



The life histories of *Meridialaris chiloeensis* (Demoulin, 1955) (Ephemeroptera: Leptophlebiidae) and *Gigantodax rufescens* (Edwards, 1931) (Diptera: Simuliidae) on a Magellanic sub-Antarctic island (55°S)

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The life histories of *Meridialaris chiloensis* (Demoulin, 1955) (Ephemeroptera: Leptophlebiidae) and *Gigantodax rufescens* (Edwards, 1931) (Diptera: Simuliidae) on a Magellanic sub-Antarctic island (55°S)

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ABSTRACT

The life histories of *Meridialaris chiloensis* (Demoulin, 1955) (Leptophlebiidae: Ephemeroptera) and *Gigantodax rufescens* (Edwards, 1931) (Simuliidae: Diptera) were studied in a Magellanic sub-Antarctic river in Navarino Island (55°S). Both species are distributed along the whole length of the watershed. Phenology was studied in the field for a period of 12 months between August 2009 and September 2010, at a site near the river's mouth (sea level). Cumulative degree-days were calculated along the gradient at five representative altitudinal locations, starting at the river's headwaters. Samples were obtained during January of 2010 at all the remaining altitudinal locations to assess possible changes in voltinism during the austral summer season through the watershed. Results show that *M. chiloensis* and *G. rufescens* have a bivoltine and multivoltine life cycle, respectively, at sea level. Based on degree-days obtained and field observations at the remaining stations, possible voltinism patterns are discussed for both species along the altitudinal gradient. These species are proposed as suitable long-term indicators for climate change studies in the sub-Antarctic ecoregion of Magallanes, as monitoring their responses will be important in the interpretation of changes in ecosystem function, community structure, and distributions of aquatic taxa in this region of the world.

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Introduction

Accumulating evidence suggests that variation in thermal regimes caused by large-scale climate change is conspicuously affecting the phenology and activity of freshwater insects (Parmesan 2007; Richter, Suhnlung, and Dietrich 2008), leading to shifts in aquatic community structure and species distribution ranges (Ryan and Ryan 2006; Woodward, Perkins, and Brown 2010). In terrestrial systems, for example, temporal uncoupling due to phenological changes such as earlier flowering of plants or earlier reproductive seasons

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in animals, are well documented and can be attributed, with high probability, to global warming (Walther et al. 2002). Furthermore, growing evidence demonstrates that aquatic ecosystems, particularly those in polar and subpolar regions, may be experiencing some of the fastest warming rates on the planet (Porter and Santana 2003; Hassan, Scholes, and Nash 2005). Freshwater ecosystems in these regions are highly dynamic, and their responses to climate change may be more immediate and evident than in their terrestrial counterparts (Spaulding, Vuver, Hodgson, Mcknight, and Verleyen 2010).

In southern South America, the subpolar region is immersed within the Magellanic sub-Antarctic ecoregion which has been identified as one of the 24 true wilderness areas remaining on the planet (Mittermeier et al. 2003). Generally, freshwater ecosystems in the southern tip of this ecoregion (55–56°S) present marked changes in microclimate with small changes in elevation (Contador, Kennedy, Ojeda, and Rozzi 2015). The modulating effect of the ocean drastically diminishes with altitude, and the tree line appears at only 600 metres above sea level (a.s.l.) (Rozzi et al. 2010). This drastic change creates steep altitudinal gradients characterised by a topography that supports a unique mosaic of evergreen and deciduous forests, peatlands, grasslands, and scrublands over a relatively small area (Pisano 1977).

Despite the uniqueness of the ecoregion and the imminent threats of climate change on its freshwater ecosystems, little research has been conducted to assess possible impacts on the phenology, development, and trophic interactions of aquatic insects in the long-term (Contador, Kennedy, and Rozzi 2012). We hypothesised that given the modulating effect of the ocean and the temperate weather conditions found in Magellanic sub-Antarctic streams, some aquatic insect species will be able to accumulate enough degree-days to complete two or more generations per year. In this context, the purposes of this study were to (1) describe the phenology of two widely distributed freshwater insects in a Magellanic sub-Antarctic watershed at sea level and (2) use the results obtained to provide a baseline for future research based on assessing the potential effects of climate change in freshwater ecosystems of southern South America in the long-term.

