Journal of Natural History
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tnah20

Predatory insects in lentic freshwater habitats from northwest Patagonia: richness and phenology

Fabián G. Jara [a] , Carmen A. Úbeda [b] & María G. Perotti [a]

[a] Laboratorio de Fotobiología , INIBIOMA (CONICET-Universidad Nacional del Comahue) , Bariloche , Argentina

[b] Departamento de Zoología , INIBIOMA (CONICET-Universidad Nacional del Comahue), Quintral 1250 , 8400 , Bariloche , Argentina

To cite this article: Fabián G. Jara , Carmen A. Úbeda & María G. Perotti (2013): Predatory insects in lentic freshwater habitats from northwest Patagonia: richness and phenology, Journal of Natural History, DOI:10.1080/00222933.2013.791932

To link to this article: http://dx.doi.org/10.1080/00222933.2013.791932

Journal of Natural History, 2013
http://dx.doi.org/10.1080/00222933.2013.791932

Taylor & Francis
Taylor & Francis Group

Predatory insects in lentic freshwater habitats from northwest Patagonia: richness and phenology

Fabián G. Jara[a]*, Carmen A. Úbeda[b] and María G. Perotti[a]

[a] *Laboratorio de Fotobiología, INIBIOMA (CONICET-Universidad Nacional del Comahue), Bariloche, Argentina;* [b] *Departamento de Zoología, INIBIOMA (CONICET-Universidad Nacional del Comahue), Quintral 1250, 8400 Bariloche, Argentina*

(*Received 22 May 2012; final version received 29 March 2013*)

The main purpose of this work was to study the richness, phenology and abundance of predatory insects throughout the hydroperiod and how they relate to the environmental parameters in lentic bodies of water in northwest Patagonia. Nineteen fishless wetlands and three wetlands with fish were studied, which are located in the surroundings of the Nahuel Huapi National Park. Biotic and abiotic variables were measured during the hydroperiod of each wetland. The dip-netting sampling technique was used to determine the richness of predatory insects and to study the phenology of the dominant species in four wetlands. Species richness in temporary wetlands ranged from one to nine species per wetland and does not differ from that observed in the permanent environments with or without fish predators. Maximum insect richness was recorded in late spring and was associated with the maximum depth of the wetland and its structural complexity as well as with the duration of the hydroperiod.

Keywords: aquatic insects; richness; hydroperiod wetland; phenology; Patagonia

Introduction

Freshwater wetlands that undergo periods of drought are essential habitats for the development, growth and reproduction of a wide range of organisms, many of which live exclusively in this type of environment (Schneider and Frost 1996; Williams 1997). Many of these ponds are biodiversity "hotspots", providing fundamental ecosystem services to wildlife (e.g. breeding and foraging habitat) and humans (flood protection, aesthetic and recreational values) (De Meester et al. 2005; Williams 2006). Despite intensive research in recent years, their ecology remains poorly understood and many of these little-known ecosystems continue to disappear at an increasing rate through agricultural expansion, alteration of flow regimens, draining and damming, and habitat fragmentation. These threats are likely to intensify with climate change so the sustainable use and effective management of these ecosystems is all the more critical (Perotti et al. 2005). Among the fauna colonizing these wetlands are different groups of invertebrates such as snails, leeches, planarians, crustaceans and insects, and vertebrates such as amphibians. The protection of these habitats, which may exist as neighbouring patches, allowing species to migrate between them (Gibbs 2000; Roe and Georges 2007), is essential to the conservation of many of these biotas. Nevertheless,

---

*Corresponding author. Email: fjara77@hotmail.com they have always been assigned less importance than other kinds of aquatic environments like rivers and lakes, and have been neglected for many years, mainly because of their small size and temporary nature, and they are often destroyed by human actions (Grillas et al. 2004a, 2004b; Williams 2006; Zacharias et al. 2007).

Predators play a key role in structuring communities; therefore any change in predator richness, whether caused by the introduction of exotic species, human impact or global warming, may alter the composition, diversity and population dynamics of lower trophic levels (Bruno and Cardinale 2008). For example, insects are one of the most diverse groups in these aquatic environments. They are recognized in food chains in these environments for their role as voracious predators of different organisms, both invertebrates (i.e. zooplankton) and vertebrates (fish and amphibian larvae). Because these environments cannot be colonized by fish because of their temporary character, insects are the top predators in temporary environments, and can attain high population densities (Wellborn et al. 1996; Wilbur 1997) generating a trophic cascade that moves through the entire food chain (Bruno and Cardinale 2008; Magnusson and Williams 2009). They have been described as gape-unconstrained predators, and can prey on one species throughout their ontogeny (Peckarsky 1982; Urban 2007). They can eat a wide range of prey sizes, even prey items larger than themselves, because some species can eat their prey either in discrete portions or by manipulating it with the mandibles (engulfers), while others can suck body fluids after injecting digestive enzymes (piercers). The richness and abundance of predators are key parameters in determining ecological processes in the population and community (Bruno and Cardinale 2008).

Predatory insects are key in aquatic ecosystems because they can exercise control over other organisms, modifying the age and size structure or delimiting their distribution (Sih et al. 1985; Batzer and Wissinger 1996; Jeffries 1996; Blaustein 1998; Magnusson and Williams 2009; Cobbaert et al. 2010). Furthermore, they are important indicators of environmental health and trophic state (Foster et al. 1989; Painter 1999; Biggs et al. 2000; Chovanec and Waringer 2001; Sahlen and Ekestubbe 2001; Chovanec et al. 2004; Nicolet et al. 2004), and are important to health because many of them eliminate or control disease vectors (Jerez and Moroni 2006; Kumar and Hwang 2006; Saha et al. 2010).

The taxonomy of insect species is fairly well known in the temporary and semi-temporary aquatic systems in Patagonia (Bachmann 1962, 1963, 1998; Trémouilles 1984; Muzón 1995; Alarie et al. 2009), but their biology and ecological role require further study. There are compilations of their geographical and ecological distributions (Muzón 1995, 1997, 2009; Archangelsky 2004; Muzón et al. 2005; Melo 2009). They are known to feed on zooplankton, other invertebrates such as mosquito larvae, anuran larvae and even their congenerics (Casanovas and Úbeda 2006; Jara and Perotti 2009, 2010; Gilbert and Diéguez 2010; Jara 2010; Moncada 2011; Jara et al. 2012). Given the scarcity of data on their phenology and abundance, and considering that knowledge of this group is key to the progress of research into aquatic ecosystems, the aims of this study are: (1) to assess the richness of predatory insects in freshwater wetlands located on a decreasing west–east rainfall gradient in the Nahuel Huapi National Park and surrounding, Río Negro Province, Argentina; (2) to analyse the species richness in relation to different environmental parameters; and (3) to analyse the phenology and abundance of the most frequent species during the hydroperiod.

Material and methods

Study area

The study area is located in northwest Patagonia, Argentina. Wetlands were selected on a strip transect along a west–east decreasing rainfall gradient. The transect runs from 71°33′ W in the west to 71°10′ W in the east, and the strip lies between 41°03′ S and 41°16′ S. Nineteen fishless wetlands and three wetlands with fish were studied: native fish species *Galaxias maculatus*, Galaxiidae (up to 9 cm), and the introduced salmonid species *Oncorhynchus mykiss* (up to 76 cm), *Salmo trutta* (up to 78 cm) and *Salvelinus fontinalis* (up to 40 cm) along the transect, which was located in the surroundings of San Carlos de Bariloche city and Nahuel Huapi National Park (Figure 1). Precipitation along the transect ranges from 1500 mm a year in the west to 800 mm a year in the east.

