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RESEARCH ARTICLE

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Reproduction in *Balanus amphitrite* Darwin (Cirripedia: Thoracica): influence of temperature and food concentration

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Abstract *Balanus amphitrite*, an acorn barnacle, is distinctly euryhaline, eurythermal and a dominant fouling organism found in warm and temperate waters throughout the world. In this study, the influence of temperature and food concentration on the reproductive biology of this species collected from a tropical habitat was evaluated. Adult barnacles were maintained at 20, 25 and 30°C temperatures at different concentrations of food (50, 100, 150 and 200 *Artemia* ind^{-1} day^{-1}). In this previously believed obligatory cross-fertilizing hermaphrodite, self-fertilization was observed. The rise in temperature from 20 to 30°C resulted in a longer interbreeding interval (6–7 days, 200 *Artemia* ind^{-1} day^{-1}; 11–13 days, 50 *Artemia* ind^{-1} day^{-1}). Computed carbon gained through feeding during the interbreeding interval indicated an inverse relationship to the temperature. At 20°C, although a greater amount of carbon was gained through feeding, the numbers of larvae produced were fivefold less when compared to those raised at 30°C. At 20°C, 2.3 µg C was required to produce a single larva, whereas at 30°C it was 0.4 µg C. A rise in rearing temperature also influenced the molting rate positively. Observations on temporal variation in the gonad development of this species in a tropical coastal environment influenced by the monsoons indicated gonad development to be positively related to chlorophyll *a* concentration.

Introduction

Balanomorph barnacles are distributed worldwide and are found in all the marine environments from high intertidal zone to the depth of the ocean. Barnacles have gained economic importance owing to their presence in the hard fouling community and have been widely used in studies of inter-specific competition, habitat selection by planktonic larva and life histories (Barnes and Barnes 1967; Hurley 1973; Crisp 1974; Wethey 1979).

Most of the balanomorph barnacles are hermaphrodites (Charnov 1987), fertilization is internal and they are usually capable of producing eggs and sperms at the same time. Exchange of sperms between adjacent individuals, leading to cross-fertilization, appears to be the rule among acorn barnacles. However, incidences of self-fertilization have also been reported (Barnes and Crisp 1956; Furman and Yule 1990; El-Komi and Kajihara 1991).

Several species of cirripedes in warm temperate and subtropical regions characteristically produce numerous small broods in rapid succession during summer. Temperature is considered to determine the length of the brooding season (Crisp 1950; Patel and Crisp 1960a, b; Hines 1978). Some cirripedes breed over a wide range of temperature, whereas others breed until a certain critical temperature is reached and are termed as eurythermic or stenothermic, respectively. Thus, temperature is an ecologically important component in determining the latitudinal distribution of cirripedes (Barnes and Barnes 1975; Lewis 1975; Barnes 1989). Within the optimum temperature range and in relatively stable conditions there is some evidence of seasonal breeding periods superimposed on a general continuous low level of reproduction, for example, in *Elminius modestus, E. plicatus* and *Chthamalus anisopoma* (Malusa 1986; Barnes 1989). It is also reported that the quantity of food plays an important role in the breeding cycle of the cirripedes. Barnes and Barnes (1967, 1975) have shown that feeding in barnacles can control the time at which egg lamellae are produced; furthermore, poor nutritional conditions can cease breeding.

Balanus amphitrite is distinctly euryhaline and eurythermal in its tolerance. The study site, Zuari estuary, is a tropical estuary and experiences a considerable quantity of fresh water during monsoon thereby lowering the

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salinity. We have presented the data relevant to recruitment of this species in this estuary (Desai and Anil 2005) and elucidated the importance of monsoon and salinity changes.

In this paper we quantified the feeding rate and evaluated its influence on breeding. The frequency of molting was observed to evaluate its relationship with the breeding pattern. Observations on the incidences of self-fertilization in the laboratory were performed in this species, which is represented as an obligatory cross-fertilizing hermaphrodite. Temporal variations in the ovarian development of barnacles collected from the nature were observed to draw inferences on the influence of ambient temperature and the quantity of chlorophyll *a*.

Materials and methods

Breeding and molting

In order to determine the effect of breeding (breeding interval and number of broods) and molting (molting interval and number of molts) several laboratory experiments were carried out. To study the breeding and molting, *B. amphitrite* was collected from the intertidal area of Dona Paula bay. Barnacles with a rostro carinal diameter (RCD) ranging between 8 and 12 mm were sorted out in the laboratory, cleaned of the epibiotic growth with a nylon brush and used to carry out different experiments. These barnacles were mounted on acrylic plates (8×3 cm^2) as solitary and in pairs (five replicates) using commercially available glue (Super Wiz). Acrylic sheets with barnacles mounted on them were immersed in filtered seawater (GF/C) in 250 ml capacity glass beakers. Seawater (35‰) in the beakers was changed daily. These barnacles were fed with newly hatched *Artemia*. The number of molts and/or the larvae released was quantified prior to change of medium and food everyday. Everyday the unconsumed *Artemia* nauplii were also counted.

Experiment 1

Observations on breeding, molting and food consumption were performed for 75 days at different temperatures (20, 25 and 30°C) and food concentrations (50, 100, 150 and 200 *Artemia* ind^{-1} day^{-1}). Throughout the experiment the barnacles were maintained in the incubator at respective temperatures.

Experiment 2

The Experiment 1 was demonstrated at a given food concentration (200 *Artemia* ind^{-1} day^{-1}). The breeding is frequent at lower temperature (20°C), whereas at higher temperature (30°C) the number of larvae produced during experimental duration was higher and this was coupled with higher frequency of molting. Taking into consideration the ambient water temperature in the surrounding waters Experiment 2 was designed to elucidate whether the production of higher number of larvae is sustainable over a longer period. Thus, Experiment 2 was carried out considering all the food concentrations (50, 100, 150 and 200 *Artemia* ind^{-1} day^{-1}) at 30°C for a longer duration (203 days). The barnacle *B. amphitrite*, also gets exposed to this temperature for a longer duration in this tropical environment compared to the other two temperatures (20 and 25°C). Food and seawater were changed everyday as mentioned earlier.

