Differential metabolic response to temperature among populations of *Cyprideis torosa* (Jones, 1850) (Ostracoda: Cytherideidae)

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ABSTRACT

Rising global temperatures reduce oxygen solubility in water bodies while increasing the metabolic demands of aquatic ectotherms. Oxygen consumption rate (OCR) varies widely across crustaceans and is influenced by developmental stage, sex, body mass, activity level, and environmental conditions such as temperature and salinity. We investigated how OCR responds to increasing temperatures in the podocopid ostracod *Cyprideis torosa* (Jones, 1850) by using optical sensor respirometry. Specifically, we compared adults and subadults from ostracod populations inhabiting distinct salinity regimes to assess how environmental history and life stage influence oxygen consumption. Results show that OCR increases with temperature across all populations, but the magnitude of this response differs markedly. Specimens from intermediate salinity (mesohaline) exhibited the highest OCR and strongest thermal response, whereas those from oligohaline and hyperhaline habitats showed lower

OCR and reduced thermal flexibility. Subadults consistently consumed more oxygen than adults, particularly at higher temperatures. These findings highlight the role of local conditions, local adaptation, and ontogeny in shaping oxygen demand in *C. torosa* and provide new insights into its physiological response in the face of temperature and salinity variability.

Keywords: Crustacea, crustacean physiology, metabolic rate, respirometry, salinity, thermal effects

INTRODUCTION

Rising global temperatures reduce oxygen solubility in water bodies while increasing the metabolic demands of aquatic ectotherms (Verberk *et al*., 2011; Breitburg *et al*., 2018). Species may experience physiological limitations that restrict their thermal tolerance when oxygen demand exceeds supply capacity (Pörtner, 2001; Whiteley & Taylor, 2015; Pörtner *et al*., 2017; Bridge *et al*., 2024). These limitations arise not only from reduced oxygen availability but also from the organism's inability to match oxygen supply with increasing metabolic demand, or from excessive energetic costs associated with doing so (Verberk & Atkinson, 2013; Rubalcaba *et al*., 2020). Shallow coastal lagoons, such as salt marshes, are particularly affected by climate change due to their limited depth, which accelerates evaporation, increases salinity, and reduces dissolved oxygen levels (Lloret *et al*., 2008; Pérez-Ruzafa *et al*., 2011; Carrasco *et al*., 2016). Although groundwater-fed lagoons typically show more stable temperatures (Andrisoa *et al*., 2019), they often experience limited water circulation, also leading to reduced oxygen renewal (Newton *et al*., 2014).

Aquatic ectotherms, such as crustaceans, rely on physiological adjustments to maintain metabolic function (Lagerspetz & Vainio, 2006; Morley *et al*., 2019; Ren *et al*., 2021). Metabolic rates, the energy consumed by organisms over a specific period of time, can

be approximated by quantifying the volume of oxygen consumed per unit time through respirometry (Lampert, 1984). Oxygen consumption rate (OCR) is known to increase with temperature (Pörtner, 2002; Brown *et al*., 2004), but it is also influenced by other factors such as developmental stage and sex (Weisse & Rudstam, 1989), body mass (Gillooly *et al*., 2001), activity level (Culver & Poulson, 1971), and abiotic conditions (Hernández-León & Ikeda, 2005; Ruiz *et al*., 2013). Early-life stages typically exhibit higher metabolic rates due to increased energy demands for growth and development (Epp & Lewis, 1979; Perera *et al*., 2007; El-Gamal, 2011; Sokolova *et al*., 2012; Sokolova, 2013). Additionally, larger individuals tend to have lower mass-specific OCR than smaller ones (Villarreal, 1990; Carvalhoa & Phanb, 1997), while food intake directly raises metabolic rates (Newell, 1973; Loreau, 1995; Crear & Forteath, 2000; Díaz-Iglesias *et al*., 2002).

Podocopid ostracods are small crustaceans (0.3–5 mm) widely distributed across marine, brackish, and freshwater ecosystems (Carbonel *et al*., 1988; Mesquita-Joanes *et al*., 2012; Smith *et al*., 2015), making them valuable models for studying respiratory processes across aquatic environments. Despite their ecological significance, most studies on ostracod respiration focus on the effects of temperature while overlooking potential metabolic differences between life-stages. Moreover, previous research mostly targeted single populations under specific conditions (Hagerman, 1969; Grant, 1983; Newrkla, 1985; Ikeda, 1990) or compared different species rather than populations (Ganning, 1971; Kaeriyama & Ikeda, 2004).

