Short Research Note

Invertebrate colonization patterns in a Mediterranean Chilean stream

Ricardo Figueroa^{1,*}, Victor Ruíz², Xavier Niell³, Elizabeth Araya¹ & Alejandro Palma² ¹Aquatic Systems Research Unit, Environmental Science Center EULA-Chile, University of Concepcion, P.O. Box 160-C, Concepcion, Chile

²Department of Zoology, University of Concepcion, P.O. Box 160-C, Concepcion, Chile

³Department of Ecology, Faculty of Sciences, University of Malaga, Malaga, 29071, Spain

(*Author for correspondence: E-mail: rfiguero@udec.cl)

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Abstract

The macrozoobenthos colonization process on artificial substrata in lotic environments was evaluated. Two seasonal periods, autumn–winter and spring–summer, of a relatively undisturbed fluvial system, the Estero Nonguén (VIII Region, Chile), have been studied. Five stations, two in riffles and three on sandy bottoms, extending from a head water stream to 5 km down river, were sampled. For all stations and for each season the results were as follows: (a) 32% of the total number of taxa found in this study colonized the artificial substrata on the first day of exposure, (b) the taxa that colonized sandy bottoms were typical for riffle, (c) the colonization process showed the same abundance, specific and cumulative richness and diversity patterns over time, and (d) equilibrium was reached approximately 2 weeks after initial exposure. This suggests that "Estero Nonguén" stream presents a nearly pristine condition and can be considered as a reference site to carry out biodiversity and ecosystem functionality studies, and giving information on time recovery for sectors previously disturbed.

Introduction

Colonization is an important mechanism in river restoration; its study is useful to predict the extent and type of conditions required for flora and fauna recovery in a disturbed ecological system (Allan, 1997; Friberg et al., 1998). The aquatic habitat is constantly being modified by the appearance of new elements, such as fallen trees, branches and other substrates, which enter the system with different periodicity and predictability (Resh & Rosenberg, 1984). Consequently, the colonization mechanism is the process by which organisms move to settle in new areas or in disturbed environments where they were previously present (recolonization). The colonization of a particular environment depends on various factors, such as the availability of certain food resources, the available surface area, temperature, and light as well as the current

speed, width, depth and slope of the channel. The substrate, as an immediate physical medium for colonization, has been shown to be the main factor on which colonization depends (Wohl et al., 1995; Matthaei et al., 1996). A zone of riffle can be quickly recolonized since it lies relatively near settlers' source areas, while the colonization of a sandy bottom area would depend on those organisms that are coming from upstream sections and have not been preyed upon by organisms of higher trophic levels. Thus, river colonization would partly depend on the distance from future settlers' source areas (MacArthur & Wilson, 1967; Gore, 1982).

Published works studying the ecology of benthic macroinvertebrates from Chilean rivers are scarce. By contrast, in the Northern Hemisphere, Australia and in New Zealand, the distribution of benthic macroinvertebrates and the colonization processes have been extensively studied for several decades. Studies have been principally undertaken to control and evaluate the degree of disturbance in fluvial systems (Downes & Lake, 1991; Matthaei et al., 1996; Peterson, 1996; Brown et al., 1997; Paltridge et al., 1997). The present study provides the possibility to compare the colonization patterns of Chilean rivers with that of other Mediterranean climate streams in Europe, Western North America, Southeast Australia and Southwestern South Africa.

Methods

The studied sites were located in the Estero Nonguén ($36^{\circ} 49'-36^{\circ} 54' S$; $72^{\circ} 57'-73^{\circ} 01' W$), a second-order fluvial system with an estimated annual flow of 1 m³ s⁻¹. It is a coastal sub-basin tributary of the Andalién River's lower course (Concepción, Chile), running over a distance of 15 km in the south–north direction, with a basin surface area of 44 km² (Fig. 1). Five stations were selected within the 5 km from the head of the stream, separated by 1 km of distance, two in the rithron area (E1 and E2), one in the intermediate area (E3), and two in the sandy bottom sector (E4 and E5) as shown in Table 1 and Fig. 1.

