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POPULATION BIOLOGY AND LARVAE OF THE ANCHIALINE CRAB *MUNIDOPSIS POLYMORPHA* (GALATHEIDAE) FROM LANZAROTE (CANARY ISLANDS)

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ABSTRACT

The galatheid *Munidopsis polymorpha* Koelbel, 1892, is found at high population density in an anchialine pool (Jameos del Agua) on Lanzarote. Ovigerous females on an average carry 1–4 eggs. Larval development is advanced. Only 2 zoeal stages, which are unable to undergo locomotion, precede molt to a small crab.

Munidopsis polymorpha is not preyed upon in the Jameos del Agua. Population density is regulated less by available food than by the number of available hiding places for resting phases. Population density is probably increased by the fact that the highly territorial crabs periodically alternate in feeding in the same grazing areas and in hiding. The percentage of ovigerous females and the average number of eggs per female is negatively correlated with the number of specimens per area.

During the years of investigation from 1976–1989, the number of ovigerous females and the average number of eggs per female have decreased considerably in parts of the pool. Consequently, the general population density has become drastically reduced. This is attributed to the construction and opening of the Jameos del Agua for tourism.

The island of Lanzarote (Canary Islands) possesses the longest known lava tube in the world. Originating at the volcano La Corona, the tunnel runs 7 km to the coast and continues below the sea for another 1.6 km. In the transition zone, an anchialine pool, the so-called Jameos del Agua, is formed (Wilkens and Parzefall, 1974; Iliffe *et al.*, 1984).

In this pool a series of more or less blind and unpigmented animal species can easily be observed, species which belong to the marine crevicular and ground-water fauna of Lanzarote (Harms, 1921; Fage and Monod, 1936; Iliffe *et al.*, 1984; Wilkens *et al.*, 1986). The most conspicuous and prominent species is the galatheid *Munidopsis polymorpha* Koelbel, 1892, which occurs at high population densities in the pool. This high density is made possible by two ceiling openings through which light penetrates and promotes a rich growth of diatoms, the basic food of *M. polymorpha* in the Jameos del Agua. Due to a high level of intraspecific aggressive behavior, the animals are distributed in a very regular pattern in the pool (Wilkens and Parzefall, 1974; Parzefall and Wilkens, 1975). Besides the rich food supply, the great number of specimens of *M. polymorpha* probably also results from the absence of species preying upon them (Harms, 1921; Fage and Monod, 1936; Wilkens and Parzefall, 1974; Garcia-Valdecasa Huelin, 1986). It is one of the purposes of these studies to evaluate the factors that regulate the population density of this anomuran crab in the pool.

About five years prior to the beginning of the following studies, the Jameos del Agua underwent construction and was opened for visitors. Therefore, it has been of further interest to analyze whether this unique ecosystem has suffered from any environmentally caused damage.

MATERIALS AND METHODS

The sampling sites were situated at the opposite ends of the anchialine pool. The Chico sampling site, which is located closer to the sea, covers the steep breakdown slope close to the Jameo Chico. It consists of large rocky boulders which enclose a system of rather large crevices. The Grande sampling site is situated in a rather flat area adjacent to the Jameo Grande breakdown. Here the ground consists mainly of gravel and small stones which leave only tiny crevices. This special situation provides for the occurrence of the amphipod *Liagoceradocus acutus* Andres, 1978, as well as for rich growth of some undetermined diatoms in the Grande region. A third sampling site was situated at the beginning of the seaward submerged lava tube. This so-called Inferior region is artificially illuminated during the day, resulting in a rich algal flora. Sampling for size measurement and sexing was performed from 0900–2200. Independently from this, 2 prominent rocks of approximately 0.25 m^2 were chosen, both in the Chico and the Grande region. On these 2 rocks the numbers of *M. polymorpha* were counted at 10-min intervals