Material and methods

Study area

The study was conducted along the altitudinal gradient of the Róbalo River watershed in Navarino Island (55°S). The river runs through the Dientes of Navarino mountain range and provides drinking water to the city of Puerto Williams, capital of the Chilean Antarctic Province and the world's southernmost town. Navarino Island lies within the Magellanic sub-Antarctic ecoregion, which occurs along a narrow but latitudinally extensive strip of land between 35° and 55°S (Armesto, Rozzi, Smith-Ramirez, and Arroyo 1998). The northern portion of the ecoregion is delimited by the Mediterranean-type scrublands and the hyper-arid Atacama Desert, while to the east lies the Patagonian steppe, and westward and southward, the Pacific Ocean (Rozzi et al. 2012). Furthermore, the island is located within the Cape Horn Biosphere Reserve, which hosts the world's southernmost-forested ecosystems, encompassing all of the islands south of the Beagle Channel, as well as the Chilean portion of Tierra del Fuego (Figure 1; Rozzi, Massardo, Anderson, Heidinger, and Silander 2006). The study site is located within this biosphere reserve and the Omora Ethnobotanical Park, part of Chile's Long Term Socio-Ecological Research Sites (LTSER) network.

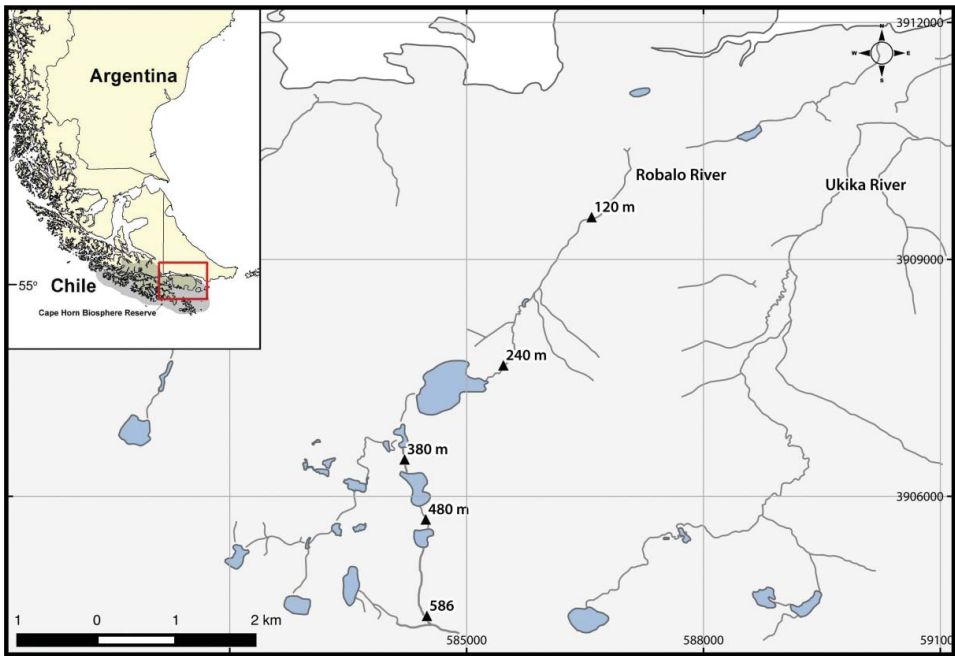


Figure 1. (Colour online) Map of Navarino Island showing its location within the Cape Horn Biosphere Reserve. The map details the location of the Róbalo River watershed, located on the northern side of the island. Sampling sites along the watershed are shown. Projection WGS84_UTM 19S, scale 1:50,000.

Climate

The climate of the area is strongly affected by westerly storm tracks coupled with precipitation induced by the high western flanks of the Andean Cordillera (McCulloch, Clapperton, Rabassa, and Currant 1997). It is also influenced by polar weather fronts from the south Pacific (Rozzi et al. 2006). The average annual temperature and precipitation recorded for Puerto Williams are 6 °C and 467 mm, respectively. The warmest month has an average temperature of 9 °C (January–March), while the coldest month averages 2 °C (May–August) (Contador, Kennedy, Ojeda, Feinsiner, and Rozzi 2014; Rozzi and Jiménez 2013).

Study organisms

For the purposes of this study, two aquatic insect species, *Meridialaris chiloeensis* (Demoulin, 1955) (Leptophlebiidae: Ephemeroptera) and *Gigantodax rufescens* (Edwards, 1931) (Simuliidae: Diptera) were chosen. Both species are distributed along the entire length of the Róbalo River. The genus *Meridialaris* Peters and Edmunds, 1972, with seven species described in Chile, has a broad distribution range (26° to 55°S), which includes the Andean-Patagonian and Magellanic sub-Antarctic streams (Pescador and Peters 1986). The genus *Gigantodax* Enderlein, 1925 is a large genus of the Neotropical Simuliini, with 68 species extending along the Andean mountain system from Mexico to Cape Horn. Its distribution ranges from sea level to high Andean (4700 metres in the tropics), but it is generally found at altitudes from 700 to 2000 metres (Wygodzinsky and Coscarón 1989).

