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DORMANCY IN AQUATIC ORGANISMS

Strong impact of temperature on hatching success of aquatic invertebrates dispersed by two waterbirds

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Abstract Waterbirds are key agents of passive dispersal for aquatic invertebrates, particularly through internal transport of their propagules. In this study, we assessed the potential dispersal of invertebrates through endozoochory by two Anatidae species, the mallard and the common shelduck, in Albufera de Valencia Natural Park. We aimed at comparing the hatching success of invertebrate propagules egested by both ducks, under two temperatures, simulating cold (15 °C) and warm (25 °C) conditions. We performed a controlled hatching experiment using faecal samples (30 per species) collected from the roosting areas of both ducks. A total of 34 invertebrate taxa hatched, including rotifers, cladocerans, copepods, ostracods, ciliates, and microturbellarians. Species richness and hatching rates were higher under warm conditions, and shelduck samples showed more diverse assemblages than mallards. Five of the detected taxa are considered invasive non-native to the region. Some of the rotifer and ostracod species found, as well as microturbellarians, represent first records of internal dispersal by waterbirds. Our findings suggest that temperature can influence hatching success and may shape the community composition of colonizing organisms through endozoochory. Moreover, Anatidae can be effective vectors for aquatic invertebrates, including non-native species, with potential implications for metacommunity dynamics and invasions in Mediterranean wetlands.

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Introduction

Metacommunities are structured by a variety of factors, including local environmental conditions, species interactions, spatial dynamics and temporal effects (Leibold & Chase, 2018). Dispersal, the main mechanism driving spatial dynamics, can control metacommunity structure by interchanging species and genetic material between sites (Gálvez et al., 2022), facilitating the movement of species between different habitats, which is essential for maintaining biodiversity. High dispersal rates can lead to homogenization of communities across sites (Heino et al., 2015), while limited dispersal can result in distinct community compositions based on local environmental conditions (Leibold et al., 2004; Heino et al., 2015).

Dispersal becomes especially relevant in aquatic ecosystems. While many aquatic organisms, including insects, amphibians, birds, reptiles, and mammals, can actively move between water bodies across land, others cannot do so, such as many invertebrates and plants. Instead, they rely on passive transportation via various vectors, whether abiotic, such as wind or waterflow (Hulsmans et al., 2007; Brendonck et al., 2010), or biotic, involving living organisms (Alekseev et al., 2007; Vanschoenwinkel et al., 2008, 2011; Sabagh et al., 2011). A wide variety of species can serve as vectors for aquatic invertebrates, ranging from fish, mammals and birds to humans themselves (Vanschoenwinkel et al., 2008, 2011; Waterkeyn et al., 2010; Valls et al., 2016).

Aquatic birds, in particular, are highly important for the dispersal of invertebrates due to their high mobility at both local and regional scales (Figuerola & Green, 2002; Green et al., 2002), playing a key role in ecosystem functioning (Green & Elmberg, 2014). While all aquatic birds can act as dispersers through epizoochory (or ectozoochory), waterfowl (Anatidae) have been identified as particularly relevant for endozoochory, facilitating the dispersal of plants (Kleyheeg et al., 2016; Soons et al., 2016; Lovas-Kiss et al., 2019) and invertebrates (Figuerola et al., 2003; Brochet et al., 2010; Valls et al., 2017; Moreno et al., 2019). Moreover, zoochory by waterbirds has been documented for a variety of invasive non-native plants and aquatic invertebrates (Reynolds et al., 2015; Green, 2016) after their initial introduction by humans.

For a successful colonisation, propagules must be transported, and the species should be able to establish and grow to maturity in the habitats they arrive. Factors such as habitat suitability, propagule traits, and the effects of gut passage are critical in this process (Green et al., 2023). Waterbirds can facilitate directional dispersal into compatible environments and increase establishment chances for aquatic organisms with high propagule pressure, as well as those capable of clonal reproduction, such as certain cladocerans, ostracods, and rotifers, allowing colonization even from a small number of propagules (Green et al., 2016, 2023; van Leeuwen et al., 2023).

Environmental conditions should be suitable for the hatching of resting propagules to establish their populations. Several factors, such as salinity, photoperiod, pH or temperature can often trigger the hatching of these propagules (Alekseev et al., 2007). A previous study in a Mediterranean coastal wetland (Bisquert-Ribes et al., 2024) indicated that the microcrustacean (cladocerans, copepods and ostracods) metacommunity differs in species composition between the coldest season, winter, and the warmest season, summer. Both seasons showed the presence of typical native species, but invasive non-native (invasive, hereafter; Soto et al., 2024) ostracods were found with a higher prevalence in summer, suggesting temperature (and probably other environmental factors) may affect community variation, particularly in temporary habitats where the egg bank serves as the core of the community that re-establishes after the drying phase (Brendonck & De Meester, 2003; Olmo et al., 2020).