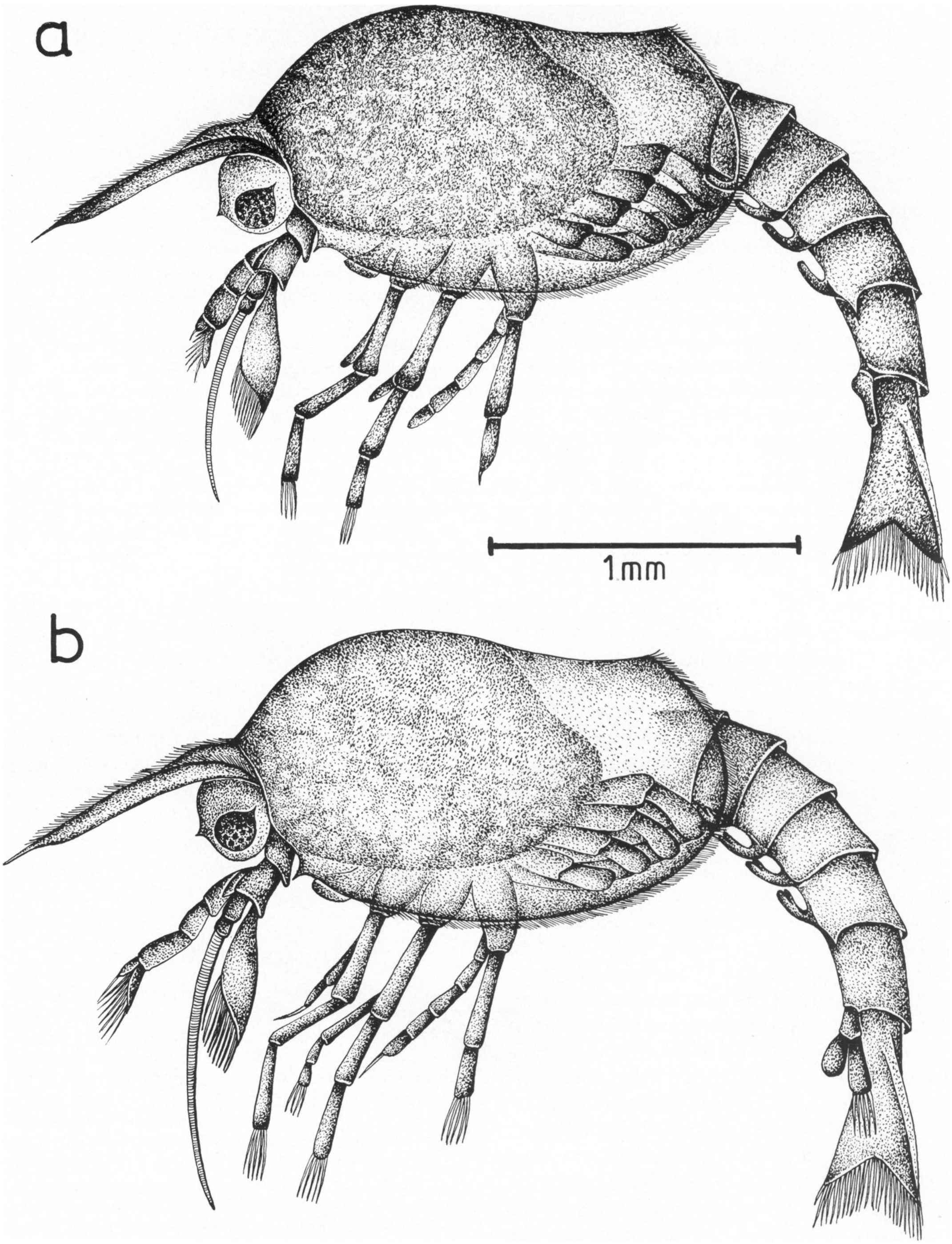

Fig. 1. *Munidopsis polymorpha.* a, first zoea; b, second zoea.

from late afternoon until darkness during 2–4 subsequent days in 1980, 1983, 1984, 1986, and 1989. During these counts the determination of sex and measurements were not made, since this would have disturbed the results. In almost all years the studies were performed in February or March. Only in 2 years observations in autumn (October) were possible.