Field phenology

To analyse seasonal variation in abundance and to describe life history patterns, nymphs and larvae were collected from riffle habitats (boulders and cobbles) at five altitudinal locations (Stations I–V) separated by approximately 100 metres of altitude each (Figure 1). Station I and Station V correspond to the highest elevation site at 586 metres a.s.l. and to the lowest site at 120 metres a.s.l., respectively. Each station selected is a representative of the Róbaló River watershed's distinct life zones, as defined by the sharp changes in vegetation, habitat, and landscape along the river's altitudinal gradient (see Contador et al. 2015). Station V was sampled at 2-week intervals for a period of 12 months starting in August of 2009. Stations I–IV were sampled once during the austral summer of 2009 and 2010 (early January), as harsh weather conditions did not allow for winter sampling. Samples were obtained using a Surber sampler (0.09 m²) with a 243- μ m mesh net. Three replicates ($n = 3$) were collected during each sampling event, preserved in 70% ethanol, and transported to the laboratory for processing. The timings of the first observations of mating, pupation (in the case of *G. rufescens*), and adult emergence in the field were noted for both species.

Gigantodax rufescens larval instars were separated by measuring head capsule lengths (mm) and widths (mm) (Wang and Kennedy 2004). Head capsule length was measured from the anterior margin of the frons to the posterior margin of the head's sclerites, while the width was measured as the distance of the head capsule across the eyes. The size of the mesothoracic wing pads in relation to segments of the thorax and abdomen combined with markings including veination and darkening during final stages, were used as a measure of *M. chiloeensis* development (Taylor and Kennedy 2006). Development classes I–V were determined as follows: I, no wing pads present; II, clear wing pads present in thoracic region; III, wing-pads with veins present in thoracic region; IV, wing-pads with veins present in abdominal region or with veins and mottling present in thoracic region; V, wing pads enlarged, with veins and dark mottling reaching abdominal region (Taylor and Kennedy 2006).

For both species, the relative abundance of each developmental stage at Station V was used to estimate cohort lines and voltinism through the year, and for the austral summer at Stations I–IV. Approximate emergence of adults at Station V was estimated by noting the time period at which a proportionally higher number of late instar larvae (and pupae) or nymphs were obtained. Specific morphometric measurements for both species were obtained using an Olympus SZH (Olympus Corporation, Tokyo, Japan) dissecting microscope coupled with a Tucsen TCA 5.0C (5 mp) camera with TSview digital imaging processing software (Fuzhou Imaging Tech co. Ltd., Fuzhou, China). Analysed individuals were deposited in the University of North Texas Elm Fork Heritage Museum, Denton, Texas (USA).

Physical and chemical parameters

Water chemistry parameters were recorded during each sampling event. Dissolved oxygen (mg/L) and conductivity (μ S) were measured using a YSI 8.5 metre (YSI Incorporated, Yellow Springs, Ohio, USA). Hobo data loggers (Model HOBO[®] Water Temp Pro v2 part # MAN–U22–001, Onset Computer Corporation, Cape Cod, Massachusetts, USA) were permanently installed at each altitudinal location starting on January of 2009 until the present. Average, maximum, and minimum daily temperatures ($^{\circ}$ C) are recorded continuously every

5 hours at each sampling site (see Contador et al. 2015). Discharge (m^3/s) and air temperature ($^{\circ}\text{C}$) data were obtained from a hydrological station located 25 metres downstream from the sampling site (Dirección General de Aguas, Chile). Statistical differences in water chemistry parameters between stations were tested using one-way Analysis of Variance (ANOVAs). All data were tested for normality (Shapiro–Wilk w statistic) and inequality of variances (Hartley's F_{max} ratio test) before proceeding with ANOVA ($\alpha = 0.05$). When significant results were determined by the ANOVA, a Tukey HSD *post hoc* test was applied (R Software version 2.9.2).

Determination of cumulative and growing degree-days

Minimum, maximum, and average daily water temperature ($^{\circ}\text{C}$) were obtained from the Hobo[®] data loggers. Cumulative (for Stations I–V) and growing degree-days (for Station V) were computed using the Modified Sine Wave Method (DegDay version 1.01). Based on field data, growing degree-days for each species were calculated by setting the hatching period and, thus, the start of a generation, at the time at which a peak in first developmental stage larvae and nymphs were recorded. The end of the cohort was defined when a proportionally higher number of individuals in the last developmental stage were significantly higher.