Sampling

Each fishless wetland was sampled during 2006–2007 including two hydroperiods corresponding to austral spring and summer. The wetlands were classified according to their location in three kinds of environments: (1) wetlands in the Patagonian Andes forest (vegetation characterized by presence of Nothofagaceae such as *Nothofagus dombeyi* and *Nothofagus pumilio*), (2) wetlands in the Patagonian steppe (with grasses such as *Stipa speciosa*, *Festuca pallescens*, and thorny shrubs such as *Mulinum spinosum*) and (3) wetlands in the ecotone between those two units (with small, isolated

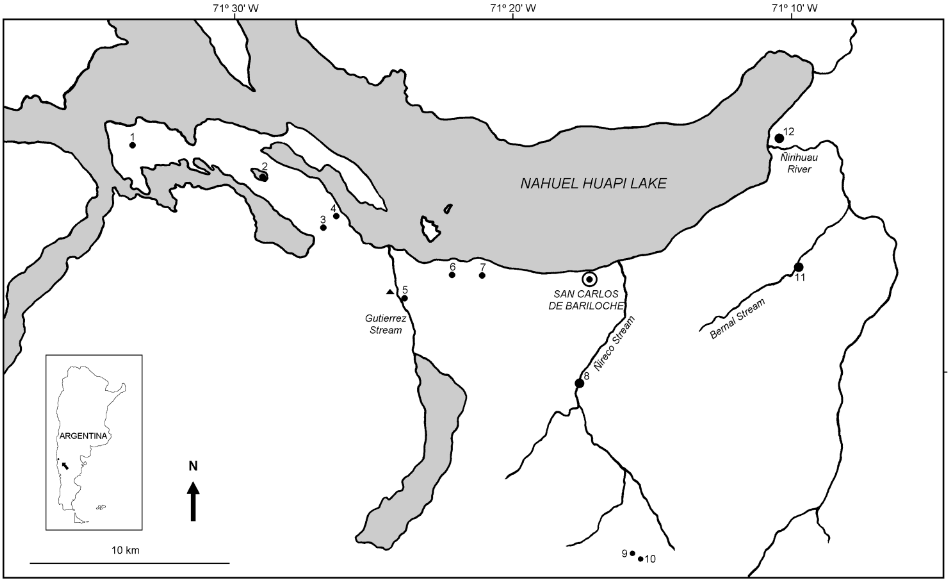

Figure 1. Map of the study area surrounding the city of San Carlos de Bariloche. Numbers refer to wetland location: 1 = Llao-Llao; 2 = Laguna El Trébol; 3 = Mallín 2 de Agosto; 4 = Laguna Fantasma; 5 = Virgen de las Nieves; 6 = Mallín Pinar de Festa; 7 = Teleférico; 8 = Mallín Ñireco, Ñireco 1 and Ñireco 2; 9 = Laguna Verde; 10 = Mallín Los Patos; 11 = Bernal 1–6; 12 = Ñirihuau 1–4. The triangle indicates the location of the meteorological station.

trees such as *Maytenus boaria*, shrubs such as *Nothofagus antarctica*, *Lomatia hirsuta*, *Schinus patagonicus* and *Berberis darwinii*). In turn, according to the duration of the hydroperiod, each wetland was classified into one of the following three categories: long-duration or permanent ponds, intermediate-duration ponds (between 6 and 9 months) and short-duration ponds (less than 6 months). Wetlands were identified using Geographic Information System technology (GPS-Garmin eTrex®).

Water temperature, dissolved oxygen and conductivity compensated for temperature were measured *in situ* using the YSI 85 multi-parameter probe. The pH was measured with the pH/ORP HANNA HI 98140. All data were collected between 11.00 h and 16.00 h. Maximum depth and maximum area were recorded. The richness of aquatic and paludal plants was determined as an estimator for the structural complexity of the habitat, for which aquatic and paludal plants were collected manually at all the wetlands, and the species or at least genera were identified.

Species richness

Insect richness was studied in both fishless wetlands and wetlands with fish, employing dip-net sweeps (net dimensions 36 × 9 × 25 cm; 5-mm mesh) in the vegetated areas during the daytime following Jara and Perotti (2010), because preliminary monitoring showed that species are concentrated in these vegetated areas during the day. The number of sweeps was determined according to the area of each pond as 30 sweeps for ponds > 1000 m^2, 15 sweeps for ponds between 1000 and 100 m^2, and five sweeps in ponds < 100 m^2. The net was swept horizontally through 2 linear metres in the littoral zone, including the bottom and the water column. The material collected was preserved in 70% alcohol to be identified subsequently in the laboratory. Other groups of arthropods such as water boatmen, caddis fly larvae and mosquito larvae were present in the samples, but were not considered in this study either because of their position in the food chains or because they are mainly collectors, gatherers or filterers. The data were recorded in a chart for insects found per wetland. Insect species richness was determined per wetland and the distribution index (frequency) was calculated for each species as: Σ wetlands with the species i/total number of wetlands sampled. The insects were classified according to feeding mode (piercers, engulfers) and hunting strategy (ambushers, searchers) following Peckarsky (1982).

Field phenology

Daily rainfall and minimum and maximum temperature were obtained from a meteorological station located at Laboratorio de Fotobiología (INIBIOMA), Bariloche, Río Negro, Argentina. To study insect phenology in the field four of the 22 wetlands were selected, represented by different hydroperiods: Ñirihuau 1, Ñirihuau 2, Laguna Fantasma and Mallín Ñireco. The wetlands were selected based on preliminary data collected in the previous season and were considered as representatives of a high abundance of more common insect predators. Samples were taken using the same methodology as describe for insect richness and were taken from June 2006 to March 2007 to describe the phenology of the most frequent and larger aquatic insects. The specimens collected were classified in the field as adult or larval stage (larvae for beetle, nymph for hemipterans and odonates). The density of each species was estimated, and was expressed as individuals per cubic meter (ind./m^3).

Statistics

One-way analysis of variance tests were used to determine whether there are differences in species richness according to the wetland hydroperiod (short, intermediate and permanent) and location (forest, ecotone and steppe). In addition, a two-sample *t*-test was used to test whether there were differences between the richness of species in permanent wetlands with and without the presence of fish. A contingency table was used to verify whether there is dependence between predatory insect species and type of wetland (short, intermediate, long without fish and long with fish). Multiple linear regression was performed to evaluate whether predatory-insect richness is affected by maximum depth, maximum area and structural complexity of the wetland. A three-way analysis of variance test for a balanced design with fixed factors was performed to determine changes in the density of insects, considering the following density-determining factors: the insect species (five levels), the wetland (four levels) and the sampling date (five levels). When analysis of variance revealed significant differences in the treatments, the Holm–Sidak method for multiple comparisons was used (SIGMASTAT 3.5).

Results

Wetland characteristics

Of the wetlands studied, 28.5% are located in the forest, 28.5% in the steppe and 43% in ecotone areas (Table 1). Regarding the duration of the hydroperiod, 14.3% of the wetlands are long duration, 33.3% short duration and 52.4% intermediate duration (Table 1). Five of the wetlands are located in protected natural areas (Laguna Fantasma, Laguna Verde, Mallín de Los Patos, Laguna Llao-Llao and Laguna El Trébol), while the other 17 are located in areas with some degree of human impact.

The environmental characterization of the wetlands surveyed showed different conductivity (17–239 μS cm^{-1}), with low values at permanent wetlands from mountain forest (Laguna Verde and Mallín de Los Patos), while higher values were observed at temporary ponds in the steppe (Table 1). In general, pH was slightly alkaline or acidic (Table 1). Temperature varied seasonally with wide daily fluctuation, with low temperatures prevailing in the morning (4°C) and high temperatures in the afternoon (up to 30°C). Dissolved oxygen values were always near saturation (Table 1).

Aquatic vegetation was present in 67% of the visited wetlands (Table 1). In some ponds the vegetation was sparse or patchy and restricted to the littoral zone, and in others it covered the entire wetland. The richness of aquatic vegetation ranged from 1 to 15 species per wetland, and was dominated by rushes (*Juncus bufonius*, *Juncus procerus*), sedges (*Eleocharis macrostachya*, *Carex aematorrhyncha*), grasses (*Puccinellia glaucescens*, *Poa* sp., *Stippa* sp.) and submerged species (*Myriophyllum quitense*, *Hydrocotyle* sp., *Veronica anagallis-aquatica*).

Distribution of insect species in the wetlands sampled

The most frequent species in the study area were coleopteran larvae and adults of the genera *Tropisternus* (Figure 2), whereas among the Odonata, *Rhionaeschna variegata* was the most frequent species of Anisoptera in the area and *Cyanallagma interruptum* was the only Zygopteran found and was widely distributed (Figure 2). Three

Table 1. Geographic location, surrounding environment, morphometric traits, physicochemical data, hydroperiod, insect richness and habitat complexity (number of aquatic plant species) in the wetlands sampled during spring and summer.