The crabs were caught with a hand net fixed to a stick 2–3 m long. The length of the crabs (rostrum to telson) was measured in the Jameos del Agua. No spec-

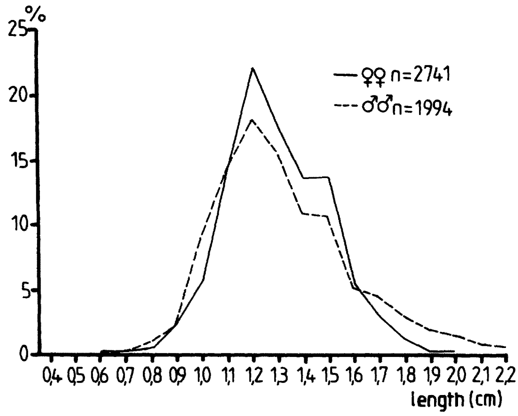

Fig. 2. Distribution of body size in *Munidopsis polymorpha.*

imen had to be killed for these studies and all were immediately set free in the middle of the pool. In order to obtain larvae, ovigerous females were kept isolated. The larvae were collected after they had dropped to the bottom and were taken into isolated glass jars for further development.

Student's *t*-test for independent samples was used.

RESULTS

Larval Development

The time necessary for the embryogenesis of *M. polymorpha* is unknown. Maternal care ends with hatching of the first larva, which is a zoea. After a further larval development of 10–14 days, it molts into a second zoea (Fig. 1a, b). First and second larvae are morphologically very similar, and about 3 mm in length. The eyes possess a cornea and are partly covered by the base of the large dorsally concave rostrum. The carapace is rounded and encloses the pereiopods, the first pair of which is chelate. The antennules, antennae, and the three maxillipeds are segmented and biramous. Differences between the two larval stages are mainly in the four pairs of pleopods which are unsegmented in both larvae but bilobed at least in the fourth pair in the second larva. Furthermore, the biramification of the uropods and the maxillipeds develops considerably in the second larva.

First and second larvae still possess a huge supply of yolk and do not feed. After hatching the first larva sinks to the bottom. Both stages are almost unable to undergo locomotion. Slight movement is achieved by beating the pleon with its large telson ventrally against the pereion. The exopodites of the maxillipeds whirl periodically, probably providing the larva with fresh water for respiration.

The first and second larvae of *M. polymorpha* are comparable to the first and second zoeae of *M. tridentata* (Esmark, 1857), as described by Sars (1890) and Samuelsen (1972). However, in contrast to *M. tridentata,* the subsequent development lacks further zoeal stages and the megalopa. Instead, after two to three weeks of development, the second zoea molts into a small crab, morphologically identical to the adult, but only 4 mm in length. The yolk is still not completely consumed. According to Gore (1979), larval development in *M. polymorpha* has to be classified as advanced.

Sex Ratio and Body Size

The population of *M. polymorpha* in the Jameos del Agua is characterized by a preponderance of female specimens. Only 42% of 4,735 crabs investigated were male.

The body length does not deviate statistically from normal distribution. Additionally, the male crabs grow a little longer (Fig. 2, Table 1). Body length was greatest in the Inferior sampling site. Between specimens from the Chico and the Grande regions a difference was not obvious (Table 1). The body lengths in the autumn did not differ

Table 1. Body size (cm) of adults of *Munidopsis polymorpha* at the different sampling sites (Chico, Grande, and Inferior).

	Males		Females	
	Mean ± SD	*N*	Mean ± SD	*N*
Chico	1.28 ± 0.22	772	1.27 ± 0.19	1,084
Grande	1.31 ± 0.27	1,012	1.28 ± 0.19	1,406
Inferior	1.56 ± 0.29	210	1.48 ± 0.20	251
Size difference ♂/♀	1.321 ± 0.267	1,994	1.294 ± 0.201	2,741
	$t = 3.961$; $P < 0.0001$			
Size difference Chico/Inferior	$t = 15.02$; $P < 0.0001$		$t = 16.04$; $P < 0.0001$	

Table 2. Body size of *Munidopsis polymorpha* in spring and autumn.