Here, we focused on the role of two waterfowl species as vectors for the dispersal of invertebrates in a coastal wetland of the Iberian Peninsula through a hatching experiment of resting propagules from faeces. Our main aim was to determine whether there was differential hatching of resting propagules under two different temperatures, simulating cold and warm conditions. We tested the following hypothesis: (1) the species composition and/or the hatching dynamics would vary between temperature treatments; (2) the two waterbird species would differ in the hatching

rates of the propagules they transport internally; (3) invasive invertebrate species, particularly ostracods and potentially cladocerans and copepods, would hatch, as they have been previously reported in the study area (Bisquert-Ribes et al., 2024); (4) invaders would appear more frequently under the warm temperature treatment, due to most of them being of tropical origin (McKenzie & Moroni, 1986; Bisquert-Ribes et al., 2023). These results may help clarify how temperature influences the emergence and the potential establishment of species whose propagules are dispersed in Mediterranean wetlands.

Material and methods

Study area and sampling methods

The Albufera Natural Park (listed as Ramsar and Natura 2000 site), spanning 21,120 ha, is a wetland complex situated on the Mediterranean coast of the Iberian Peninsula. This protected area consists of a shallow hypertrophic lake, surrounded by over 15,000 ha of rice fields and other aquatic systems such as marshes, freshwater springs, and temporary ponds. This area is remarkable within the broader context of European wetlands, particularly concerning aquatic birds, as it provides breeding, migratory stopover, and wintering habitats for a wide array of waterbirds. During the winter of 2021, over 66,000 waterbirds were recorded in the region. The most numerous groups included gulls (ca. 28,000), waterfowl (ca. 20,000), glossy ibises (ca. 11,600), and waders (ca. 5,000), among others (SEO BirdLife, 2021a).

The mallard (*Anas platyrhynchos* Linnaeus, 1758) is the most abundant Anatidae in the region, with over 8,000 individuals recorded in winter (SEO BirdLife, 2021a) and approximately 2,500 breeding pairs (SEO BirdLife, 2021b). The common shelduck (*Tadorna tadorna* Linnaeus, 1758), in contrast, is primarily a wintering species in the Albufera, exceeding 2,000 individuals in 2021 and with a small local breeding population restricted to protected areas like Racó de l'Olla (SEO BirdLife, 2021a; b). Seasonally, mallards remain in the region year-round but increase in number due to winter migrants arriving from northern and central Europe (Díaz et al., 1996; SEO BirdLife, 2012). Shelducks are mostly resident in southwestern Europe (Patterson, 1982), however, in the Albufera, they arrive in autumn and reach their peak between December and February before leaving for other areas in March (SEO BirdLife, 2021a; b). Both species exhibit short-range dispersal within the area in response to habitat availability and disturbance. Shelducks show a preference for saline or brackish wetlands and mallards can be most frequently found in shallow, vegetated freshwater areas, in association with many different habitats of the Albufera (SEO BirdLife, 2021b).

In the context of our study, both species are relevant for their potential role in the passive endozoochorous dispersal of aquatic invertebrate propagules (e.g. Green et al., 2008; Valls et al., 2017; Lovas-Kiss et al., 2018). Their winter foraging behaviour, particularly in rice fields and marshes, involves techniques like dabbling, upending, head dipping, and sieving sediments (Liordos, 2010). These practices facilitate the ingestion of resting propagules directly from the sediment, plants and by the ingestion of adults carrying the propagules. Both species access prey items in shallow water and soft sediments, although shelducks often prefer saline and deeper environments for roosting (SEO BirdLife, 2021a).

Faecal samples were collected from resting/roosting areas of both duck species. Mallard samples were gathered at Tancat de l'Illa (39° 16′ 41″ N, 0° 17′ 29″ W). This is a managed freshwater wetland that functions as a green filter with nutrient-rich shallow waters and abundant submerged vegetation (Rodrigo et al., 2013a,b). In contrast, shelduck samples were obtained at Racó de l'Olla (39° 19′ 54″ N, 0° 19′ 02″ W), a restored brackish lagoon hydrologically isolated from the main lake and characterized by deeper waters and elevated salinity levels, habitat that is usually preferred by the shelduck (SEO BirdLife, 2021a).

Sampling was conducted prior to the major migratory movements involving these species, which occur in March in this area (SEO BirdLife, 2021a). Specifically, mallard faeces (45 faeces) were collected on February 3rd (24 samples) and 11th (21 samples), 2021, while 50 shelduck faeces were collected on February 23rd, 2021. Fresh faeces were collected ensuring that they were firm enough to be handled without disintegration. Each sample was visually inspected to detect any attached sediment. If sediment was observed, it was carefully removed using a clean knife to minimize the risk of contamination from soil propagules. Faeces were carefully collected with a

separation of at least 1 m from each other and stored individually in a paper bag. In the laboratory, samples were dried in open bags at air temperature and stored in dark conditions for three months until the beginning of the experiment. This procedure aimed to prevent predation, fungal growth and sample degradation, and to allow latency periods for those propagules that may need it before hatching (Alekseev et al., 2007).

