ORIGINAL ARTICLE

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Potential effects of physiological plastic responses to salinity on population networks of the estuarine crab *Chasmagnathus granulata*

Abstract *Chasmagnathus granulata* is a South American crab occurring in estuarine salt marshes of the Brazilian, Uruguayan and Argentine coasts. Life history is characterized by an export strategy of its larval stages. I reviewed information on experimental manipulation of salinity during embryonic and larval development (pre- and posthatching salinities), and on habitat characteristics of *C. granulata* in order to determine potential effects of larval response to salinity in the field and to suggest consequences for the population structure. Local populations are spread over coastal areas with different physical characteristics. Benthic phases occupy estuaries characterized by different patterns of salinity variation, and release larvae to coastal waters characterized by strong salinity gradients. The zoea 1 of *C. granulata* showed a strong acclimatory response to low salinity. This response operated only during the first weeks of development (during zoeae 1 and 2) since subsequent larval survival at low posthatching salinities was consistently low. Larvae developing at low salinity frequently followed a developmental pathway with five instead of four zoeal stages. The ability to acclimate and the variability in larval development (i.e. the existence of alternative developmental pathways) could be interpreted as a strategy to buffer environmental variability at spatial scales of local or population networks. Early survivorship and production of larvae may be relatively high across a rather wide range of variability in salinity (5–32‰). Plastic responses to low salinity would there-

fore contribute to maintain a certain degree of population connectivity and persistence regardless of habitat heterogeneity.

Keywords Crab · Invertebrate · Larvae · Population · Plasticity · Uruguay

Introduction

Estuarine crabs show a highly patchy distribution at large scales. Juveniles and adults inhabit estuarine sandflats, salt marshes, or mangroves, but do not occupy other habitats, such as oceanic beaches or rocky shores. Although benthic phases distribute in isolated patches, connection among them may be ensured through larval migration. Depending on peculiarities of life history, the spatial scale at which local population processes take place varies from one species to another. For instance, the larvae of the estuarine crabs *Callinectes sapidus* (McConaugha 1988; Prager 1996) and *Chasmagnathus granulata* develop in coastal waters, with the megalopa reinvading the estuarine habitats. Growth and reproduction occur in the estuarine habitat (D'Incao et al. 1992; Anger et al. 1994; Stella et al. 1996; Pile et al. 1996; Tankersley et al. 1998). Larvae are thus exported from estuarine waters, and although they may be retained in continental shelf waters, they may be spread over tens to hundreds of kilometres along the coastline. As a consequence local population processes take place at large spatial scales that include a single larval pool supplying individuals to several estuaries. For species such as *Rhithropanopeus harrisi*, whose larvae are retained in estuarine waters (Cronin 1982; Morgan 1987) or *Armases miersii*, which develop in supratidal pools (Anger 1995), local population processes occur at smaller scales, perhaps leading to an isolation of larval pools.

Several species of estuarine crabs are distributed over several thousands of kilometres. For instance, *Callinectes sapidus* can be found from Nova Scotia to Uruguay (Rugolo et al. 1998); *Chasmagnathus granulata* is dis-

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tributed over a coastal area of about 4,000 km of extension, from Cabo Frío, Brazil (21°S) to Gulf of San Matías, Argentina (43°S) (Boschi 1964; Spivak 1997). A first consequence of such a widespread distribution is that there may be more than a single larval pool within the area of distribution. Duration of larval development restricts transport to a period of about 3–6 weeks (see Ismael et al. 1997 for *Chasmagnathus granulata*; Epifanio 1995 for *Callinectes sapidus*). Larvae may be retained within the bounds of mesoscale coastal oceanographic structures (see Roman and Boicurt 1999; Epifanio and Garvine 2000; Natunewicz et al. 2001 for *Callinectes sapidus*). Hence, at the largest scale, species may form one or more networks of local populations, each one consisting of a set of estuarine habitats harbouring juveniles, adults, and embryos (the benthic component) and a coastal cell containing the larval pool (pelagic component). Population networks of estuarine crabs may arise through occasional larval migration among pools; otherwise they should be considered either as isolated populations (no migration between larval pools) or a large heterogeneous population (permanent migration). Such population networks may be common in species with export strategies but rare in those with larvae retained within the estuaries.

