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Article

Factors Explaining the Distribution of *Physella acuta* (Draparnaud, 1805) in Freshwaters of Morocco

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Abstract: Invasive species are a major threat to global biodiversity. Therefore, it is crucial to monitor their presence and expansion within invaded areas and carry out studies to improve our knowledge of their biology and ecology. One of the most effective and spectacular invaders among freshwater snails is the acute bladder snail (Physella acuta) (Draparnaud, 1805). This study aims to update the available data on P. acuta in Morocco and determine the main environmental factors that favor its distribution and expansion in this country. Field surveys were conducted in northern Morocco between 2014 and 2023, with a focus on protected areas such as Ramsar sites, and especially great geographical barriers such as the Middle Atlas Mountains and the Sebou and Moulouya River basins. The gastropods were collected using Surber samplers (20 \times 25 cm surface area, 400 μ m mesh), together with measurements of the physicochemical parameters of the water and other abiotic factors. The bladder snail is probably the most widespread freshwater snail in Morocco, where the species appears to be highly adaptable and can thrive in different habitats, including degraded ones, showing great plasticity in terms of the physicochemical parameters of the water. The main factor limiting the geographical distribution and abundance of P. acuta in the study area was water velocity and conductivity. However, further studies are required to address the future range of expansion of P. acuta in relation to climate change. Although one of the consequences of climate change is reduced water flow speed, which may promote its range of expansion in Morocco, salinization of streams may also reduce its ability to colonize new environments.

Keywords: aquatic invasion; invasive snail; environmental risk; North Africa; salinization; range expansion; climate change



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1. Introduction

The introduction of exotic species is considered one of the main factors endangering the biodiversity of aquatic ecosystems [1–3]. In recent years, the introduction of exotic species has also been seen as a new form of global change [4], especially in aquatic ecosystems; the significant growth of international trade and concurrent increases in transport capacities have accelerated the rate of introduction of alien species throughout the world [5]. Invasive species have important worldwide consequences on native biodiversity [6], but also on public health [7] and local economy [8,9].

Among freshwater invaders, non-native freshwater gastropods can have an important effect on the biodiversity of colonized areas. Indeed, many snail species have proved to be very successful invaders in recent decades, even able to cross oceans and continents [10–13]. In addition, freshwater snails can be carriers and transmitters of several parasites and pathogens [14–17] that spread through being carried by their hosts. A good example of

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a successful biological invasion among the Gastropoda class is the acute bladder snail (*Physella acuta*) (Draparnaud, 1805)—an aquatic pulmonate snail with a left-handed light and glossy yellowish corneous shell and pointed apex, and no operculum. The body is greyish. The upper mantle under the shell is covered with spots; the animal has digitations (finger-like processes) along the edge of the mantle against the columella and there is no pseudobranch (false gill). The shell has six sinistral fast increasing whorls, slightly convex with a clear suture, which is in many specimens whitish, as the columellar border, and shell size varies between 8 and 15 mm high and from 5 to 7 mm wide. It may be confused in North Africa with the species *Physa fontinalis* (Linnaeus, 1758), which has a generally smaller shell with an obtuse apex, whereas *P. acuta* has an acute apex [18].

Although the type locality of *Physella acuta* is in the Garonne River basin (France) [19] (it was once thought to be native to the Mediterranean), the origin of the acute bladder snail is from the Nearctic (native to the northeastern United States and adjacent Canada) [20]. It was believed that the original description was made when the species was already introduced to Europe [13], as for another North American invader *Gammarus trigrinus* described in England. The invasive species may have spread from North America to France across Europe and is now considered cosmopolitan, invading all continents except Antarctica and colonizing different habitats representing a wide range of abiotic factors [21–23]. The invasive species is often referred to in the literature as *Physa acuta* (Draparnaud, 1805) or sometimes *Haitia acuta* (Draparnaud, 1805). In this study, we used *Physella acuta* following Vinarski [13].

The first record of *P. acuta* in Morocco probably dates back to 1972. This species, like most of the non-native species known in Morocco, was certainly established either from aquarium plants or with fish species introduced into Moroccan freshwaters after the Second World War [24]. Since then, the species has been recorded all over the country and is now considered common in its continental waters [25–29]. However, its ecological niche and geographical range of expansion have been little monitored following the first report in Morocco. In this study, we first aim to update the available data on *P. acuta* in Morocco and to determine the main environmental factors that favor its distribution in this country, while trying to confirm its ecological plasticity. The second goal of our study is to estimate the potential impact of climate change on its future range of expansion in Morocco and adjacent countries.

2. Materials and Methods

2.1. Field Surveys

Field surveys were conducted between 2014 and 2023 in 140 sampling sites covering various environmental conditions and types of water bodies (estuaries and streams, irrigation canals, lagoons, ponds, and brackish and salty marshes) observed in Morocco, with a particular focus on protected areas such as Ramsar sites and sites of ecological and biological interest (known as SEBI or SIBE). Quantitative samples of the different microhabitats present on the site were taken against the current between 10am and noon. The choice of microhabitats was based on their biogenic capacity (favorable for aquatic life), their representativeness within the site and the different classes of current velocity at the sampled site. We collected relative estimates of macroinvertebrate taxa, focusing primarily on $P.\ acuta$ in different microhabitats surveyed at each locality. Macroinvertebrates were collected using sweep nets, dip nets and Surber samplers (surface area 20×25 cm; 8 samples equating to 0.40 m²). Abundance data were converted to density per m² (see the Suplementary file for the complete list of localities and $P.\ acuta$ abundance).