Cyprideis torosa (Jones, 1850) plays a key ecological role in brackish ecosystems (Gusakov *et al*., 2021) and stands out among podocopid ostracods as euryhaline and eurythermal, with a high tolerance to environmental fluctuations (Heip, 1976; Mezquita *et al*., 2000; Boomer *et al*., 2017). As a benthic organism, *C. torosa* is particularly exposed to oxygen depletion (Jahn *et al*., 1996), as diffusion from the water column is limited and

atmospheric exchange is restricted (Vaquer-Sunyer & Duarte, 2008). Its broad ecological tolerance, well-documented fossil record, and (morphological and geochemical) sensitivity to environmental change have led to its recognition as a model for ostracod research (De Deckker & Lord, 2017). The only previous study that quantified oxygen consumption in *C. torosa* focused on subadults from a single population in northern Europe (Belgium) while providing limited data on adults (Herman & Heip, 1982). Expanding upon this work, our study investigated how OCR is adjusted to increasing temperature in three populations of *C. torosa* from habitats with different environmental conditions. Using optical sensor respirometry, we estimated OCR from adults and subadults to further assess whether this adjustment is influenced by life stage.

METHODS

Sampling sites

The three populations selected for our study originated from two locations in southeastern Spain (Fig. 1): Ullal de Baldoví (UdB) and Salinas de Santa Pola, which included two sampling sites: Aguas Dulces (AD) and Charco Llis (ChL). Table 1 summarizes the environmental conditions measured from the sampling locations. UdB is an oligohaline pond (according to the Venice system; Anonymous, 1958) within the Albufera Natural Park (Sueca, Valencia), fed by a groundwater spring, which provides stable environmental conditions (Rueda *et al*., 2013). This environmental stability supports a persistent population of *C. torosa* throughout the year (F. M.-J., personal observation). Salinas de Santa Pola comprises water bodies across a wide salinity gradient and its shallow character results in fluctuating temperatures. The sampling site AD is located within the Bras del Port saltern and receives water from a canal connected to inland wetlands (Fondo d'Elx) and the Vinalopó River, therefore exhibiting moderate (mesohaline) salinity conditions. By contrast, ChL is

located 250 m from AD, within an operational salt flat used for seawater evaporation and it is hyperhaline (Marco-Barba *et al*., 2012).

<Fig. 1; Table 1>

Sampling procedure

All locations were sampled at the beginning of spring during late morning. Populations ChL and AD populations were sampled in 2022 and UdB in 2024. Approximately 600 individuals of *C. torosa* were collected from each site by sweeping the sediment multiple times with a 250 µm hand net in submerged areas. Specimens were transferred into 1-l containers partially filled with site-specific water to maintain aeration during transport. *In situ* measurements of water conductivity, pH, dissolved oxygen, and temperature were taken using a ProQuatro portable multiparameter meter (YSI, Yellow Springs, OH, USA).

Specimen processing and maintenance

After collection, ostracods were manually separated from the sediment in the laboratory using an MZ 125 stereomicroscope (Leica Biosystems, Wetzlar, Germany), and a fine-tipped paintbrush. The isolated ostracods were transferred using plastic Pasteur pipettes to Petri dishes containing site-specific water. Adult males, females and subadults (A-1 stage) of *C. torosa* were classified following Mezquita *et al*. (2000). Males were distinguished from females based on their morphology: female bodies are shorter and exhibit a broader posterior part in dorsal view than males. Subadults were identified by their smaller size and less pronounced morphological features compared to adults.

Individuals from each population were maintained under controlled laboratory conditions (20°C, dark) for acclimation. Experimental trials were performed within one week after each sampling campaign, both in 2022 and 2024, ensuring that all measurements reflected the physiological condition of freshly collected animals. A total of 450 individuals per site (150 males, 165 females, and 135 subadults) were transferred into 50 ml containers

filled with site-specific water. Experimental water solutions were prepared to replicate the salinity conditions of each collection site: 10 psu for AD, 50 psu for ChL and 1.7 psu for UdB. The solutions were filtered using Branchia^{TM} (47 mm, medium flow rate) microfiber glass filter paper (Labbox Labware, Premià de Dalt, Barcelona, Spain) and sterilized by autoclaving at 160°C for 2 h to ensure sterility and remove impurities. To prevent cross-contamination and ensure experimental consistency, males, females, and subadults from each population were kept in separate containers until the experiments began.