Wetland	Location	Elevation (m a.s.l.)	Surrounding environment	Area (m^2)	Depth (m)	Temperature (°C)	pH	Dissolved O_2(mg l^{-1})	Conductivity (μS cm^{-1})	Hydroperiod duration	Predatory insect richness	Habitat complexity
Llao-Llao	41° 2′ 58″S; 71° 33′ 58″W	821	Forest	150	0.4	6.4–24	7–8	5–8	–	Intermediate	9	s/d
Laguna Fantasma	41° 5′ 35″S; 71° 27′ 4″W	794	Forest	10,000	2	11–24	7–7.6	6.4–7	98–114	Intermediate	8	10
Laguna el Trébol*	41° 4′ 15″S; 71° 29′ 25″W	790	Forest	43,000	12	_	7.53	8.7	93.3	Long	7	5
Mallín 2 de Agosto	41° 5′ 49″S; 71° 27′ 35″W	791	Forest	90	0.5	13.6–28	7–7.8	8.6–12	94.6–124.6	Intermediate	8	6
Virgen de las Nieves*	41°7′60″S; 71° 24′ 51″W	801	Ecotone	550	1	13.3–16.9	7.89–8.96	8.8	57.7	Long	8	10
Mallín Pinar de Festa	41° 7′ 32″ S; 71° 23′ 6″W	830	Forest	13	0.4	11–28	6.5–7.5	–	52.6–201	Intermediate	4	4
Teleférico	41° 7′ 40″S, 71° 22′ 6.0″W	816	Ecotone	257	1.7	8.4–23.6	7–7.29	7.29–13.8	201–239	Intermediate	7	7
Mallín Ñireco*	41° 10′ 53″S; 71° 19′ 14″W	899	Ecotone	1000	0.88	8.1–25.5	6.6	7.7–9.8	58–61	Long	10	15
Ñireco 1	41° 10′ 51″S; 71° 19′ 10″W	906	Ecotone	240	1.4	8.3–30	7–8	8.9–9.1	73.1–75.9	Short	1	1
Ñireco 2	41° 10′ 55″S; 71° 18′ 59″W	906	Ecotone	20	0.3	16.5–30	7.74–8.38	8.6–8.9	82.8–86.7	Short	1	0
Mallín Los Patos*	41° 15′ 44″S; 71° 17′ 45″W	1461	Forest	1010	0.7	–	–	–	–	Long	6	s/d
Laguna Verde*	41° 15′ 37″S; 71° 17′ 54″W	1525	Forest	3540	6	–	6–7.2	–	17–20	Long	4	3
Bernal 1	41° 8′ 49″S; 71° 11′ 0.07″W	837	Steppe	556	0.38	8-30	6.24–8.25	7.9–8.3	54.1–86.1	Intermediate	2	4

(*Continued*)

Table 1. (Continued).

Bernal 2	41° 8′ 49″S; 71° 11′ 0.07″W	837	Steppe	234	0.45	13.5–28.5	–	7.3–8.8	22–36.8	Short	2	2
Bernal 3	41° 8′ 49″S; 71° 11′ 0.09″W	838	Steppe	543	0.46	13.6–30	6.36–7.5	7.2–9.4	31.6–124.1	Short	1	4
Bernal 4	41° 8′ 38″S; 71° 10′ 37″W	838	Steppe	87	0.4	9–26.5	6–7.5	7.3–9.9	53.4–112.9	Short	1	2
Bernal 5	41° 8′ 34″S; 71° 10′ 21″W	844	Steppe	33	0.3	19–28.8	–	7.1–9.6	52.5–68.5	Short	1	2
Bernal 6	41° 8′ 33″S; 71° 10′ 25″W	837	Steppe	15	0.4	18–25.5	8–8.25	7.7–9	70.5–98.3	Short	1	0
Ñirihuau 1	41° 4′ 57″S; 71° 10′ 47″W	771	Ecotone	1000	0.7	8.7–26.5	6.5–7.8	6.1–9.5	65.15–91.15	Intermediate	7	7
Ñirihuau 2	41° 4′ 60″S; 71° 11′ 1″W	771	Ecotone	6837	0.6	12.73–25	6.66–7.75	6–8	63.1–129.33	Intermediate	5	10
Ñirihuau 3	41° 5′ 1″S; 71° 11′ 5″W	771	Ecotone	15.1	0.6	13.17–24	7.14	6–7.5	81.9–108.1	Intermediate	4	5
Ñirihuau 4	41° 5′ 17″S; 71° 10′ 48″W	777	Ecotone	651.5	0.5	17–30.5	7.48	7.45–8.05	58.7–80.3	Intermediate	3	2

The hydroperiod classification of each wetland is provided in the Material and Methods. The values of the physicochemical variables show the minimum and maximum values recorded during sampling between 11.00 h and 16.00 h. * indicates permanent wetland.

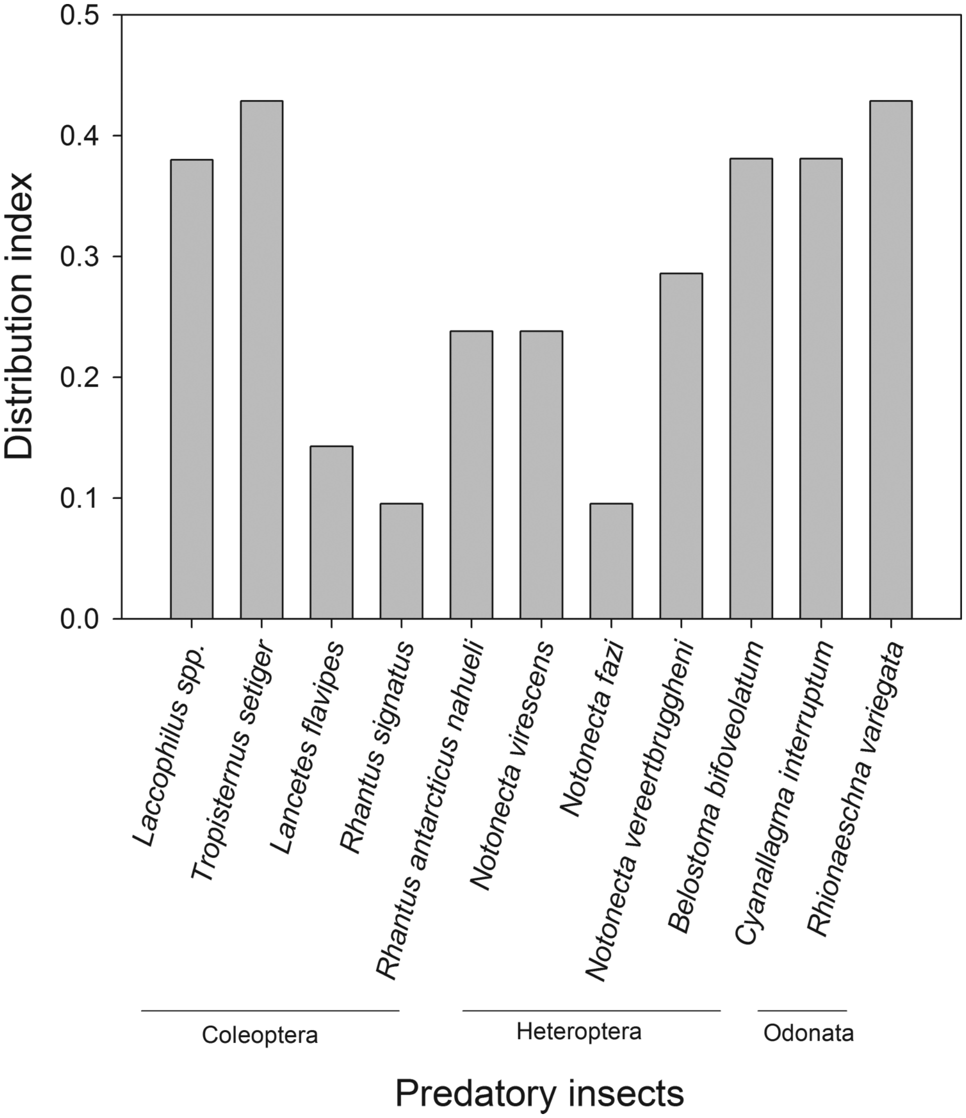

Figure 2. Predatory insect distribution in the study area. Distribution index was obtained by the ratio: number of wetlands with species i/total number of wetlands sampled.

species of notonectid were found (*Notonecta vereertbruggheni*, *Notonecta virescens* and *Notonecta fazi*), of which the most frequent were *N. vereertbruggheni* and *N. virescens* (Figure 2).