A second consequence of a widespread distribution is that the benthic component of a local population or a population network most probably occupies a diverse collection of estuarine habitats varying in size and quality. Habitat quality in estuaries may be defined by various factors such as vegetation, sediment type, food availability, temperature and salinity. Salinity is one of the key variables characterizing estuarine environments and affecting species distribution (Kinne 1971). Variability in salinity may also affect estuarine populations throughout effect on survival or growth rate (see Costlow et al. 1960, 1962; Anger et al. 1990 for effects of salinity on larval survival) depending on their degree of tolerance to osmotic stress.

Here, I will discuss how osmotic stress and adaptations to variable environments may affect structure of population networks of estuarine crabs through effects on recruitment, and thus connectivity and mortality rate, among local benthic habitats or populations. Connectivity is one of the important issues for how species are organized in local populations or higher-level structures. If connectivity among larval pools is too low or absent, a species is organized in a collection of isolated local populations. After an event of local extinction, the probability of recolonization from adjacent larval pools may be too low. Under high levels of connectivity, several pools may fuse into a single one, connecting benthic components permanently. Under intermediate levels of connectivity a population network may arise, with a reduced but still important level of migration of larvae between adjacent larval pools. This level of connectivity will ensure recolonization after local extinction, but some degree of independence of local population dynamics. If local populations are not large, a metapopu-
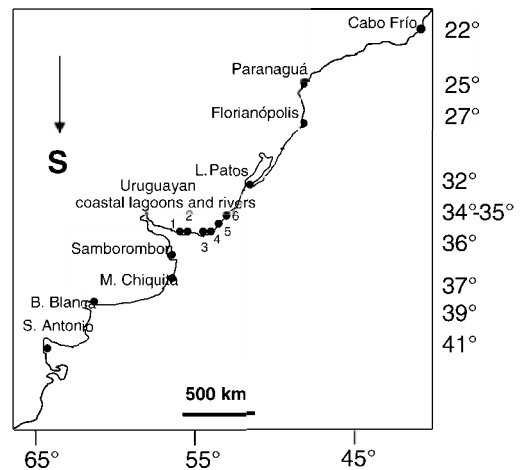

Fig. 1 *Chasmagnathus granulata*. Geographical location and latitude of estuarine habitats along the Atlantic coast of South America, occupied by adults (source: Boschi 1964; Bier 1985; Cardezo 1989; Jorcín 1993; Spivak 1997; L. Giménez, personal observation). Uruguayan sites are *1* Santa Lucía, *2* Solís Grande and Solís Chico, *3* Maldonado (rivers and flows), *4* José Ignasio and Garzón, *5* Rocha, *6* Balizas-Castillos (lagoons)

lation structure should arise. Thus, I discuss (1) recent information on adaptations of the estuarine crab *Chasmagnathus granulata* to cope with salinity stress, and (2) some information about the physical characteristics of coastal waters on the Atlantic coast of South America.

Environmental conditions for survival and distribution of *Chasmagnathus granulata*

As mentioned above, *Chasmagnathus granulata* is an estuarine crab common on the Atlantic coast of South America (Fig. 1). Larvae are exported to the open sea and development occurs through either four or five zoeal stages and a megalopa. The reproductive cycle is seasonal (Spivak et al. 1996), with females breeding from spring (October) to autumn (March); females produce 19,000–80,000 eggs (Ruffino et al. 1994; Stella et al. 1996; Luppi et al. 1997). Larval release starts in spring and continues through summer until autumn. Recruitment maxima occur from summer (February) to the end of winter (August); few individuals recruit in spring (Luppi 1999). There is no information about larval transport and dispersal in open waters. Larvae may be retained within continental-shelf waters, leading to a variable number of larval pools (Fig. 2) depending on oceanographic conditions. Larval transport may be mainly affected by buoyancy and wind forcing, as in *Callinectes sapidus* (Natunewicz et al. 2001). Thus, larvae should remain within estuarine plumes, as that of Río de la Plata or coastal lagoons, retained near the coast by onshore wind-driven currents, such as those existing along the coast (Piola et al. 1999), or by fronts, such as those of the North Patagonian shelf (Bakun and Parrish 1991). Larval pools may be structured as a single patch or a col-
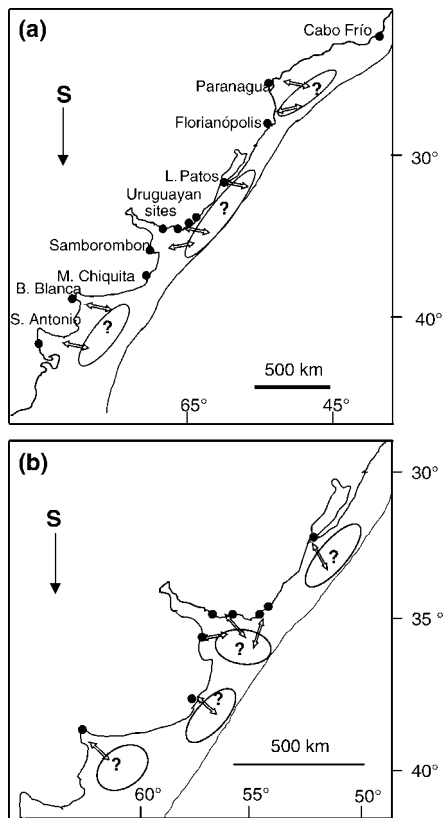
Fig. 2a, b *Chasmagnathus granulata.* Two possible scenarios for occurrence and distribution of larval pools (*ovals containing question marks*). These are either: **a** a few larval pools of several hundred kilometres' extension in the longshore axis; or **b** many larval pools (only the southern sector of the area of distribution is shown) of several tens of kilometres of extension. *Arrows* show presumed exchange of larvae between continental shelf and rivers or coastal lagoons

