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How Salinity Changes in an Intertidal Zone May Affect Population Dynamics of *Littorina scabra* (Linaeus 1758) in Northern Coasts of Persian Gulf

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Abstract

The effects of salinity on the growth rate and survival of juvenile *Littorina scabra* gastropods reared in the laboratory from the young of young females collected in estuarine, intermediate, and marine habitats were studied. The optimum growth conditions of juveniles were dependent on the salinity regime in their original habitat. The young group of females from the marine site showed maximum survival at a salinity of 40‰, the value corresponding to the normal salinity in their native habitat during the breeding period, while at 30‰, the growth of juveniles from this population was strongly suppressed. Juveniles originating from the estuarine habitat were able to maintain equally high growth rates at 40 and 30‰; however, at 30‰, they grew significantly faster than juveniles from the marine site. The progeny of females from the intermediate habitat showed intermediate growth rates at 30‰. Fluctuating salinity (40–10–40‰) had an adverse effect on the growth of juvenile *Littorina*, irrespective of the parental habitat. The differences in survival, size, and growth rates of the progeny of *L. scabra* in habitats with different salinity regimes are discussed in relation to their potential adaptive significance to life in estuaries

Keywords: *Littorina scabra*, survival, salinity.

Introduction

In most organisms, all the early ontogenetic phases (embryos, larvae, and young) are critical (De Bruyne, 2003; Hughes, 1995; Kinne, 1971; Remane, and Schlieper, 1971) and salinity is among the most important environmental factors and exerts various effects on the vitality of marine organisms. It acquires particular importance in marine areas with unstable salinity regimes, such as river estuaries, salt marshes, etc. Only organisms with effective adaptations to unfavorable salinity can live in such habitats. In this case, the so-called critical phase of development, which is characterized by the smallest adaptive capabilities in respect to the unfavorable environmental factors, often plays a crucial role in the development of stable populations of a certain species and in their further survival. The gastropod mollusk *Littorina scraba* (Linnaeus 1758) is one of the basis of the estuarine intertidal fauna of the Persian gulf. The specific features of reproduction and life cycle in Littorinids (internal fertilization (within group), ovoviviparity, and the absence of free-swimming larvae), in combination with the low mobility of adults, provide a significant degree of isolation between populations located at distances of only several tens of meters from each other (Janson, 1983) and, therefore, renders impossible the survival of stable estuarine populations of this species based on larvae from elsewhere and the formation of pseudopopulations. These animals feed principally on algae and live in the intertidal zone of mud flats and rocky coasts, on rocks and among seaweed. The subfamily littorininae contains the majority of species. They occure in both warm and colder maritime environments (De Bruyne, 2003) It is evident that the estuarine populations of *L. scraba* are capable of reproduction within little communities; therefore, in all stages of ontogenesis, these animals should have effective adaptations against the unfavorable salinity regime of estuaries (Sokolova, 1995; Sokolova, 1997) Numerous studies on the responses of *L. scabra* to changes in environmental salinity provide evidence of the high degree of euryhalinity of adult Littorinids (Byrne *et al*., 1990). On the other hand, significantly less is known about the salinity adaptations of the early ontogenetic stages of this species (Byrne *et al*., 1990; Sokolova, 1997). The aim of this study was to study the effects of decreased and fluctuating salinities on the survival and growth rate of young *L.*

scabra immediately after transition to independent existence and to compare these parameters in animals from habitats with different salinity regimes.

Materials and Methods

Samples were collected during the first third of January 2010, *i.e*., the period when, in nature, the youngs of this species are already hatched (Hughes, 1978), in three populations of *L. scabra* located in the south coast of Queshm island (Figure 1):

(1) Estuarine population A located at the limit of *L. scabra* penetration into the coast of the Queshm city

(2) Intermediate population B where the effects of the freshwater river runoff from the Salakh

(3) Marine population C (Namakdan) from a habitat with normal salinity, where constant freshwater coastal runoff was absent.