Experiment 3

In order to understand the breeding of *B. amphitrite* raised in the laboratory from cypris instar and to compare it with those barnacles collected from the field this experiment was carried out. The nauplii released by the paired barnacles maintained at 30°C (fed with 200 *Artemia* ind^{-1} day^{-1}) were collected and reared till they developed into the cypris stage in the laboratory using *Chaetoceros calcitrans* (unicellular diatom) as food at a cell concentration of 2×10^5 cells ml^{-1}. These cyprids were transferred into 5 ml capacity polystyrene multiwells for settlement. The settled cyprids (spat) were provided with unicellular algae (*C. calcitrans*) and *Artemia* as food. Once these juveniles attained a size of 5 mm (RCD) they were separated into solitary and paired individuals, and maintained at 30°C at a food concentration of 100 *Artemia* ind^{-1} day^{-1}. The numbers of molts and broods were monitored every day prior to change of food and seawater.

Carbon quantification

Carbon quantification was done by calculating the quantity of food intake by counting the unconsumed *Artemia* and subtracting it from the total number of *Artemia* provided which was fed into each of the beakers every day. The *Artemia* nauplii used for hatching to feed the barnacles were from the same batch of cysts, and all were hatched for similar duration; it was assumed that they would have almost similar carbon. As single *Artemia* nauplius corresponds to ~ 0.52 µg C (Omori and Ikeda 1984), the total number of nauplii fed were multiplied by this factor to get the energy gained in terms of carbon and was expressed as microgram C assimilated.

Field observation of gonads

Studies on temporal variations in the ovarian development were carried out for the *B. amphitrite* population at Dona Paula bay from March 1997 to September 1999. Observations on gonads were taken every fortnight. Collection of the barnacles was done as solitary (having no other barnacle in the vicinity of 5–6 cm as cross-fertilization would not be possible) and crowded. Barnacles with ripe ovaries were measured for their size (RCD) before taking the observations on the status of the ovary.

Results

Breeding, molting and food consumption (Experiment 1)

Breeding

The paired individuals produced higher number of broods when compared to the solitary individuals at all temperatures and food concentrations (Fig. 1a–c). In the case of solitary individuals at 30°C, breeding was observed at all the food concentrations (Fig. 1c). In solitary individuals breeding interval was comparatively longer than the paired ones. For solitary individuals the maximum breeding interval was 43 days at 30°C (50 *Artemia* ind^{-1} day^{-1}; Fig. 1f), and the minimum interval was 19 days at 20°C (150 *Artemia* ind^{-1} day^{-1}; Fig. 1d). In case of paired individuals, an increase in food concentration resulted in an increase in the number of broods at almost all the temperatures (Fig. 1a–c). However, the maximum numbers of broods were observed at 20°C (Fig. 1a). Two-way ANOVA results indicated mode of occurrence as solitary, and paired individuals significantly influenced the breeding interval at 100, 150 and 200 *Artemia* ind^{-1} day^{-1} (Table 2). Similarly, temperature also significantly affected the breeding at all the food concentrations. Multiway ANOVA results for the influence of mode of occurrence, food concentration and temperature indicated that mode of occurrence as solitary, and paired individuals with respect to temperature significantly