Hatching experiment design

Thirty faeces of each duck species (60 in total) were randomly selected from those sampled in the field and weighed (ESM Table 1) before the beginning of the experiment. Two temperatures were established, 15 °C (to simulate cold conditions) and 25 °C (warm conditions), with half of the samples (15 faeces of each duck species, 30 in total) allocated to each treatment. A cycle of 12 h light and 12 h darkness was established for all samples, and the light cycle was initiated at the beginning of the inundation. Average light intensity in the chambers was 20 µE m^{-2} s^{-1}. The two culture chambers used for the experiment, each programmed at one of the selected temperatures, were BINDER™ KBW 240 (E 5.1) and 720 (E 5.1) (Tuttlingen, Germany), and containers were randomly distributed over the chamber shelves.

The hatching experiment was conducted between May 11th and July 1st, 2021, in plastic containers measuring 10 × 10 × 5 cm (0.5 L). Each container included one faecal sample and was filled with 300 mL of sterilised deionised water. The containers were sealed with a transparent plastic cover to prevent contamination with air droplets between them. Four small holes (1 cm diameter) were drilled in each cover to allow air renewal. Four blank control containers (two in each chamber), with water but without faeces, were added to monitor the possible circulation of propagules in the chambers. The emergence of invertebrates in the containers, including controls, was checked on days 1, 3, 5, 7, 10, 13, 16, 23, 30, 37, and 51 after filling. The procedure consisted of filtering the water through a 20-µm mesh and pouring it carefully. The filtered water was not discarded but was stored temporarily. The 20-µm filter with the faecal material and organisms was washed with deionised water on a Petri dish and examined under a stereomicroscope at 10–40 × to sort and collect all observed invertebrates. Hatched rotifers were collected with Pasteur pipettes, isolated in plastic tubes, and immediately fixed with 70% ethanol. In order to identify crustaceans to species level (and particularly those with indirect development), emerged juveniles were isolated individually in multiwell plates and placed in the same experimental chamber until reaching adulthood, at which point they were also fixed. During this growth period, copepods and branchiopods were fed every two days with the green algae *Raphidocelis subcapitata* (Korshikov) Nygaard, Komárek, Kristiansen & Skulberg 1987 from a pure laboratory culture; juvenile ostracods were fed with frozen spinach following Schmit et al. (2007). After extracting all observed invertebrate individuals, the Petri dish with the faecal material, the filtered water and the remains of resting propagules captured during the filtration process were returned to their corresponding container to avoid the loss of viable resting propagules. Water loss and evaporation were compensated by adding sterilised deionised water up to the level of 300 mL. The containers were then randomly placed back into the chamber until the next checking period. Water conductivity, oxygen concentration and pH were measured three times (days 6, 16 and 28) in each container (including the controls) during the incubation period with a WTW® Multi 3430 multiparameter probe (with TetraCon 925 for conductivity, FDO 925 for oxygen and WTW® SenTix 940 for pH).

All individuals emerged during the experiment were counted and identified following Koste (1978) for rotifers, Alonso (1996) for branchiopods, Błędzki & Rybak, (2016) and Dussart (1967) for copepods and Meisch (2000) and Karanovic (2012) and references therein for ostracods. Identifications were done at the species level whenever possible. Observed organisms of other taxonomic groups including Ciliophora and Rhabdocoella platyhelminthes (microturbellaria) were also detected and removed (except for ciliates), and their presence was noted during the experiment, although they were not counted or identified to lower taxonomic levels. To identify species as invasive we rely on previous works in the study area in which they discuss the possible origin of the species (Bisquert-Ribes et al., 2023, 2024).

Data analysis

The index for timing of hatching (ITH) was calculated as the average number of days (incubation period) required by each taxon to hatch, as described by Vandekerkhove et al. (2004). This calculation was performed for the entire dataset as well as separately for each duck species and temperature treatment. To assess differences in ITH between temperatures and between ducks, paired t-tests were applied.

To compare the species composition of microinvertebrate communities between temperatures and ducks, we first applied the Hellinger transformation to the species abundance matrix obtained from the experiment in order to reduce the influence of rare and ubiquitous species (Legendre & Gallagher, 2001) using the function *decostand* of the *vegan* R ver. 4.3.1 package (Oksanen et al., 2022; R Core Team, 2023). Then, we obtained a distance matrix with a Bray–Curtis dissimilarity index using the function *vegdist* of the same package. This was used to test for differences in species composition between ducks, temperature treatments and along the experiment by means of PERMANOVA with the function *adonis2* of the *vegan* package.

Finally, to assess the main patterns in the ordination of the microinvertebrate assemblages for the four datasets (two ducks x two temperatures), we performed a nonmetric multidimensional scaling analysis (NMDS) using the function *metaMDS* of the *vegan* package.