To estimate the specific features of the salinity regime in these habitats, we used data on the changes in salinity over the course of one tidal cycle obtained in June-September 2009. Adult female *L. scraba* specimens were collected at the middle intertidal horizon, in the band of brown macrophyte *Fucus vesiculosus*, and were transferred to the laboratory, where they were maintained at a temperature of 10 to 15°C and salinity of 40‰ for 2–3 days. The size of sampled population was about 200 individuals in each point. The temperature at which they were acclimated in the laboratory corresponded to the water temperature in the natural periwinkle habitat at the time of sampling (10-15°C). The specimens were then dissected, and completely developed active young were isolated from their brood pouches. Altogether, 150 young specimens were obtained from 20–25 females in each of the examined populations. The size (shell diameter) of the mollusks was measured under a dissection microscope using an eyepiece graticule with an accuracy of 25 µm. The *L. scabra* youngs sampled from each of the populations were randomly divided into 3 groups of 50 specimens each. Each group was placed in a closed, well-aerated aquarium with stones covered with microalgal fouling. In our experiments, we used three salinity regimes: series 1, a stable salinity of 40‰; series 2, a stable salinity of 30‰; and series 3, a fluctuating salinity (for 4 hours a day, the mollusks were kept at 10‰, whereas the salinity was 40‰ throughout the rest of the day). The experiments were performed at a temperature of 10 to 15°C and constant illumination throughout the day, which corresponded to the natural light regime during the period of the experiment. Experimental cultivation of *L. scabra* showed that the mollusks are suppressed if kept constantly under water (Koehn and Bayne, 1989; Hughes, 1995). Therefore, at the same time every day, the water from the aquariums was removed and the mollusks were left without water for 4 hours. The humidity of the air in the aquariums remained sufficiently high throughout this period, and the mollusks remained active.

In the course of the experiment (79 days), we performed three surveys. All the mollusks were taken out of the experimental vessels and shell diameter was measured. Furthermore, we determined the number of dead mollusks, which were removed from the aquariums during each survey. The mortality of the young was calculated as a part of dead specimens collected throughout the period of the experiment. Proceeding from the results of four series of measurements (one at the beginning and one for each of the three surveys), we determined changes in mean shell size for each experimental group. This is considered below as the growth rate. The mean sizes of the young sampled from the brood pouch of the females and their survival under conditions of different salinity regimes were compared using standard statistical methods: a monofactorial

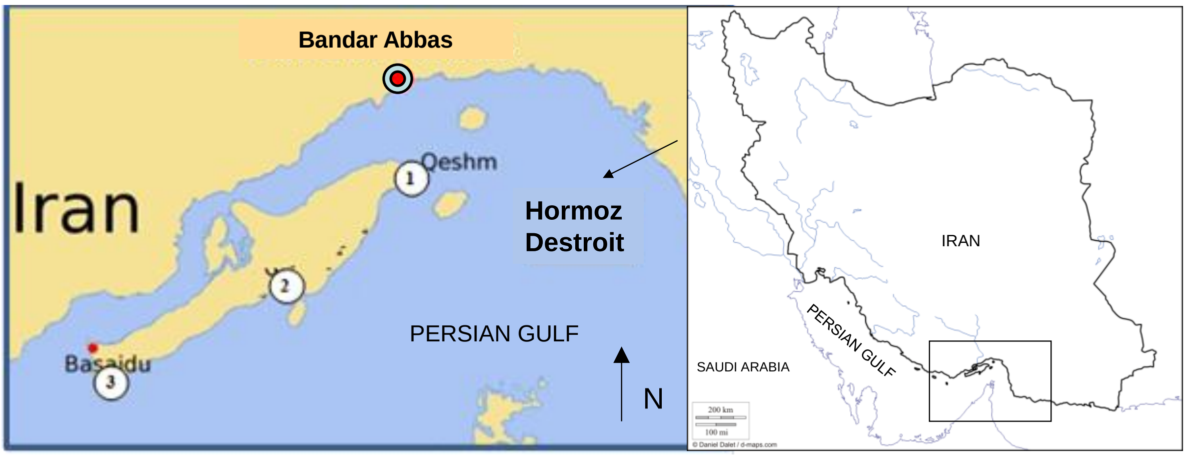

Figure 1. Queshm island location in Hormoz strait and three selected study stations. (1)Estuarine population A located at the limit of L. scabra penetration into the coast of the Queshm city. (2)Intermediate population B with the effects of the temporal freshwater runoff of the Salakh. (3)Marine population C (Namakdan) from a habitat with normal salinity, where constant freshwater coastal runoff was absent.

dispersion analysis (Model I ANOVA) and χ^2 criterion, respectively (Sokal and Rohlf, 1995; Warwick, 1983). The parameters of regression equations describing the growth rates in the Littorinids were calculated using the least-squares method (Sokal and Rohlf, 1995; Suissi-Ben, 2008). To compare the latter, we used Student's t-tests, with the modification of Urbakh (Urbakh, 1964).