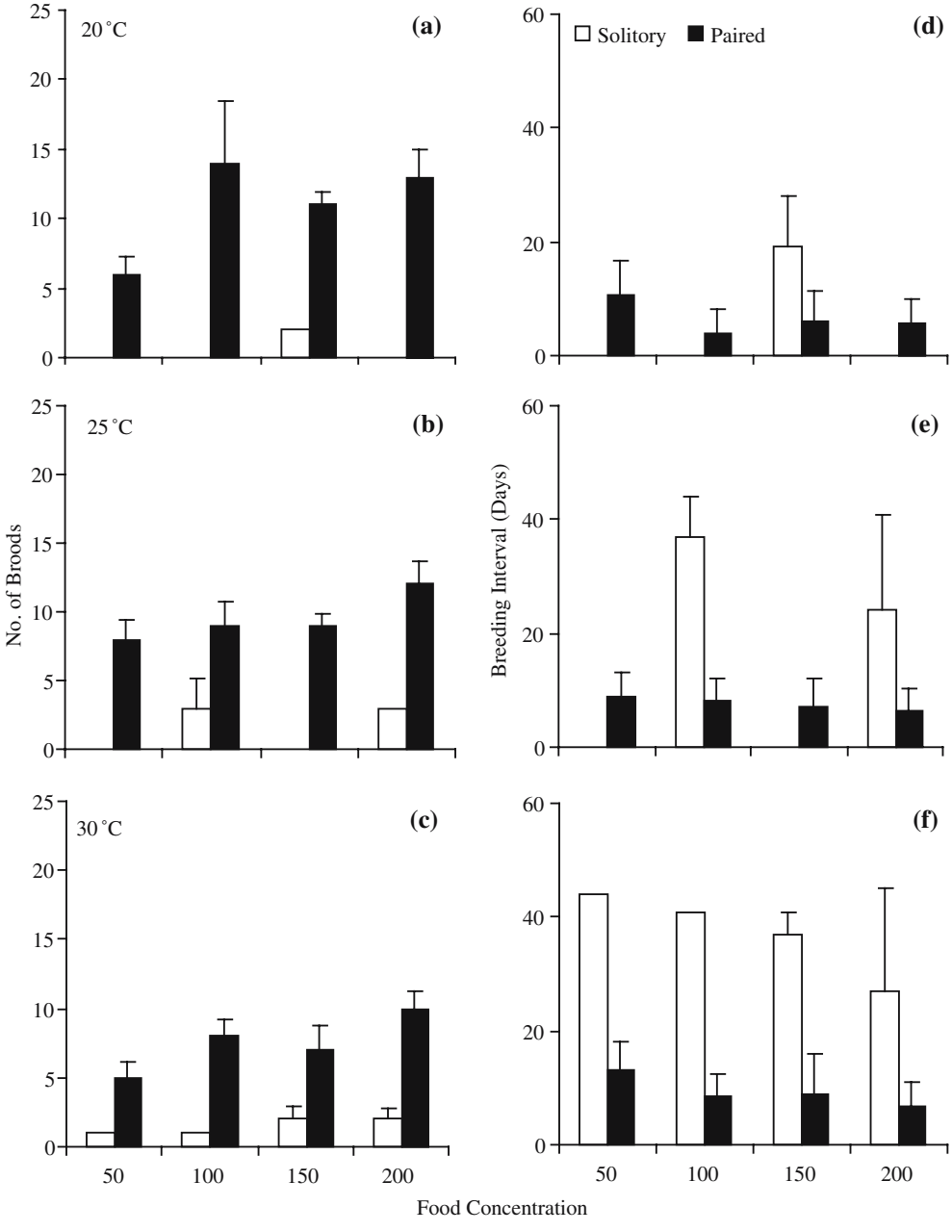

Fig. 1 Number of broods (**a**, **b**, **c**) and breeding interval (**d**, **e**, **f**) for barnacles reared at different temperatures and food concentrations for 75 days. *Vertical lines* indicate the standard deviation from the mean

affected the breeding interval ($P \leq 0.025$). The paired individuals released maximum number of larvae at 200 *Artemia* ind^{-1} day^{-1} at 30°C (Tables 1, 2). However, at 20 and 25°C at similar food concentrations, the number of larvae released was less (Table 1). A similar situation was evident at the other food concentrations (150, 100 and 50 *Artemia* ind^{-1} day^{-1}) at all of the temperatures (Table 1) except at 50 *Artemia* ind^{-1} day^{-1} at 20°C, where maximum larvae per brood were observed. In case of solitary individuals the maximum number of larvae (2,700 brood^{-1}) was released at 150 *Artemia* ind^{-1} day^{-1} (20°C) but no larvae were produced at the other food concentrations at this temperature (Table 1). At this temperature, the number of molts between the two broods was less compared to 25 and 30°C (Table 1).

Regression analysis between the numbers of larvae released versus the number of days (experimental schedule) for which the barnacles were raised indicated that the number of larvae released increased with the age of the barnacles. This increase was significant in the case of barnacles maintained at 30°C and fed with 150 ($m = 24.4$, $P \leq 0.02$) and 200 ($m = 37.5$, $P \leq 0.02$) *Artemia* ind^{-1} day^{-1}, and at 25°C fed with 200 ($m = 22.99$, $P \leq 0.01$) *Artemia* ind^{-1} day^{-1}.

Molting

The maximum number of molts was found at 30°C (Fig. 2c) and decreased with the decrease in the temperature (Fig. 2a, b); however, the number of molts increased with an increase in food concentration (from 50 to 200 *Artemia* ind^{-1} day^{-1}) irrespective of the rearing temperatures (Fig. 2a–c). In general, solitary individuals had less molts compared to paired individuals (Two-way ANOVA; $P \leq 0.025$). At 20°C, the molting interval was longer (two-way ANOVA; $P \leq 0.025$) (Fig. 2d) compared to 25 and 30°C (Fig. 2e, f). The results indicated a significant influence of temperature and mode of occurrence (solitary/paired) on the number of molts at all the food concentrations (Table 3); however, the interaction between mode of occurrence and temperature significantly influenced the molting at 100, 150 and 200 *Artemia* ind^{-1} day^{-1} (Table 3).

Table 1 Average carbon gained between successive breeding, average number of larvae produced per brood, average number of molts between successive breeding and total number of broods, larvae and molts produced at different temperature and food concentration by paired barnacles

	Food concentration	Carbon gained (μg C)	Number of larvae	Number of molts	Total number of broods	Total number of larvae	Total number of molts
Experiment 1	Observation for 75 days						
20°C	200	688 (± 356)	300 (± 250)	2 (± 1)	13	2,829	21
	150	479 (± 350)	500 (± 290)	2 (± 1)	11	4,556	17
	100	272 (± 200)	300 (± 225)	2 (± 1)	14	3,752	15
	50	255 (± 150)	1,500 (± 1,900)	2 (± 1)	6	9,290	12
25°C	200	603 (± 370)	800 (± 700)	2 (± 1)	12	8,935	23
	150	513 (± 380)	460 (± 260)	2 (± 1)	9	4,606	21
	100	392 (± 178)	1,300 (± 500)	2 (± 1)	9	12,005	17
	50	210 (± 108)	460 (± 350)	2 (± 1)	8	3,410	12
30°C	200	576 (± 335)	1,500 (± 1500)	3 (± 1)	10	14,585	28
	150	660 (± 556)	1,500 (± 750)	3.5 (± 2)	7	10,690	23
	100	400 (± 172)	1,400 (± 600)	2 (± 1)	8	11,585	22
	50	303 (± 147)	750 (± 760)	3 (± 1)	5	3,730	14
Experiment 2	Observation for 203 days						
30°C	200	808 (± 615)	1,700 (± 1,500)	4 (± 2)	23	34,700	70
	150	622 (± 350)	1,600 (± 1,700)	3 (± 2)	21	31,000	52
	100	424 (± 292)	1,300 (± 1,400)	4 (± 3)	19	21,850	60
	50	340 (± 400)	700 (± 600)	6 (± 5)	11	8,100	47

Numbers in the parenthesis indicate the standard deviation from the average

Table 2 Two-way ANOVA of the influence of temperature and mode of occurrence (solitary/paired individuals) on breeding interval at different food concentrations

Factor	50 *Artemia* ind^{-1} day^{-1}				100 *Artemia* ind^{-1} day^{-1}			150 *Artemia* ind^{-1} day^{-1}			200 *Artemia* ind^{-1} day^{-1}		
	df	SS	MS	Fs	SS	MS	Fs	SS	MS	Fs	SS	MS	Fs
A. (Solitary /paired)	1	57	57	4.1 NS	1,582	1,582	101*	586	586	273*	512	512	1,341*
B. Temperature	2	2,252	1,126	82*	1,744	872	56*	1,172	586	273*	701	351	919*
A × B	2	1,646	823	60*	1,336	668	43*	896	448	209*	614	307	805*
Within sub. Gr. err.	12	165	14		187	16		26	2.1		5	0.4	
Total	17	4,120			4,849			2,680			1,832		

df degrees of freedom, *SS* sum of squares, *MS* mean of squares, *Fs* Fischer constant, *NS* not significant
*$P \leq 0.001$