Results

A total of 34 species were identified from the experiment, including rotifers and crustaceans (cladocerans, copepods, and ostracods; Table 1). More than twice as many species (26) were detected in the 25 °C treatment (warm conditions) compared to the colder (15 °C) temperature treatment (12 species). Out of the 15 rotifer species, 13 hatched exclusively at the higher temperature, with none hatching at both temperatures. Among the 19 crustacean species identified, nine (eight ostracods and one cladoceran) hatched only at 25 °C, six (four ostracods, one cladoceran, and one copepod) hatched only at 15 °C, and four ostracods hatched at both temperatures (Table 1). When comparing the two duck species, 30 different invertebrates were recorded in the shelduck samples, whereas only 11 were detected in the mallard samples. In the combined treatment analysis (temperature x duck), more species were found in the shelduck samples (11 and 23 species at cold and warm conditions, respectively) than in the mallard samples (three and nine species, respectively). The most frequently occurring species were the ostracods *Ilyocypris gibba*, *Heterocypris incongruens*, and the rotifer *Lecane tenuiseta*, each detected in nine different samples, followed by *Heterocypris* sp. 3, which appeared in six samples. Among the detected species, five invasive ostracods were found (Table 1), appearing exclusively in shelduck samples and at the 25 °C treatment, except for *Sarscypridopsis* sp. B (ostracod), which appeared in both temperature treatments. Individuals belonging to Rhabdocoela were observed in one shelduck sample at 25 °C. Members of Ciliophora were present in 10 different samples of the experiment including both temperatures and duck species. A significant percentage of the samples, 52% (31 out of 60 samples), showed no hatching throughout the experiment. When comparing the two temperatures, the proportion of non-hatching samples was considerably higher at 15 °C, with 80% of the samples (24 out of 30 samples) failing to hatch, while at 25 °C, only 23% of the samples (seven out of 30 samples) did not hatch. In terms of duck species, over half of the samples showed no hatching in both cases, with 50% in mallards and 53% in shelducks.

Since hatchlings began to emerge, the accumulated species richness for shelduck was consistently higher than that for mallards across both temperature treatments (Fig. 1). In the warmer treatment, no individuals appeared before the 7th day of the experiment. Particularly noteworthy was the shelduck treatment at 25 °C, which accumulated species richness did not appear to stabilize throughout the experiment. In contrast, mallard samples at 25 °C exhibited fewer species and showed two stabilization periods: one at the beginning and another between days 30 and 40 of the experiment, with a slight increase in new species towards the end. In the cold treatment, hatchlings took up to 30 days to appear in both duck species. Shelduck at 15 °C exhibited species accumulation values similar to those of mallard at 25 °C, ultimately surpassing it in species count by the end of the experiment. As with the other temperature treatment, mallard showed fewer species than shelduck

Table 1 Index for timing of hatching (ITH) values for invertebrate species hatched from faecal samples in the experiment, separated by duck species (mallard and shelduck) and temperature treatment (15 °C and 25 °C)

Species list	Species code	ITH (days)				
		Total	Mallard	Shelduck	15 °C	25 °C
Rotifera						
Brachionus calyciflorus Pallas 1766	Bra caly	13†		13†		13†
Cephalodella cf. *obvia* Donner 1950 **(FR)**	Cep obvi	33	33		33	
Cephalodella gibba (Ehrenberg 1838) **(FR)**	Cep gibb	32	38	29		32
Cephalodella sp. 1 **(FR)**	Cep sp1	51		51		51
Collotheca sp. **(FR)**	Col sp	51†		51†		51†
Encentrum cf. *longipes* Wulfert 1936 **(FR)**	Enc long	37		37		37
Itura cf. *aurita* (Ehrenberg 1830) **(FR)**	Itu auri	51		51	51	
Lecane bulla (Gosse 1851) **(FR)**	Lec bull	51		51		51
Lecane cf. *hornemanni* (Ehrenberg 1834) **(FR)**	Lec horn	51	51			51
Lecane closterocerca (Schmarda 1859) **(FR)**	Lec clos	51†		51†		51†
Lecane tenuiseta Harring 1914 **(FR)**	Lec tenu	42	47	42		42
Lepadella patella (O. F. Müller 1773) **(FR)**	Lep pate	43		43		43
Proales cf. *similis* de Beauchamp 1907 **(FR)**	Pro simi	51†	52†			51†
Proales cf. *syltensis* Tzschaschel 1979 **(FR)**	Pro sylt	51	51	51		51
Trichocerca cf. *cavia* (Gosse 1886) **(FR)**	Tri cavi	41	41			41
Branchiopoda						
Daphnia magna Straus 1820	Dap magn	37†		37†	37†	
Macrothrix laticornis (Jurine 1820)	Mac lati	13†		13†		13†
Copepoda						
Calanoida	Calan	51†		51†	51†	
Ostracoda						
Cypretta cf. *maya* Cohuo-Durán et al. 2013 * **(FR)**	Cyp maya	30		30		30
Cypridopsis vidua (Müller 1776)	Cyp vidu	49		49		49
Cypris decaryi Gauthier 1933 * **(FR)**	Cyp deca	30†		30†		30†
Eucypris virens (Jurine 1820)	Euc vire	47	44	51	47	
Hemicypris exigua Broodbakker 1983 * **(FR)**	Hem exig	45		45		45
Heterocypris incongruens (Ramdohr 1808)	Het inco	40	41	39	41	40
Heterocypris salina (Brady 1868)	Het sali	13†		13†		13†
Heterocypris sp. 1 **(FR)**	Het sp1	27		27		27
Heterocypris sp. 3 **(FR)**	Het sp3	37	36	37	39	37
Ilyocypris biplicata var. *anomala* (Koch 1838) **(FR)**	Ily bipl	51†		51†	51†	
Ilyocypris getica Masi 1906 **(FR)**	Ily geti	40		40		40
Ilyocypris gibba (Ramdohr 1808)	Ily gibb	39	30	39	43	38
Isocypris beauchampi (Paris 1920) * **(FR)**	Iso beau	16†		16†		16†
Sarscypridopsis aculeata (Costa 1847)	Sar acul	39		39	39	
Sarscypridopsis sp. B * **(FR)**	Sar spB	41		41	40	41
Trajancypris clavata (Baird 1838) **(FR)**	Tra clav	51		51	51	
Mean ± SD		39.5 ± 12.0	42.1 ± 7.4	38.9 ± 12.6	43.6 ± 6.4	37.8 ± 12.7

