

Diel locomotor activity and shelter use in the Patagonian catfish *Hatcheria macraei* under experimental conditions

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Abstract Diel locomotor activity and shelter use was experimentally evaluated in *Hatcheria macraei* under three different light regimens: natural and inverted photoperiods, and during constant darkness. The results demonstrate clear nocturnal activity and highlight the negative phototactic behaviour of *H. macraei*, proving that light is the external factor that triggers the seeking of shelter and the subsequent hiding action. Locomotor activity was maximal in darkness, intermediate at dawn and dusk, and minimal (maximum shelter use) in full light. During free-running experiments (i.e. constant darkness) *H. macraei* continued to exhibit the same diel pattern of resting (or hiding) and swimming as under natural light conditions. Nocturnal activity and negative phototactic behaviour appear to be important mechanisms which have enabled *H. macraei* to withstand the effects of salmonid introduction in lotic environments where other native fishes have suffered negative effects.

Keywords Circadian rhythm · Artificial photoperiod · Hiding behaviour · Refuge · Swimming activity

Introduction

Activity patterns in animals have evolved to cope with the time structure of their environment in order to anticipate predictable events (Yerushalmi and Green 2009). The most evident environmental cycle is the day-night alternation which follows a 24-h pattern. Light–dark successions have strong implications in the physiology, behaviour and ecology of fish, and ultimately model their activity rhythms (Reebs 2002).

Locomotor or swimming activity is mostly related to feeding or reproductive processes; in contrast, shelter use is mainly associated with predation avoidance. In this context, the most recognized trade-off is between food acquisition and shelter use, which is a central ecological fact in small fish (e.g., Werner and Hall 1988; Walters and Juanes 1993; Borcharding 2006). When fish forage they are usually exposing themselves to some risk of predation; in contraposition, a safe place can often be inadequate for optimal feeding (Lima and Dill 1990). The choice made at this dichotomy is determined by changes in light intensity during the 24-h cycle.

The small benthic catfish *Hatcheria macraei* (Girard 1855) is a species of pencil catfish of the Trichomycteridae family. It mainly inhabits Atlantic drainages, including both headwater and lowland habitats of Patagonian rivers (Unmack et al. 2009, 2012). In contrast to other native fish species which are very scarce nowadays in rivers, *H. macraei* is widely distributed and often abundant in the rivers where it occurs (Unmack et al. 2012). Currently, Patagonian freshwater communities are largely dominated by salmonids (Pascual et al. 2007), *Oncorhynchus mykiss* being the most widespread species (Aigo et al. 2008). Notwithstanding the absence of native fish abundance data previous to their introduction, salmonids (in particular *O.*

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mykiss) seem to have had a major impact on small streams, where they appear to have displaced native fishes almost completely (Aigo et al. 2008; Habit et al. 2010), with the exception of *H. macraei*.

Within complex and dynamic environments like rivers, fish activity patterns may vary on both spatial and temporal scales (Reebs 2002; Kronfeld-Schor and Dayan 2003). These have ecological implications; for example, diel temporal partitioning of resources may facilitate coexistence between competitors and between predators and prey. This mechanism could be key to the coexistence of *O. mykiss* and *H. macraei*. *Oncorhynchus mykiss* has generally been reported to perform diurnal activity (Chen et al. 2002), although it seems to prefer daytime when constrained mostly by foraging considerations, and night-time when predator avoidance is more important (Reebs 2002). *Hatcheria macraei*, in contrast, displays negative phototaxis (Menni 2004), is a bottom-dweller and highly cryptobiotic with great variation in its spot patterns (Barriga et al. 2015), hiding most of the time and using interstitial space during daylight. For this reason the diurnal microhabitat use of this catfish is associated with large substrate sizes which have conspicuous interstitial space (Barriga et al. 2013). Although their nocturnal behaviour is known (Ringuelet et al. 1967), no studies have been carried out in order to elucidate the relationship between light variation, shelter use and locomotor activity during a 24-h cycle. The main goal of this study was to evaluate, under experimental conditions, the behaviour of the Patagonian catfish *H. macraei* in terms of locomotor activity and shelter use in relation to light intensity during a 24-h cycle of light–dark (L:D). The effect of light intensity decoupled from the natural 24-h cycle was also studied, in order to assess the existence of internal regulation in a free-run experiment (D:D), or the inhibitor effect of light in an inverted photoperiod (D:L) cycle.