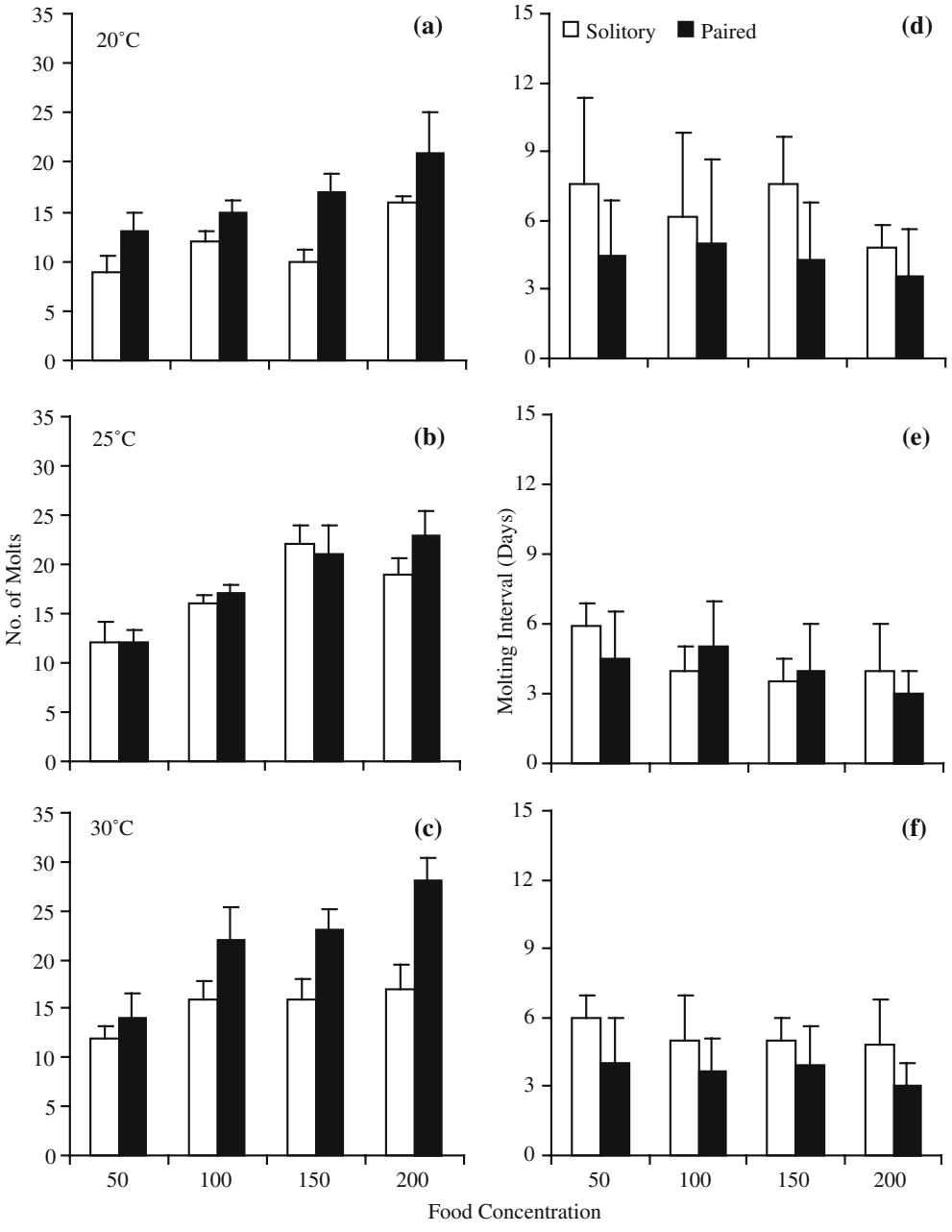

Fig. 2 Number of molts (**a**, **b**, **c**) and molting interval (**d**, **e**, **f**) for barnacles reared at different temperatures and food concentrations for 75 days. Vertical lines indicate the standard deviation from the mean

Table 3 Two-way ANOVA of the influence of temperature and mode of occurrence (solitary/paired individuals) on number of molts at different food concentrations

Factor	50 *Artemia* ind^{-1} day^{-1}				100 *Artemia* ind^{-1} day^{-1}			150 *Artemia* ind^{-1} day^{-1}			200 *Artemia* ind^{-1} day^{-1}		
	df	SS	MS	Fs	SS	MS	Fs	SS	MS	Fs	SS	MS	Fs
A. (Solitary/paired)	1	24	24	24*	8	8	8**	20	20	23*	168	168	189*
B. Temperature	2	13	6	6**	79	39	39*	119	60	67*	55	27	31*
A × B	2	7	3	3 NS	67	33	33*	119	60	67*	59	29	33*
Within sub. Gr.err.	12	12	1		12	1		11	1		11	1	
Total	17	56			166			269			293		

NS not significant
*$P \leq 0.001$; **$P \leq 0.025$

Food consumption

The food consumption rate was similar for both solitary and paired individuals at all the food concentrations. Feeding rate was not uniform throughout the experimental duration. At several instances, prior to/or during larval release there was a general decrease in the food consumption rate and this was more prominent at higher temperatures.

The number of larvae released and molts between successive breeding varied with the quantity of carbon gained through feeding (Table 1). The quantity of carbon gained between the successive broods was maximum at 200 *Artemia* ind^{-1} day^{-1} at 20°C (Table 1). At 20°C, maximum number of larvae was released at 50 *Artemia* ind^{-1} day^{-1} even though the carbon gained was more at 200 *Artemia* ind^{-1} day^{-1} (Table 1). It was observed that at 50 *Artemia* ind^{-1} day^{-1} six broods were produced; however, at 200 *Artemia* ind^{-1} day^{-1} it was 13 broods (Table 1). Regression analysis between the carbon gained versus number larvae and number of molts produced between successive breeding indicated a significant increase in the production of larvae and molts with an increase in the carbon gain and this was generally observed at higher food concentration (Table 4).

