ABSTRACT

The production of diapause eggs is a strategy for survival adopted by microcrustaceans living under adverse environments. This strategy also aids dispersion and colonization in new environments. In the long term, this colonization process can enhance genetic isolation as the first step in the process of species evolution. The present study is: (a) a wider review of the diapause process in inland water crustaceans and its ecological, evolutionary, and biogeographical implications, and (b) its application to microcrustacean assemblages in inland waters in southern Patagonia. In the literature, the diapause strategy was described from anostracans, cladocerans, and copepods as microcrustaceans, and amphipoda in malacostracan crustaceans. High crustacean species richness was recorded from southern Patagonia, this region having species of southern South American and Sub-Antarctic islands origin. Their spatial distribution is probably explained by the presence of migratory birds. Also, many habitats of the microcrustaceans are ephemerals that would be studied under metapopulation and metacommunities view point.

Key words: diapause, colonization, metapopulations, metacommunities, anostracans, cladocerans, copepods.

RESUMEN

Los microcrustáceos tienen como estrategias del ciclo de vida la generación de huevos en estado de diapausa bajo condiciones ambientales adversas, esta estrategia provee facilidades para la dispersión que generan procesos de colonización los que estimulan procesos de aislamiento genético como primer
Microcrustaceans such as Branchiopoda, Copepoda and Ostracoda have diapause egg production - the generation of resting eggs - as a life strategy for species perpetuation under adverse environments, specifically drying of their habitats (Alekseev, 2007a;b;2010; Alekseev et al. 2007; Muñoz, 2009). This life strategy has many ecological, systematic and evolutionary implications. Resting eggs, can be spread by agents such as wind and other fauna and initiate the colonization process in new habitats or habitats where microcrustaceans have been reduced or disappeared from. This could have impacts on metapopulations and metacommunities (Altermatt, 2008). This spreading and colonization dynamics would have evolutionary and systematic implications as, if the resting eggs colonize new habitats with environmental heterogeneity, selection pressure would eliminate all individuals other than those with optimal genes for survival and reproduction, and as a consequence would create genetic isolation as the first step in the speciation process (De los Ríos & Zúñiga, 2000; Gajardo et al. 1995; 2004; Ebert et al. 2002). This scenario, over a wide spatial and temporal scale could create zones where certain taxa could originate, spread and colonize new, more distal habitats as the first step in a potential speciation process, that could be described using biogeographical techniques, such as track analysis or endemicity parsimony analysis (Morrone, 2004; 2006).

In Patagonia (38-54° S) there are many ephemeral pools (formed in spring, and disappearing over the other seasons), that would contain crustaceans that generate resting eggs. These subsequently hatch when the environmental conditions are optimal (De los Ríos-Escalante, 2010). From a biogeographical view point, Patagonia has species from Southern South America and Sub-Antarctic islands (Menu-Marque et al. 2000; Pugh et al. 2002; Dos Santos et al. 2008). Within this scenario, the aim of the present study is to review diapause strategies of microcrustaceans in general with emphasis on biogeographical and ecological implications and apply this to a study of microcrustacean (Branchiopoda, Copepoda, and Amphipoda) species distribution in Patagonian inland waters.