Materials and methods

Fish collection

Hatcheria macraei individuals were captured in Pichileufu River, Río Negro province, Argentina (41°05'24''S, 70°49'42''W, 926 m a.s.l.) using a 24-V DC backpack electrofishing unit, model 12-B (Smith-Root Inc., Vancouver, WA, USA) and hand nets. Fishing was performed in riffle sections during April and August 2010 and April 2012. Captured fish ($N = 30$, 7.83 ± 1.86 cm total length, 2.07 ± 0.67 g weight) were transported inside insulated containers to the facilities of Centro de Ecología Aplicada de Neuquén (CEAN) in the city of Junín de los Andes, Neuquén province, Argentina, in order to perform the experimental work.

Experimental trial design

Fish were acclimatized to experimental conditions for at least 1 week in 500-l tanks with a continuous water supply from Chimehuín River. Tanks were prepared with substrate to provide shelter, similar to conditions in the wild (Barriga et al. 2013), in order to diminish fish stress. During this period fish were fed daily with live prey, mainly macroinvertebrates, and also with artificial food. The feeding process was carried out at different times of day and night in order to prevent learning behaviour on the part of the individuals.

Experiments were performed in a 20-l aquarium (20 cm height \times 25 cm width \times 40 cm length) with a slow water turnover rate, which was artificially illuminated by a light-emitting diode (LED) device. The bottom of the aquarium was covered with gravel from 4 to 50 mm in size and a shelter was recreated using a hollow brick (4 \times 4 \times 15 cm) placed in a corner. Both the aquarium and LED device were placed inside a chamber of 1 \times 1 \times 2 m constructed with black opaque plastic in order to isolate them from natural light. A Sony digital video camera (DCR-HC54) with night vision (i.e. infrared vision) was used to register fish locomotor activity and an additional infrared light was used to increase nocturnal visibility. A gridded acrylic sheet (20 cm height \times 40 cm length) was placed directly behind the aquarium, opposite the camera, as a reference for the analysis of locomotor activity from the videos.

Three types of experiment were performed to evaluate the locomotor activity and shelter use of *H. macraei* under different light regimens during a 24-h cycle. The first was carried out under a L:D regimen similar to the natural cycle. The second was performed with an inverted photoperiod (D:L) exactly opposite to the natural cycle. The third experiment was run in constant darkness (D:D). Thirty individuals were used in total, ten fish per series of experiments. However, data from one individual in the first experiment were ruled out due to the anomalous behaviour of this fish (i.e. extremely active with spastic swimming). Each trial was carried out with one fish and lasted 2 days in total: 1 day for acclimatisation and 1 day for video recording of locomotor activity. The photoperiod of each series was maintained without alteration during both trial days. Fish were not fed during this 2-day period. The first series of trials were carried out from 3 May 2010 to 1 June 2010 (austral autumn), the second series from 21 August 2010 to 11 September 2010 (austral winter), and the third series from 1 to 26 April 2012 (austral autumn). The water in the experimental aquarium was maintained at room temperature: for the first series at 7.6 ± 1.4 °C (mean \pm SD), for the second series at 6.3 ± 1.8 °C, and for the third series at 10.7 ± 1.7 °C.