Results

Physical and chemical parameters

Dissolved oxygen (mg/L) and pH were not significantly different (8.9–12.6 mg/L ; 8.3–8.9, respectively) between sites throughout the altitudinal gradient (one-way ANOVA, $P = 0.53$ and 0.89, $\alpha 0.05$) and conductivity ranged from 26S to 60– μS from higher to lower altitudes. Maximum water temperature ($^{\circ}\text{C}$) was reached during austral summers (December–March) and ranged between 13 $^{\circ}\text{C}$ and 16 $^{\circ}\text{C}$ from the headwaters to the mouth of the Róbalo River watershed. Minimum temperatures below 0 $^{\circ}\text{C}$ were recorded during austral winters (June–August) (Table 1, Figures 2 and 3). Distinct changes in cumulative degree-days (CDD) were recorded every 100 metres of altitude through the altitudinal gradient, and ranged from 365 to 2051 CDD, from the headwaters to the mouth (Table 1). Discharge (m^3/s) sharply increases with higher temperatures during the austral summer, with significant peaks during the months of January and February.

Table 1. Average, maximum, and minimum water temperatures and total cumulative degree-days (CDD) registered between 2009 and 2010 through the altitudinal gradient of the Róbalo River watershed, Navarino Island (55 $^{\circ}\text{S}$).

Altitude (m)	Temperature ($^{\circ}\text{C}$)			CDD ($^{\circ}\text{C}$)
	Average ($\pm\text{SD}$)	Max	Min	
120	5.66 (4.36)	15.92	0.00	2051.00
240	4.55 (3.89)	13.45	−0.55	1650.00
380	2.69 (2.29)	8.94	0.02	944.00
486	1.40 (1.99)	10.00	−0.09	508.00
586	1.01 (1.14)	5.70	0.05	365.00

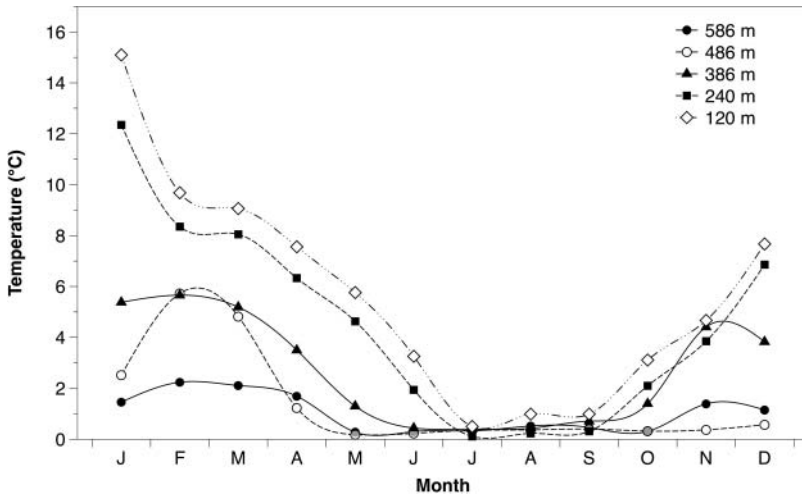


Figure 2. Average monthly water temperature at each of the permanent stations for long-term studies of freshwater insects, along the altitudinal gradient of the Róbalo River, Omora Park (55°S).

Determination of *Gigantodax rufescens* larval instars and voltinism through the altitudinal gradient

Larval instars

Five distinct larval instars were obtained for *G. rufescens* by plotting head capsule length and width (mm) (Figure 4). Generally, members of the family Simuliidae may have up to seven larval instars, therefore, it is likely that the sampling method used failed to collect the first two instars (Ross and Craig 1979). This is based on the observation that larvae bearing an egg burster on the cephalic apotome were not collected. The terminal instar was confirmed based on the presence of the dark gill histoblast (Ross 1979). Head capsule

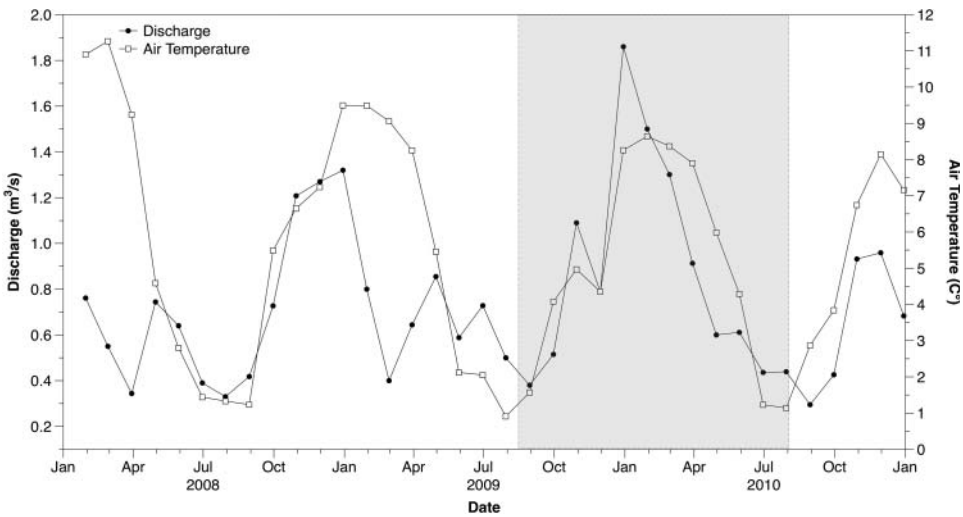


Figure 3. Average monthly discharge (m³/s) and air temperature (°C) at station V (120 m a.s.l.) from 2008 to 2010. Sampling period is shaded in light grey.