Total ITH was calculated using all individuals of the same species that hatched in the experiment. ITH values with the symbol † correspond to species with only one individual hatched, so ITH does not represent mean but unique values. An asterisk (*) next to species names indicates the species is invasive. Species not detected in previous zoochory studies have been indicated as first record (FR) next to the species name

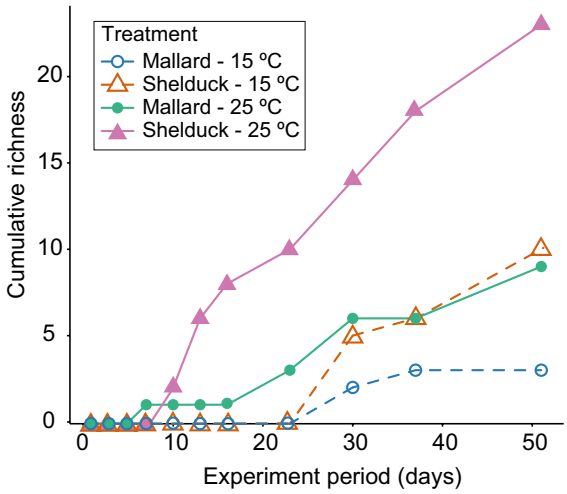

Fig. 1 Cumulative species richness for each treatment (duck species x temperature) along the hatching experiment

in cold conditions. Regarding water characteristics along the experiment, when comparing both temperature treatments, we found very similar values of water conductivity (318 ± 106 µS/cm and 353 ± 130 µS/cm, respectively) and pH (7.6 ± 0.5 and 8.0 ± 0.6, respectively). Oxygen saturation in the cold treatment of the experiment was 69 ± 25%, slightly lower than in the warm treatment (80 ± 16%).

The ITH indicated that species took an average of approximately 40 days to hatch (Table 1). At 15 °C, the average hatching time was delayed to 44 days, whereas at 25 °C it was about six days earlier. However, this difference was not statistically significant ($t = 1.46$; d.f. = 3; $p = 0.24$). Similarly, when comparing between duck species, the average ITH was about 42 days for mallard and 39 days for shelduck, but again, the difference was not significant ($t = -0.06$; d.f. = 6; $p = 0.95$).

The PERMANOVA analysis revealed that the invertebrate species composition varied between temperatures ($F = 2.49$; $p = 0.01$). This variation was evident in the NMDS ordination (Fig. 2), which separated samples along the second axis in relation to experimental temperature: most warm samples were positioned on the positive side of the axis (with some on the negative side), while cold samples were ordered on the negative side. Additionally, PERMANOVA indicated differences in species composition between duck species ($F = 5.16$; $p = 0.01$), throughout the experiment ($F = 1.65$; $p < 0.01$), and in the interaction between temperature and duck