Composition, feeding modes and hunting strategies

Fourteen species of predatory insects were recorded in temporary wetlands, of which at least nine are exclusive to Patagonia (Table 2). Insect richness in temporary wetlands ranged from one to nine species (Table 1). The assemblage of predatory insects in the

Table 2. Predatory insects found in the wetlands studied; maximum body size recorded for each species and its presence in the three types of wetland defined according to surrounding environment.

Predatory insects	Maximum body size observed (mm)	Forest wetlands	Ecotone wetlands	Steppe wetlands	Feeding mode	Predator strategy
Hemiptera						
Notonectidae						
Notonecta vereertbruggheni Hungerford 1928 (*)	14	X	X		P	S
Notonecta virescens Blanchard 1853 (*)	9	X	X	X	P	S
Notonecta fazi Hungerford 1930 (*)	13.5	X			P	S
Gelastocoridae						
Nerthra ranina Herrich-Schäffer 1853†	7		X		P	A
Belostomatidae						
Belostoma bifoveolatum Spinola 1852 (*)	25	X	X		P	A
Coleoptera						
Ditiscidae						
Rhantus antarcticus nahueli Trémouilles 1984 (*)	35	X	X		P/E	A/S
Rhantus signatus (Fabricius 1775)	30	X			P/E	A/S
Rhantus sp.	23			X	P/E	A/S
Lancetes flavipes Zimmerman 1924	28	X			P/E	A/S
Lancetes sp.	20	X	X		P/E	A/S
Laccophilus spp.	6	X	X		P/E	ND
Hydrophilidae						
Tropisternus setiger (Germar 1824)	24	X			P/E	A/S
Tropisternus sp.	18	X	X	X	P/E	ND
Odonata						
Zygoptera						
Coenagrionidae						
Cyanallagma interruptum (Selys 1876) (*)	15.9	X	X		E	A
Anysoptera						
Aeshnidae						
Rhionaeschna variegata (Fabricius 1775)	38.7	X	X		E	A/S
Libellulidae						

(*Continued*)

Table 2. (Continued).

Predatory insects	Maximum body size observed (mm)	Forest wetlands	Ecotone wetlands	Steppe wetlands	Feeding mode	Predator strategy
Erythrodiplax connata (Burmeister, 1839) (*)†	16	X	X		E	A
Gomphidae						
Neogomphus sp. (*)†	15	X			E	A
Cordulidae						
Rialla villosa Rambur, 1842 (*)†	23	X			E	A

Note: * = species exclusive to the Patagonia region. P = piercer, E = engulfer, A = ambusher, S = searcher, M = mixed strategy (A/S), ND = no data available. † = species observed only in permanent wetlands. In the case of beetle, P/E = indicate that larval stages of beetle are piercing but then in the adult stage they are engulfers.

wetlands studied was dominated by coleopterans, represented by four genera (eight species), followed by Heteroptera (Hemiptera) with three genera (four species) and Odonata with two genera (two species) (Table 2). Three species of odonate larvae were exclusively from permanent wetlands (Table 2). The two feeding modes were piercers (28.5%), e.g. *Belostoma* and *Notonecta* species (Table 2), and engulfers (14.3%); 77.2% belong to both feeding modes because the beetle species change their feeding method during ontogeny, the larvae are piercers and the adults are engulfers. Of the total species found in temporary wetlands, 23% were exclusively searchers and 15% were exclusively ambushers. The remaining 62% of the species used a mixed hunting strategy characterized by alternating periods of searching and resting on perches from which the prey can be ambushed (e.g. *Rhionaeschna* and *Rhantus*) (Table 2).

Species richness and environmental influences

Species richness varied according to the hydroperiod ($F_{2,18} = 20.71$, $P < 0.001$), but there were only differences in the richness of predatory insects between short hydroperiod wetlands and the other two categories (long versus short $t = 5.58$, $P = 0.017$; intermediate versus short $t = 5.50$, $P = 0.025$; Figure 3). Richness increased throughout spring in almost all the wetlands, attaining maximum values in early summer (Figure 4). Average insect richness varied according to the environment surrounding the wetlands ($F_{2,18} = 7.5$, $P = 0.004$). In wetlands located in the forest, average insect richness was 6.28 ± 0.8 species per wetland (with a total of 17 species of insects), in wetlands located in the ecotone, it was 4.75 ± 1.11 (11 species) and in wetlands located in the steppe it was 1.33 ± 0.21 (three species) (Table 2). The predatory insect richness between permanent wetlands with and without fish did not differ significantly (long duration without fish: species richness = 5 ± 1, long duration with fish = 8.33 ± 0.8; $t = 2.45$, $P = 0.09$). Also, predatory insect species were associated with the type of wetland ($\chi^2 = 96.23$, $P = 0.0027$).

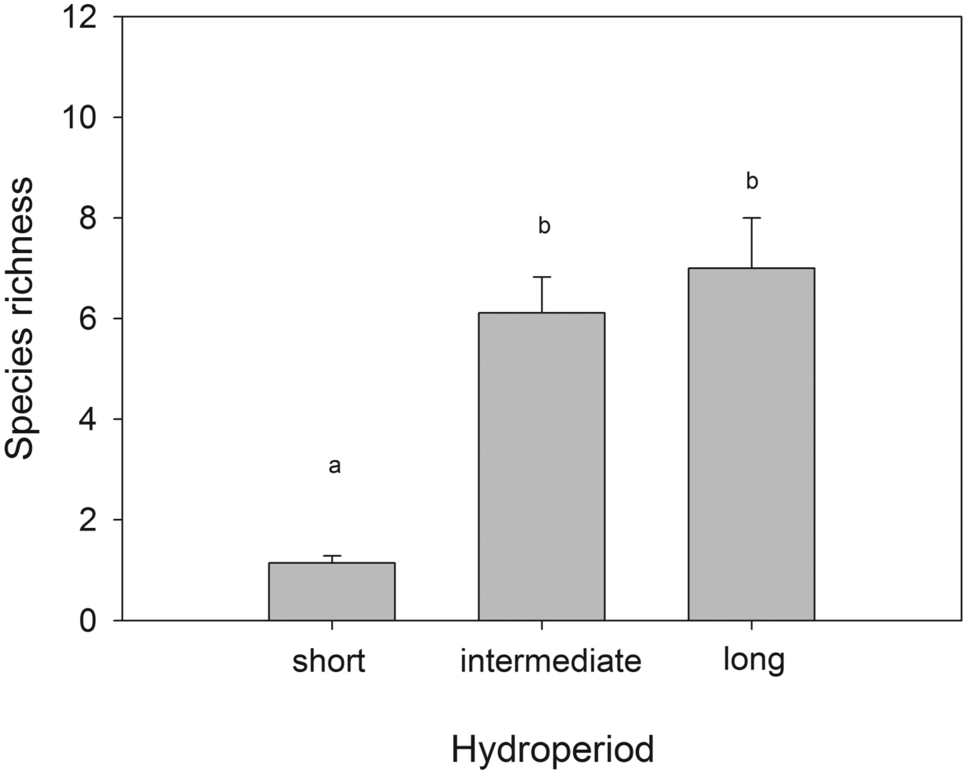

Figure 3. Comparison of the richness of predatory insects in three types of wetlands, classified according to the duration of the hydroperiod. Different letters indicate significant differences in species richness ($P < 0.01$).

The relationship between insect richness and maximum area, maximum depth and structural complexity of the wetland was significant and positive ($F_{3,13} = 20.77$, $P < 0.001$, $R^2 = 0.827$). Not all these variables explained insect richness; a significant relationship was only found with maximum depth (coefficient = 2.16, $P = 0.005$) and structural complexity (coefficient = 0.291, $P = 0.002$) of the wetland. The greatest insect richness was found in the deepest, most structurally complex wetlands (greater number of species of aquatic plants). In contrast, very shallow (i.e. short duration) wetlands without vegetation were poor in insect species, with only two coleopteran species represented.