Respirometry experimental setup

For each locality (AD, ChL and UdB), a total of 10 experimental units (replicates) were prepared: 7 adult replicates and 3 replicates with only subadults. Each replicate consisted of 15 individuals. In adult replicates, the composition included approximately equal numbers of males and females (7 or 8 of each). Subadult replicates were composed exclusively of subadults. All were placed in 2.7 ml SV-PSt5 glass vials (PreSens^{TM}, Regensburg, Germany), with integrated optical oxygen sensor, filled with previously sterilized experimental water solutions. Ostracods remained in the same vials throughout the experiment, without being moved or transferred between cycles. Two additional vials containing only the experimental water solutions, without ostracods, served as controls.

The experimental and control vials were placed over an SDR SensorDish Reader (PreSens^{TM}), a 24-channel system for real-time optical oxygen measurement. The system was placed inside a KBW 240 (E 5.1) (Binder, Tuttlingen, Germany) climate chamber under dark conditions, where it remained throughout the entire experiment. The reader was connected to an external computer via an RJ45 cable and a splitter, allowing continuous data recording using SDR v4.0.0 software (PreSens^{TM}). Oxygen saturation measurements were recorded from the start of the trial every 3 min for approximately 2 h. Each locality was tested using three consecutive temperature cycles (10°C, 20°C, and 30°C), selected to represent a broad

and ecologically relevant range for the species (Heip, 1976; Mezquita *et al*., 2000; Roberts *et al*., 2020). A 10°C rise is typically associated with a two- to threefold increase in metabolic rate in aquatic ectotherms (Dell *et al*., 2011).

Estimation of oxygen consumption rates

OCRs were estimated from the slopes of linear regressions fitted to oxygen concentration decline over time for each experimental vial. Only the final 50 min (~16 data points) per session were used to ensure stable measurements. Background oxygen changes were corrected by subtracting the mean slope from control vials. Replicates with persistent positive slope values after correction were excluded (four replicates: one adult and one subadult from ChL at 10°C, one adult each from ChL at 20°C and from UdB at 20°C).

Slopes were normalized by the mean dry weight per replicate to obtain mass-specific OCR. Dry weights for ChL and AD individuals were obtained from the literature (Herman & Heip, 1982). Since UdB ostracods were visibly larger, individuals from this site were weighed following a modified protocol (Heiri *et al.*, 2001) to allow reliable comparisons and consider potential mass differences related to habitat-driven body size variation (Mezquita *et al*., 2000). Ostracods were sorted by stage and sex and dried (105°C, 4 h) in previously dried aluminum pans (60°C for 24 h). After cooling to room temperature, they were weighed three times on a precision balance with ± 0.01 mg resolution (SM635i-ION, Avantor, Gliwice, Poland).

The resulting OCR values were subsequently plotted to visualize interpopulation and life stage differences. The Q_{10} coefficient was calculated for each temperature interval and developmental stage to quantify the change in OCR with each 10°C increase. A global Q_{10} was also calculated for the full 10–30°C range to capture the general response across the temperature gradient.

Statistical modelling

Given that oxygen consumption values used in our dataset were positive (after multiplying the obtained negative slopes by –1) and displayed a right-skewed distribution, we used generalized linear models (GLMs) with a Gamma error distribution and a log-link function. Regression coefficients (β) were used to interpret the influence of each factor, with positive values indicating an increase and negative values indicating a decrease in oxygen consumption relative to the reference group. Models were fitted using adults from the AD population at 20°C as the reference level (intercept), as this population represents intermediate environmental conditions. Adults were chosen as the reference life stage due to their more stable metabolic rates compared to subadults. We used AICc model selection to obtain the best model among a set of possible variants considering all the different combinations of the explanatory variables: population, life stage, and temperature. Models were fitted using the glm function of the stats base package and the AICcmodavg package (Mazerolle, 2025) for model selection, in R v4.4.1 (R Core Team, 2024).

