, while the two grapsoid species, *Hemigrapsus oregonensis* from the North Pacific and *C. granulata* from the South Atlantic, showed a stronger influence. These observations suggest that planktotrophic first-stage crab larvae, in general, may not necessarily require a continuous availability of concentrated food, because they are capable of efficiently exploiting briefly available food sources and to accumulate sufficient nutritional energy to survive subsequent periods of starvation, even if these last 4–6 times longer than the preceding period of satiated feeding. However, the nutritional vulnerability of the Zoea-I stage appears to vary significantly among brachyuran taxa; this should be tested in future comparative studies.

Chasmagnathus granulata: intraspecific variability among broods and interacting effects of salinity

As in our other test species, the effects of limited access to prey on the Zoea-I stage were also in *C. granulata* generally weak, with a reduction of survival rate mostly <34% (in 8 out of 12 hatches); only in one hatch increased mortality by >50%. Comparison of the response patterns in larvae originating from 12 different females showed that there was significant intraspecific variability among broods in the tolerance of food limitation. This suggests that future studies should pay more attention to this potentially confounding factor. Unlike in some previous experiments (Giménez, 2002; Giménez and Anger, 2003), however, variability in survival or development duration was not significantly correlated with brood-specific variation in initial larval biomass at hatching. This may be explained by a different range of biomass values found in the larvae that were used in this study (2.0–4.0 µg C per zoea) compared to previously used materials ranging from 1.8 to 3.0 µg C (Giménez and Anger, 2003). In a previous study (Giménez, 2002), correlations between C content and duration of development were found only under extreme conditions of starvation, e.g. when larvae were initially starved for at least one day, or they were initially fed for two days and subsequently starved for longer periods. In these experiments, the biomass values were rather high, varying between 2.2 and 3.2 µg C per larva, which may have decreased the variability in survival or growth under conditions of food limitation.

Effects of limited access to prey on early zoeal survival in *C. granulata* were independent of the salinity conditions during larval or embryonic development. The delay of development due to food limitation, however, was significantly stronger in larvae reared in decreased salinity (20 salinity) than in those exposed to seawater (32 salinity).

Since the zoeae of *C. granulata* are released in estuaries and brackish coastal lagoons varying greatly in salinity (Giménez, 2003), larvae originating from different local or regional populations should have similar abilities of tolerating short-term food limitation in terms of survival at expenses of lengthening the duration of development.

In *C. granulata*, previous observations on larval starvation tolerance (Giménez, 2002) may be compared with the present data of survival and growth in the first zoeal stage, allowing for a preliminary evaluation of the importance of the time scale of variation in food availability. For instance, only one day of initial starvation may lead to an increase of 1 day in the duration of development as compared with well-fed larvae (Giménez, 2002). This delay is similar to that obtained as a cumulative effect of 4 h of daily access to prey through a period of 5–6 days.

Tolerance of continually limited access to prey in *C. granulata*

While limited access to prey had only weak effects on survival and development in the Zoea-I stage of *C. granulata*, later larval stages were strongly affected by continued conditions of food limitation. Most mortality occurred during the zoeal stages II–IV, although the larvae in these stages are larger and should thus capture *Artemia* nauplii more efficiently than the small Zoea I, while high (*ad libitum*) food concentrations prevented a decline in food availability due to the consumption of prey items. This suggests a cumulative effect of daily food limitation.

If the experimental conditions with a continually limited access to prey resemble those occurring in nature, most natural mortality should be a consequence of cumulative nutritional stress effects. Thus, in nature limited access to prey should have a big impact on the survival of *C. granulata* larvae. As alternative or additional conclusions, however, it should be considered that (i) *Artemia* nauplii might have a lower nutritional quality than natural zooplankton prey, (ii) daily periods of access to prey in the natural environment may be longer than 4–6 h, (iii) the larvae may use also other food sources including phytoplankton or detritus (Sulkin and van Heukelem, 1980; Harms *et al.*, 1991, 1994; Sulkin and McKeen, 1999) and (iv) some prey should be available also outside concentrated food patches. High rates of survival and growth in larvae fed *ad libitum* with *Artemia* suggest that this food cannot be inadequate. However, the prey quality may eventually affect the survival in advanced developmental stages of brachyuran larvae (Sulkin and McKeen, 1999). Low prey quality may translate to decreased recruitment or fitness in the subsequent juvenile phase of the life cycle (Phillips, 2002; Giménez *et al.*, 2004), leading to a reduction in population growth as suggested for copepods (Jones and Flynn, 2005).

During the course of vertical migration, larvae may regulate the time spent within a food patch, as observed for instance in copepods (Tiselius, 1992) and in non-crustacean invertebrate larvae (Metaxas and Young, 1998; Burdett-Coutts and Metaxas, 2004). Survival and fitness may be enhanced by greater diversity in the types and quality of prey, as suggested for a diatom–copepod–fish food chain (Jones and Flynn, 2005), and this may eventually enhance the recruitment success in the benthos. Survival may be enhanced also in stratified environments, in particular, if feeding takes place near the thermocline, where food tends to accumulate, and larvae migrate downward where lower temperatures should decrease the metabolic rate, and thus, the rate of reserve utilisation during periods of poor food availability. Progress in the understanding of how brachyuran crab larvae are able to cope with highly variable food conditions is important for the understanding of benthic–pelagic coupling. This may be provided from comparative laboratory experiments using various species and simulating (i) scenarios of limited access to a higher diversity of zooplankton and phytoplankton prey, (ii) food patches associated with pycnoclines and (iii) combined effect of temporal changes in food availability and temperature.

ACKNOWLEDGEMENTS

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