	Males		Females	
	Mean ± SD	N	Mean ± SD	N
Spring	1.32 ± 0.27	1,420	1.29 ± 0.20	1,840
Autumn	1.32 ± 0.27	574	1.30 ± 0.21	901

from those in spring (Table 2). Contrary to this, specimens caught in the morning were on the average slightly larger than those collected in the afternoon or in the evening (Table 3). Body size remained more or less unchanged during the first ten years of the investigation (Table 4). In 1989, however, the average size of male and female specimens was lower. This is a statistically significant difference from those of the preceding years (Table 4).

Number of Eggs and Fecundity

The reproduction time of *M. polymorpha* is not restricted to a single season, but takes place throughout the year. As in all species of this genus investigated (Gurney, 1942; Samuelsen, 1972), relatively large eggs are produced. They have a diameter of 1.2–1.3 mm and show yellowish coloration. Ovigerous females continuously clean their eggs with the fifth pair of pereiopods. The maximum number of simultaneously carried eggs is positively correlated with the size of the ovigerous females (Fig. 3). Eight to ten eggs may be found on the largest specimens. On the average, however, only 1–3 eggs are carried beneath the pleon (Fig. 4).

In spring as well as in autumn only some of the females were ovigerous. There is evidence that the proportion of egg-carrying females fluctuates seasonally. At least in 1976 and 1977, the percentage of ovigerous individuals was remarkably higher in autumn than ever observed in the respective localities during spring (Fig. 5). The percentage of ovigerous females differed between the Chico and the Grande sampling sites (Fig. 5). In the Chico region they fluctuated around 20% from 1976 until 1986. Contrary to this, the percentage was originally much higher in the Grande region. It is characteristic, however, that in the Grande sampling site a continuous decline has taken place. From 60% ovigerous specimens in 1976, a reduction to the level of the Chico sampling site of less than 20% was reached in 1984 and 1986 (Fig. 5, Tables 5, 6). In 1989 an increase of ovigerous females was observed both in the Chico and the Grande localities. In the Chico locality it became higher than ever found there before during spring, and was identical to the values of autumn 1976 and 1977.

When calculating the mean number of eggs per female of the sample, curves result which parallel those found for the proportional share of ovigerous females (Fig. 5). In the Chico locality the egg rate fluctuated between 0.4 and 0.6 per female. Only in 1989 a remarkable increase was observed. In the Grande locality the average rate was considerably higher in 1976 and 1978, but decreased in the following years. In 1983 the level of the Chico site was reached. Calculation of the average number of eggs per ovigerous female shows that in the Grande site a continuous decrease took place during

Table 3. Body size of *Munidopsis polymorpha* sampled in the sampling sites Chico and Grande at different times of day.

Time	Males		Females	
	Mean ± SD	N	Mean ± SD	N
0900–1400	1.32 ± 0.27	654	1.32 ± 0.21	1,171
1400–1800	1.30 ± 0.25	163	1.30 ± 0.20	293
1800–2000	1.28 ± 0.24	967	1.27 ± 0.19	1,277
Statistics				
0900–1400 versus 1800–2000	$t = 3.058$; $P < 0.005$		$t = 6.158$; $P < 0.001$	

Table 4. Body size of *Munidopsis polymorpha* in the years of investigation in the sampling sites Chico and Grande.

	Males		Females	
Years	Mean ± SD	*N*	Mean ± SD	*N*
1976	1.32 ± 0.26	324	1.28 ± 0.18	469
1977	1.28 ± 0.25	324	1.26 ± 0.20	523
1978	1.32 ± 0.25	218	1.28 ± 0.17	263
1980	1.33 ± 0.28	354	1.28 ± 0.19	408
1983	1.31 ± 0.24	273	1.31 ± 0.20	330
1984	1.31 ± 0.26	224	1.28 ± 0.19	287
1986	1.33 ± 0.27	89	1.24 ± 0.18	116
1989	1.19 ± 0.29	54	1.19 ± 0.21	94

Statistics of size difference:
1976–1986 versus 1989: $t = 4.786$; $P < 0.001$.
Mean = 1.286 ± 0.216 ($N = 4{,}216$) versus
mean = 1.191 ± 0.238 ($N = 148$).

the investigation period (Fig. 5). In the Chico site extreme oscillations developed. The average egg rate there was highest, while the percentage of ovigerous females was very low.