For the first and second series of experiments, dawn was simulated by means of a progressive linear increment of light intensity from 0 to 630 lx (or lumen m⁻²) in 1 h. The inverse situation was generated in the case of dusk, namely a progressive linear decrement from 630 to 0 lx in 1 h. As the beginning of each twilight was set according to the natural cycle, the 24-h cycle was divided as follows: 1 h of dawn, approximately 11 h of maximum light intensity (at 630 lx), 1 h of dusk, and approximately 11 h of darkness (at 0 lx). For the third experiment the 24-h cycle was run at 0 lx. Four 1-h sessions of video recording were performed each day for the first and second series of experiments. These sessions coincided with dawn, dusk, midday (from 12:00 to 13:00 h) and midnight (from 0:00 to 1:00 h); totalling 4 h per day. The beginning of dawn ranged from 7:34 to 8:01 h, and of dusk from 18:25 to 18:49 h for the first series of experiments. During the second series, the beginning of dawn ranged from 6:53 to 7:27 h and of dusk from 19:11 to 19:31 h. Two 1-h sessions of video recording were performed each day for the third series of experiments, at midday and at midnight.

The recorded videos were digitized, transferred to a personal computer and subsequently analysed with a standard multimedia player. To evaluate activity and shelter use, fish behaviour was characterized as: swimming, resting, or hiding. The fish was considered as ‘swimming’ when it was actively moving, ‘resting’ when it was immobile on the substrate (hereafter called ‘bottom time’) and ‘hiding’ when it was registered as inside the shelter. Accordingly, each 1-h video was divided into three mutually exclusive periods, corresponding to the three fish behaviours. The swimming velocity of each individual was also estimated considering total time and total distance recorded during the ‘swimming’ period.

The differences in both time and intensity in *H. macraei* locomotor activity at different times of the day during experiments were assessed using ANOVA. Mann–Whitney and Kruskal–Wallis analyses were used when normality or homoscedasticity assumptions of the data failed. A multiple comparison procedure (Tukey test) was used to detect differences between each pairwise comparison.

Results

Direct photoperiod (L:D)

Catfish under natural photoperiod conditions showed a clear nocturnal locomotor activity pattern. Differences were found in relation to the time of the day (Kruskal–Wallis, $H = 18.32$, d.f. = 3, $P < 0.001$): time spent on swimming activity (i.e. swimming time) was greatest at midnight, intermediate at dusk and lowest during midday

and dawn (Fig. 1). The lowest swimming time was recorded at midday or at increasing light intensity (i.e. dawn). No differences were found in swimming velocity at the different times of day analysed (ANOVA, $F_{2, 13} = 0.379$, $P = 0.692$, Table 1). Due to the low level of activity registered at midday, only one measurement of velocity was registered, which was ruled out for statistical analysis. In addition, a remarkable difference in shelter use (i.e. hiding time) was found throughout the 24-h cycle (Kruskal–Wallis, $H = 24.81$, d.f. = 3, $P < 0.001$). Catfish remained hidden inside the shelter during almost the entire midday period, while they came out of hiding during the midnight period. The time spent in the shelter during midnight was the lowest, and differed significantly from the time spent sheltering at the other three moments of the day (Tukey, $P < 0.05$, Fig. 1).

Inverted photoperiod (D:L)

When the photoperiod was inverted, swimming time was low for all four times of the day, and no differences were found between them (Kruskal–Wallis, $H = 7.61$, d.f. = 3, $P = 0.055$, Fig. 2). A difference in shelter use was found, however, under the inverted light cycle conditions (Kruskal–Wallis, $H = 11.81$, d.f. = 3, $P = 0.008$). Hidden time