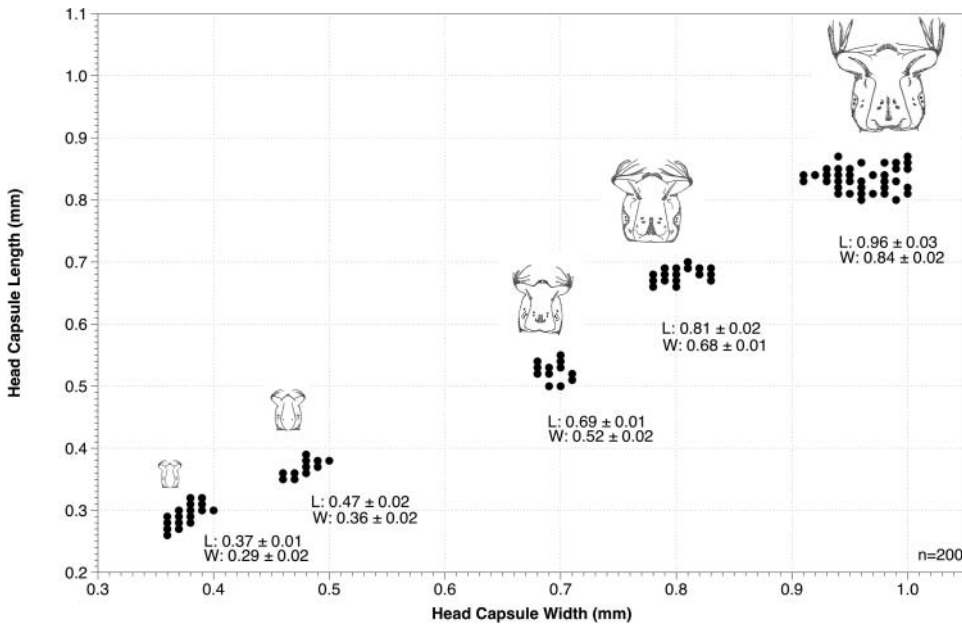


Figure 4. Scatter plot of *Gigantodax rufescens* (Edwards, 1931) head capsule length and width (mm) indicating larval instars. Mean length and width (mm) \pm SD are indicated below each instar category.

lengths ranged from 0.37 mm (early instar) to 0.96 mm (final instar), while head capsule widths ranged from 0.29 mm (early instar) to 0.84 mm (final instar) (Figure 4).

Voltinism

A higher abundance of *G. rufescens* earliest larval instars was observed during December, March, and June (Figure 5), while a higher abundance of final larval instars was observed during February, May, and December. The highest relative abundances of final larval instars coincide with the highest numbers of total pupae collected. Based on this interval, it is estimated that it takes approximately 336 degree-days for *G. rufescens* to complete one generation. Using this estimate, we concluded that at 120 metres a.s.l., where the total CDD per year are 2051, *G. rufescens* has a multivoltine life cycle, with three generations per year and with adult emergence times occurring during February, May, and December (Figure 5). Based on the measured CDD, field observations and austral summer sampling, it could be hypothesised that the life history of *G. rufescens* could vary from univoltine (one generation per year), at the river's headwaters, to multivoltine (three generations per year) at its mouth.

Determination of Meridialaris chiloeensis developmental classes and voltinism through the altitudinal gradient

Nymphal developmental classes

Five distinct nymph developmental classes were obtained for *M. chiloeensis* by describing the developmental stage of the mesothoracic wing pads (Taylor and Kennedy 2006) (Figure 6). The first developmental stage was characterised by the absence of wing pads