BRANCHIOPODA

The branchiopods described for Patagonia include Anostracos (families Artemiidae and Branchinectidae), and Cladocerans (families Daphniidae, Bosminidae, Chydoridae), with both endemic and cosmopolitan species (De los Ríos-Escalante, 2010). Both Anostracan families Artemiidae and Branchinectidae are present in saline and freshwater lakes and pools respectively (De los Ríos-Escalante, 2010). The Artemiidae is represented by the species Artemia persimilis (Piccinelli & Prosdocimi, 1968), found in two saline lakes in the Magallanes region, Laguna Amarga (51° 00’ S: 72° 48’ W) in Torres del Paine National Park and Laguna de los Cisnes (53° 14’ S: 70° 23’ W) close to Porvenir on Tierra del Fuego (De los Ríos-Escalante & Gajardo, 2010). The population in Laguna Amarga is permanent and practically exclusive to the zooplankton of this habitat (Campos et al., 1996), whereas the popula-
ción en Laguna de los Cisnes depende de variaciones en salinidad: puede estar presente a altos niveles de salinidad, pero si la salinidad disminuye, la población desaparece (De los Ríos-Escalante & Gajardo, 2010). Para Branchinectidae, los especies Branchinecta gaini y B. granulosa se reportan en la región Magallanes en 53° y 51° S respectivamente, B. vuriloche desde la región Ayens a 45° S (Rogers et al., 2008) y juveniles en lodos costeros de la Araucanía en 38° S (De los Ríos-Escalante et al., 2010). Branchinecta se encuentran en cuerpos de agua efimeros presentes solo en primavera, y este género es probablemente confinado a oligotróficos y baja conductividad de aguas continentales (De los Ríos et al., 2008). Los cladoceros tienen especies con distribuciones cosmopolitas y especies endémicas (De los Ríos-Escalante, 2010) como Ceriodaphnia dubia Richard, 1894, Daphnia ambigua Scourfield, 1947, D. dadayana, Paggi, 1999, D. pulex Leydig, 1860; Scapholeberis exsipinifera (Nicolet, 1849); Simosa exsiposa (De Geer, 1778), Neobosmina chilensis (Daday, 1902), Ilyocryptus spinifer Herrick, 1884; Alona poppei Richard, 1897, A. pulchella King, 1853, A. quadrangularis (O.F. Müller, 1776), A. clathratula (G.O. Sars, 1896), Alonella exsipe (Fisher, 1854), Camptocercus rectirostris (Schoedler, 1862), Pleuroxus aduncus (Jurine, 1820), Chydorus sphaericus (O.F. Müller, 1785), Leydigia leydigi (Schoedler, 1863) y Paralona nigra (G.O. Sars, 1862). Los cladoceros de la región norte del hemisferio que producen huevos diapausa se han estudiado (Altermatt, 2008; Muñoz, 2009) y aunque existe una estrategia de vida sexual y sexual no reportado, esta situación no ha sido reportada para poblaciones continentales del hemisferio sur (Adamowicz et al., 2002).

COPEPODA

Los copepodos efímeros y temporales, tales como B. brasiliensis (Lubbock, 1855), B. brevicaudata (Brady, 1875), B. michaelseni (Mrázek, 1901), B. poppei (Mrázek, 1901) y Parabroteas sarsi (Ekman, 1905). Entre los Copepoides hay especies endémicas de América del Sur (De los Ríos-Escalante, 2010), tales como Acanthocyclops michaelseni (Mrázek, 1901), A. vernalis (Fisher, 1853), Eucyclops ensifer Kiefer, 1936, Eucyclops serrulatus (Fisher, 1851), Macrocylops albidus (Jurine, 1820), Mesocyclops araucanus (Löffler, 1962), Metacyclops mendocinus (Wierzejski, 1892), Microcyclops aniceps (Richard, 1897), Paracyclops fimbriatus chiltoni (Thomson, 1882) y Tropocyclops prasinus meridionalis Kiefer, 1927. Solamente el especie Mesocyclops logisetus (Thiébaut, 1912) se ha distribuido en todos los gradientes geográficos en el hemisferio sur. No se han reportado estudios de diapausa en Aguanos de América del Sur, donde las especies de copepodos efímeros y temporales, la información disponible es de Nueva Zelanda copepodos (Cough et al., 2001; Hall & Burns, 2001; Banks, 2007; Taylor, 2010), y para la población antártica de B. poppei (Jiang et al., 2012). No obstante, la presencia de las especies anteriores en cuerpos de agua efímeros indicaría la presencia de estrategias de vida diapausable en copepodos (De los Ríos-Escalante, 2010).