The artificial substrata used were plastic net baskets of $20 \times 20 \times 8$ cm full with natural stones standardized in color, texture and size classes. The stones were washed with 10% HCl to eliminate all organic remains, and then rinsed with freshwater. The mesh aperture was 2.5 cm² to allow free passage of organisms. In each station, 36 artificial substrates were randomly placed in a tract measuring no more than 10 m² in surface area during May-July 1999 (autumn-winter) and October-December 1999 (spring-summer). A 3-month exposure period was considered sufficient to study the benthic community response (Towsend & Hildrew, 1976; Mackay, 1992). The four artificial substrates were collected from each station, and in each period at 1, 3, 7, 10, 16, 28, 45, 65 and 85 days



Figure 1. Study area and location of sampling stations (E1-E5).

Site Code Bedrock Latitude (S) Longitude (W) Altitude Distance from (m.a.s.l)source (m) 36° 52′ 12″ 72° 59' 26" Essbio E1Boulders, cobbles and pebbles 72 1036 Boulders, cobbles and pebbles 36° 51' 41" 72° 59' 48" 2071 Bridge M. Elena E2 34 Pebbles and coarse sand Bridge Seguel E3 36° 51' 22" 72° 59' 48" 28 3040 36° 51' 07" 72° 59' 57" Lake sector E4 Coarse and medium sand 17 3968 School sector E5 Coarse and medium sand 36° 50' 41" 73° 00' 19" 13 4956

Table 1. General characteristics of sampling stations

after exposure. They were individually stored in plastic bags and transported to the laboratory.

Identification was made at the lowest possible taxonomic level using available literature (e.g. CSIRO, 1991; Fernández & Domínguez, 2001). Results were recorded in an abundance matrix $(N m^{-2})$ and in a biomass matrix (wet-weight m⁻²) for each station. Biomass was determined using an Analytic Precisa 240A balance (0.0001 g sensitivity). Starting from a density matrix (Number of individuals m^{-2}) elaborated for each sampling period and each station, the stations were compared and grouped to define areas with similar biological composition. Additionally, the taxa were grouped by an analysis of conglomerates (UPGMA) using a similarity matrix Bray–Curtis (1957). Other variables determined included abundance, specific richness, Shannon diversity $\log_2(H')$, evenness (J) and Simpson diversity (D).

Colonization curves representing the number of individuals and specific richness over time t were assumed to behave according to the function proposed by Sheldon (1977): $N_t = at^b$, where a and b are constants. To obtain the colonization parameters, data were fitted with regression analysis to the linear model of the proposed equation: log $N_t = \log a + b \log t$. Differences in the intercepts and the slopes of the regression lines among stations and among seasonal periods were tested for significance with ANOVA. In order to establish the time at which the community reached its equilibrium (MacArthur & Wilson, 1967), the rates of immigration and emigration were plotted.

Results

The fauna of macroinvertebrates colonizing the artificial substrates during the entire study period

consisted of 92 identified taxa (See Supplementary material¹). The community parameters of the five sampling stations and both seasonal periods are showed in the Supplementary material. The artificial substrates from stations with sandy bottoms were colonized in both sampling periods by characteristic taxa of riffle areas. No apparent differences in colonization were observed (p > 0.05). The curves of the accumulative number of species and the cumulative number of individuals colonizing the substrata became asymptotic in each station and seasonal period between day 15 and day 22 (Fig. 2). Shannon's diversity index was relatively constant among all the stations. For the second season (spring-summer), the variation observed among stations was even lower. During both seasonal periods and in all stations, the community equilibrium was reached between day 15 and 17 (Fig. 2; see Supplementary material). A single station (station 2) reached its equilibrium on day 10 in the period of autumn-winter and on day 21 in the period of spring-summer.

During the period of autumn-winter, of the total number of species found in this study, 34% colonized the artificial substrata in the first day of sampling, 52% did so at the time of community equilibrium, and 65% colonized the artificial substrata at the end of the experiment (day 85). During the spring-summer period, the colonization rates for the same sampling dates were, respectively, 30, 44 and 64%. In the first day of colonization, the dominant taxa in both seasonal periods were Diptera (Chironomidae and Simulidae) with more than 53% of total abundance (see Supplementary material). At the time of

¹ Electronic supplementary material is available for this article at http://dx.doi.org/10.1007/s10750-006-0214-0.