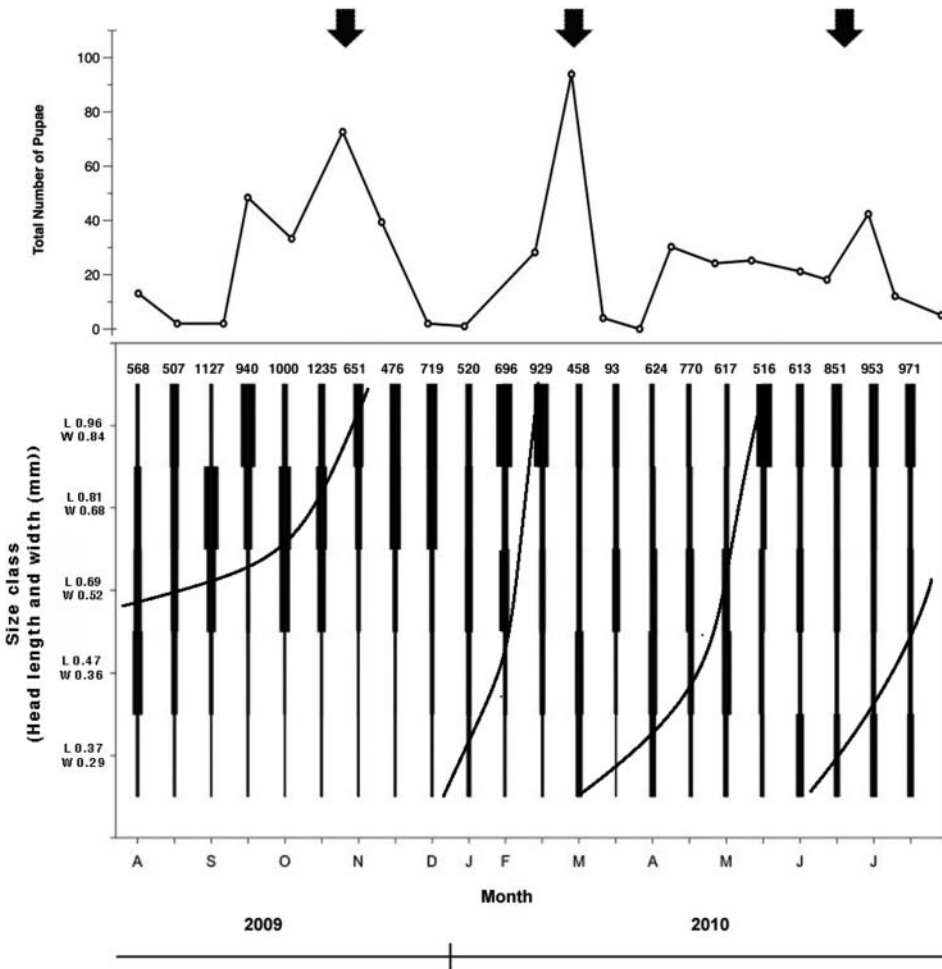


Figure 5. Relative abundance of larval instars and total number of pupae of *Gigantodax rufescens* (Edwards, 1931) from the Róbalo River watershed, at station V (120 m a.s.l.), from August of 2009 through August of 2010. Bar thickness represents the relative proportion of individuals in each instar. Bold, curved lines indicate proposed cohorts derived from cumulative degree-days data obtained from the field.

and well-defined compound eyes, while the second primarily by the absence of wing pads. The third developmental stage presents clear wing pads on the first thoracic segment, and the fourth and fifth has wing pads with veins, expanding from the first thoracic segment to the mid portion of the second thoracic segment, and darkened wing pads, expanding to the mid portion of the third thoracic segment, respectively (Figure 6).

Voltinism

A high proportion of nymphs in the first developmental stage were observed during December and January, while the fifth developmental stage was more abundant through the end of March (Figure 7). At the same time, a high proportion of first and fifth stage nymphs were observed during April and December, respectively, showing the