RESULTS

In situ measurements of environmental parameters confirmed a clear contrast between the three study sites, and were generally consistent with previously reported values, except for a slight deviation in the ranges of salinity at UdB and temperature in AD (Table 1). Salinity and conductivity values varied markedly across sites, with ChL presenting the highest levels, indicative of hyperhaline conditions, and UdB the lowest (oligohaline). Aguas Dulces exhibited intermediate values (mesohaline). In addition to these environmental patterns, the measured weight of adult males (119.39 µg) and subadults (42.00 µg) from UdB were slightly higher, and those of adult females (91.56 µg) slightly lighter than the weights

obtained from the literature (Herman & Heip, 1982) and considered for the individuals from the other two more saline sites.

Figure 2 displays the OCR across life stages, populations, and temperatures (see also Supplementary material Table S1). OCR increased with temperature across all populations, but the extent of this increase varied significantly among these and between life stages. OCR variation was generally wider in AD, particularly in subadults at 30°C, and narrower in ChL across all conditions. The highest OCR was recorded in subadults from AD at 30°C (1.668 µl h^{-1} mg^{-1}), and the lowest in adults from ChL at 10°C (0.052 µl h^{-1} mg^{-1}).

<*Fig. 2*>

According to life stage, differences were also observed, especially in AD, which gradually enlarged with increasing temperature and became significant at 30°C. Global Q_{10} values (Table 2) for the full 10–30°C range were generally lower in subadults (1.26–1.98) than in adults (1.86–2.10), except for AD. In UdB, subadults showed a low Q_{10} between 10–20°C (0.68), whereas adults reached a high value in the same interval (4.77), followed by a decrease between 20–30°C (0.86). Q_{10} values were overall more consistent in AD (~2.0 for both stages) among populations, whereas larger stage-related differences appeared in ChL and UdB.

<*Table 2*>

These observations were supported statistically. The best-fit GLM model, selected based on the lowest AICc (–101.86), included only main effects of temperature, population, and life stage, all of which had significant effects on OCR (Table 3). The estimated β coefficients indicated that population differences (e.g. ChL: $\beta = -1.18$, $P < 0.001$; UdB: $\beta = -0.66$, $P < 0.001$) and life stage (subadults $\beta = 0.62$, $P < 0.001$) had effect sizes comparable to or greater than those associated with a 10°C temperature change (30°C: $\beta = 0.49$, $P = 0.005$; 10°C: $\beta = -0.73$, $P < 0.001$). Subadults consistently showed higher OCRs than adults, and

OCRs were lower in ChL and UdB relative to AD, consistent with the observed means (Fig. 2). Variation across populations was also reflected in differences in the dispersion of OCR values, particularly the reduced variability in ChL.

<Table 3>

DISCUSSION

Our study provides the first evidence of consistent population-specific respiratory patterns in ostracods under different temperature conditions and across life stages. Previous research focused mainly on single populations and adult stages of ostracods (e.g. Ikeda, 1985; Peper, 1986; Kaeriyama & Ikeda, 2004) with limited attention to oxygen consumption in subadults (Ikeda, 1990). Our results expand upon earlier work by Herman & Heip (1982), demonstrating that oxygen consumption in *C. torosa* is shaped by a combination of temperature and developmental stage, with population origin and local environmental factors also modulating respiratory response.

As ectotherms, crustaceans generally increase metabolic rate with increased temperature (Ikeda *et al*., 2001; Manush *et al*., 2004; Winch & Hodgson, 2007). The strength of this thermal response differed markedly among the populations we studied. Similar population-level differences in survival and metabolic performance have been documented in other crustaceans (Lascio *et al*., 2011; Foucreau *et al*., 2014; Šargač *et al*., 2022; Turner *et al*., 2025). Our results showed that the population inhabiting intermediate salinity conditions exhibited the greatest increase in respiratory rate with temperature, whereas OCR responses were weaker in in both low- and high-salinity populations. These results are consistent with the niche theory, which predicts reduced performance when environmental conditions deviate from the optimum (Grinnell, 1917; Chase & Leibold, 2003). Reduced metabolic rates under stressful conditions, such as high or low salinity, have been documented in fishes and insects (Haney & Nordlie, 1997; Waters & Harrison, 2012).