Results

The measurements of salinity performed during one tidal cycle in all three surveyed populations confirmed the existence of significantly different salinity regimes at these points (Figure 1). In population A, the salinity was decreased throughout the tidal cycle and ranged from 5–6‰ at high tide to 1–3‰ at low tide. Synchronic conditions of decreased salinity and high tidal fluctuations were also recorded in population B, where, at different phases of the tidal cycle, it varied from 16–17 to 5–6‰. In population C, the salinity equaled 35–40‰ throughout the tidal cycle. These values correspond to the normal salinity of the surface waters of the Persian Gulf during the summer–autumn period (Kozminskii *et al*., 1995). During the experiment, the mortality of the young was recorded in all aquariums except for the sample from population C that was maintained under constant high salinity conditions (40‰) (Figure 2). The highest mortality of young from population C was recorded under conditions of constantly decreased salinity (30‰) ($P<0.05$). No significant, salinity-dependent differences in the mortality of *L. scabra* young from populations A were found. The survival of young from population C at a salinity of 40‰ was significantly greater than in the samples from the other two populations ($P<0.01$). No differences in survival were found between the samples from populations A and B. At 30‰, the survival of young was similar in the samples from all three examined populations ($P>0.05$). Under conditions of fluctuating salinity (40–10–40‰), statistically significant differences in mortality were only recorded in samples from populations C and A (10 and 40‰, respectively) ($P<0.05$). The young from population B were characterized by intermediate survival values. The size of the young sampled from the brood pouches of *L. scabra* differed in different populations ($P<0.05$). Our data, summarized for three series of experiments, show that the largest and the smallest mollusks were found in the brood pouches of females from populations A and C, respectively (704±77 and 577 ±46 µm, respectively). The young from the brood pouches of Littorinids from population B were intermediate in size (672±68 µm). Under constant high salinity conditions (40‰), the highest growth rate was found in the young from population C ($P<0.05$). The respective index for mollusks from populations A and B were of the same value. The differences in growth rate caused the initially existing differences in the size of young from different populations to disappear by the end of the experiment (Table 1, Figure 3a).

Under constantly decreased salinity (30‰), the growth rate of the young from all the surveyed populations showed significant differences (see table, Figure 3b). The highest and the lowest growth rates were found in the mollusks from population A and population C, respectively. Therefore, the initial differences in the size of young were not only maintained to the end of the experiment, but even increased. After 79 days of culturing, at a salinity of 30‰, the young from population A were the largest (1225±25 µm) and those from population C were the smallest (931±14 µm). The young from population B were intermediate in size (110±25 µm). Dispersion analysis showed the statistical significance of these differences ($P<0.05$). Under conditions of fluctuating salinity (40–10– 40‰), the growth rate of young in all three surveyed populations was the same ($P>0.05$)

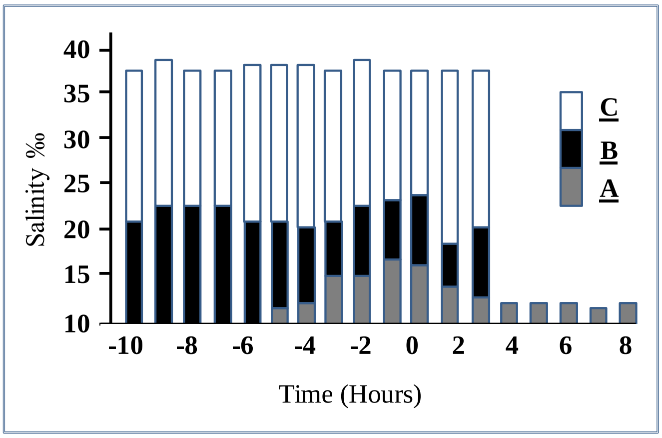

Figure 2. Salinity fluctuations in the surface water layer in the course of a semidiurnal tidal cycle in the area of surveyed populations of *L. scraba*; A, Queshm city; B: Salakh coast and C: Namakdan region marine population. The time is indicated relative to the moment of daily high tide (0 h is the high water point; –6 and +6 h are the low water points).