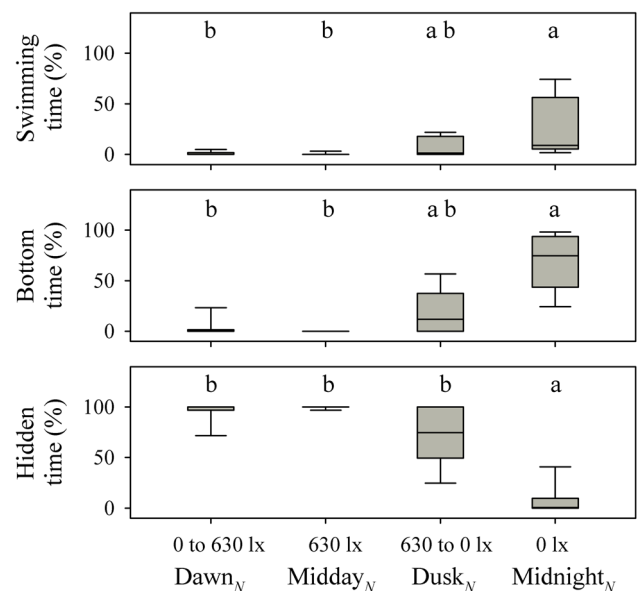


Fig. 1 Diel activity of *Hatcheria macraei* during the direct experiment (L:D) represented by median, quartiles and data outside 10th and 90th percentiles. One-hour videos from 9 individuals are divided into percentage of time *inside* shelter (*Hidden*), on the *bottom* but *outside* the shelter (*Bottom*) and active (*Swimming*), and clustered by light intensity (in lx) of the experiment. The relationship between experimental light intensity and the 24-h natural cycle (Dawn_N, Midday_N, Dusk_N, and Midnight_N) is also indicated. Significant differences between times of the day are indicated by *different letters* (Tukey, $P < 0.05$)

Table 1 Fish swimming velocity (mean \pm SD, in m sec^{-1}) during direct (L:D), inverted (D:L) and free-run (D:D) experiments throughout the 24-h cycle

Treatments	Natural light cycle			
	Dawn	Midday	Dusk	Midnight
L:D ^a	0.038 \pm 0.012 (0 \rightarrow 630 lx)	0.073 ^d (630 lx)	0.035 \pm 0.017 (630 \rightarrow 0 lx)	0.043 \pm 0.014 (0 lx)
D:L ^b	0.022 \pm 0.011 (630 \rightarrow 0 lx)	0.022 \pm 0.012 (0 lx)	0.043 \pm 0.031 (0 \rightarrow 630 lx)	0 \pm 0 (630 lx)
D:D ^c	–	0.026 \pm 0.019 (0 lx)	–	0.046 \pm 0.029 (0 lx)

Relationship between natural and artificial (light intensity in brackets) cycles is shown. Differences between times of the experiment for each treatment are also indicated

^a (ANOVA, $P > 0.05$)

^b (Kruskal–Wallis, $P > 0.05$)

^c (Mann–Whitney, $P < 0.01$)

^d Only one measurement recorded, ruled out for statistical analysis

was significantly longer at 630 lx (i.e. at natural midnight) than at 0 lx (Tukey, $P < 0.05$, Fig. 2). Bottom time varied throughout the day (Kruskal–Wallis, $H = 12.46$, d.f. = 3, $P = 0.006$). Regarding time spent on the bottom, results found were the opposite to shelter use. *Hatcheria macraei* spent more time on the bottom at 0 lx (natural midday) than at 630 lx (natural midnight) (Tukey, $P < 0.05$, Fig. 2). No differences were found between times of day

regarding swimming velocity (Kruskal–Wallis, $H = 0.54$, d.f. = 2, $P = 0.765$, Table 1).

Comparing D:L and L:D cycles, swimming time at 0 lx decreased in the D:L cycle (at natural midday) and also when light decreased from 630 to 0 lx (at natural dawn). Hiding time increased at 0 lx in D:L as compared to L:D. In other words, catfish displayed lower activity levels and more hiding in D:L when there was a total absence of light.