Breeding, molting and food consumption (Experiment 2)

Breeding

The observations on breeding for a longer duration (203 days) at 30°C indicated an increase in the breeding rate with an increase in the food concentration (two-way ANOVA; $P \leq 0.001$) (Fig. 3) and the results (Fig. 3a, c) were similar to those obtained in Experiment 1 (Fig. 1c, f). Regression analysis indicated a significant increase in the number of larvae released with the age of the barnacle (1–203 days) only at 200 *Artemia* ind^{-1} day^{-1} ($m = 10.854$, $P \leq 0.02$). The maximum numbers of larvae released were 7,000 brood^{-1} at 150 *Artemia* ind^{-1} day^{-1}. However in general, numbers of larvae released were more at 200 *Artemia* ind^{-1} day^{-1}.

Molting

The barnacles maintained for a longer duration (203 days) did not show any marked difference in the molting interval with reference to food concentration (Fig. 3b, d), and the interval was similar to that observed in Experiment 1; 30°C (75 days; Fig. 2f).

Production of molts was significantly influenced by the mode of occurrence and the food concentration (two-way ANOVA; $P \leq 0.01$). In case of paired individuals a maximum of 14 molts were observed at 50 *Artemia* ind^{-1} day^{-1} between two successive breeding (48 days interval), and the number of molts was less at higher food concentrations (Table 1; Experiment 2). While in the case of solitary individuals a maximum of 22 molts (90 days) were observed between successive breeding at 100 *Artemia* ind^{-1} day^{-1}.

Food consumption

The food consumption at all the concentrations was similar for both paired and solitary individuals. The results

Table 4 Regression analysis between the carbon gained versus number larvae and number of molts produced between successive breeding at different temperature and food concentration

	Food concentration	Number of larvae				Number of molts			
		m	*r*	*n*	*P*	*m*	*r*	*n*	*P*
Experiment 1	Observation for 75 days								
20°C	200	0.75	0.949	10	$P \leq 0.001$	0.005	0.45	10	NS
	150	0.71	0.84	9	$P \leq 0.01$	0.005	0.65	9	$P \leq 0.05$
	100	0.442	0.43	12	NS	0.002	0.47	11	NS
	50	10.22	0.772	6	$P \leq 0.05$	0.003	0.47	6	NS
25°C	200	1.11	0.704	11	$P \leq 0.01$	0.002	0.56	10	$P \leq 0.05$
	150	0.24	0.35	9	NS	0.002	0.84	9	$P \leq 0.01$
	100	1.95	0.607	9	$P \leq 0.05$	0.002	0.62	9	$P \leq 0.05$
	50	0.92	0.265	8	NS	0.004	0.706	6	NS
30°C	200	3.585	0.66	10	$P \leq 0.05$	0.002	0.6	9	$P \leq 0.05$
	150	0.999	0.723	7	$P \leq 0.05$	0.003	0.929	7	$P \leq 0.001$
	100	2.41	0.65	8	$P \leq 0.05$	0.002	0.524	8	NS
	50	1.432	0.278	5	NS	0.002	0.315	5	NS
Experiment 2	Observation for 203 days								
30°C	200	1.539	0.62	20	$P \leq 0.001$	0.003	0.739	20	$P \leq 0.001$
	150	2.426	0.5	20	$P \leq 0.02$	0.004	0.705	20	$P \leq 0.001$
	100	3.22	0.674	17	$P \leq 0.01$	0.007	0.7514	15	$P \leq 0.001$
	50	−0.692	0.481	11	NS	0.011	0.963	9	$P \leq 0.001$

NS not significant

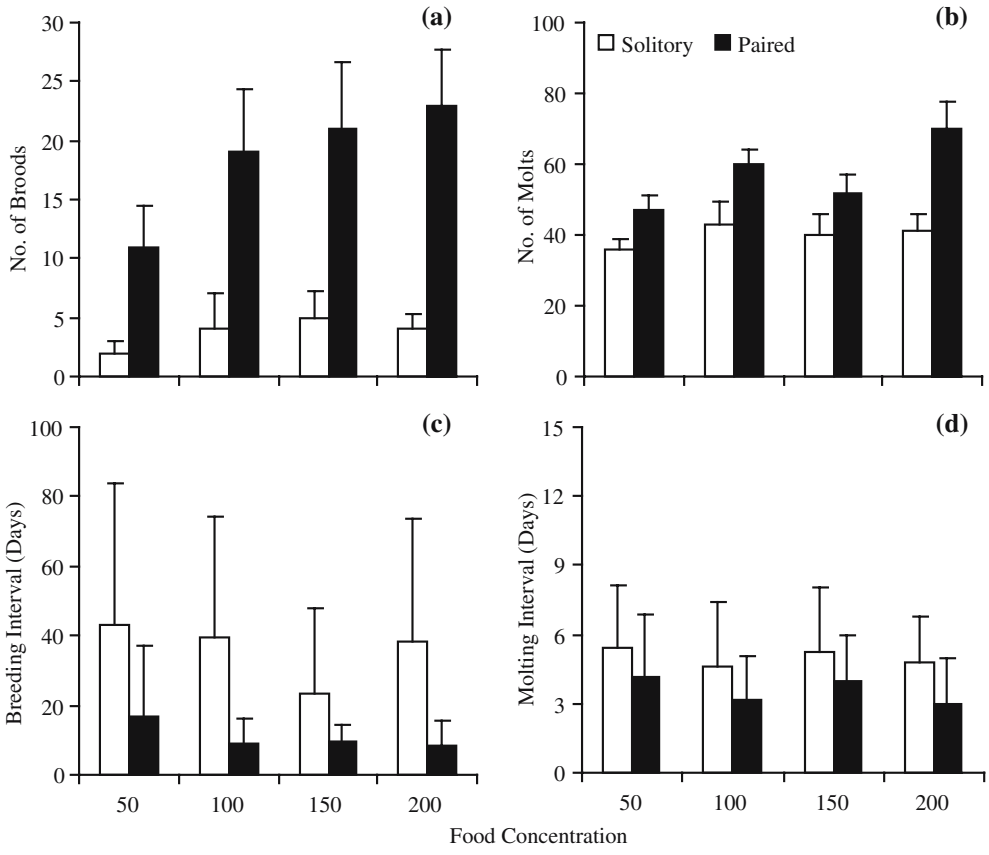

Fig. 3 Variations in **a** number of broods **b** number of molts **c** breeding interval **d** molting interval of the barnacles reared for 203 days at 30°C at different food concentrations. Vertical lines indicate the standard deviation from the mean