Fig. 3 *Chasmagnathus granulata.* Mean salinities experienced by larvae released to coastal waters in Río de la Plata and adjacent shelf areas (sources: Mazzetta and Gascue 1995; Guerrero et al. 1997). *Arrows* show expected area of larval release from Rocha, Valizas Castillos and Mar Chiquita lagoons, Maldonado, and Solís Chico flows, Santa Lucía river and Samborombon Bay

lection of patches of larvae resembling those of *Callinectes sapidus* (Natunewicz and Epifanio 2001; Natunewicz et al. 2001).

Information on physical oceanography (Guerrero et al. 1997) clearly shows that larvae of *Chasmagnathus granulata* are released into estuarine waters with high temporal and spatial variability in salinity. Temporal changes in the timing of larval release will lead to larvae experiencing different osmotic conditions. In estuarine environments salinity changes at hourly (e.g. Mar Chiquita lagoon: Anger et al. 1994), daily (e.g. Solís Grande river: Calliari et al. 2001), and monthly (e.g. Rocha lagoon: Conde et al. 1999), or longer (e.g. Uruguayan coast: Mazzetta and Gascue 1995) time scales (see Fig. 3 for location of sites). Besides, spatial gradients of salinity characterize the sites of larval release. Larvae from different estuaries are therefore released under different salinity conditions. For instance, zoeae 1 released at Santa Lucía river (Fig. 3) should be transported to Río de la Plata and, at least temporarily, exposed to low salinities (5–15‰). However, those released in Mar Chiquita lagoon should be immediately transported to coastal
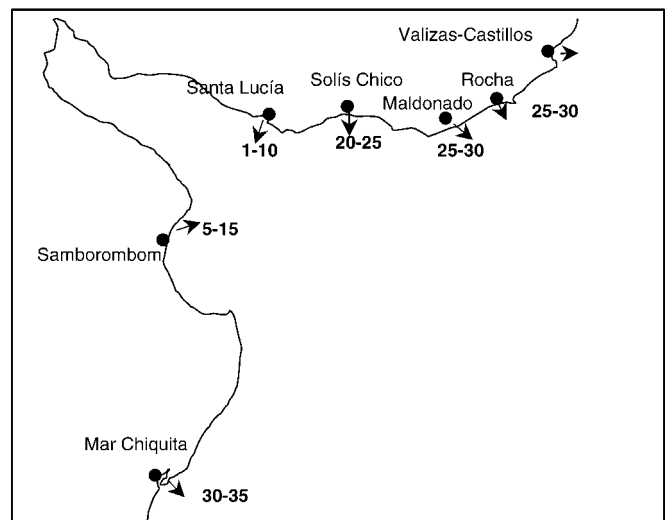
waters (Anger et al. 1994) with salinities of about 34‰. There are additional sources of variability in salinity: some coastal lagoons (e.g. Rocha, Valizas-Castillos, Garzón) have an intermittent connection with the open sea, i.e. sand bars temporarily obstruct the inlet of the lagoons. Several periods of isolation and connection may occur within a year, lasting from days to months, depending on freshwater discharge, wind direction, and other factors. During the periods of isolation, freshwater tends to accumulate, leading to a decrease in salinity until the breakage of the sand bar. After water discharge, a period of intrusion of seawater may occur, leading to an increase in salinity within the lagoon (Conde et al. 1999). When lagoons are isolated, larvae must face osmotic stress, while in other habitats, at the same time, larvae will be rapidly transported to the open sea. In summary, *C. granulata* is distributed over a heterogeneous collection of habitat patches with regard to salinity. There may be additional sources of heterogeneity in habitat quality (e.g. temperature, food items, abundance of predators) that may contribute to additional heterogeneity.