Figure 2. Community variables of the artificial substrates for five sampling stations over time and across emigration/immigration curves.

equilibrium and at the end of the experiment, Diptera (Chironomidae and Simuliidae spp.) and Naididae (*Nais* sp.) were again the most abundant taxa, while the second most abundant colonizers were Hydropsychidae (*Smicridea* sp.), Leptophlebiidae (*Meridialaris* spp.) and Gripopterygiidae (*L. jaffueli*).

The colonization curves displayed a similar stabilization pattern for species richness and the number of individuals over time (see Fig. 3). ANOVA analysis showed that within the same season, differences in the slopes and the intercepts of the colonization curves among the five stations were not significant (p > 0.05).

Within the same station, no significant differences between seasons in the slopes and the intercepts of the curves were obtained (Table 2). The stability was reached approximately after 2 weeks of colonization in most of the stations and for both sampling periods; except in station E2 and E5, where stability was reached, respectively, in day 5 and 21. The classification of the sampling stations according to the taxonomic composition

Figure 3. Colonization slope of number of individuals $(LN_N^{\circ}IND)$ and specific richness (LN_RICH) over the time for total benthos.



	d.f.	MS error	F	р
Autumn-winter				
Intercepts	4	1.3673	0.9994	0.4517
Slopes	4	0.0002	0.9535	0.4731
Spring-Summer				
Intercepts	4	0.0003	0.2015	0.9318
Slopes	4	0.0022	0.0346	0.9973
Both periods				
Intercepts	9	0.6838	1.0007	0.4706
Slopes	9	0.0013	0.1558	0.9965

Table 2. ANOVA analysis between stations and periodical samplings of the intercepts and slopes of the lineal colonization curves between

found in the artificial substrates at the end of the experiment showed more than 70% similarity between sampling stations in both sampling periods (Fig. 4).

Discussion

The "Estero Nonguén" stream has nearly pristine conditions at its headwaters. These conditions favor a high biodiversity, making this stream an important study area for Chile where diversity studies of aquatic invertebrates practically do not exist. In this study, in a section only 5 km long corresponding to a drainage area of 44 km², a diversity of 92 taxa were found, whereas in other fluvial systems of Chile, the following number of taxa have been listed: 108 for the Biobío river (Arenas, 1995; hydrographical basin of 24,260 km²), 56 taxa for the Itata river (Habit et al., 1998; hydrographical basin of 11,000 km²) and 77 taxa for the Damas river (Figueroa et al., 2003; hydrographical basin of 513 km²).

Colonization is a recurrent process in the rivers (Gore & Milner, 1990; Mackay, 1992). In 5-km segment of the river studied, similar habitats existed and the entire segment behaved like a single habitat with the benthic macrofauna responding with equal colonization patterns for the studied stations and seasonal periods in terms of species richness, abundance and diversity index. The high diversity observed during the first day of exposure already suggests a pre-competitive colonization, "the empty niche model" proposed by Bazzaz (1975) and described by Niell & Varella (1985) in stones exposed to marine environments. This high diversity could be due to the continuous drift of organisms (Water, 1965; Williams & Hynes, 1976; Fenoglio et al., 2002), which facilities the processes of random colonization, reflected in a high initial diversity (S > 2). Diversity decreases as equilibrium is reached and later increases to obtain constant values (see Supplementary material, Fig. 2).

According to Mackay (1992), the point where the immigration and emigration curves cross (community equilibrium) is close to the time when the stability is reached. In our study, the community equilibrium always occurred between 2 and 5 days after community stability establishment. According to Gore (1982), this happens because the community needs an adjustment period before reaching the equilibrium, which would coincide with the incursion of the predators. This subtle difference allows us to see that the theoretical point of the balance could be expressed as the moment when the stability is maximized. Some studies have shown that the colonization is completed in a very short time period, within 4–6 days, although it can take from 1 to 9 weeks. However, the range of the colonization period is usually between 10 and 25 days (Towsend & Hildrew, 1976; Lake & Doeg, 1985; Mackay, 1992); which coincides with the results obtained in the present study (Fig. 4), where both seasons are very similar in taxonomic composition and time at the end of the experiment.