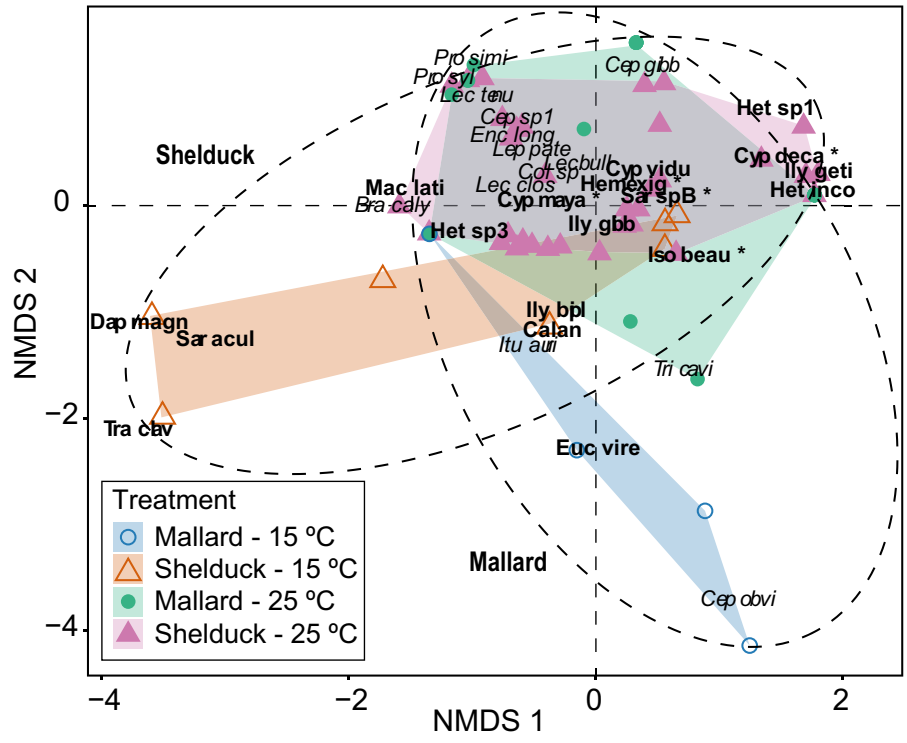

Fig. 2 Non-metric multidimensional scaling (NMDS) ordination of the experiment samples and invertebrate species hatched, according to duck species and temperature. The shaded areas encompassing the samples (convex hull) correspond to each treatment. An asterisk (*) next to the species code indicates the species is invasive, species codes in italics indicate rotifers and bold type indicates crustaceans. See Table 1 for species codes

species ($F = 1.96$; $p = 0.01$). The NMDS ordination also showed a clear differentiation between the two duck species at 15 °C, likely due to the emergence of different species, but not so much at 25 °C. Under cold conditions, the crustaceans *Trajancypris clavata* (ostracod) and *Daphnia magna* (branchiopod) were dominant in shelduck samples, whereas the ostracod *Eucypris virens* and the rotifer *Cephalodella* cf. *obvia* were prevalent in mallard samples. In warm samples, the NMDS showed a similar and overlapping dispersion between the two species. Shelduck samples were widely dispersed across the area, while mallard samples were more concentrated around the outer edges. This distribution likely contributed to the differences in species composition between the two temperature treatments for mallard, as indicated by the PERMANOVA pairwise test analysis (ESM Table 2). The analysis also revealed significant differences in most other comparisons, except between the two temperature treatments for shelduck. This exception might be due to three shelduck samples at 15 °C having a species composition very similar to some samples at 25 °C, contrasting with the other four samples, which were more distinct (Fig. 2).

Discussion

This study aimed to assess the role of two waterfowl species on the dispersal through endozoochory of aquatic invertebrates in a Mediterranean wetland, with a focus on how temperature influences hatching success and community composition. We found higher species richness and hatching rates at warmer conditions, and shelducks showed a more diverse invertebrate assemblage than mallards, including several invasive ostracods. We recorded 34 taxa belonging to a broad array of organisms: rotifers, ostracods, cladocerans, copepods, ciliates, and rhabdocoelans. Several rotifers and ostracods we detected (e.g., *Collotheca* sp., *Lepadella patella*, *Isocypris beauchampi*, and *T. clavata*, see Table 1), so as microturbellarians, represent, to our knowledge, the first records of internal transport by waterbirds. We found five invasive ostracod species in our samples, including *Hemicypris exigua, Cypris decaryi* and *Sarscypridopsis* sp. B, which, as far as we know, have not previously been reported in endozoochory studies, although bird-dispersal of species of the same genera has been documented elsewhere (Proctor & Malone, 1965; Proctor et al., 1967; Valls et al., 2017; Lovas-Kiss et al., 2018). Our findings, along with previous studies (Lovas-Kiss et al., 2018; Martín-Vélez et al., 2022), illustrate that passively dispersing species, irrespective of their origin, benefit from waterfowl endozoochory, which can have an influence on ecosystems at local, regional, and continental scales (Green et al., 2002; Reynolds et al., 2015; Green, 2016).