Salinity can modulate thermal responsiveness: populations within favorable ranges of salinity show enhanced oxygen consumption with warming, as observed in the larvae of the caridean shrimp *Palaemon serratus* (Pennant, 1777) (Yagi *et al*., 1990) and *Artemia* Leach, 1819 (Dey *et al*., 2023), whereas populations further from the optima exhibit comparatively weaker responses, as found for the copepod *Tigriopus californicus* (Baker, 1912) (DeBiasse *et al*., 2018). *Cyprideis torosa* is of marine ancestry but commonly thrives in brackish waters, with an estimated optimum salinity of approximately 22 psu in populations from the eastern Iberian Peninsula (Mezquita *et al*., 2005). Temperatures around 18–20°C may be close to the species' thermal optimum (Heip, 1976; Mezquita *et al*., 2005), while established populations tolerate a broader thermal range between 0°C and 32°C (Heip, 1976; Mezquita *et al*., 2000). While salinity variation was not directly tested for each population, our results suggest that local regimes may influence oxygen consumption patterns. The broader and more variable salinity range in Salinas de Santa Pola compared to UdB may contribute to the observed differences, possibly reflecting local adaptation as reported in other aquatic invertebrates (Lee *et al*., 2023; Ross *et al*., 2023; Vafeiadou *et al*., 2018). Populations inhabiting conditions away from their optimal range may consequently have a reduced ability to cope with thermal variation, as indicated in previous work for other crustaceans (Torres *et al*., 2011; Whiteley *et al*., 2001).

Significant differences between life stages were detected, with subadults exhibiting higher OCR than adults. This trend is consistent with expectations for actively growing crustaceans, where increased metabolic demand supports tissue growth and elevated cellular activity (Winch & Hodgson, 2007; Pörtner, 2010; Wittmann *et al*., 2011; Small *et al*., 2016). A previous study by Herman & Heip (1982), conducted on a single *C. torosa* population from a brackish-water pond also reported ontogenetic differences in OCR. Likewise, we found this pattern in the intermediate salinity population (10 psu), where subadults showed a notably

higher OCR than adults. By contrast, the ontogenetic effect was less evident in the low and high salinity populations. This result agrees with the idea that intermediate salinity conditions may better support the respiratory requirements of developing individuals (Anger *et al*., 2000; Anger, 2001). While we detected consistent differences between adult and subadult life stages, we did not address sex as a biological factor in our experimental design. Since previous work have reported sex differences in respiratory performances in crustaceans (Valverde *et al*., 2009; Willett, 2010; Augusto & Masui, 2014), it will be noteworthy to consider this factor in future research on podocopid ostracods.

As emphasized by recent syntheses (Reddin *et al*., 2020; Gruber *et al*., 2021; Torres *et al*., 2021), integrative approaches are essential to understand species responses to multifactorial environmental stressors across spatial scales and ontogenetic variation. Overall, our study suggests that the respiratory performance of *C. torosa* is influenced by local environmental conditions, and that this influence is not equivalent across life stages. Podocopid ostracods will be a worthy candidate for testing respiratory responses using such an integrative approach.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

S1 Table. Mean oxygen consumption for each life stage and population at different temperatures.

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List of figure captions

Figure 1. Sampling sites for *Cyprideis torosa* in the Valencian Community, Spain. The map highlights the geographic distribution of the sites along the Mediterranean coast. Photographs illustrate the typical environmental conditions at Ullal de Baldoví, an oligohaline spring, Aguas Dulces, a brackish (mesohaline) pond, and Charco Llis, a hyperhaline saltpan pond. Scale bar = 40 km.

Figure 2. Oxygen consumption rates per unit weight of *Cyprideis torosa* at different temperatures (10°C, 20°C, and 30°C), categorized by population (Aguas Dulces, Charco Llis, and Ullal de Baldoví) and life stage (subadults in yellow, adults in blue).

Table 1. Ranges of *in situ* measurements of temperature, water electric conductivity (EC), salinity, pH, and dissolved oxygen (DO_2) at the three study sites. Values in parentheses correspond to previously published range values from the same locations (References). Coordinates are given in decimal degrees (WGS84 datum). AD, Aguas Dulces; ChL, Charco Llis; UdB, Ullal de Baldoví.

Population	Coordinates	Temperature (ºC)	EC (mS cm^{-1})	Salinity (psu)	pH	DO_2 (mg l^{-1})	References
AD	38.1820,–0.6133	11.5 (13.3–32.9)	15.7	9.1 (4.1–12.7)	7.5	12.06	Marco-Barba *et al*., 2012
ChL	38.1697,–0.6802	12.4 (11.8–28.9)	72.4	48.8 (43.7–71.8)	7.4	8.09	Marco-Barba *et al*., 2012
UdB	39.2504, –0.3164	20.1 (13–21.4)	3.26	1.7 (2–3)	7.18	6.82	Rueda *et al*., 2013

Table 2. Q_{10} values for different temperature ranges, populations, and life stages of *Cyprideis torosa*. AD, Aguas Dulces; ChL, Charco Llis; UdB, Ullal de Baldoví.