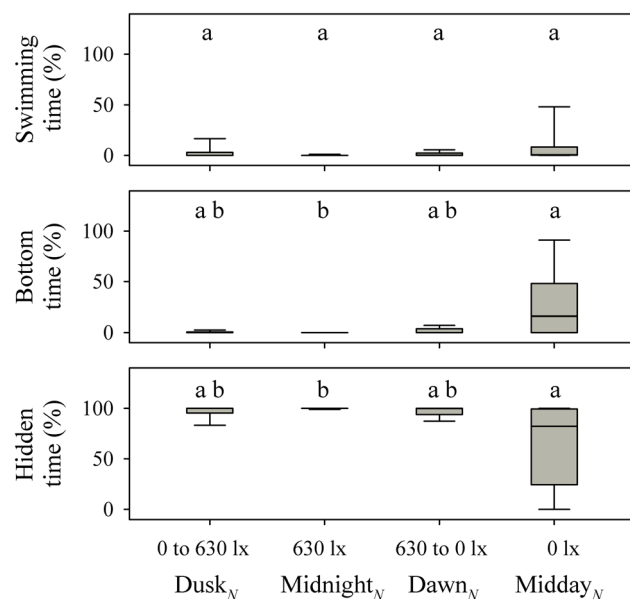


Fig. 2 Diel activity of *Hatcheria macraei* during the inverted experiment (D:L) represented by median, quartiles and data outside 10th and 90th percentiles. One-hour videos from 10 individuals are divided into percentage of time *inside* shelter (*Hidden*), on the *bottom* but *outside* the shelter (*Bottom*) and active (*Swimming*), and clustered by light intensity (in lux) of the experiment. The relationship between experimental light intensity and the 24-h natural cycle (Dusk_N, Midnight_N, Dawn_N, and Midday_N) is also indicated. Significant differences between times of the day are indicated by *different letters* (Tukey, $P < 0.05$)

Continuous darkness photoperiod (D:D)

No significant differences were detected concerning time spent outside (including both bottom and swimming times) (Mann–Whitney, $U = 71$, $P = 0.097$) or inside the shelter (Mann–Whitney, $U = 29$, $P = 0.097$) when comparing subjective midday and subjective midnight under natural photoperiod conditions (Fig. 3). However, more time was spent swimming (Mann–Whitney, $U = 96$, $P < 0.001$, Fig. 3), and swimming was faster (Mann–Whitney, $U = 85$, $P = 0.009$, Table 1) during subjective midnight than during subjective midday.

Discussion

The results of the present study confirm clear nocturnal activity and highlight the negative phototactic behaviour of *H. macraei*, proving that light is the external factor that triggers the seeking of shelter and the subsequent hiding action. Locomotor activity was maximal in darkness, intermediate at dawn and dusk, and minimal (maximum shelter use) in full light. Nocturnal locomotor and feeding activities have been registered in many catfish species (Menni 2004; Schulz and Leuchtenberger 2006; Kasai et al. 2009; Ramteke et al. 2009; Mazzoni et al. 2010; Carvalho et al. 2014); furthermore, Ringuélet et al. (1967), reported