AMPHIPODS

Los amphipods reportados de la Patagonia incluyen especies reportadas para el sur de América del Sur (De los Ríos-Escalante et al., 2012) como Hyalella costera González & Watling, 2001, H. chiloensis González & Watling, 2001, H. curvispina Schoemaker, 1942, H. franciscae González & Watling, 2003, H. patagonica (Cunningham, 1871), H. rionegrina (Grosso & Peralta, 1999) y H. simplex (Schellenberg, 1943). Aunque no se han realizado estudios de diapausa en especies de agua dulce en el sur de Chile, la presencia de especies de cuerpos de agua efímeros y pantanos con el agua se evapora y flotando periodos, tales como Tres Puente, pantanos cerca de Punta Arenas, y algunas áreas de agua efímeras, pantanos cerca de Puerto Natales, indicaría la presencia de mecanismo de diapausa para explicar la presencia de estos amphipods (De los Ríos-Escalante, personal observations, February 2012). Diapausa ha sido observado para Hyalella azteca (Bayley et al., 2005; Doobay 2011; Alekseev, 2007a), un especies anteriores de América del Sur (De los Ríos-
Escalante et al., 2012), nevertheless there are no published accounts of diapause in South American amphipods.

ECOLOGICAL IMPLICATIONS

In ecology, the metapopulation and meta-communities concepts are currently widely used to explain the presence of interconnected sub-units where individuals continuously migrate with the consequent local colonization and extinction process (De los Ríos-Escalante, 2012). In this scenario, metapopulation and metacommunities can be used to explain faunal populations in plains such as coastal zones (Puauco sand beaches), flooded after rainy season or mountain zones such as Cañi Park or zones close to Lonquimay in Araucania region, or pools close to Balmaceda airport in the Aysen region, or in the Magallanes region (De los Ríos-Escalante, 2010; 2012). The main characteristic of these habitats is the presence of many isolated pools during spring. In summer these habitats dry out, and in autumn and winter these can be snow covered (in for example the Lonquimay, Balmaceda or Magallanes pools), or filled with water from winter rains (Puauco pools) (De los Ríos-Escalante, 2012). The exceptions are the pools in Cañi which can remain water-filled in summer (De los Ríos & Roa, 2010). These pools are characterized by a relatively homogeneous species diversity regulated mainly by trophic status and/or conductivity (De los Ríos & Roa, 2010; De los Ríos-Escalante 2012). No systematic studies have been conducted on the occurrence and distribution of pools on the Patagonian plains. These are however present only one or two months after winter rains, and inhabited by characteristic crustaceans for each region, for example Boeckella poppei, Daphnia dadayana and Parabroteas sarsi in central and southern Patagonia, or Boeckella gracilis and Daphnia pulex in northern Patagonia (De los Ríos, personal observations; De los Ríos-Escalante, 2010; 2012). In Laguna de los Cisnes lagoon, where there are marked variations in response to seasonal salinity variations, it is proposed that these might result in the presence of only Artemia persimilis at high salinity, but at intermediate salinity the Artemia can coexist with other halophilic copepods such as harpacticoids and B. poopoeensis, and at low salinity A. persimilis is not found and is replaced by B. poopoeensis and harpacticoid copepods (De los Ríos-Escalante & Gajardo, 2010).

It was reported in the literature that diapause egg production can be induced by direct or indirect predator exposure, specifically the presence of fish kairomones (semiochemicals emitted by the fish which benefit the recipient organism) that induced diapause process reproduction in large bodied cladocerans (Santangelo et al., 2010; Slusarczyk, 2010; Slusarczyk et al., 2012). None of the sites studied in the Magallanes and Aysen region had zooplanktivorous fishes, and in these pools the main predator would have been the large-bodied copepod Parabroteas sarsi (De los Ríos-Escalante, 2010), an active zooplankton predator in Patagonian inland waters (Vega, 1996, 1997, 1998, 1999). However no studies have been carried out on chemical communication between predator and prey in Patagonian inland waters.