Population	Life stage	Temperature interval (°C)		
		10–20	20–30	10–30
AD	subadults	1.38	2.82	1.98
	adults	2.15	1.60	1.86
ChL	subadults	1.14	1.64	1.37
	adults	1.75	2.51	2.10
UdB	subadults	0.68	2.35	1.26
	adults	4.77	0.86	2.02

Table 3. Generalized linear model (GLM) of the effects of temperature, life stage, and population on oxygen-consumption rates in *Cyprideis torosa*. The reference group corresponds to the adult population from Aguas Dulces (AD) at 20°C. ChL, Charco Llis; UdB, Ullal de Baldoví; A-1, subadults.

Parameter	**Level**	**β**	**Std. Error**	***t* value**	***P* value**
Temperature	10ºC	–0.73	0.174	–4.226	< 0.001
	30ºC	0.49	0.171	2.878	0.005
Population	ChL	–1.18	0.171	–6.901	< 0.001
	UdB	–0.66	0.170	–3.887	< 0.001
Stage	A-1	0.62	0.154	4.053	< 0.001

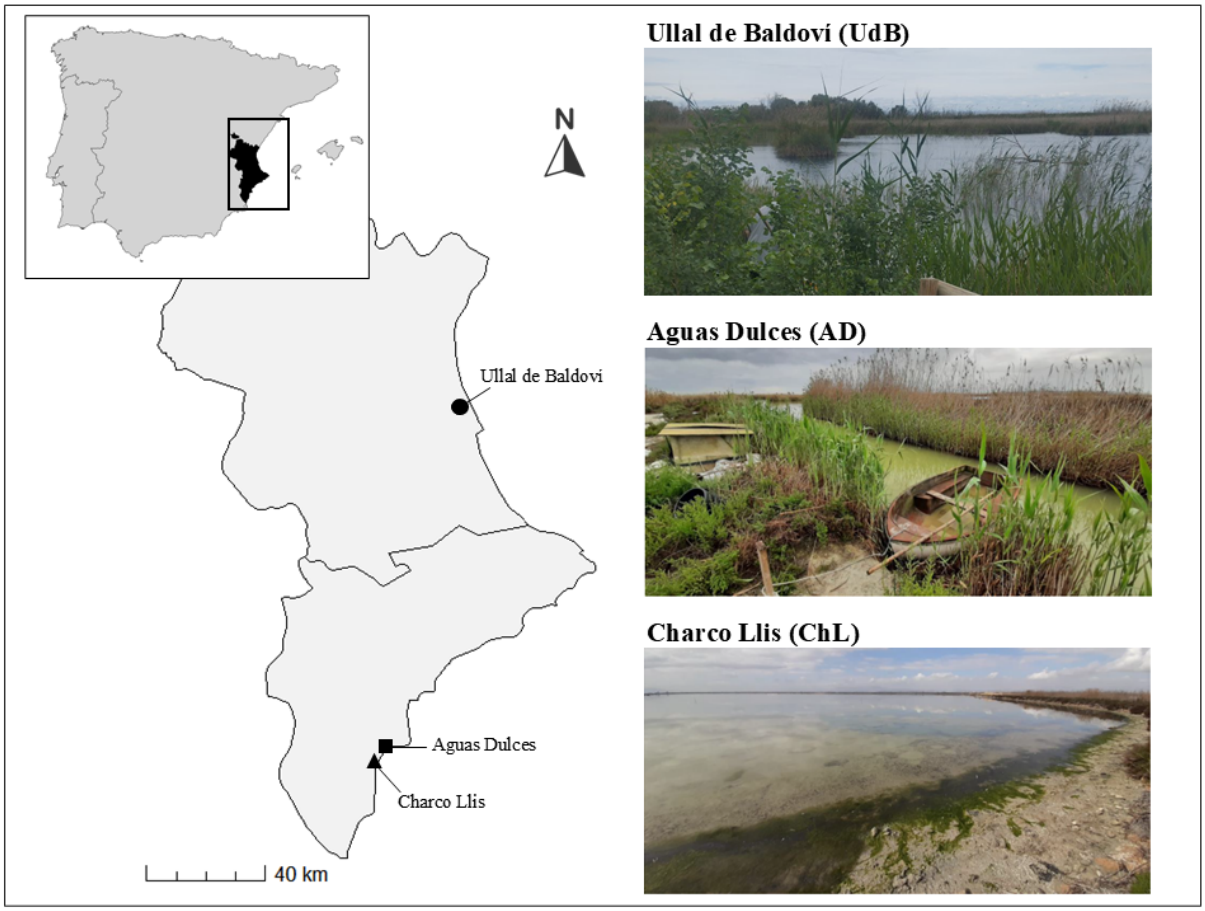
N
Ullal de Baldovi
Aguas Dulces
Charco Llis
40 km
Ullal de Baldovi (UdB)
Aguas Dulces (AD)
Charco Llis (ChL)