Field phenology

The phenology of these insects followed a seasonal pattern in temporary wetlands (short and intermediate duration) (Figure 5). According to the hydroperiod of the wetlands, abundance was found to vary in each wetland as spring progressed (Figure 6). The species, type of wetland and sampling date all affected the insect population density (species $F_{4,48} = 5.03$, $P = 0.002$; wetland $F_{3,48} = 56.98$, $P < 0.001$; time $F_{4,48} = 9.02$, $P < 0.001$). In the three temporary wetlands (Ñirihuau 1, Ñirihuau

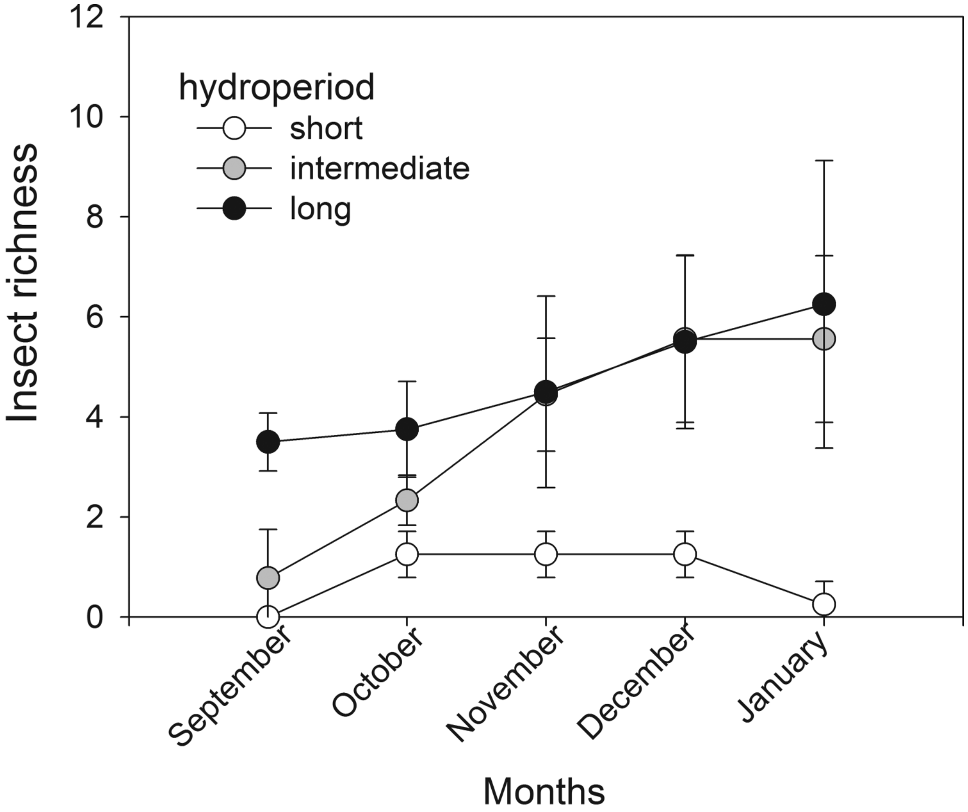

Figure 4. Monthly variation in predatory insect richness in the wetlands studied, showing mean richness (± SE) for the wetlands classified according to their hydroperiod.

2 and Laguna Fantasma) predatory insects first appeared in October, in contrast to the permanent wetland (Mallín Ñireco), where insects were varied and abundant as from September (Figure 6). Insect density in Mallín Ñireco differed significantly from the rest of the wetlands ($P < 0.05$ for all comparisons) and had higher densities, with dominance of *N. vereertbruggheni* and *Cyanallagma interruptum* (Figure 6). The wetlands Ñirihuau 1 and Ñirihuau 2 formed a homogeneous group, as did Ñirihuau 1 and Laguna Fantasma ($P > 0.05$ for both groups). September and October did not differ regarding abundance of aquatic insects between wetlands and had the greatest abundance of insects, but differed significantly from the rest of the months studied ($P < 0.05$ for all comparisons). In the wetland Ñirihuau 1, *Belostoma bifoveolatum* was dominant and the first species to colonize the environment, whereas *N. vereertbruggheni* attained its highest density in January; both species maintained significantly higher densities than the rest of the species throughout the study period ($P < 0.05$). The wetland Ñirihuau 2 differed from Ñirihuau 1 because of the presence of *Cyanallagma interruptum* in late summer and the presence of *Rhantus antarcticus* in December (Figure 5). Significant differences were found between the densities of the different species in November and December, though not in January ($P < 0.05$ for *Rhantus* and *Belostoma* versus the rest of the species in November and for *Belostoma* versus the rest of the species in December and January).

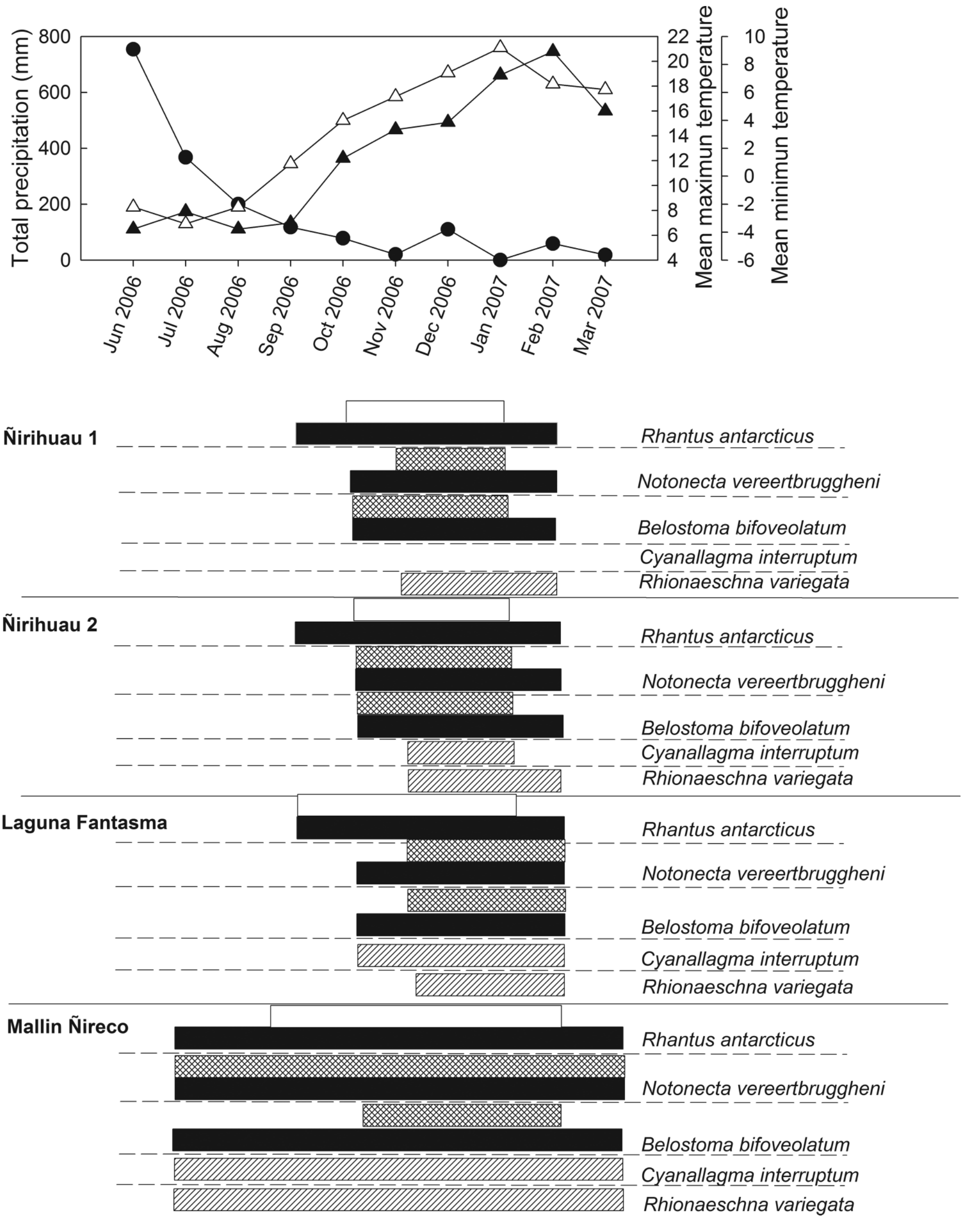

Figure 5. Phenology of predatory insects (black bar = adult stage; white bar = coleopteran larva; single-hatched bar = odonate nymph; double-hatched bar = hemipteran nymph), and climate data (precipitation = black circles; minimum temperatures = white triangles; maximum temperatures = black triangles) from June 2006 to March 2007.