The first settlers in both periods were Chironomidae and Simuliidae, with more than 53%, and the second most abundant settlers Naididae, Hydracarina, Baetidae, Leptophlebiidae, Gripopterygiidae, Diamphipnoidae, Hydropsychidae, Elmidae and Psephenidae. Chironomidae have been shown to be one of the most important primary settlers, like Oligochaeta and Simuliidae (Mathooko, 1995). The Simuliidae have been described as the first settlers of the high and middle sectors of rivers (Moor et al., 1986) since they prefer clear substrata to adhere to their disks and need high-speed currents to capture their food. Baetidae have been reported as an abundant family of early colonizers (e.g. Ulfstrand et al., 1974; Lamberti et al., 1991). The same occurs with Leptophlebiidae in New Zealand (Sagar, 1983) and Australia (Lake & Doeg, 1985; Boulton et al., 1988).



Figure 4. Sampling station ordering at the end of the experiment (Bray-Curtis cluster analysis): (a) Autumn-winter, (b) Spring-summer.

The previously mentioned data allows us to show that the MacArthur & Wilson (1967) model is adequate for organisms in running waters, even though the original theory was developed for species that colonize and reproduce in "islands", while the permanence of the freshwater organisms in the "patches" is transitory. The principal source of immigrants corresponds to the immediately adjacent areas in the case of the exposed substrata in a riffle environment, and from upstream waters in the case of the sandy bottoms. These types of studies have been performed for several decades in Mediterranean rivers of North America, Europe and Australasia, but are scarce for the South American continent, especially in Chile (Gasith & Resh, 1999). Recent studies in Chile have focused on the use of aquatic macroinvertebrates as bioindicators for water quality and general description (Arenas, 1995; Figueroa et al., 2003), and have provided only a limited knowledge of the ecological performance of fluvial systems, a problem that appears also when comparing the fauna, since many of the families are endemic to the Neotropical region or Chile. However, the behavior of the macroinvertebrates in this study seems to coincide with the behavior from other similar climatic regions in the world.

The colonization in the lotic system is an important continuous mechanism, which can give important information on recovery time of sectors previously disturbed. From this point of view, the features of "Estero Nonguén" stream, which has nearly pristine conditions at its headwaters, are very important as reference sites to carry out biodiversity and ecosystem functionality studies.

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References

- Allan, D. J., 1997. Stream Ecology: Structure and Function of Running Waters. Chapman & Hall, London, 388 pp.
- Arenas, J. N., 1995. Composición y distribución del macrozoobentos del curso principal del río Biobío, Chile. Medio Ambiente 12(2): 39–50.
- Bazzaz, F. A., 1975. Plant species diversity in old-field successional ecosystem in southern Illinois. Ecology 56: 485–488.
- Boulton, A. J., G. M. Spangaro & P. S. Lake, 1988. Macroinvertebratess distribution and recolonization on stones subjected to varying degrees of disturbance – an experimental approach. Archiv für Hydrobiologie 113: 551–576.
- Bray, J. R. & J. T. Curtis, 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27: 325–349.
- Brown, S. C., K. Smith & D. Batzer, 1997. Macroinvertebrate responses to wetland restoration in northern New York. Environmental Entomology 26(5): 1016–1024.
- CSIRO, 1991. The Insects of Australia. A Textbook for Students and Research Workers. Melbourne University Press and Cornell University Press: Vol. I–II, 1137 pp.