Table 1. Parameters of linear regression equations describing the dependence between the mean size of *L. scraba* youngs (µm) and the duration (days) of culturing at different salinities

population	Slope of curve µm. Day^{-1}	Crossing with the Y-axis, µm	Correlation coefficient	R^2, %	N
Salinity of40‰					
C	8.5a	593.9	0.960	92.2	196
B	6.9b	718.7	0.844	71.2	187
A	6.2b	743.4	0.797	63.5	193
Salinity of30‰					
C	4.6a	567.3	0.832	69.2	178
B	5.8b	665.2	0.835	69.7	210
A	7.1c	647.7	0.843	71.1	156
Salinity of 40–10–40‰					
C	4.4	577.7	0.841	70.7	196
B	4.3	669.2	0.778	60.5	201
A	4.0	729.7	0.767	58.8	175

N is the number of measurements of mollusks from four surveys. R^2 is the fraction of overall variability of the complex described by the linear regression model. The curve slopes marked by the same letters do not differ significantly within each salinity range at a 5% significance level.

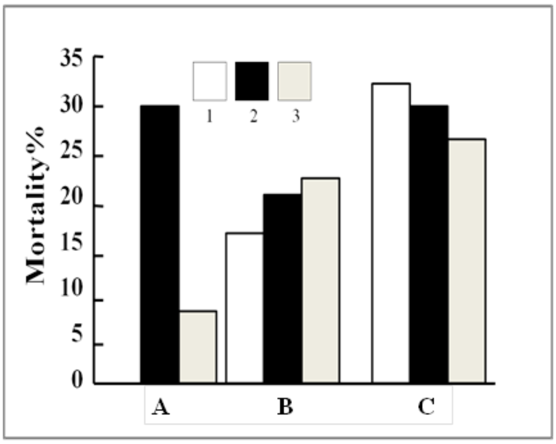

Figure 3. Mortality of L. scraba young from (A) estuarine, (B) intermediate, and (C) marine populations under conditions of different salinity regimes: (1) salinity of 40‰; (2) salinity of 30‰; (3) fluctuating salinity of 40–10–40‰. N=50 individuals

(see table, Figure 4c). Therefore, the differences in mean size of specimens from different populations recorded by the end of the experiment seemed to reflect initial size differences. Dispersion analysis showed that, by the end of the experiment, the mean shell diameter of the young from population C (927±19 µm) was significantly smaller than in samples from populations B and A (996±21 and 1022±21 µm, respectively). In general, (Table 1), the effects of the salinity regime on the growth rate of mollusks were different in different populations. The highest growth rate of Littorinids from population C was recorded at a salinity of 40‰. With a constantly decreased and fluctuating salinity, the growth rate was similar and significantly lower than at a salinity of 40‰ ($P<0.05$). In samples from population B, the young growth rates in the three series of experiments were significantly different from one another. The greatest shell increase was recorded at a constant salinity of 40‰; the smallest increase was observed under fluctuating salinity. The young from population A showed a similar growth rate at a constant salinity of 30 and 40‰ ($P>0.05$), and the growth of Littorinids from this population was significantly suppressed only under the fluctuating salinity regime ($P<0.05$).

Discussion

The studies of survival and growth rate of young *L. scraba* under conditions of different salinity regimes show significant interpopulation differences. The obtained data allow us to hypothesize that the optimum conditions for growth of *L. scabra* young correlate with the salinity regime in the habitats of the parental specimens. In the offspring of Littorinids from the marine population, the salinity in which the greatest growth rate and the lowest mortality was recorded is close to the natural environmental salinity in this habitat (35–40‰) during the summer–autumn period, when the young hatch in the natural populations of *L. scabra* in the Persian Gulf

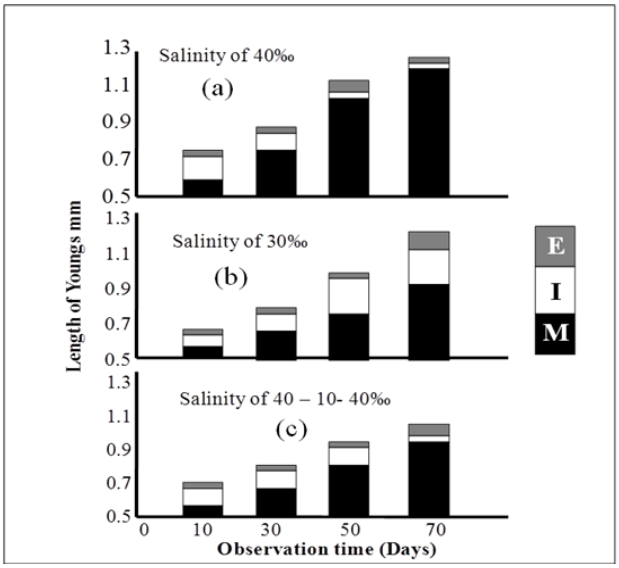

Figure 4. Growth rate of young L. scraba (a) Queshm city, (b) Salakh region, and (c) Namakdan populations under conditions of different salinity regimes. (a) Salinity of40‰; (b) salinity of 30‰; (c) fluctuating salinity of 40–10–40‰. the absence of the bars means that confidence interval values are smaller than the size of the mark.