of the interbreeding carbon gain at different food concentrations indicated that it decreased with the food concentration (Table 1). Food concentration significantly influenced the breeding interval (two-way ANOVA; $P \leq 0.001$) (Fig. 3c) and also the numbers of larvae released were less (Table 1; Experiment 2). A significant increase in the number of molts and number of larvae was observed with an increase in the amount of carbon gain (Table 4; Experiment 2).

Breeding and molting (Experiment 3)

The observations on the breeding of barnacles raised in the laboratory indicated that in the case of solitary individuals the interval of self-fertilization was comparatively higher (Fig. 4c) than the barnacles used in Experiment 1 (collected from wild) (Fig. 1f). The breeding interval was 54 days for the laboratory-raised individuals and 43 days for the individuals collected from the field and kept solitary. However, in the case of paired individuals the breeding interval was slightly shorter compared to Experiment 1 (Figs. 4c, 1f). For the laboratory-reared barnacles in the case of paired individuals, the numbers of larvae released were more (3,000 brood^{-1}) compared to solitary individuals (one-way ANOVA; $P \leq 0.025$).

Barnacles raised in the laboratory from cyprids showed a shorter molting interval (2.7 ± 1.6 days; Fig. 3d) when compared to those individuals brought from the field (3.2 ± 1.9; Fig. 2f).

Field observations of gonads

Barnacles with ripe ovaries were found throughout the year; however, the percentage varied with the seasons (Fig. 5). The percentage of individuals with ripe ovaries was high during late post-monsoon and early pre-monsoon months. During monsoon months this percentage was low. Maximum percent of ripe ovary were found during December 1998 to March 1999 (50–37%) followed by December 1997 and January 1999 (31 and 33%). Percentage of ripe ovaries was minimum during late pre-monsoon (April and May; 1997: 4 and 9%, 1998: 12 and 17%, 1999: 9 and 8%) and early monsoon months (June and July; 1997: 14 and 18%, 1998: 4 and 0%, 1999: 12 and 7%).

It was observed that barnacles occurring as solitary individuals also showed ripe ovaries; however, their percentage was comparatively lower than those observed in pairs (one-way ANOVA; $P \leq 0.025$; Fig. 5). In summary, relatively high percent of ripe ovaries are found in pre-monsoon months (29–50%), while the rest of the months showed lower values (4–23%). It was observed that the average minimum size of individuals at which mature broods are produced varied with the seasons. It was 4.35 mm RCB in post-monsoon, 5.65 during monsoon

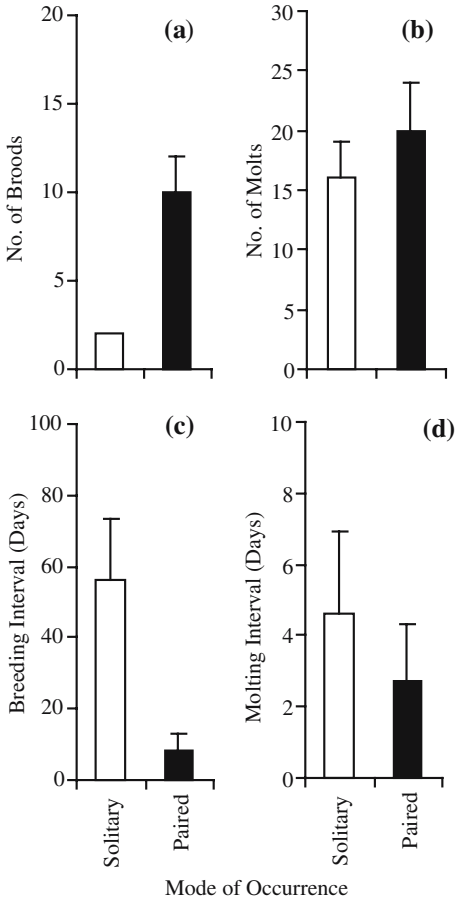

Fig. 4 Variations in **a** number of broods **b** number of molts **c** breeding interval **d** molting interval for the laboratory-raised *B. amphitrite*. *Vertical lines* indicate the standard deviation from the mean

and 6.3 mm RCB during pre-monsoon (Fig. 6). When the effect of temperature and chlorophyll on the size at maturity was analyzed, it was observed that during low temperature and high chlorophyll *a* content the size of the barnacles to produce mature broods was small (Fig. 6). Regression analysis indicated a significant decrease in the size at maturity of barnacles with an increase in the chlorophyll *a* content of the seawater (Fig. 7). The regression analysis between the temperature and the size at maturity of barnacles did not show a significant relation; however, it indicated an increase in size with rise in temperature (Fig. 7).

Discussion

Balanus amphitrite has euryhaline and eurythermal survival and breeding capability, and can breed at temperatures as low as 15°C (Crisp and Costlow 1963; Iwaki 1981; Anil 1991; Anil et al. 1995). In Indian waters, *B. amphitrite* breeds round the year (Karande 1965). Though exchange of sperm between adjacent individuals leading to cross-fertilization generally occurs as seen in the present study (El-Komi and Kajihara 1991) incidences of self-fertilization are also observed. The individuals that were kept solitary in this study released larvae. However, the breeding interval varied between the laboratory-raised and the field-collected individuals. The solitary individuals collected from the field showed ripe ovaries after an interval of 43 days, whereas this interval for laboratory-raised barnacles was 54 days. Such self-fertilization is stated to occur under circumstances when gametogenesis is completed without the occurrence of copulation (Barnes and Crisp 1956; Patel and Crisp 1961).