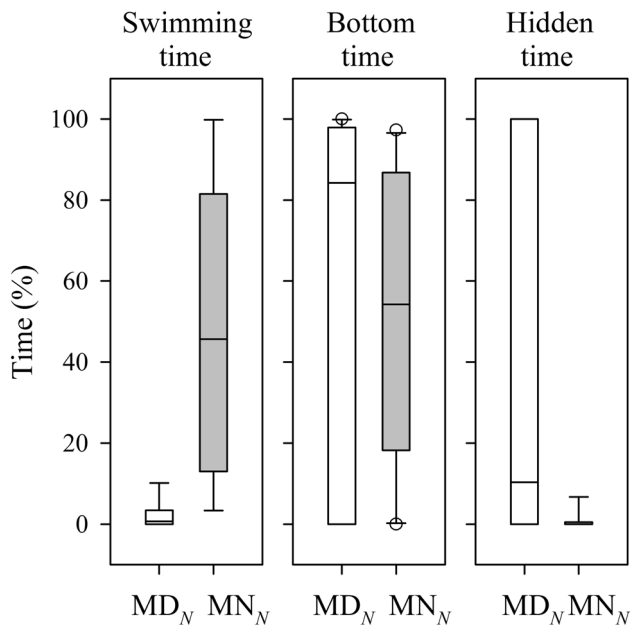


Fig. 3 Diel activity of *Hatcheria macraei* during free-run experiments (total darkness) expressed by median, quartiles and data outside 10th and 90th percentiles. One-hour videos from 10 individuals are divided into time of activity, time on the *bottom* but outside the shelter and time *inside* shelter. The midday (MD_N) and midnight (MN_N) of the natural cycle are also indicated. Difference between MD_N and MN_N was significant only for swimming time (Mann-Whitney, $P < 0.05$)

in their first work that *Pygidium* (now *Trichomycterus*) and *Hatcheria* were negatively phototactic genera.

Low values for swimming time were found at natural midday (L:D) as well as inverted midnight (D:L). During the inverted cycle at 630 lx (i.e. natural midnight), the time of the day when the catfish would be more active under L:D cycle, activity was inhibited by light. The phase shift provoked when the photoperiod was inverted resulted in a low swimming time throughout the entire day. That is to say, these results emphasize that light has a negative masking effect on normal locomotor activity rather than causing a fundamental shift in the diel pattern, irrespective of what an internal clock might dictate at that particular time of day.

When fish are phase-shifted from natural L:D to D:L cycle and there is endogenous control of locomotor activity, they require several days to synchronize their rhythms to the new phase (Kasai et al. 2009). In contrast, when fish resynchronize to the new cycle within a day, this suggests that the control is mainly driven by exogenous factors (Vera et al. 2011). The former situation seems to be the case in phase-shifted cycles in *H. macraei*. Moreover, the time of activity observed during the free-running experiments (D:D) continued to exhibit the same pattern of resting (or hiding) and swimming as under natural light

conditions (L:D experiments), at least during the 24 h of the trial. Both situations seem to correspond to endogenous control, but long-term experiments are required in order to confirm the endogenous nature of diel activity in this species.

Although a clear pattern of nocturnal activity was observed in *H. macraei*, the differences found between direct (L:D) and inverted (D:L) photoperiod experiments regarding hidden time could alternatively be due to a seasonal effect on diel activity. Despite the fact that the experimental temperature was similar for the direct (7.6 ± 1.4 °C) and inverted (6.3 ± 1.8 °C) experiments, they were performed at different times of the year: the former during austral autumn and the later during austral winter. For this reason, it cannot be ruled out that the difference in hidden time (higher in D:L) was also due to a seasonal effect. That is, this species could have a tendency to be less active (more hiding) in winter in relation to the low water temperature. Whatever the case, during the inverted experiment hidden time was significantly lower and bottom time was significantly higher at 0 lx than at 630 lx.

Hatcheria macraei is a small, elongated fish with morphological adaptations to a benthic life style, such as a flattened head with subterminal mouth and a prognathic upper lip, three pairs of barbells and very small dorsal eyes (Arratia and Menu-Marque 1981; Barriga and Battini 2009). All these characteristics indicate that this fish seeks its prey using tactile rather than visual sense. For this reason, feeding activity is probably maximized in darkness rather than during light periods.

Hatcheria macraei mostly inhabits microhabitats presenting substrates with considerable interstitial space, preferably those present in riffles or runs with faster water velocity (Barriga et al. 2013). Their hiding behaviour during daytime is in agreement with our experimental data. The use of shelter was almost total during light periods, providing evidence of the negative phototaxis previously reported in this species (Menni 2004).