Population Density

Munidopsis polymorpha shows a negative phototactic behavior (Parzefall and Wilkens, 1975). Consequently, all observations between 1976 and 1986 revealed that the density of feeding specimens on the rocks and the substrate increased with decreasing light intensity in the evening. Originally at night parts of the pool were covered with maximum numbers of 150 crabs per m^2 (Wilkens and Parzefall, 1974) (Fig. 6a, b). In 1989 the density of crabs considerably decreased. In the Chico test area, for example, only two specimens were counted at 2000, where originally more than 30 had been found. Furthermore, contrary to results of previous studies, the number of grazing specimens no longer increased in the evening, and even decreased at night, although the light conditions had not changed. This decrease was confirmed by observations made between 2300 and 0200 (Fig. 6a, b).

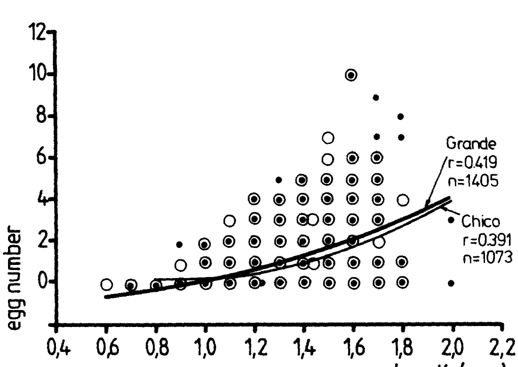

Fig. 3. Correlation between number of eggs and body size of ovigerous females of *Munidopsis polymorpha* (open circles = Grande, solid dots = Chico sampling site).

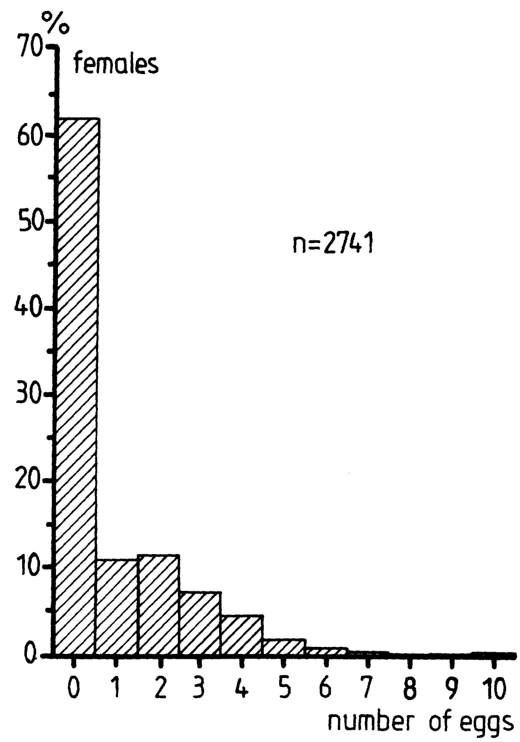

Fig. 4. Percentage of females of *Munidopsis polymorpha* carrying a specific number of eggs.

Discussion

These studies led us to hypothesize that observed population density in adult *M. polymorpha* is regulated by two factors, food supply and available hiding habitats. In the Chico site the number of ovigerous females as well as the egg number per female is lower than in the Grande locality during most years. The density of *M. polymorpha* is probably higher in the Chico region because of the greater number of hiding places. Due to the higher population density, less food is available there for an individual. In contrast, the Grande locality has fewer hiding places. Hence, the population density is