What may be the consequence of such variability in salinity for larval survival and dispersal? Changes in salinity may lead to heterogeneity in larval production and quality if reproductive activities, embryogenesis, larval survival and growth are sensitive to osmotic stress. Juveniles and adults tolerate low and variable salinities quite well, as they survive in habitats of salinity as low as 5‰. However, embryonic and larval phases are less tolerant to osmotic stress (Bas and Spivak 2000; Giménez 2000; Giménez and Anger 2001; Charmantier et al. 2002). Present information allows a first view on how *C. granulata* may respond to variability in salinity at the population level.

Larval survival in relation to salinity

Under controlled laboratory conditions, I investigated (1) how salinity experienced by embryos affected initial larval biomass, (2) how tolerant larvae are to low salinity, and (3) whether prehatching salinity and initial individual larval biomass affected larval salinity tolerance, survival under food stress and growth. Details on methodology and results are given in Giménez (2000), Giménez and Anger (2001), Spivak et al. (2001), Charmantier et al. (2002), Giménez (2002), Giménez and Torres (2002), Giménez and Anger (in press). Embryonic development took place at different salinities (range: 15–32‰) by keeping ovigerous females isolated from egg laying to hatching of larvae. Freshly hatched larvae were used to estimate individual biomass (dry weight, carbon and nitrogen), and for experiments to determine larval survival. Survival was measured in various experiments by rearing the larvae under different salinities (range: 5–32‰) or feeding periods. Growth of larvae was evaluated under ad libitum food and near optimal salinity conditions.

Information on embryonic survival in relation to salinity experienced by females is still lacking. Eggs laid at 15‰ were in general larger in diameter and had higher carbon and nitrogen content than those laid at 32‰; energy loss during embryogenesis was higher at lower salinities (Giménez and Anger 2001).

Under ad libitum food conditions, survival of zoeal stages was higher and duration of development shorter in larvae with higher biomass at hatching if they were maintained at 15–32‰. Survival of the megalopa was independent of biomass at hatching except for larvae reared at 32‰ (Giménez and Anger, in press). Growth depended also on biomass of freshly hatched zoea (Giménez and Torres 2002). There was a significant positive correlation between biomass at postmoult zoea 4 and at hatching. *C. granulata* develops through either a short or a long developmental pathway with four or five zoeae, respectively (Pestana and Ostrensky 1995). The proportion of larvae following the long pathway increases with decreasing biomass at hatching (Giménez and Torres 2002) or if early zoeal stages are incubated at low salinities (e.g. 15‰: Giménez and Anger, in press). These larvae metamorphose into larger megalopae than those from the short pathway.

Also under ad libitum food conditions, survival of zoea 1 at low salinities (5–10‰) depended on the salinity experienced by embryos, showing an acclimatory response (Giménez and Anger, in press). For instance, at 5‰ all zoeae 1 died if hatched from embryos incubated at 32‰. However, an average of 70% of the larvae reached the second stage if they hatched from embryos reared at 15 or 20‰. At higher salinities (15–32‰), survival of zoeae 1 varied from 20% to 100% depending on biomass at hatching. Such pattern can also be observed when survival of zoea 1 from hatching to premoult is plotted against time (Fig. 4). When larvae that hatched from embryos maintained at 32‰ were incubated at 5‰, all individuals died within the first 24 h
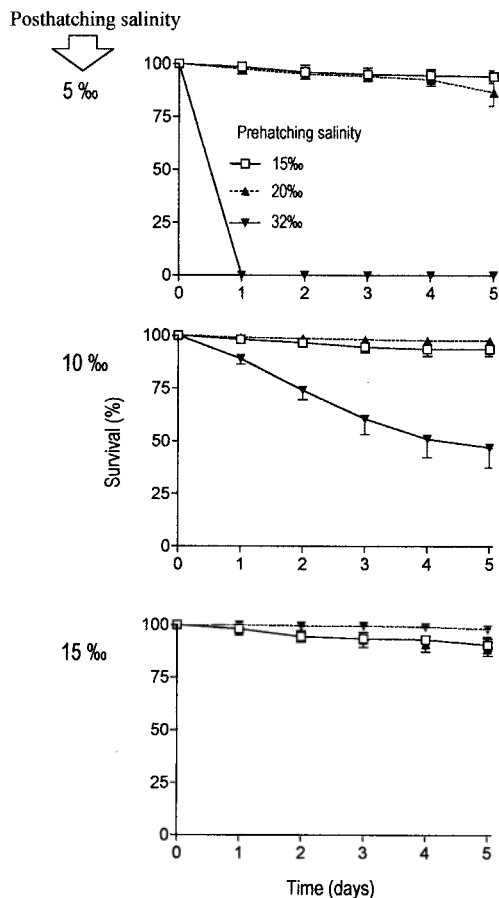