From a broad point of view, their nocturnal activity habits could have conferred adaptive advantages to *H. macraei* in environments like Pichileufu River. On the one hand, this behaviour enables temporal segregation or temporal resource partitioning with diurnal species, hence avoiding any possible competitive effect (e.g. food resource). On the other hand, hiding during daytime favours predation avoidance, not only from fish species, but also from birds or mammals. For example, the neotropical cormorant (*Phalacrocorax brasilianus*) preys actively on both exotic and native fishes, these items constituting an important component of its diet (86 % frequency occurrence); however, no records of *H. macraei* in their diet (pellet) analysis have been reported (Alarcón et al. 2012).

For this reason, a nocturnal habit, and thus temporal partitioning of resource use between *O. mykiss* and *H. macraei*, appears to be an important mechanism in enabling these species to co-exist in low-order streams, as inferred from the wide distribution and high density of *H. macraei* in Patagonia. In line with this, Glova et al. (1992) observed nocturnal displacement of the feeding time of one New Zealand galaxiid, *Galaxias vulgaris*, due to the presence of brown trout. Whether an induced or innate behaviour, this strategy could have enabled *H. macraei* to withstand the effects of salmonid introduction in lotic environments where these fish have had a negative effect on other native fishes (Pascual et al. 2002, 2007, 2009, Baigún and Ferriz 2003, Aigo et al. 2008).