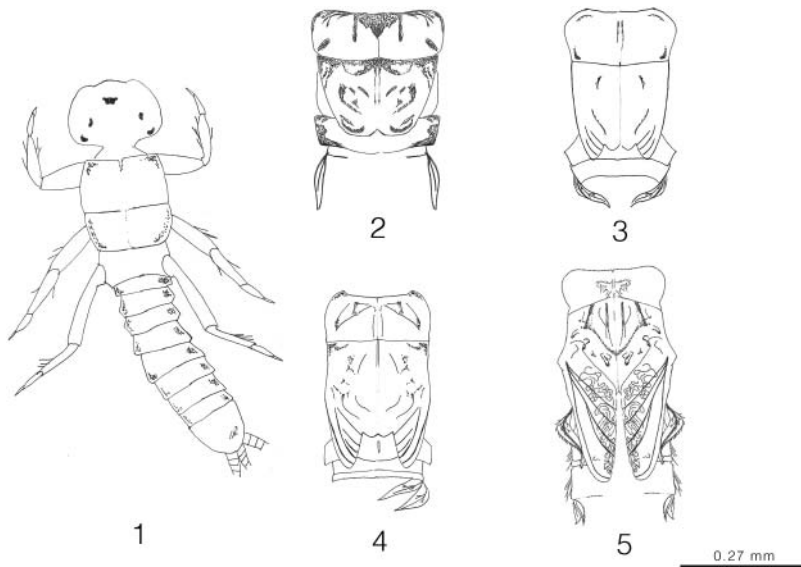


Figure 6. Mesothoracic wing pad developmental stages for *Meridialaris chiloeensis* (Demoulin, 1955). (1) Absence of wing pads and well-defined compound eyes; (2) absence of wing pads; (3) clear wing pads on the first thoracic segment; (4) wing pads with veins, expanding from the first thoracic segment to the mid portion of the second thoracic segment; (5) darkened wing pads, expanding to the mid portion of the third thoracic segment.

development of a second, slower-growing generation during the winter. Based on these population dynamics, it was estimated that it takes approximately 1185 degree-days for *M. chiloeensis* to complete one generation. With this estimate, we concluded that at 120 metres a.s.l., *M. chiloeensis* has a bivoltine life cycle, with adult emergence times occurring during January– February and March–April (Figure 7).

Discussion

Although life history studies have been carried out for many years in the Northern Hemisphere, little is known about the phenology of aquatic insects in the Magellanic sub-Antarctic ecoregion (Contador, Kennedy, and Rozzi, 2012). This is the first study to report on the life history of any freshwater insect inhabiting the sub-Antarctic Magellanic ecoregion of southern Chile. Our results indicate that *G. rufescens* and *M. chiloeensis* have a multivoltine and bivoltine life cycle, respectively, at sea level. In agreement with other studies conducted in the Patagonian ecoregion, *M. chiloeensis* exhibits an asynchronous bivoltine life cycle (Epele, Miserendino, and Pessaq 2011; Hollmann and Miserendino 2008), while *G. rufescens* exhibits a synchronous multivoltine pattern. Based on CDD data and field observations, we could hypothesise that the life histories of these species could potentially vary throughout the altitudinal gradient of the Róbaló River, with *G. rufescens* varying from univoltine to multivoltine from the headwaters to the mouth and with *M. chiloeensis* varying from merovoltine to bivoltine.

Most aquatic insects in high latitudes exhibit a seasonal phenology defined by the interaction of temperature, photoperiod, and local climate conditions (DeWalt, Stewart,

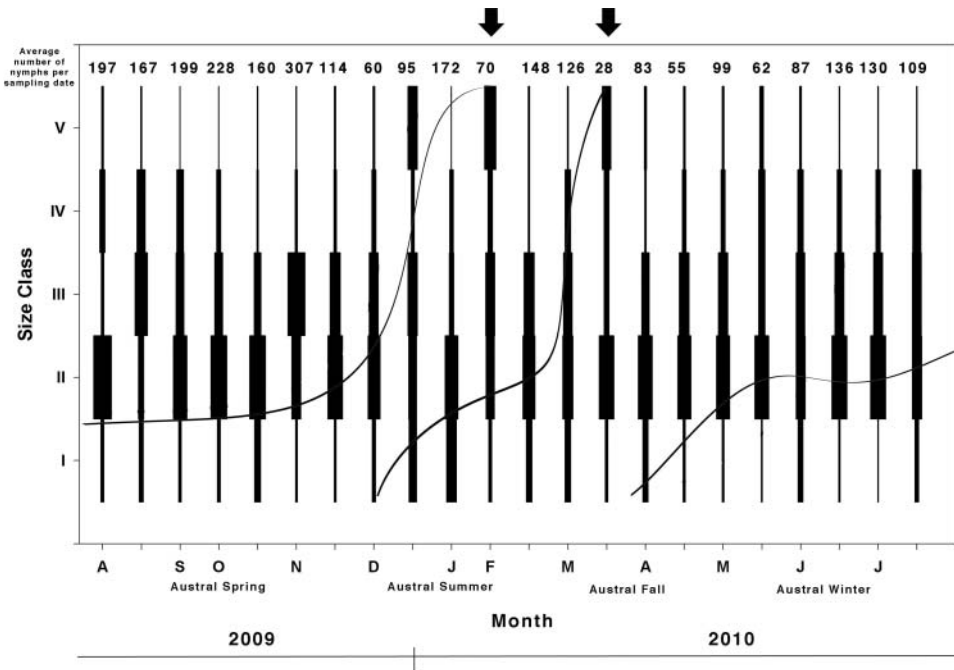


Figure 7. Relative abundance of *Meridialaris chiloeensis* (Demoulin, 1955) nymph developmental classes from the Róbalo River watershed, at site V (120 m a.s.l.), from August of 2009 through August of 2010. Arrows correspond with emergence peaks. Bar thickness represents the relative proportion of measured individuals in each developmental class. Bold lines indicate proposed cohorts derived and represent estimated developmental rates derived from a combination of developmental class frequency, emergence, and DD estimates from continuous field water temperatures.