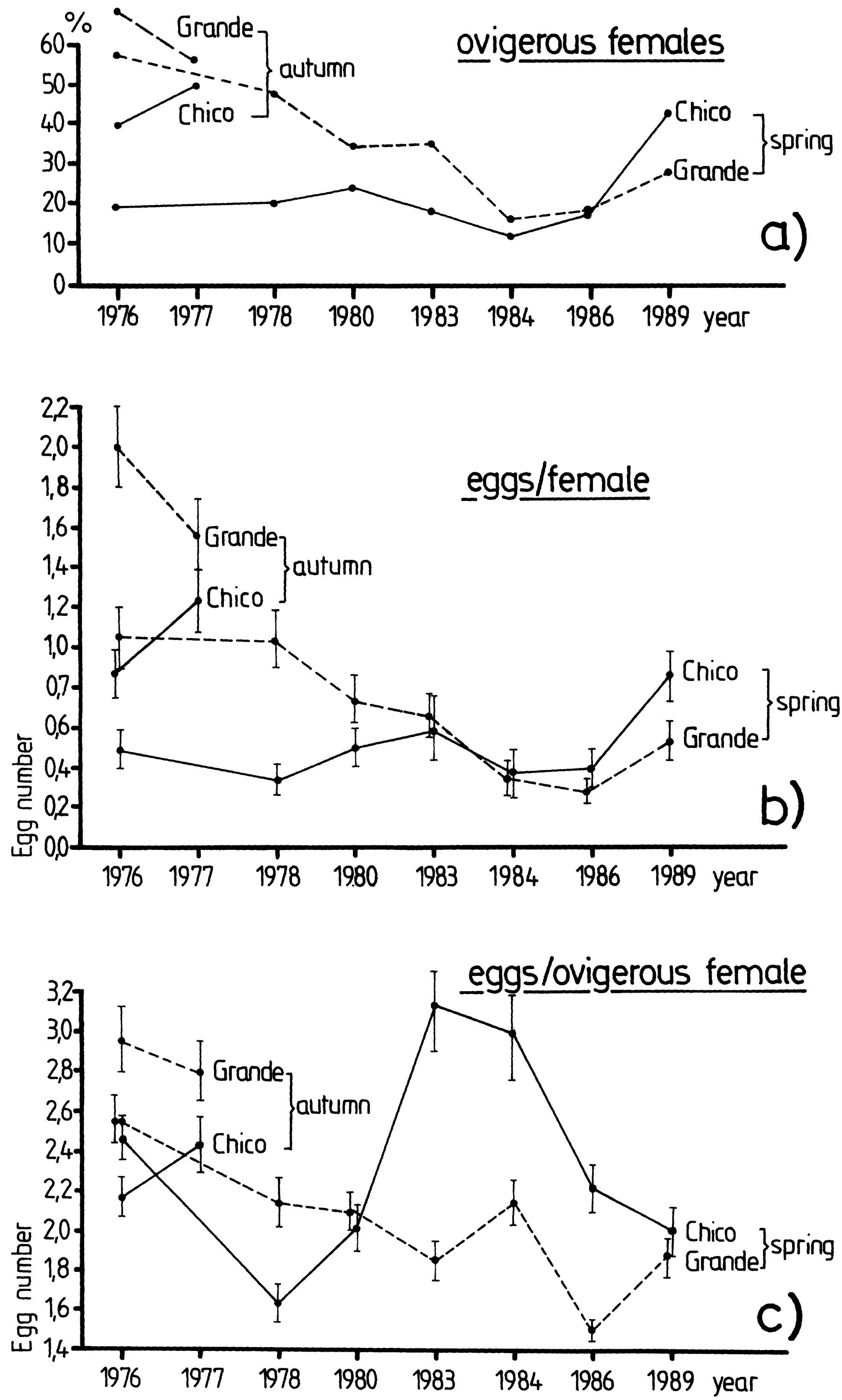

Fig. 5. Percentage of ovigerous females of *Munidopsis polymorpha* (a) and mean number and standard deviation of eggs in relation to the total number of sampled females (b) with respect to the ovigerous ones (c) in the Chico and Grande locality.

Table 5. Percentage of ovigerous females of *Munidopsis polymorpha* in the Chico (C) and Grande (G) sampling sites.