Discussion

The richness of predatory insects in the study area is represented by several species of beetles, notonectids and odonates. Our results agree with the latitudinal decrease in species diversity, which determines that the richness of most plant and animal groups

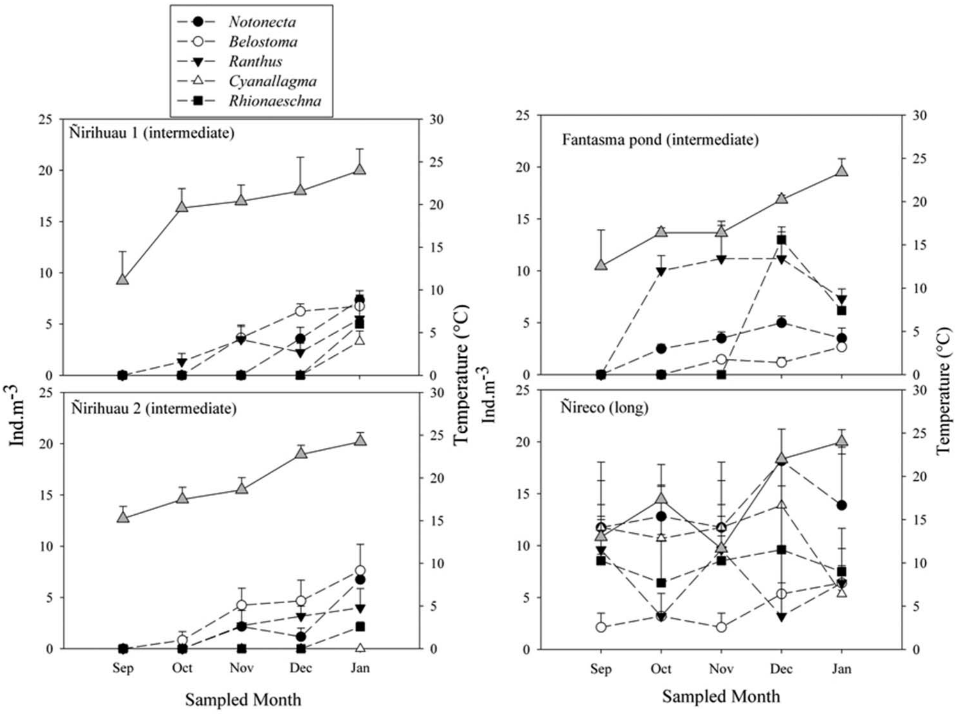

Figure 6. Seasonal variations in dominant insect species abundance at four wetlands with different hydroperiods (given between brackets in each figure). In addition, for each wetland, average monthly water temperature recorded between 11.00 and 16.00 h is plotted (grey triangles).

declines from the equator towards the poles (Rosenzweig 1995; Mittelbach et al. 2007). For example *Rhionaeschna variegata* is the only odonate species registered in wetlands from Tierra del Fuego, and therefore the most austral of the planet (Muzón 2009). The species richness recorded in this study is lower than for other temporary environments in temperate and subtropical regions in Argentina (Fischer et al. 2000; Fontanarrosa et al. 2004; Fontanarrosa 2009).

The permanent wetlands studied maintain a stable insect richness throughout almost the entire year, whereas the temporary wetlands (short and intermediate hydroperiod) have a seasonal colonization pattern that begins in early spring, in agreement with the findings of other authors (Fontanarrosa et al. 2009). In these north Patagonian aquatic systems, the wetland hydroperiod seems to determine the insect population size and species richness. Considering the models proposed for the functioning of wetlands in temperate regions, which can be situated along a hydroperiod gradient (from short-duration to permanent wetlands) and predator composition (Schneider and Frost 1996; Wellborn et al. 1996), permanent fishless wetlands are considered richer in insect species. However, some studies of temporary environments in temperate regions have shown that species richness is similar to that of permanent environments (Williams 1996; Boix et al. 2001). Here, the species richness in the permanent wetlands with and without fish predators and temporary wetlands in the study area do not differ greatly in predatory insect richness, and the differences were mainly due to species composition. In the analysis of the contingency table, there is a strong association between the species and the type of wetland. For example, the Odonata *Erythrodiplax connata*, *Neogomphus* sp. and *Rialla villosa* and the Heteroptera *Nerthra ranina* were only present in permanent forest and ecotone wetlands with fish, whereas among the representatives of the genus *Notonecta*, only *N. fazi* was found in permanent wetlands without fish in upland forests, where it might replace *N. vereertbruggheni* and *N. virescens*, which are mainly present in temporary ecotone wetlands and steppe in the case of *N. virescens*. For certain groups, like odonates, more species were recorded in permanent environments, where up to four species have been found (Jara personal observation). The only odonate species capable of using the temporary environments studied were *Cyanallagma interruptum* and *Rhionaeschna variegata*.

Several studies have shown that the presence of top fish predators could impact on invertebrate communities, such as insects (Wellborn et al. 1996 and references therein). The permanent wetlands with fish predators (introduced and native fish) showed an increase of insect richness, particularly those wetlands in which plentiful littoral vegetation grows, providing refuge for insects. Gilinsky (1984) found that fish predation was not effective on invertebrates in the littoral vegetation, so this might explain why the presence of fish did not affect the richness of predatory insects in our studied area. Additionally, Diehl (1992) suggested that invertebrate predators such as insects continue being the key predators in the littoral vegetation even when fish are present in the wetland.

The insect assemblage studied shows a dominance of Coleoptera, followed by Hemiptera and Odonata. This pattern is also found in other temperate temporary environments (Fontanarrosa et al. 2004; Fischer and Schweigmann 2008). It was also observed that both feeding modes (piercer and engulfer) were well represented among the species and the dominant hunting strategy was a mixed strategy (ambusher–searcher), which may make them highly efficient prey consumers. In general, the aquatic insect species in this study are considered to be generalists because of their morphological characteristics and the type of prey they select (Urban 2007). There is a wide range of prey in these Patagonian environments, with predominance of rotifers, calanoid and cyclopoid copepods, cladocerans, ostracods, mosquito larvae and anuran larvae (Perren 2008; Trochine et al. 2008; Jara and Perotti 2009, 2010; Coviaga 2011; Diéguez and Gilbert 2011; Jara et al. 2012). The colonization process observed, which begins in spring, and the appearance of the first larval stages late in the season, reflect a use of the environment for both feeding and development, which are favoured by the high productivity and warmer spring temperatures of these environments in spring.

The duration of the hydroperiod influenced the richness of predatory insects, with higher richness in environments with intermediate to long hydroperiods. The maximum richness (10 species) was found in the long-duration or permanent wetland (Mallín Ñireco). The hydroperiod is an important variable regulating the number of species that can become established in a wetland because only species that are able to adjust their life cycles to the period in which the wetland contains water can live there. For example, species that need to spend at least one winter in the water to complete their life cycles cannot live in intermittent or temporary environments. However, other species have developed strategies enabling them to live in these temporary environments in Patagonia. Diapause is mentioned among these strategies, as is the case for cladocerans, which remain in a resistance stage until the environments refill with water during the autumn rains (Perren 2008). Predatory insect species also have a certain degree of plasticity in their life cycles, which they can shorten or lengthen in response to environmental changes, as has been observed by other authors (e.g. environmental desiccation, De Block et al. 2008). These plastic responses have also been found for amphibian larvae, which accelerate their growth rate according to the duration of the hydroperiod (Jara 2010; Perotti et al. 2011). Predatory insect richness was found to be closely related to other variables such as maximum depth of the wetland and structural complexity given by the aquatic vegetation, which determines a wider diversity of microenvironments. These microenvironments are varied regarding temperature, shelter and feeding sites, allowing a greater number of insects to become established.

Although the results of this study show that the forest wetlands have greater predatory insect richness, Muzón et al. (2005) found that some permanent wetlands located in the Patagonian steppe with abundant aquatic vegetation can contain high insect richness. These data, plus the results of this study, confirm that the presence of aquatic vegetation and the duration of the hydroperiod would have a marked influence on insect richness, more than the surrounding environment (forest or steppe) per se.