Moulton, and Kennedy 1994). Generally, where climates are cold, rapid development is rare, and species with several generations per year are unusual (Danks 2007). Indeed, many Arctic/Antarctic and alpine species have life cycles that last more than one year, with multivoltine life histories occurring most frequently at lower latitudes (i.e., 34°N), while at higher latitudes (i.e., 50°N, 42°S), univoltine, semivoltine, and merovoltine life histories are more frequent (Danks 2007). For example, the diving beetle *Lancetes angusticollis* (Curtis 1839) (Coleoptera: Dytiscidae) exhibits a semivoltine life cycle in South Georgia Island, one of the coldest subantarctic islands, with summer temperatures that range between -5°C and 10°C (Rodney and Convey 1998). Furthermore, the stoneflies *Notoperla fasciata* McLellan, Miserendino, and Hollman, 2006 and *Notoperla magnispina* McLellan, Miserendino, and Hollman, 2006 (Plecoptera: Gripopterygidae) exhibit semivoltine and merovoltine life cycles in Patagonian streams, where temperatures range from 1°C to 12°C (Beltran and Miserendino 2011). The presence of multivoltine and bivoltine life cycles in the Magellanic sub-Antarctic ecoregion could be explained by climatic and geographic events. In the high latitudes of southern South America, the climate is modulated by a largely oceanic climate, with mild winters and cool summers, whereas in the high latitudes of the northern North America, the climate is continental, characterised by very cold winters contrasted with warm summers (Rozzi and Jimenez 2013). In this context, the small thermal fluctuations experienced on most Sub-Antarctic islands could

result in little or no seasonal structure to the life cycle, and no true diapauses in response to environmental cues (Convey 1996). Hence, cool temperatures year-round, combined with a low or non-existent risk of extreme winter lows, could allow for continuous development and for the completion of multiple generations through the year (Convey 1996).

Temperature and discharge seem to be important environmental constraints in Patagonian (Epele et al. 2011) and Magellanic sub-Antarctic streams. During the austral summer, discharge increases at Station V (120 metres a.s.l.) and temperature remains stable and warm throughout April and March (Figure 3), allowing for the supply of a variety of food resources (Miserendino and Pizzolon 2000). Under these conditions, aquatic insects are almost certainly able to achieve the number of degree-days needed to complete their development (Sweeney 1984), allowing for hatching to occur during the months of January, February, March, and April.

Gigantodax rufescens and Meridialis chiloeensis as potential indicators of climate change in South American sub-Antarctic streams

Climate change has the capacity to change aquatic community structure and species geographical distributions (Ryan and Ryan 2006; Winterbourn, Cadbury, Ilg, and Milner 2008). Several studies have shown that aquatic ecosystems are as vulnerable to global change as terrestrial and marine ecosystems (Heino, Virkkala, and Toivonen 2009), although the evidence is unbalanced across ecosystems and information from streams is scarce (Durance and Ormerod 2007). Lentic and lotic ecosystems are considered to be most sensitive to climate change at a global scale, with aquatic ecosystems at high latitudes being strongly threatened by it (Heino et al. 2009). With increasing temperatures in Magellanic sub-Antarctic watersheds, species may not be able to meet their low temperature thresholds for proper egg and larval development to occur (Winterbourn et al. 2008), causing changes in trophic structures, distributions, or even local extinction of cold-stenothermal specialists.

In this context, a monitoring programme at Omora LTSER was established to identify potential indicators of biologically significant changes in the long-term. The programme started with *G. rufescens* and *M. chiloeensis*, as described in this study, and has added other species with distributions sharply limited by altitude and temperature. Although the studied species do not show distribution restrictions throughout the altitudinal gradient, they are proposed as potentially good indicators of global warming in the long-term for at least three reasons: (1) their wide latitudinal and altitudinal distribution could allow for the monitoring and prediction of large-scale distributional changes between different latitudes and altitudes, (2) both are highly abundant in the sub-Antarctic Magellanic ecoregion, and (3) their life cycle could potentially vary from merovoltine to multivoltine through a short gradient, allowing for a close monitoring of their phenology at all altitudinal locations. Finally, the Róbalo River watershed and the Dientes de Navarino mountain range host a representative mosaic of the Cape Horn archipelago (Rozzi et al. 2010), which can be reached throughout a relatively short distance and altitude. The monitoring of the freshwater insects discussed here, along with long-term water temperature data, will provide a barometer to assess the potential influence of global warming on the freshwater fauna of the sub-Antarctic ecoregion of southern South America.

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Disclosure statement

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