A few studies have documented the survival of copepods after waterbird gut passage. Frisch et al. (2007) and Lovas-Kiss et al. (2018) reported the presence of harpacticoids and cyclopoids, while Valls et al. (2017), similarly to our findings, reported an unidentified calanoid species. However, in all these studies, other groups were more abundant than copepods. The apparently low importance of internal dispersal of copepods by waterbirds may be related to the fact that most copepod species do not produce resting eggs (Alekseev et al., 2007; Błędzki & Rybak, 2016). Instead, many of them enter dormancy at the copepodite stage, a developmental instar that may be more susceptible to digestive degradation during gut passage than more resistant resting eggs, potentially limiting their capacity for successful endozoochory dispersal. Although not the primary focus of this study, the detection of Rhabdocoela and Ciliophora in several samples is notable. While ciliates have been reported before (Valls et al., 2017; Silva et al., 2021), the presence of Rhabdocoela, as far as we know, has not been reported in previous endozoochory studies, and their occurrence here can suggest that they may also be capable of passive dispersal via waterbirds. A previous work by Rogers (2014) mentions the culture of turbellarian cocoons, but he did not specify if these cocoons were obtained from bird faces or gastrointestinal samples, or either from mud collected from pools, boots or vehicle. Further research could explore the potential dispersal dynamics of these groups by endozoochory. Ducks are also likely to disperse other groups of organisms whose propagules do not hatch easily under laboratory conditions, such as plumatellid bryozoans (Martín-Vélez et al., 2022).

Comparing temperature treatments, more species hatched at the warmer treatment, and they did it earlier on average. The species that hatched at both temperatures were different as well. Some species that typically appear in winter conditions in the region,

such as *D. magna*, *S. aculeata*, *T. clavata*, and *E. virens* (Bisquert-Ribes et al., 2024), hatched only at the lower temperature tested. Conversely, many species typical of summer conditions in the area appeared at the higher temperature, including the branchiopod *Macrothrix laticornis*, and the invasive ostracods *C. decaryi*, *Cypretta* cf. *maya*, and *H. exigua*, (Bisquert-Ribes et al., 2024). In this previous work in the study area, all crustacean species reported in the present work were detected except for *Heterocypris* sp. 1, *T. clavata* and *I. biplicata* var. *anomala*. However, the first two species were detected in another study in the rice fields of the Albufera (Bisquert-Ribes et al., 2023). This may suggest that temperature can influence the hatching success and species composition, as it has been reported as a highly relevant factor for the emergence of resting propagules (Alekseev et al., 2007). Indeed, temperature changes can trigger specific life-cycle phases in aquatic organisms, such as the development or hatching of diapausing eggs (Alekseev et al., 2007; Bonacina et al., 2023).

In our study, we focused exclusively on temperature as a factor influencing hatching success, however, other factors can be determinant too. For example, latency period can be relevant, as many resting propagules require relatively long latency periods before hatching (Alekseev et al., 2007). In this study, more species typical of summer temperatures hatched, perhaps because their resting eggs were present since the previous summer, so they may have had a longer latency period that allowed them to quickly respond to inundation triggering hatching. In contrast, most resting propagules of typical wintering species (which would probably hatch at lower temperatures) may have been produced during the winter of the same year in which the samples were collected, and the experiment was conducted, and therefore were younger. Thus, it is possible that species requiring longer latency periods did not hatch. Further research is needed to verify this hypothesis.

Other environmental factors such as salinity (Valls et al., 2017; Conde-Porcuna et al., 2018), photoperiod, or even the interaction between different factors may also have appreciable effects in the hatching success (Conde-Porcuna et al., 2018). In this sense, unlike other studies that isolate resting eggs before incubation (e.g., Brochet et al., 2010; Martín-Vélez et al., 2022), we used entire faecal samples, which may have altered water chemistry within experimental containers. For instance, organic matter and microbial or algal growth could have influenced oxygen levels, potentially masking or modifying temperature effects. This could be the case of the unexpected lower oxygen levels detected in the colder treatment of this study. Possibly, a higher concentration of heterotrophic bacteria in some samples of the cold treatment or algal activity in the warmer samples may have increased respiration or photosynthesis, respectively, leading to differences in oxygen content. These methodological aspects should be considered when interpreting our results and suggest the need for more controlled approaches and for testing the interaction among multiple environmental factors affecting propagule hatching (Spencer & Blaustein, 2001; Alekseev et al., 2007). Nevertheless, it should be noticed that the eggs of some aquatic invertebrates, such as ostracods, are deposited attached to physical or organic structures in the sediment (e.g., sand grains, shells, leaves…) (Aguilar-Alberola & Mesquita-Joanes, 2013), and therefore standard methods used to separate eggs through density centrifugation may not be appropriate to uncover all the diversity of propagules in a given sample.

Gut passage and retention time (García-Álvarez et al., 2015), bird diet (Clark, 2021), or propagule traits such as size (Santamaría et al., 2023) can also be determinant for the hatching success of invertebrate propagules. Some studies have shown that the shape and volume of propagules can provide an advantage to invaders over native species (García-Álvarez et al., 2015; Lovas-Kiss et al., 2023). While invasive species may experience less propagule pressure, favourable environmental characteristics or conditions, or even the characteristics of their propagules, may facilitate their establishment.