Year		Spring		Autumn	
		%	*N*	%	*N*
1976	C	19.82	111	40.00	105
	G	57.14	112	68.57	140
1977	C			49.78	231
	G			55.82	292
1978	C	20.34	118		
	G	48.28	145		
1980	C	24.50	151		
	G	34.55	246		
1983	C	18.62	145		
	G	35.14	185		
1984	C	12.20	123		
	G	16.50	164		
1986	C	17.30	52		
	G	18.80	64		
1989	C	43.20	37		
	G	28.10	57		

lower there and each individual can graze in a larger feeding territory. Additionally, the richer occurrence of some species of diatoms provides a better food supply.

The influence of food supply on egg number and percentage of ovigerous females could also be demonstrated by a seasonal fluctuation of these values. Both show an increase in autumn. This might be caused by the preceding sunny period enhancing the development of the algae. Contrary to this, reduced algal growth in winter might be hypothesized as the reason for a decrease of fecundity in spring.

Feeding activity seems to be rhythmic. This can be concluded from the observation that during different times of day the samples of feeding specimens show statistically different mean body sizes. From this it can be concluded that different individuals were active. Within a certain area individuals inhabit different hiding places while resting, but alternate in the same feeding territory. The rhythmic feeding and resting pattern was further confirmed by observations on the population density in special grazing areas in 1989. During their main activity at night the crabs fed for some hours, but then rather simultaneously retreated into the crevicular system.

This phenomenon of a rhythmic behavior did not become apparent at the beginning of these studies. At that time it was characteristic that all stones were continuously and densely populated at least at night. As explained, this was probably due to an alternating (rotating) interaction between feeding and resting individuals. However, under the recent conditions of low population density, gaps within the continuous

Table 6. Mean and standard deviation of number of eggs per female of *Munidopsis polymorpha* sampled in spring (* = sampled in autumn). C = Chico, G = Grande sampling site.

Year		Eggs per female		Eggs per ovigerous female	
		Mean ± SD	*N*	Mean ± SD	*N*
1976	C	0.49 ± 1.08	111	2.46 ± 1.01	22
	G	1.46 ± 1.59	83	2.56 ± 1.26	35
1976*	C	0.87 ± 1.25	99	2.17 ± 1.03	36
	G	2.03 ± 1.92	139	2.96 ± 1.62	95
1977*	C	1.21 ± 1.59	231	2.44 ± 1.45	115
	G	1.56 ± 1.80	292	2.80 ± 1.52	163
1978	C	0.33 ± 0.77	118	1.63 ± 0.92	24
	G	1.03 ± 1.38	145	2.14 ± 1.25	70
1980	C	0.50 ± 1.05	140	2.03 ± 1.13	26
	G	0.73 ± 1.19	246	2.11 ± 1.08	85
1983	C	0.59 ± 1.56	145	3.15 ± 2.25	27
	G	0.65 ± 1.09	185	1.85 ± 1.08	65
1984	C	0.37 ± 1.24	123	3.00 ± 2.24	15
	G	0.35 ± 0.91	164	2.15 ± 1.10	27
1986	C	0.39 ± 0.95	52	2.22 ± 1.09	9
	G	0.28 ± 0.63	64	1.50 ± 0.52	12
1989	C	0.87 ± 1.29	37	2.00 ± 1.27	16
	G	0.53 ± 1.00	57	1.88 ± 1.03	16