Fig. 4 *Chasmagnathus granulata.* Time course of survival of zoeae 1 from hatching to premoult at different salinities (posthatching salinities) and hatched from embryos maintained at different salinities (prehatching salinities)

(Fig. 4). However, the number of survivors decreased only slightly for larvae incubated at 5‰ but that hatched from embryos at 15 or 20‰. As at 5‰, larval survival at 10‰ also depended on the salinity experienced by embryos (Fig. 4b), although the effect was less pronounced. Finally at 15‰, larval survival changed with time only slightly irrespective of the salinity experienced by embryos (Fig. 4). Considering subsequent stages, survival at a 15‰ salinity was low compared with 32‰; at 15‰ very few individuals reached the first crab instar independently of salinity experienced by embryos, suggesting that acclimatory response is restricted to early larval stages. Further experiments showed that the acclimatory response was based on an enhanced osmoregulatory capacity in the first zoea, and that the response was strongly decreased in subsequent stages (Charmantier et al. 2002). Enhanced survival as a consequence of acclimation to low salinity was therefore limited to the first 2 weeks of larval life.

Under limited food conditions (short initial starvation period at 20‰), a higher biomass at hatching led to lower mortality and shorter development time of zoea 1 (Giménez 2002). Effects of acclimation to salinity under

limited food conditions were found for zoeae 1 cultured under a short initial feeding period and subsequent starvation at 20‰: zoeae 1 hatched from 15‰ and 20‰ showed lower mortality and shorter development time than those hatched from 32‰. This might have occurred because these larvae accumulated a higher proportion of biomass during the initial feeding period (Giménez 2002).

Discussion

Larval survival was the consequence of the interaction of different pre- and posthatching factors. Prehatching salinity affected initial biomass, loss of energy during embryogenesis, larval salinity tolerance, survival under limited starvation periods, and initial larval growth of *C. granulata* in a complex fashion (summarized for zoea 1 in Fig. 5). For instance, negative effects of low (5–10‰) posthatching salinities did not appear under moderate (15–20‰) prehatching salinities (Fig. 5b). Such findings lead to the conclusion that for *C. granulata*, as for other species, population dynamics should be studied considering the life cycle as a whole rather than from studies on each life phase separately, i.e. considering pre- and posthatching as well as pre- and postsettlement processes/factors. These processes may be important to explain large-scale population dynamics. The facts that (1) egg size and prehatching salinity affect the frequency of larvae developing through the long pathway; (2) these larvae metamorphose into larger juveniles that exhibit tolerance to stress (L. Giménez, unpublished data), further suggest that life-history characteristics of different life phases are strongly linked in *C. granulata*. This may also occur in other crustaceans (Rosenberg and Costlow 1979; Laughlin and French 1989; Qiu and Qian 1999).