Species richness may vary even within one wetland. For example, one of the wetlands in this study, Laguna Fantasma, remained inundated all year in 2010–2011, as a result of the increased precipitation in June 2010 (840 mm, whereas the average in the last 10 years was 224 mm). These exceptional climate conditions enabled many insect species that would normally migrate in the dry season to remain in the pond, so increasing species richness (seven species found in September), compared with the values recorded in 2006 (three species).

Typically, adult aquatic insects, having overwintered in some permanent body of water, disperse in early spring in search of newly formed ponds, eggs are laid and the young grow quickly under conditions of plentiful food and reduced competition (Williams 1997). In this study, the five permanent wetlands contained aquatic insects all year (Table 1). In addition, like other organisms, insects were observed overwintering in permanent wetlands in different stages of their life cycles, as observed by other authors (e.g. Merrit and Cummins 1996). For example, among the species found in the wetlands studied, coleopterans overwinter as adults, notonectids overwinter as advanced nymphs or adults, belostomatids overwinter as adults and odonates overwinter as larvae in different stages (Jara, personal observation). It was also found that some species (notonectids, beetles and odonates) within the same body of water can have two types of life cycle: a short one (approximately 4 months) from spring to early summer, and a long one in which the larvae overwinter in the water (Jara, personal observation).

Many aquatic organisms have temperature-dependent physiological processes. The gradual warming of the habitats, particularly the aquatic phase in this study, accelerates growth and development rates and stimulates early reproduction in insects (Gilbert and Raworth 1996). For example, the aquatic invertebrates at the top of the food chains (e.g. aquatic insects) might mature faster, metamorphose at a small size and reproduce more frequently (Arnell et al. 1995). This study found that abundance, richness and the appearance of larval stages of different insect species increased as wetland water temperature increased. Although there is no information on the possible effects of annual variations in temperature on the physiology of these species, it could be that warmer, drier summers shorten the hydroperiods, determining a smaller size at metamorphosis in these insects, leading to a decline in survival and reproductive potential and hence a decline in population numbers, as shown in other studies (McPeek and Peckarsky 1998).

The richness and the density of predatory insects in these Patagonian wetlands suggest the importance of this group when studying and modelling these environments. Moreover, their diversity and abundance were shown to be related to certain environmental parameters, such as temporality of the aquatic environments and attributes such as area, depth and vegetation. On the other hand, these wetlands not only supply habitats for these organisms, but also offer sites for the reproduction and the development of different aquatic species. Their role as top-predators in these communities, great variety of body size and different feeding modes suggest that these predators could have strong effects on prey communities, altering the size structure or density of prey species populations. In conclusion, the results indicate that the assemblages of predatory insects found in these Patagonian wetlands are diverse and, for some of the insect taxa, highly abundant. Also, insect abundance was changing and increasing with advancing spring. Such a fluctuating phenological pattern could have a powerful influence at lower trophic levels and could also influence competitive interactions for the available resources.

Acknowledgements

This research was performed under the Animal Care guidelines established by Argentinean animal protection law and Administracion de Parques Nacionales, Argentina. Administración de Parques Nacionales de Argentina provided the authorization to collect the samples and living animals in ponds within the Nahuel Huapi National Park (APN Nos 498–730), and San Carlos de Bariloche Municipality provided authorization for sampling in areas under its jurisdiction. We are grateful to S. Mazzucconi, J. Muzón and M. Archangelsky for their help with identification of the insect species. C. Brion, C. Ezcurra, J. Puntieri and J. Grosfeld determined the aquatic plants. This work was supported by UNComahue B04-153 and B04-166 grants, FONCyT 13550, a CONICET postdoctoral fellowship and the Neotropical Grassland Conservancy.

References

Alarie Y, Michat MC, Nilsson AN, Archangelsky M, Hendrich L. 2009. Larval morphology of *Rhantus* Dejean, 1833 (Coleoptera: Dytiscidae: Colymbetinae): descriptions of 22 species and phylogenetic considerations. Zootaxa. 2317:1–102.

Archangelsky M. 2004. Nuevas citas de Coleoptera acuáticos y Megaloptera para la provincia de Chubut (Argentina). Rev Soc Entomol Argent. 63:66–68.

Arnell N, Bates B, Lang H, Magnuson JJ, Mulholland P. 1995. Hydrology and freshwater ecology. In: Watson RT, Zinyowera MC, Moss RH, Dokken DJ, editors. Climate change 1995: impacts, adaptations, and mitigation of climate change, scientific-technical analyses. Cambridge (UK): Cambridge University Press.

Bachmann AO. 1962. Apuntes para una hidrobiología argentina. V. Los hemípteros acuáticos de los parques nacionales Lanín, Nahuel Huapi y Los Alerces y zonas vecinas (Insecta-Hemipt.). Physis (Buenos Aires). 23:103–107.

Bachmann AO. 1963. Apuntes para una hidrobiología argentina. VI. Los Hemiptera Cryptocerata de la Patagonia extracordillerana. Physis (Buenos Aires). 24:35–37.

Bachmann AO. 1998. Heteroptera acuáticos. In: Morrone JJ, Coscarón S, editors. Biodiversidad de artrópodos argentinos. Una perspectiva biotaxonómica. Ediciones Sur, La Plata.

Batzer DP, Wissinger SA. 1996. Ecology of insect communities in nontidal wetlands. Annu Rev Entomol. 41:75–100.

Bay EC. 1974. Predator-prey relationships among aquatic insects. Ann Rev Entomol. 19:441–453.

Biggs J, Williams PJ, Whitfield M, Fox G, Nicolet P, Howard S. 2000. A new biological method for assessing the ecological quality of lentic waterbodies. In Wicherek S, editor. L'Eau, de la Cellule au Paysage. Paris: Elsevier.

Blaustein L. 1998. Influence of the predatory backswimmer, *Notonecta maculata*, on invertebrate community structure. Ecol Entomol. 23:246–252.

Boix DJ, Sala J, Moreno-Amich R. 2001. The faunal composition of Espolla pond (NE Iberian Peninsula): the neglected biodiversity of temporary waters. Wetlands. 21:577–592.

Bruno JF, Cardinale BJ. 2008. Cascading effects of predator richness. Front Ecol Environ. 6:539–546.

Casanovas P, Úbeda CA .2006. *Alsodes gargola*. Predation. Herpetol Rev. 37:439–440.

Cobbaert D, Bayley SE, Greter J-L. 2010. Effects of a top invertebrate predator (*Dytiscus alaskanus*; Coleoptera: Dytiscidae) on fishless pond ecosystems. Hydrobiologia. 644:103–114.

Coviaga CA. 2011. Estudio del ciclo de vida de ostrácodos (Crustacea) de ambientes temporarios en Patagonia Norte. Licenciatura thesis. San Carlos de Bariloche, Universidad Nacional del Comahue.

Chovanec A, Waringer J. 2001. Ecological integrity of river-floodplain systems-assessment by dragonfly surveys (Insecta: Odonata). Regul Rivers Res Manage. 17:493–507.

Chovanec A, Waringer J, Raab R, Laister G. 2004. Lateral connectivity of a fragmented large river system: assessment on a macroscale by dragonfly surveys (Insecta: Odonata). Aquat Conserv Mar Freshwat Ecosyst. 14:163–178.

De Block M, McPeek MA, Stoks R. 2008. Life-history evolution when *Lestes* damselflies invaded vernal ponds. Evolution. 62:485–493.

De Meester L, Declerck S, Stoks R, Louette G, Van De Meutter F, De Bie T, Michels E, Brendonck L. 2005. Ponds and pools as model in conservation biology, ecology and evolutionary biology. Aquat Conserv Mar Freshwat Ecosyst. 15:715–725.

Diehl S. 1992. Fish predation and benthic community structure: the role of omnivory and habitat complexity. Ecology. 73:1646–1661.

Diéguez MC, Gilbert JJ. 2011. Daphnia-rotifer interactions in Patagonian communities. Hydrobiologia. 662:189–195.

Fischer S, Marinone MC, Fontanarrosa MS, Nieves M, Schweigmann N. 2000. Urban rain pools: seasonal dynamics and entomofauna in a park of Buenos Aires. Hydrobiologia. 441:45–53.

Fischer S, Schweigmann N. 2008. Association of immature mosquitoes and predatory insects in urban rain pools. J Vector Ecol. 33:46–54.