Fig.1

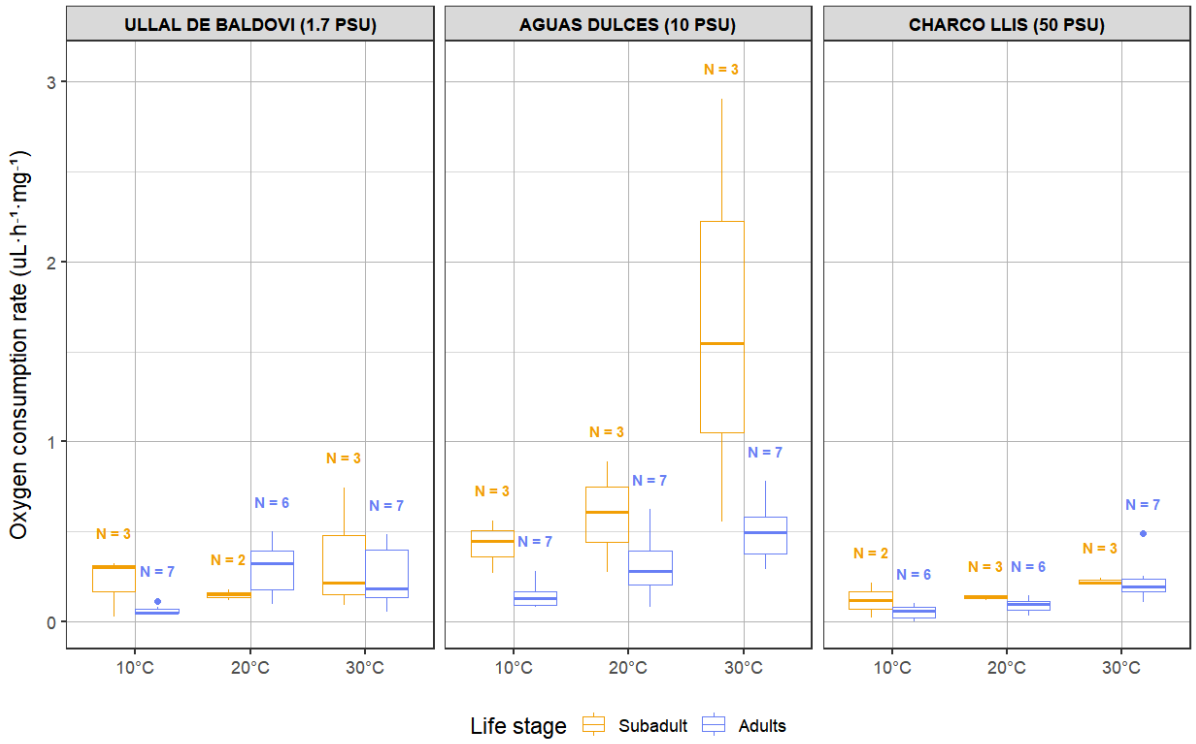
ULLAL DE BALDOVI (1.7 PSU)
AGUAS DULCES (10 PSU)
CHARCO LLIS (50 PSU)
Oxygen consumption rate (uL·h⁻¹·mg⁻¹)
0
1
2
3
N = 3
N = 7
N = 2
N = 6
N = 3
N = 7
N = 3
N = 7
N = 3
N = 7
N = 2
N = 6
N = 3
N = 6
N = 3
N = 7
10°C
20°C
30°C
Life stage
Subadult
Adults

Fig. 2