Importance of acclimation on larval production

An increased loss of embryonic biomass at low salinity seemed to be compensated by increased initial biomass at egg laying. Initial larval biomass is a consequence of the balance between initial egg biomass and energy loss during embryogenesis. Effects of initial larval biomass on subsequent survival and development duration were particularly important when zoea 1 were under food deprivation immediately after hatching, or under near-optimal salinity and food conditions. Initial larval biomass also affected growth rate, since larger freshly hatched zoeae 1 led to larger postmoult zoea 4, and increased the proportion of larvae following the short pathway, i.e. that reached metamorphosis in a shortest time. An increased initial egg biomass as a response to low salinities must have an adaptive value, as it should reduce or eliminate negative effects of energy loss on larval survival or growth. Thus, variability in energy loss among broods from estuarine habitats with different salinities may be at least partially eliminated, as well as their effects on larval survival.
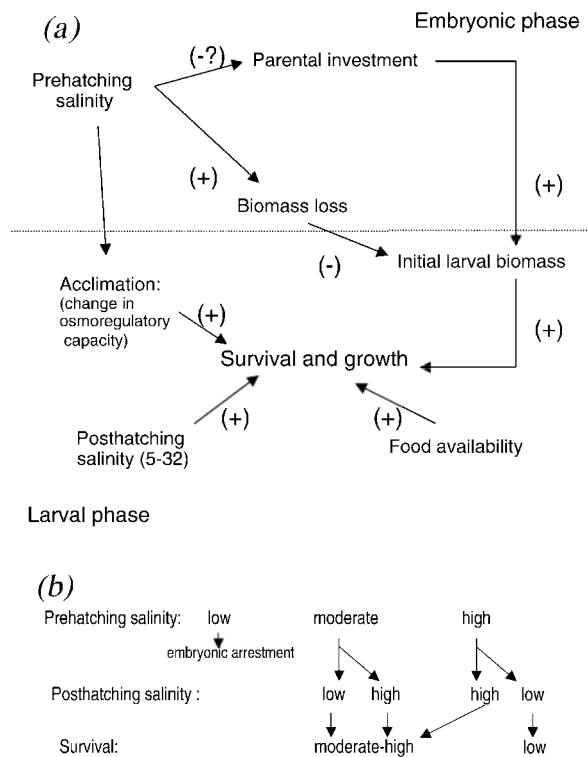

Fig. 5a, b *Chasmagnathus granulata.* **a** Flow diagram showing the effects of prehatching salinity (15–32‰), posthatching salinity (5–32‰) and food availability on physiological processes, and the consequences on larval growth and survival. *Signs associated with each connecting arrow* show the nature of the relationship between components of the diagram. **b** Effects of interactions between pre- and posthatching salinity (low: 5‰, medium: 15–20‰, high: 32‰) on larval survival (low: 0–20%, high: 40–100%)

Expected initial and total larval survival rates could be calculated from salinity fields and survival data from laboratory experiments. Extrapolation of laboratory results to predict larval survival in the field is not indisputable, as other factors (e.g. predation, parasites, food availability, pollutants) may interact with salinity to explain larval survival. Therefore, such figures should be interpreted as a possible scenario for variability in larval output and as a way to help further discussion. Figure 6 shows the expected survival for larvae released in the Uruguayan and part of the Argentinian coast with and without acclimation to reduced salinities. At least in the short term, acclimation should buffer larval survival against the high variability in salinity that characterize this area. For instance, the larvae released from Santa Lucía river would die within the first day of life if acclimation during embryogenesis were not possible. Acclimation should allow these larvae to be transported and reach areas of higher salinity. Besides, acclimation may be highly important for survival of larvae released in temporarily isolated lagoons if the period of isolation is shorter than 2 weeks. These two kinds of habitats are candidates for sinks or pseudosinks if larval acclimatory capacity were lacking or low. Their environmental con-
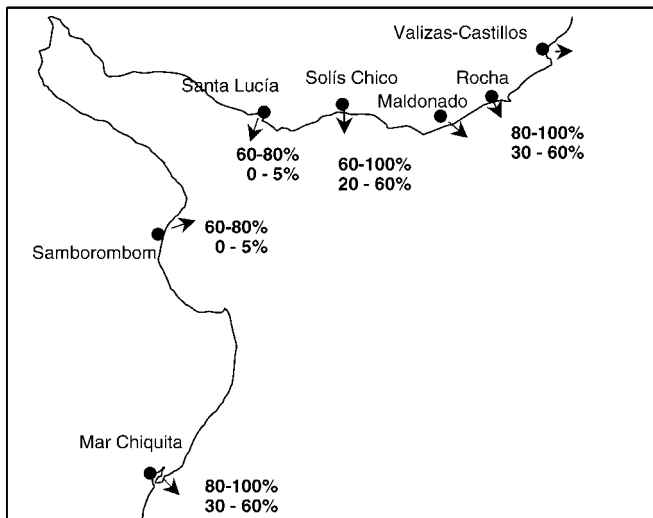
Fig. 6 *Chasmagnathus granulata.* Expected range of initial survival with (*upper values*) and without (*lower values*) acclimation to low salinities during embryonic development for larvae released from different nursery habitats. Ranges were calculated using values of salinities from Fig. 4 and survival data from Giménez (2000)