(Kuznetsov and Matveeva 1948; Bjerregaard and Depledge, 1994; Sokolova, 1995). In this case, a constantly decreasing or a fluctuating salinity had equally harmful effects on the growth of young from this habitat. The mortality of the young from the marine population also increased under fluctuating and, especially, under constantly decreased salinity regimes. For Littorinids from the intermediate population, the salinity of 40‰ also appeared to be optimal. At a salinity of 30‰, the growth rate was somewhat decreased; however, the growth was suppressed to the maximum degree under conditions of fluctuating salinity. On the other hand, the growth rate in the offspring of females from the estuarine population was the same both at 40 and 30‰, and growth was significantly retarded only with sharp fluctuations of salinity. The mortality of young from the estuarine and intermediate populations in the experiment was not dependent on salinity regime and seemed to be related to some other factor, which we cannot reveal based on the results obtained. The unstable salinity regime appeared to be the least favorable for early growth in all the surveyed populations due to sharp drops and rises in salinity, which changed by 15‰ over a few seconds. Such an amplitude and rate of salinity fluctuation is too great to allow normal periwinkle growth. It is pertinent to note that, even in estuarine habitats, the range of tidal salinity fluctuations is significantly smaller (Figure 1). Thus, the growth rates of the offspring of Littorinids from different settlements differed significantly, even if the young were maintained at similar conditions for a long time (79 days), i.e., 6–8 times longer than necessary to complete acclimation to new salinity conditions (Janson, 1983). This suggests the existence of a genetic (or irreversible nongenetic) component in these differences. However, it is worth noting that the phenomenon of irreversible nongenetic adaptation seems to occur rarely in animals; only a few examples of nongenetic phenotypic changes arising in the course of ontogenesis under the influence of the environment have been described(Kinne, 1962; Suissi -Ben, 2008; Warwick, 1983; Wright and Mason, 1999). Therefore, at present, the genetic component of the growth rate seems to be the most probable explanation for the stable differences in this index in Littorinids from habitats with different salinity regimes. The assumption about the existence of a significant genetic component in the interpopulation variability of growth rate in *L. scabra* has already been advanced by different authors when studying the growth of Littorinids of the Persian Gulf (Behrens Yamada, 1987; Janson, 1982; Janson, 1983). In general, the data about the growth rate of young under conditions of different salinity regimes allow us to hypothesize that the offspring of Littorinids from estuarine populations in the early stages of ontogenesis already possess adaptations that facilitate their rapid growth under conditions of decreased salinity. It seems that a high growth rate, combined with the larger size of the young by the moment of transition to independent existence, might be of adaptive value for the estuarine populations of Littorinids. It is known that salinity resistance depends on periwinkle size: the smaller specimens are less effective in sealing the mantle cavity and show increased mortality under conditions of extremely low salinity (Behrens Yamada, 1987; Berry and Hunt, 1980; Hughes, 1978). This dependence is clearly pronounced before the animal attains maturity. After a certain critical age is reached, no size-dependent differences in tolerance are revealed (Byrne *et al*., 1990; Koehn and Bayne, 1989). Thus, the larger initial size of *L. scabra* young and their relatively high growth rate might be of crucial importance in estuaries, allowing greater survivorship. These animals rapidly attain a critical size when the tolerance against the unfavorable effects of salinity is the greatest (Suissi -Ben, 2008; Zamer and Mangum, 1979). It is pertinent to note that the increase in size of the youngs in the brood pouches of Littorinids has also been recorded in populations from the estuaries and salt marshes of the North Atlantic (Hughes, 1978, 1995; Roberts and Hughes, 1980; Ross and Berry, 1991). However, in the framework of this study, potentially adaptive interpopulation differences in the growth rate of young under conditions of different salinity regimes have been studied and experimentally proven for the first time.

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