Another important consideration is the likely underestimation of the number of taxa effectively dispersed by wintering waterfowl in the Albufera. Our sampling represents only a small fraction of the approximately 20,000 ducks that arrive each winter to the area (SEO BirdLife, 2021a). Moreover, although ducks have been documented as a very relevant group for the efficient endozoochoric dispersal of aquatic invertebrates (Figuerola et al., 2003; Brochet et al., 2010; Valls et al., 2017; Moreno et al., 2019), other bird groups such as gulls and shorebirds, are also known to disperse aquatic invertebrate propagules (Conde-Porcuna et al., 2018; Lovas-Kiss et al., 2018;

Martín-Vélez et al., 2022), and consequently the great variety of invertebrates being dispersed by birds are most probably underestimated in our study.

Our results suggest that both duck species, shelduck and mallard, can serve as effective dispersers of invertebrate propagules, consistent with previous studies (Valls et al., 2017; Green et al., 2023). However, shelduck samples showed a higher diversity of invertebrates compared to mallard samples. Mallard and shelduck are both plastic species that adapt their foraging methods according to several environmental variables, such as habitat and prey availability (Ferns & Reed, 2009; Viain et al., 2011; Bezzalla et al., 2019). Their feeding behaviour involves techniques like upending, head dipping, and sieving sediments (Liordos, 2010) that may have favoured the ingestion of the studied species. The abundance of rotifer genera typically found in the littoral (*Lecane*, *Cephalodella*, *Lepadella*) or in the benthos (*Encentrum*, *Itura*, *Proales*, see Koste, 1978), also supports this feeding behaviour. Regarding niche and foraging habitat preferences, both species overlap during winter, foraging in flooded rice fields in the area, although shelducks often prefer saline and deeper environments for roosting (SEO BirdLife, 2021a). This aligns with the detection of the ostracod *Heterocypris salina*, a common species in halophilic environments (Meisch, 2000), particularly in the area (Rueda et al., 2006). Variations in the egg bank composition of the sediments from which the birds feed could also explain the differences in species composition detected between the two waterbirds. Many invertebrate species have patchy distributions, so their propagule egg banks are heterogeneous (Brendonck & De Meester, 2003; Pinel-Alloul & Ghadouani, 2007), affecting the diversity of resting propagules ingested by the birds. In any case, this study highlights the strong potential of both duck species to disperse propagules from a wide range of invertebrate groups, including rotifers, crustaceans, ciliates, and flatworms. However, previous studies have shown that dispersal by these birds is not limited to resting propagules; they are also capable of dispersing organisms such as aquatic beetles (Laux & Kölsch, 2014) and snails (Cadée, 2011; van Leeuwen et al., 2012).

Given the ability of these birds to effectively disperse a wide array of invertebrates, their movements across regions could be determinant in the spread of invasive species, which this study shows they are capable of dispersing. Mallard is the most abundant Anatidae in the Albufera in winter, and a relevant portion of the population remains in the region to breed (SEO BirdLife, 2021a; b). As a result, its potential for long-distance dispersal to other regions may be somewhat reduced. Nevertheless, mallard are also highly abundant throughout Europe (Drilling et al., 2020), and their seasonal migrations, southward to warmer regions for overwintering and northward for breeding (Díaz et al., 1996; SEO BirdLife, 2012), make it a strong candidate for interregional dispersal of aquatic organisms, including invasive ones. Shelduck has experienced a positive population growth trend in Europe (Fouque et al., 2009; Martínez-Abraín et al., 2016; Nagy & Langendoen, 2020), including the wintering population in the Albufera, which has increased significantly to exceed 2,000 birds in last years (SEO BirdLife, 2021a). This population growth, along with its generalist habitat preferences with selection for artificial wetlands such as rice fields (Walmsley & Moser, 1981; Rendón et al., 2008), as well as its seasonal movements (Cimiotti et al., 2024) and migratory patterns between populations in central and southern Europe (Cimiotti et al., 2025), position the common shelduck as a potential vector for the spread of invasive species. This is particularly relevant in our study area, where previous research has documented a high diversity of invasive ostracods in ricefields (Bisquert-Ribes et al., 2023, 2024). In a global change scenario, increasing mobility and range expansion of waterbirds (Pavón-Jordán et al., 2015; Ramírez et al., 2018) may further facilitate the spread of such invasive species across a variety of European wetlands.

Conclusions

This study provides new evidence that mallards and shelducks can disperse a taxonomically diverse assemblage of aquatic invertebrates via endozoochory, including several invasive ostracod species and other groups previously unreported, such as flatworms. By testing the effect of temperature on hatching success, we show that warmer conditions may favour the emergence of more species, including invaders, and reveal differences in the dispersal capacity between the two bird species. We acknowledge the importance of considering other

environmental factors, such as photoperiod, conductivity, pH, and their potential interactions, as they can also significantly influence the hatching success of many propagules (Alekseev et al., 2007). Including these variables in future studies will help improve our understanding of how bird-dispersed resting propagules respond to environmental conditions and how the resulting species may impact local aquatic communities.

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Data availability Raw data and R scripts of this study are available at Zenodo (https://doi.org/10.5281/zenodo.14640283).

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

Ethical approval No approval of research ethics committees was required to accomplish the goals of this study because work was conducted with chitinized remains.

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