Molting was observed at all of the rearing temperatures and food concentrations. The number of molts was high at higher temperatures and food concentration, indicating that food concentration along with temperature affects the molting process. The breeding frequency also increased with an increase in food concentration; however, with an increase in temperature the breeding rate decreased. It has been shown that embryonic development is a function of temperature in several barnacles, *B. amphitrite* var. *denticulata*, *E. modestus*, *Semibalanus balanoides* (Crisp 1959; Patel and Crisp 1960a, b; Barnes 1963; Crisp and Costlow 1963). Thus, the nutritional condition and temperature seem to play an important role in the breeding and molting processes in barnacles.

While studying the energy budget in *Balanus glandula*, Wu and Levings (1978) reported a loss of a large quantum

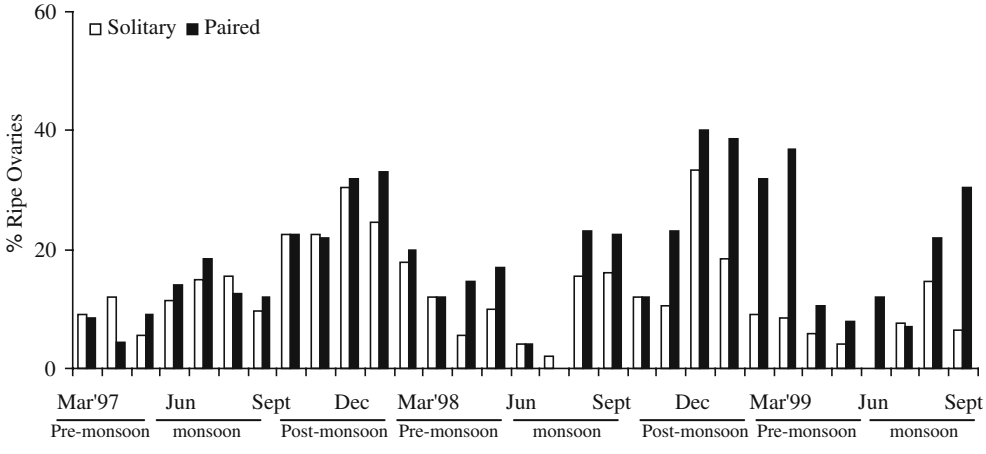

Fig. 5 Temporal variation in the percentage of barnacles (solitary and paired) with ripe ovary

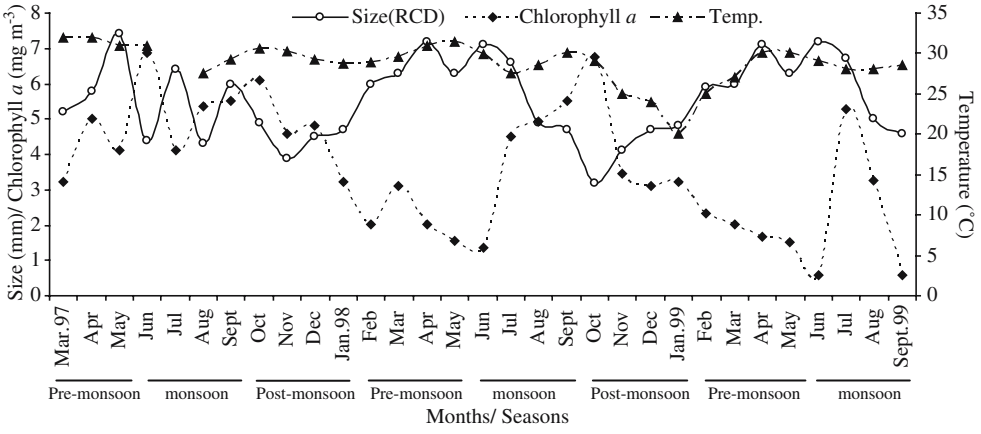

Fig. 6 Temporal variation in the average minimum size of barnacles with mature broods, chlorophyll *a* content and temperature of seawater. *RCD* Rostro Carinal Diameter

of energy in respiration, the second most important budget item was for egg production, followed in decreasing order by shell production, production of body tissue and molting. These observations indicate that the energy allocated for reproduction is less at higher temperatures and explain the faster breeding observed at lower temperatures in this study. In the present investigation it was observed that at lower temperature the carbon gained through feeding was greater compared to higher temperature. At 200 *Artemia* ind^{-1} day^{-1} the carbon gain was 688 µg C and they could produce 300 larvae. This translates to 2.3 µg C to produce single larva (and molt twice during the inter breeding period averaging to 6 days), whereas at 30°C, at similar food concentration, the carbon gain was 576 µg C, and could produce 1,500 larvae (fivefold more compared to 20°C) translating to 0.4 µg C per larva (and molt three times during the interbreeding period averaging to 7 days).

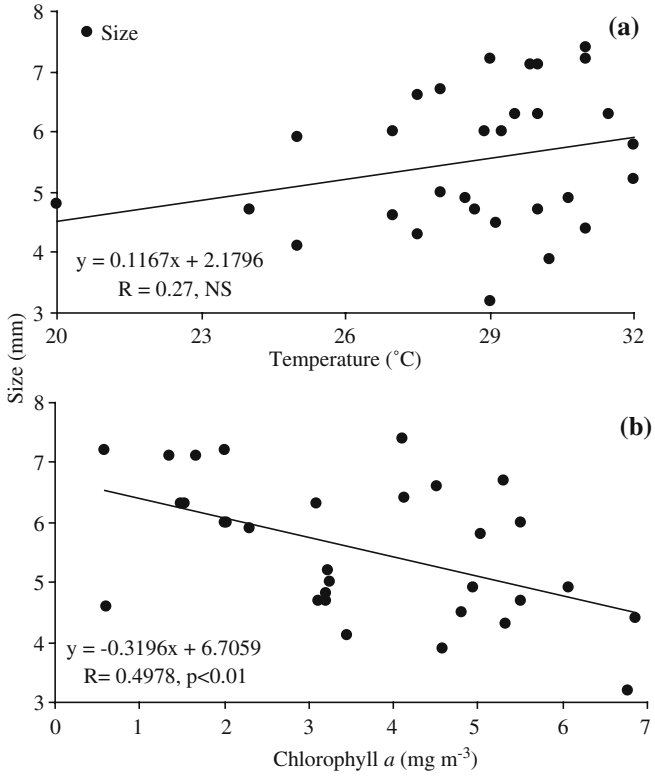

Fig. 7 Relationship between **a** seawater temperature **b** chlorophyll *a* content on the size at maturity of barnacles