- Downes, B. J. & P. S. Lake, 1991. Different colonization patterns of two closely related stream insects (*Austrosimulium* spp.) following disturbance. Freshwater Biology 26(2): 295–306.
- Fenoglio, S., P. Agosta, T. Bo & M. Cucco, 2002. Field Experiments on colonization and movements of stream invertebrates in an Apennine river (Visone, NW Italy). Hydrobiologia 474: 125–130.
- Fernández, H. R. & E. Domínguez, 2001. Guía para la determinación de los artrópodos bentónicos sudamericanos. Serie Investigaciones. Edit. Universitaria de Tucumán, 282 pp.
- Figueroa, R., C. Valdovinos, E. Araya & O. Parra, 2003. Macroinvertebrados bentónicos como indicadores de calidad de agua de ríos del sur de Chile. Revista Chilena de Historia de Natural 76: 275–285.
- Friberg, N., B. Kronvang, H. O. Hansen & L. M. Svendsenv, 1998. Long-term, habitat-specific response of a macroinvertebrate community to river restoration-Aquatic Conservation. Marine and Freshwater Ecosystem 8(1): 87–99.
- Gasith, A. & V. H. Resh, 1999. Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. Annual Review of Ecology and Systematic 30: 51–81.
- Gore, J. A., 1982. Benthic invertebrate colonization: source distance effects on community composition. Hydrobiologia 94: 183–193.
- Gore, J. A. & A. M. Milner, 1990. Island biogeographical theory: can it be used to predict lotic recovery rates?. Environmental Management 14: 737–753.
- Habit, E., C. Beltrán, S. Arévalo & P. Victoriano, 1998. Benthonic fauna of the Itata river and irrigation canals (Chile). Irrigation Sciences 18: 91–99.
- Lake, P. S. & T. J. Doeg, 1985. The macroinvertebrate community of stones in an Australian upland stream. Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie 22: 2141–2147.
- Lamberti, G. A., S. V. Gregory, L. R. Ashkenas, R. C. Wildman & K. M. S. Moore, 1991. Stream ecosystem recovery following a catastrophic debris flow. Canadian Journal of Fisheries and Aquatic Sciences 48: 196–208.
- MacArthur, R. H. & E. O. Wilson, 1967. The Theory of Island Biogeography. Princeton Univ. Press, Princeton, NJ.
- Mackay, R. J., 1992. Colonization by lotic macroinvertebrates: a review of processes and patterns. Canadian Journal of Fisheries and Aquatic Sciences 49: 617–628.
- Mathooko, J. M., 1995. Colonization of artificial subtrates by benthos in a second-order high altitude river in Kenya. Hydrobiologia 308(3): 229–234.
- Matthaei, C. D., U. R. S. Uehlinger, E. Meyer & A. Frutiger, 1996. Recolonization by benthic invertebrates after experimental disturbance in a Swiss prealpine river. Freshwater Biology 35: 233–248.
- Moor, F. C., F. M. Chutter & I. J. Moor, 1986. Drift behaviour and microhabitat selection in the preimaginal stages of *Simulium chutteri* (Diptera Simuliidae). Hydrobiologia 133: 143–154.
- Niell, X. & M. Varella, 1985. Initial colonization stages on rocky coastal substrates. Marine Ecology 5(1): 45–56.
- Paltridge, R. M., P. L. Dostine, C. L. Humphrey & A. J. Boulton, 1997. Macroinvertebrate recolonization after rewetting of a tropical seasonally-flowing stream (Magela

Creek, Northern Territory, Australia). Marine and Freshwater Research 48(7): 633–645.

- Peterson, C. G., 1996. Mechanisms of lotic microalgal colonization following space-clearing disturbances acting at different spatial scales. Oikos 77(3): 417–435.
- Resh, V. & D. M. Rosenberg, 1984. The Ecology of Aquatic insects. New York, Westport, Connecticut, London: 615 pp.
- Sagar, P. M., 1983. Invertebrate recolonization of previously dry channels in the Rakaia River. New Zealand Journal of Marine and Freshwater Research 17: 377–386.
- Sheldon, A. L., 1977. Colonization dynamics of aquatic insects. In Resh, V. H. & D. M. Rosenberg (eds), The Ecology of Aquatic Insects. Praeger, NY, 401–429.
- Townsend, C. R. & A. G. Hildrew, 1976. Field experiments on the drifting, colonization and continuous redistribution of stream benthos. Journal of Animal Ecology 45: 759–773.

- Ulfstrand, S., L. M. Nilsson & A. Stergar, 1974. Composition and diversity of benthic species collectives colonizing implanted substrates in a south Swedish stream. Fauna Entomológica Scandinavica 5: 115–122.
- Water, T. F., 1965. Interpretation of invertebrate drift in stream. Ecology 46: 327–334.
- Williams, D. D. & H. B. N. Hynes, 1976. The recolonization mechanisms of stream benthos. Oikos 27: 265–272.
- Wohl, D. L., J. B. Wallace & J. Meyer, 1995. Benthic macroinvertebrate community structure, function and production with respect to habitat type, reach and drainage basin in the southern Appalachians (U.S.A.). Freshwater Biology 34: 447–464.