It is recorded in the literature that the diapause can be induced by climate changes that affect it at metapopulation and metacommunity levels (Altermatt & Ebert, 2008; Altermatt et al., 2008). Drying periods directly affect diapause activity. The dormant eggs hatch during the flooding period (Altermatt & Ebert, 2008; Altermatt et al., 2008), and the hatching process is enhanced by optimal temperature and photoperiod conditions (Vandekerkhove et al., 2005; Depuis & Hann, 2009), resulting in a synchronized process in confined habitats (Nevalainen & Sarmaja-Korjonen, 2008). Resting eggs can survive in sediments of ephemeral water bodies over many seasons, and when they hatch can give rise to individuals with different genetic characteristics from other individuals of the same species, which have hatched from more recent eggs. This would generate an effect of improvement in community robustness (Brendonck & De Meester, 2003). On a population or species scale, the diapause is a rapid life strategy to obtain many resting eggs that can have marked genetic heterogeneity. When these eggs are spread to different environments, this could enhance the survival of optimal genes as a first step in a long term speciation process such as has successfully been recorded in the Daphnia genus (Coulborne et al., 1997; Taylor et al. 1998; Keerfoot & Weider, 2004; Kerfoot et al. 2004).
BIOGEOGRAPHICAL IMPLICATIONS

From a biogeographical view point, the diapause process can encourage dispersion, mainly by biological agents such as animals that transport dormant eggs. This scenario involves colonization at long distances to habitats with different environmental conditions (Jenkins & Underwood, 1998; Suatoni et al., 2006), and would generate genetic isolation because only individuals with optimal genetic conformation would survive (Gajardo et al., 1995; Suatoni et al., 2006). In this scenario, genetic isolation would generate a long term speciation process with consequent reproductive isolation (De los Ríos & Zúñiga, 2000; Gajardo et al., 2004; Suatoni et al., 2006). For this scenario to occur, any specific geographical zone would need to have the potential first ancestors, that would generate the respective spreading and colonization by resting eggs or other similar strategy (Suatoni et al., 2006). According to Menu-Marque et al. (2000), southern Patagonia is a dispersion zone from a common ancestor, which would explain the presence of both South American and Antarctic species together (Menu-Marque et al., 2000; Morrone, 2004; 2006). If we consider these records of the presence of an ancestor, and the dispersion of dormant eggs by biological agents such as migratory aquatic birds moving from south to north, this could explain the widespread distribution of Sub-Antarctic species in southern Patagonia. On the other hand, the presence of southern South American species in Southern Patagonia, can be probably due to dormant eggs being carried north to south by migratory aquatic birds. This proposal would agree with center of origin idea, that indicates the presence of defined geographical zones that have the potential ancestors, where many varieties and greatest dominance of the taxon, can be found and the direction from the origin is indicated by the migration routes of birds (Crisci et al. 2003).

This could explain the presence of similar zooplankton communities structures in central and southern Patagonian plains between 46-53° S (De los Ríos-Escalante, 2010; 2012). A different situation would occur with another similar widespread species (B. gracilis) which is found in coastal and mountain ephemeral pools, in mountain zones in Patagonia and tropical South America (Menu-Marque et al., 2000). The marked differences between inland water fauna in Patagonia and the north of South America (Menu-Marque et al., 2000; De los Ríos-Escalante et al., 2012) are due the absence of the physical barrier of the Andes mountains preventing species dispersion and the presence of migratory aquatic birds. This would explain the distribution patterns of branchiopods and copepods in the region (De los Ríos & Zúñiga, 2000; Menu-Marque et al., 2000). This mechanism agrees with observations of Agius (2006), in a lake exposed to volcanic activity that had been recently colonized by Branchinecta gaini and Boeckella poppei. Nevertheless, there is still no evidence about diapause and dispersion process in Amphipods, to explain the geographical distribution of some widespread species such as H. chiloensis and H. patagonica.

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