Fig. 7a, b *Chasmagnathus granulata.* Expected structure of population network without (**a**) and with (**b**) the capability for acclimation, plotted in the demographic space defined by Compensation and Mobility axes, birth (*B*), death (*D*), emigration (*E*) and immigration (*I*) rates (see text for explanation). *Arrows* in **a** show the displacement effect produced by acclimation to salinity: habitat patches with local populations or benthic components located near the sink extreme of demographic space are displaced farther than those located towards the source extreme. Different *sizes and shading of circles* denote position in the three-dimensional space

ditions may allow colonization by megalopae, subsequent growth, and reproduction, due to higher osmotic tolerance of these stages. However, low rates of embryonic and/or early larval survival would lead to virtually no larvae reaching the open sea. For habitats open to coastal areas of highly variable salinity, acclimation would reduce temporal variability in larval output.

As well as acclimatory capacity, *C. granulata* showed the ability to follow an alternative developmental pathway under salinity stress. The existence of alternative developmental pathways (i.e. variable development) has been found in other estuarine crabs (Costlow 1965; Montú et al. 1990; Anger 1991). Variable development has been interpreted as a strategy to priorize survival in spite of morphogenic processes (Knowlton 1974), and thus it should lead to a high average, but a low variance in survival in spite of variable environmental conditions. The consequences of following an alternative larval development are not easy to ascertain, as this includes a lengthening of larval period and an increased size at settlement (Giménez 2000). Lengthening the larval period may favour connectivity among benthic habitats or even among larval pools. However, it may reduce settlement rate due to predation or offshore transport. Delaying the timing of settlement may not be favourable for *C. granulata*, since inter-cohort cannibalism may be an important source of postsettlement mortality (Luppi et al. 2001). However, this may be reduced by the fact that juveniles originated from larvae that followed the long pathway are larger than those originated from the short one (L. Giménez, unpublished results).
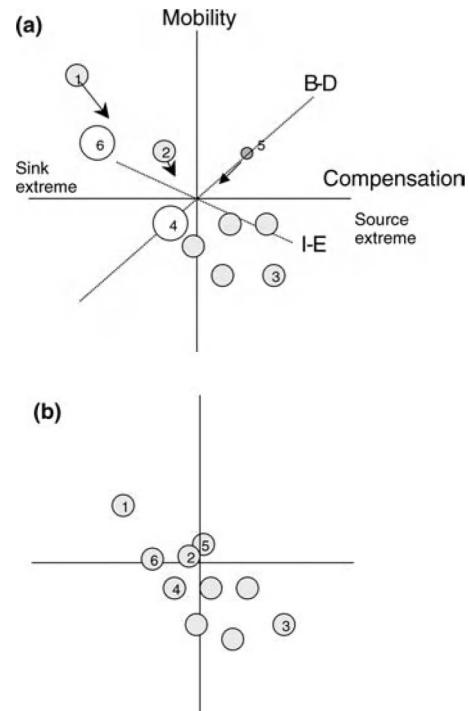
Importance of acclimation for structure and dynamics of population networks

I will follow Thomas and Kunin (1999) to describe population networks. They consider that most population types (e.g. mainland–island, metapopulation) intergrade so that it is possible to locate them within a continuous demographic space defined by a combination of the birth (*B*), death (*D*), emigration (*E*) and immigration (*I*) rates (Fig. 7). In the demographic space a "compensation axis" is defined as the line $(I-E)+(B-D)=0$, so that population units towards the extremes characterized by high *I* and *D* rates are sinks and those at the other extremes (with high *E* and *B*) are sources. In the middle lies the classical population (i.e. *I=E* and *B=D*), and towards the left side are the pseudosinks (see Figure 1 in Thomas and Kunin 1999). A "mobility axis" describe the importance of regional and local processes, as the line $(I+E)-(B+D)=0$, where $(I+E)$ summarizes the importance of interaction among population units and $(B+D)$ summarizes local events. Local populations located in the plane defined by both axes (CM plane) should be at equilibrium. As those outside equilibrium should be located outside the CM plane, the demographic space has three dimensions (see Figure 2c in Thomas and Kunin 1999). Any

local population may change its position in the demographic space. For instance demographic and environmental stochasticity may move populations away from the CM plane, and denso-dependent processes should tend to return them to that plane (Thomas and Kunin 1999).