Fontanarrosa MS, Torres PLM, Michat MC. 2004. Aquatic insect communities of temporary pools and permanent ponds in Buenos Aires City (Argentina). Rev Soc Entomol Argent. 65:55–65.

Fontanarrosa MS, Collantes MB, Bachmann AO. 2009. Seasonal patterns of the insect community structure in urban rain pools of temperate Argentina. J Insect Sci. 9:1–17.

Foster GN, Foster AP, Eyre MD, Bilton DT. 1989. Classification of water beetle assemblages in arable fenland and ranking of sites in relation to conservation value. Freshwater Biol. 22:343–354.

Gibbs JP. 2000. Wetland loss and biodiversity conservation. Conserv Biol. 14:314–317.

Gilbert N, Raworth DA. 1996. Insects and temperature: a general theory. Can Entomol. 128:1–13.

Gilbert JJ, Diéguez MC. 2010 Low crowding threshold for induction of sexual reproduction and diapause in a Patagonian rotifer. Freshwater Biol. 55:1705–1718

Gilinsky E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology. 65:455–468.

Grillas P, Gauthier P, Yavercovski N, Perennou C. 2004a. Mediterrane and temporary pools; Volume 1. Issues relating to conservation, functioning and management. Station biologique de la Tour du Valat.

Grillas P, Gauthier P, Yavercovski N, Perennou C. 2004b. Mediterranean Temporary Pools, Volume 2. Species information sheets. Station biologique de la Tour du Valat.

Jara FG, Perotti MG. 2009. Toad tadpole responses to predator risk: Ontogenetic change between constitutive and inducible defenses. J Herpetol. 43:82–88.

Jara FG. 2010. Plasticidad fenotípica en anuros patagónicos de los géneros *Pleurodema* y *Rhinella*: respuestas al hidroperíodo y a los depredadores. Doctoral thesis. San Carlos de Bariloche. Universidad Nacional del Comahue, Centro Regional Universitario Bariloche.

Jara FG, Perotti MG. 2010. Risk of predation and behavioral response in three anuran species: influence of tadpole size and predator type. Hydrobiologia. 644:313–324.

Jara FG, Perotti MG, Diéguez MC. 2012. Distribution of backswimmers in shallow ponds of Patagonia and their predatory role on a common tadpole–copepod assemblage. NZ J Mar Fresh. DOI:10.1080/00288330.2012.707130.

Jeffries M. 1996. Effects of *Notonecta glauca* predation on cyphon larvae (Coleoptera: Scirtidae) populations in small, seasonal ponds. Arch Hydrobiol. 136:413–420.

Jerez V, Moroni J. 2006. Diversity of freshwater beetle of Chile. Gayana. 70:72–81.

Kumar R, Hwang J-S. 2006. Larvicidal efficiency of aquatic predators: a perspective for mosquito biocontrol. Zool Stud. 45:447–466.

Magnusson AK, Williams DD. 2009. Top-down control by insect predators in an intermittent pond- a field experiment. Ann Limnol – Int J Lim. 45:131–143.

McPeek M, Peckarsky BL. 1998. Life histories and the strengths of species interactions: combining mortality, growths, and fecundity effects. Ecology. 79:867–879.

Melo MC. 2009. Biodiversity of aquatic and semiaquatic Heteroptera (Hemiptera) from Argentinean Patagonia. Rev Soc Entomol Argent. 68:177–185.

Merrit RW and Cummins KW. 1996. An introduction to the aquatic insects of North America.

Mittelbach GG, Schemske DW, Cornell HV, Allen AP, Brown JM, Bush MB, Harrison SP, Hurlbert AH, Knowlton N, Lessions HA, McCain CH, McCune AR, McDade LA, McPeek MA, Near TJ, Price TD, Ricklefs RE, Roy K, Sax DF, Schluter D, Sobel JM, Turelli M. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecol Lett. 10:315–331.

Moncada C. 2011. Patrones reproductivos y de desarrollo larval de un ensamble de anuros en una laguna de un mallín de bosque nordpatagónico. Licenciatura thesis. San Carlos de Bariloche. Universidad Nacional del Comahue.

Muzón J. 1995. Los odonata de la patagonia argentina. Rev Soc Entomol Argent. 54:1–14.

Muzón J. 1997. Odonata (Insecta) from Patagonia: species richness and distributional patterns. Biogeographica. 73:123–133.

Muzón J, Spinelli GR, Pessacq P, Von Ellenrieder N, Estévez AL, Marino PI, Perez Goodwyn PJ, Angrisano EB, Díaz F, Fernández LA, Mazzuconi S, Rossi G, Salomón OD. 2005. Insectos acuáticos de la Meseta del Somuncura, Patagonia, Argentina. Inventario preliminar. Rev Soc Entomol Argent. 64:47–68.

Muzón J. 2009. Current knowledge of Patagonian Odonata. Rev Soc Entomol Argent. 68:163–167.

Nicolet P, Biggs J, Fox G, Hodson MJ, Reynolds C, Whitfield M, Williams P. 2004. The wetland plant and macroinvertebrate assemblages of temporary ponds in England and Wales. Biol Conservat. 120:261–278.

Painter D. 1999. Macroinvertebrate distributions and the conservation value of aquatic Coleoptera, Mollusca and Odonata in the ditches of traditionally managed and grazing fen at Wicken Fen, UK. J App Ecol. 36:33–48.

Peckarsky BL. 1982. Aquatic insects predator-prey relations. BioScience. 32:261–266.

Perotti MG, Diéguez MC, Jara FG. 2005. Estado del conocimiento de humedales del norte patagónico (Argentina): aspectos relevantes e importancia para la conservación de la biodiversidad regional. Rev Chil Hist Nat. 78:723–737.

Perotti MG, Jara FG, Úbeda CA. 2011. Adaptive plasticity of life-history traits to pond drying in three species of Patagonian anurans. Evol Ecol Res. 13:415–429.

Perren G. 2008. El banco de resistencia de cladóceros de lagunas temporarias del norte patagónico: estructura y patrones de abundancia y distribución. Licenciatura thesis. San Carlos de Bariloche. Universidad Nacional del Comahue.

Roe JH, Georges A. 2007. Heterogeneous wetland complexes, buffer zones, and travel corridors: landscape management for freshwater reptiles. Biol Cons. 135:67–76.

Rosenzweig ML. 1995. Species diversity in space and time. New York (NY): Cambridge University Press.

Sahlen G, Ekestubbe K. 2001. Identification of dragonflies (Odonata) as indicators of general species richness in boreal forest lakes. Biodiversity Conserv. 10:673–690.

Schneider DW, Frost TM. 1996. Habitat duration and community structure in temporary ponds. J N Am Benthol Soc. 15:64–86.

Sih A, Crowley PH, McPeek MA, Petranka JW, Strohmeier K. 1985. Predation, competition and prey communities: a review of field experiments. Ann Rev Ecol Syst. 16:269–311.

Saha N, Aditya G, Saha GK, Hampton SE. 2010. Opportunistic foraging by heteropteran mosquito predators. Aquat Ecol. 44:167–176.

Trochine C, Balseiro E, Modenutti B. 2008. Zooplankton of fishless ponds of Northern Patagonia: insights into predation effects of *Mesostoma ehrenbergii*. Int Rev Hydrobiol. 93:312–327.

Trémouilles ER. 1984. El género *Rhantus* Dejean en la Argentina (Coleoptera, Dysticidae). Physis (Buenos Aires). 102:9–24.

Urban M. 2007. Predator size and phenology shape prey survival in temporary ponds. Oecologia. 154:571–580.

Wellborn GA, Skelly DK, Werner EE. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Ann Rev Ecol Syst. 27:337–363.

Williams DD. 1996. Environmental constraints in temporary fresh waters and their consequences for the insect fauna. J N Am Benthol Soc. 15:634–650.

Williams DD. 1997. Temporary ponds and their invertebrate communities. Aquat Conserv. 7:105–117.

Williams DD. 2006. The biology of temporary waters. New York (NY): Oxford University Press.

Wilbur HM. 1997. Experimental ecology of food webs: complex systems in temporary ponds. Ecology. 78: 2279–2302.

Zacharias I, Dimitriou E, Dekker A, Dorsman E. 2007. Overview of temporary ponds in the Mediterranean region: threats, management and conservation issues. J Environ Biol. 28:1–9.