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References

- Aigo J, Cussac V, Peris S, Ortubay S, Gómez S, López H, Gross M, Barriga J, Battini M (2008) Distribution of introduced and native fish in Patagonia (Argentina): patterns and changes in fish assemblages. *Rev Fish Biol Fisher* 18:387–408
- Alarcón PAE, Macchi PJ, Trejo A, Alonso MF (2012) Diet of the Neotropical cormorant (*Phalacrocorax brasilianus*) in a Patagonian freshwater environment invaded by exotic fish. *Waterbirds* 35:149–153
- Arratia G, Menu-Marque S (1981) Revision of the freshwater catfishes of the genus *Hatcheria* (Siluriformes, Trichomycteridae) with commentaries on ecology and biogeography. *Zool Anz* 207:88–111
- Baigún C, Ferriz RA (2003) Distribution patterns of native freshwater fish in Patagonia (Argentina). *Org Divers Evol* 3:151–153
- Barriga JP, Battini MA (2009) Ecological significances of ontogenetic shifts in the stream-dwelling catfish, *Hatcheria macraei* (Siluriformes, Trichomycteridae), in a Patagonian river. *Ecol Freshw Fish* 18:395–405
- Barriga JP, Espinós NA, Chiarello-Sosa JM, Battini MA (2013) The importance of substrate size and interstitial space in the microhabitat selection by the stream-dwelling catfish *Hatcheria macraei* (Actinopterygii, Trichomycteridae). *Hydrobiologia* 705:191–206
- Barriga JP, Chiarello-Sosa JM, Juncos R, Battini MA (2015) Photo-identification and the effects of tagging on the Patagonian catfish *Hatcheria macraei*. *Environ Biol Fish* 98:1163–1171
- Borcherding J (2006) Prey or predator: piscivorous 0 + perch (*Perca fluviatilis*) in the trade-off between food and shelter. *Environ Biol Fish* 77:87–96
- Carvalho MS, Zuanon J, Ferreira EJG (2014) Diving in the sand: the natural history of *Pygidianops amphioxus* (Siluriformes: Trichomycteridae), a miniature catfish of Central Amazonian streams in Brazil. *Environ Biol Fish* 97:59–68
- Chen W, Naruse M, Tabata M (2002) Circadian rhythms and individual variability of self-feeding activity in groups of *Oncorhynchus mykiss* (Walbaun). *Aquac Res* 33:491–500
- Girard CF (1855) Contributions to the fauna of Chile. Report to Lieut. James M. Gilliss, U. S. N., upon the fishes collected by the U. S. Naval Astronomical Expedition to the southern hemisphere during the years 1849-50-51-52, Washington
- Glova G, Sagar P, Naslund I (1992) Interaction for food and space between populations of *Galaxias vulgaris* Stokell and juvenile *Salmo trutta* L. in a New Zealand stream. *J Fish Biol* 41:909–925
- Habit E, Piedra P, Ruzzante DE, Walde SJ, Belk MC, Cussac VE, Gonzalez J, Colin N (2010) Changes in the distribution of native fishes in response to introduced species and other anthropogenic effects. *Global Ecol Biogeogr* 19:697–710
- Kasai M, Yamamoto T, Kiyohara S (2009) Circadian locomotor activity in Japanese sea catfish *Plotosus lineatus*. *Fish Sci* 75:81–89
- Kronfeld-Schor N, Dayan T (2003) Partitioning of time as an ecological resource. *Annu Rev Ecol Syst* 34:153–181
- Lima SL, Dill M (1990) Behavioural decisions made under the risk of predation. *Can J Zool* 68:619–640
- Mazzoni R, Moraes M, Rezende CF, Iglesias-Rios R (2010) Diet and feeding daily rhythm of *Pimelodella lateristriga* (Osteichthyes, Siluriformes) in a coastal stream from Serra do Mar—RJ. *Braz J Biol* 70:1123–1129
- Menni RC (2004) Peces y ambientes en la Argentina continental. Monografías del Museo Argentino de Ciencias. Naturales, Buenos Aires
- Pascual MA, Macchi PJ, Urbansky J, Marcos F, Riva Rossi C, Novara M, Dell'Arciprete P (2002) Evaluating potential effects of exotic freshwater fish from incomplete species presence-absence data. *Biol Invasions* 4:101–113
- Pascual MA, Cussac V, Dyer B, Soto D, Vigliano P, Ortubay S, Macchi PJ (2007) Freshwater fishes of Patagonia in the 21st century after a hundred years of human settlement, species introductions, and environmental change. *Aquat Ecosyst Health* 10:1–16
- Pascual MA, Lancelotti J, Ernst B, Ciancio J, Aedo E, García-Asorey M (2009) Scale, connectivity, and incentives in the introduction and management of non-native species: the case of exotic salmonids in Patagonia. *Front Ecol Environ* 7:533–540
- Ramteke AK, Poddar P, Pati AK (2009) Circadian rhythms of locomotor activity in Indian walking catfish, *Clarias batrachus*. *Biol Rhythm Res* 40:201–209
- Reebs SG (2002) Plasticity of diel and circadian activity rhythms in fishes. *Rev Fish Biol Fisher* 12:349–371
- Ringuelet RA, Aramburu RH, Alonso A (1967) Los peces argentinos de agua dulce. Provincia de Buenos Aires, Comisión de Investigación Científicas, Buenos Aires
- Schulz UH, Leuchtenberger C (2006) Activity patterns of South American silver catfish (*Rhamdia quelen*). *Braz J Biol* 66:565–574
- Unmack PJ, Habit EM, Johnson JB (2009) New records of *Hatcheria macraei* (Siluriformes, Trichomycteridae) from Chilean province. *Gayana* 73:102–110
- Unmack PJ, Barriga JP, Battini MA, Habit EM, Johnson JB (2012) Phylogeography of the catfish *Hatcheria macraei* reveals a negligible role of drainage divides in structuring populations. *Mol Ecol* 21:942–959
- Vera LM, Al-Khamees S, Hervé M (2011) Stocking density affects circadian rhythms of locomotor activity in African catfish, *Clarias gariepinus*. *Chronobiol Int* 28:751–757
- Walters CJ, Juanes F (1993) Recruitment limitation as a consequence of natural selection for use of restricted feeding habits and predation risk taking by juvenile fishes. *Can J Fish Aquat Sci* 50:2058–2070
- Werner EE, Hall DJ (1988) Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology* 69:1352–1366
- Yerushalmi S, Green RM (2009) Evidence for the adaptive significance of circadian rhythms. *Ecol Lett* 12:970–981