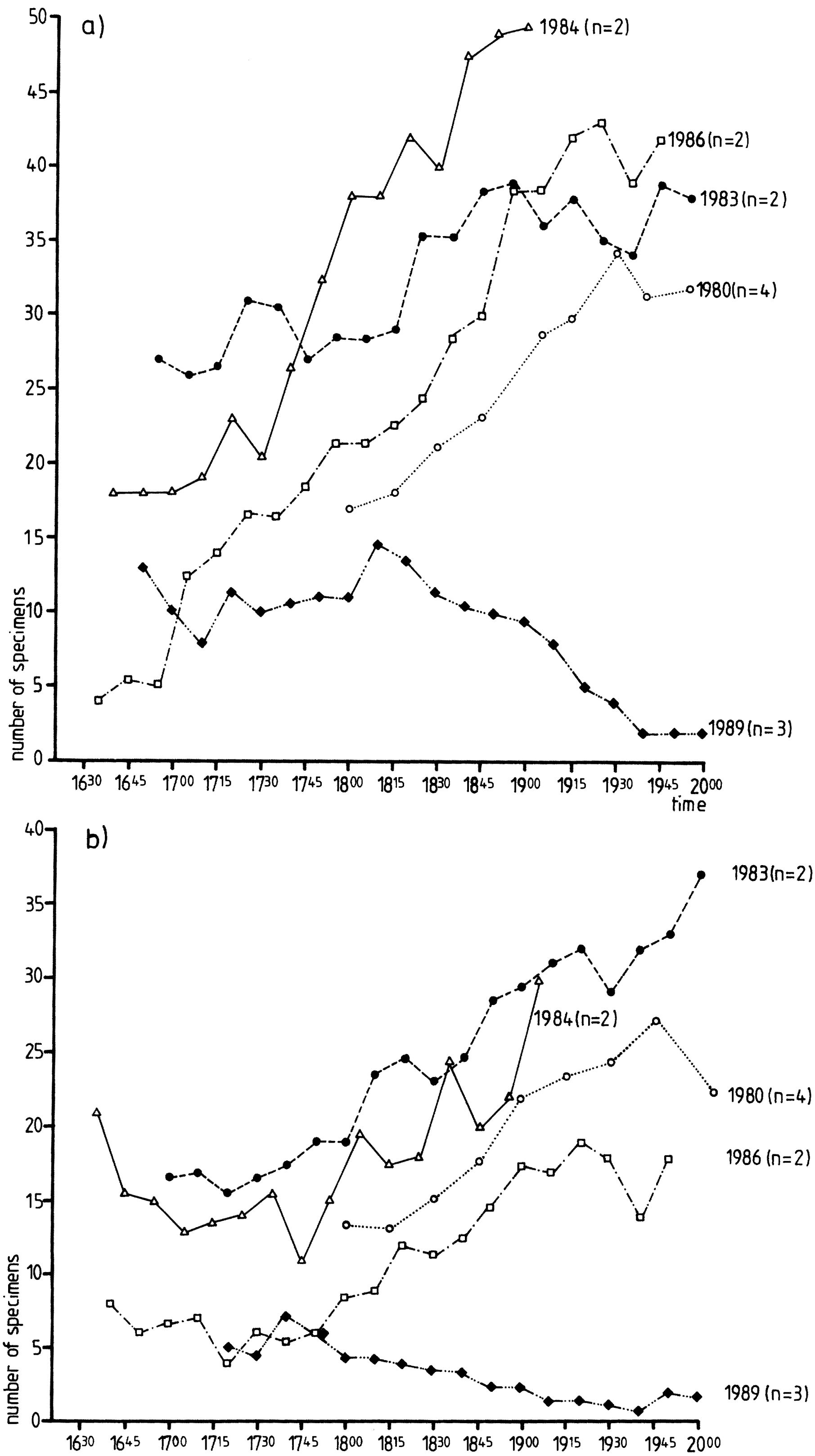

Fig. 6. Mean density of *Munidopsis polymorpha* within specific test areas, a, Chico region; b, Grande region. Test area = 0.25 m², n = number of observations. Observations made at 15-min intervals.

process of feeding specimens became visible.

The population of *M. polymorpha* in the Jameos del Agua has been subjected to deteriorating environmental influences since the time this pool was opened for visitors. The most obvious observation is that female fecundity has decreased by more than 50% in some parts of the pool. This has led to a continuous reduction of the originally extremely high population density. In 1989, for the first time, periods could be observed even at the nightly main activity time, during which almost no crabs were feeding. It can also not be excluded that the lower mean average body size found in 1989 is a result of the above-mentioned influences. It could be hypothesized that due to the above-mentioned environmental influences , the crabs no longer lived as long as in the original years and therefore are on the average smaller at present.

The increase of ovigerous females in 1989, however, might indicate that the environmental impact in the Jameos del Agua has relaxed at least to some extent. If this should be true, population density should again increase in the following years.

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