Breeding potential at any given temperature was regulated by food concentration. At 20°C, more larvae were released at 50 *Artemia* (9290; Table 1) than at 200 *Artemia* ind^{-1} day^{-1} (2829; Table 1). However, the numbers of broods produced at higher food concentration were more. The release of more number of larvae at low food concentration can be attributed to the greater quantum of energy accumulated by the animal during the longer interbreeding interval. Thus, the longer breeding interval at the lower temperature may help the individuals to accumulate more energy through feeding, to produce more larvae. Such a phenomenon may be of importance to cold-water species to sustain the diversity by producing more larvae with less number of broods. It was observed for *S. balanoides* that the energy available for egg production is distributed among 4,000–10,000 small eggs approximately, according to the size of the adult, which hatch into planktotrophic nauplii. Egg size is a compromise between two extremes: the smaller the egg, the greater the fecundity, yet the greater its energy reserves, the greater its probability of survival (Crisp 1986).

It was observed at many instances that the liberation of brood is accompanied by a molt. The intermolt period of ovigerous barnacles is longer than the unfertilized ones owing to the presence of egg masses in the mantle cavity (Patel and Crisp 1961; Fyhn and Costlow 1977). Molting while embryos are present may therefore be disadvantageous. Thus, extending the intermolt period while the egg masses are developing minimizes the danger. Low molting and breeding was observed at 50 *Artemia* ind^{-1} day^{-1} food concentration; however, the maximum number of larvae was observed at this food concentration at 20°C. Hence, the decrease in molting can be attributed to the presence of egg masses in the mantle cavity, for which the animal may delay its molting.

It was observed that during or prior to larval release the feeding rate decreased indicated by the presence of more number of unconsumed *Artemia* nauplii. There could be two possible explanations: (1) there may be actual halting of feeding activity during breeding or prior to larval release, (2) the interval of observation period was 24 h and within this period, the adult could have fed on its own larvae. However, the incidence of reduced feeding, a day prior to the release of larvae indicates the earlier reason for reduced feeding a greater probability.

The observations on the gonad index of the field-collected *B. amphitrite* showed seasonal changes and also varied between solitary and crowded individuals. The percentage of ripe ovaries was low in solitary individuals when compared to those of the crowded ones. Low percentages of ripe ovaries were observed during monsoon season and can be attributed to low salinity. The study site being a tropical estuary receives comparatively large amount of fresh water run-off during monsoon season that lowers the salinity down to 4‰, and this could be a reason for low breeding in monsoon. Barnes (1989) also suggested that the effect of salinity on the breeding season is particularly important in estuarine habitats where fresh water run-off due to river discharge is excessive. Pillay and Nair (1972) indicated restricted brooding of *B. amphitrite communis* in the monsoon period and attributed this to low salinity and food availability. In cirripedes, those producing more than one brood per year, the time between the laying down of egg masses is important. In warm-water species, those producing several broods a year, and settling early in the year will reach maturity and they themselves reproduce during that year. Age can also affect the number of eggs/larvae produced by an adult. It was observed that the minimum size of adults at which mature broods (stage IV ovary) observed varied with the seasons. This size was minimum during post-monsoon, followed by monsoon and maximum during pre-monsoon. In general, the surface water temperature was slightly lower during post-monsoon months compared to pre-monsoon months; however, there is difference in the size at maturity of the individuals, indicating that temperature plays an important role in the growth and reproduction of this species. However, a significant decrease in the size at maturity of barnacles with an increase in the chlorophyll *a* content of seawater was observed. Inter-annual seasonal averages (March 1997–September 1999) showed that the size at maturity was minimum (4.35 mm) when chlorophyll *a* was 4.39 mg m^{-3} and temperature was 27°C in post-monsoon season and the average maximum size (6.3 mm) was during pre-monsoon season when chlorophyll *a* was 2.7 mg m^{-3} and temperature was 31°C. Earlier studies have reported that phytoplankton abundance is more during post-monsoon compared to other seasons at this study site (Patil 2003). It was observed that the minimum size at maturity of the laboratory-raised barnacle is 6.7 mm. The difference in the maturity size of laboratory-raised and the field-collected barnacles can be attributed to the available diet. Nichole (2005) suggested that growth of filter feeding benthic invertebrates (*Polycipes polymerus, B. glandula* and *Mytilus californianus*) to be largely dependent upon the productivity. Dattesh and Anil (2005) reported low growth rate of *B. amphitrite* during monsoon season compared to post- and pre-monsoon and correlated to low food availability during monsoons. In the laboratory they were raised with a monospecies animal diet (*Artemia* sp.), whereas in the field the adults are exposed to a mixed diet (phytoplankton and zooplankton) that could have possibly rendered faster growth and maturity. This indicates that the quality of food and seawater temperature determines the growth in this species and needs further validation.

Recently satellite-derived environmental data is used to forecast the climatic changes. Issues related to remote sensing of optically complex waters are frequently encountered, for example, in coastal regions and in lakes. Water masses of this kind are often designated as "Case 2" waters. It is generally recognized that Case 2 waters are more complex in their composition and optical properties and interpretation of optical signal from these water can therefore be rather difficult. To date, remote sensing of ocean color has focused largely on the relatively simple Case 1 waters, and it is well recognized that the standard algorithms in use today for chlorophyll retrieval from satellite data break down in Case 2 waters (Sathyendranath 2000). Observations of the present study showed a significant relation between the chlorophyll *a* values and the size of this barnacle species. With further refinement, the reproduction index and growth can be used as a proxy for changes in the environmental parameters.

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