In the case of a population network of a species without acclimation distributed over a heterogeneous collection of patches, a mixed type of population, including sinks, pseudosinks, classical and source populations, is the most likely situation (Fig. 7a). If some patches experience environmental stochasticity, local populations should frequently be moved away from the CM plane (Fig. 7a). In the case of *C. granulata* the capability to acclimate should affect several processes. A relatively high number of larvae produced in a local population characterized by low salinities should lead to relatively high E and low D rates. Hence, this population should be located towards the centre of the space (compare positions of population 1 in Fig. 7a, b). As the effect of acclimation was only observed at low salinities (5–10‰) the shift in the position of populations should be larger if they are located towards the sink extreme, i.e. towards areas with lower salinity (compare positions of populations 1, 2 and 3 in Fig. 7a, b). This shift may move populations along the Compensation axis (Fig. 7); effects of acclimation on the shift of populations along the Mobility axis should depend on its effect on E and D rates of local populations. If hydrodynamic conditions usually transport most larvae to other populations, acclimation should increase the importance of regional processes (i.e. most surviving larvae are exported). The importance of local processes should be affected if larvae are usually retained (most surviving larvae increase local population size). Furthermore, variability in salinity may be an important source of environmental stochasticity, as a consequence of temporal changes in precipitation rates and hence in river discharge. Such changes have been reported in Patos lagoon, where they influence primary (Ciotti et al. 1995) and shrimp production (Castello and Möller 1978). Acclimation should tend to reduce the effects of that environmental stochasticity, so that at a given moment only few local populations may be located away from CM plane. Therefore, the consequence of acclimation capability is that the population network is compressed towards the lower right part of the CM plane, i.e. it is dominated by local populations with relatively high birth and emigration rates and with low probabilities for local extinction. Hence, acclimation to salinity should stabilize a population network of C. granulata located in a heterogeneous environment.

Perspectives

Although future research on biology and ecology *C. granulata* should take many different aspects into account (see Spivak et al. 2001), I would like to suggest some that I consider to be central for the understanding of population dynamics. Future approaches should combine different levels of organization and spatial scales. For example, studying larvae hatched from ovigerous females from Mar Chiquita, we found that acclimation was based on a change in osmoregulatory capacity (Charmantier et al. 2002). However, due to genotypic differences, this capacity may vary among individuals from different habitats. Thus, a higher level of physiological responses, based on genetic heterogeneity, may be found at large spatial scales. In order to evaluate this possibility, we should carry out studies taking into account scales large enough to cover several local populations.

It is also necessary to quantify how heterogeneous different patches and local populations are. Some local benthic components, such as those located in the southern limit of distribution or under extreme osmotic conditions, are especially interesting, since they are under particular combinations of environmental conditions (see also Spivak et al. 2001). Food availability may determine variability in egg and initial larval biomass; predation rate in the benthos and in the water column should affect larval output. At the larger scales, different oceanographic conditions seem to prevail: as well as differences in temperature, northern upwelling areas off the South Brazilian coast may constitute a different habitat than southern estuarine plumes in the Uruguayan and Brazilian coast or shelf-fronts in Argentina. The importance of pre- vs postsettlement processes may change from one habitat to another as a consequence of large-scale differences in habitat quality.

Studies on local populations or networks of populations should also be carried out in the context of conservation. *C. granulata* is a key species in estuarine salt marshes, as it processes large quantities of matter and can affect sediment stability (Iribarne et al. 1997; Bortolus and Iribarne 1999; Botto and Iribarne 2000). High levels of pollutants enter the estuarine areas (e.g. Río de la Plata: Gómez-Erache et al. 2001) possibly affecting the benthic and pelagic stages. A study in Mar Chiquita (Iribarne et al. 2000) showed that debris (mainly plastics) retained in areas populated by crabs and burrows acted as a passive trap. Land reclamation may reduce the habitat available for the establishment of juveniles and adults. Whether present effects of debris or reduction in habitat size or quality are still unimportant is not yet known. They may lead to metapopulation effects either in connectivity among local benthic components or in extinction rates.

Studies on *C. granulata* should involve more than one working group, rather a network of them (see Olmi and Orth 1995 and references therein as an example), perhaps addressing different aspects of the ecology and biology of particular species. For such studies, connectivity among working groups would turn out to be as important as connectivity among local populations.

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