2.2. Environmental Data

Water pH, electrical conductivity ($\mu s \cdot cm^{-1}$) and dissolved oxygen concentrations were measured directly on the field with a portable apparatus (WTW, MPP350) and the water temperature was measured (± 0.1 °C) using both a digital and mercury thermometer. The flow velocity (in m.s⁻¹) was measured as the time taken by a floating body (a cork stopper)

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to cover at least one meter. Elevation was measured using a GPS device (Garmin eTrex 10, Schaffhausen, Switzerland). In addition, we analyzed the physicochemical parameters of the waters harboring P. acuta. For each station, two replicates of each water sample were collected in 500 mL polyethylene bottles and preserved with 2 mL of concentrated hydrochloric acid. Samples were carried out in a cooler according to the ISO 5667-6, ISO 5667-2 and ISO 5667-3 [30–32] standards. Sulfates (SO_4^{2-} in in $mg \cdot L^{-1}$), the biological oxygen demand after 5 days (BOD_5 in $mg \cdot L^{-1}$), and orthophosphate (PO_4^{3-} in $mg \cdot L^{-1}$) and nitrate ($N-NO_3^-$ in $mg \cdot L^{-1}$) concentrations were measured in the laboratory according to AFNOR standards [33] and Rodier et al. [34].

2.3. Statistical Analysis

Out of the 140 sampled sites, 74 were chosen to ensure homogeneous data, and 44 of these 74 sites harbored *P. acuta*. Other sites harboring *P. acuta* were not included in the following analyses because some environmental parameters were missing. To compare physicochemical parameters between sites, we used ANOVAs followed by Tukey's test if conditions of normality and/or homoscedasticity were satisfied; otherwise, we used the Kruskal–Wallis test followed by Wilcoxon tests. The analyses were carried out using R software version 4.1.3, and the *ggeffects*, *MASS* and *ggplot2* packages.

To investigate the relationship between environmental factors and the presence of *P. acuta*, we firstly conducted a principal component analysis (PCA) with the *ade4.0*, *factoextra* and *ggeffects* packages. We applied a logistic regression to determine the environmental factors explaining the distribution of *P. acuta* in Morocco using *MASS*, *ggplot2* and *agricolae* packages. Logistic regression is a modeling tool that primarily attempts to forecast and clarify the outcomes of a binary categorical parameter Y using a set of continuous, discrete or binary variables X. Abundance data were transformed into presence/absence data before conducting a logistic regression [35]. We implemented a step-by-step top-down selection approach to enhance the explanatory model. We evaluated the quality of the final model based on the Akaike information criterion (AIC), whereby lower values indicate better model performance. We considered the model valid and accepted when it satisfied the logistic regression assumptions, including sufficient cases and no overdispersion.

2.4. Gathering Distribution Data

To complete and update the distribution map of *P. acuta* in Morocco, the geographical coordinates were compiled from the Global Biodiversity Information Facility GBIF [36] and an extensive literature search of published articles [24–29,37].

3. Results

Physella acuta is widely distributed throughout Morocco, with the southernmost record from the Laayoune-Sakia El Hamra region (Figure 1).

The species was detected at 96 sites (out of 140 sampled sites) along the northern part of Morocco, occupying a wide range of habitats: high-altitude lakes (e.g., Sidi Ali, Zerrouka and Tifounassine), the potamal section of big rivers (e.g., Moulouya and Sebou) or anthropogenic habitats (e.g., the artificial canal of Saidia). Most of the surveyed inland Ramsar sites were infested by the invasive gastropod. In the sites surveyed, *P. acuta* was often found in association with shallow, stagnant or slowly flowing waters. Future surveys could reveal other populations of this species and extend its known range in Morocco. The complete list of records for *P. acuta* in Morocco is provided in the Supplementary Material.

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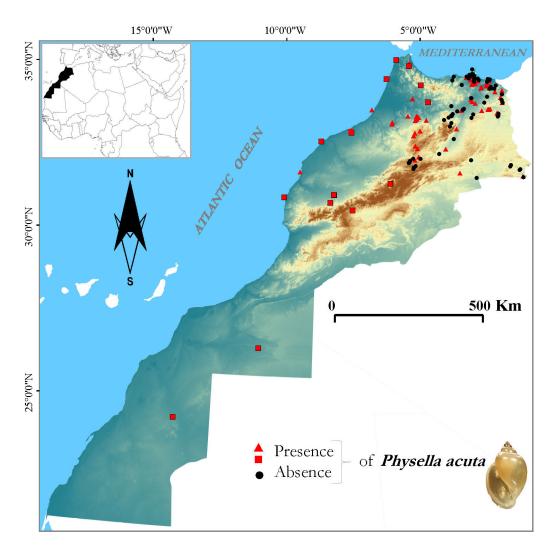


Figure 1. Updated map of *P. acuta* distribution in the continental waters of Morocco. Red triangles: own records; red squares: bibliographic records from GBIF and published articles [24–29,36,37].

The bladder snail showed great plasticity in terms of the physicochemical parameters of the water, as illustrated by the abundance of P. acuta according to the physicochemical parameters of the water and abiotic factors in each new locality (Table S1 in the Supplementary File). Regarding electrical conductivity in particular, P. acuta was recorded in low mineralized waters with a minimum of 213 $\mu s \cdot cm^{-1}$ at Ain Sfa (perennial spring in the Oriental region of Morocco) and in the brackish waters of the coastal system, with a maximum of $30,340 \,\mu s.cm^{-1}$ registered at Sidi Boughaba Lake (a Ramsar site on the Atlantic coast of Morocco). The species appears to tolerate significant spatiotemporal fluctuations in dissolved oxygen levels; it has been observed in both highly oxygenated waters, with a concentration of 9.6 mg.L⁻¹ at Dardoura River, an affluent of the Marchica lagoon (Ramsar site on the Mediterranean coast of Morocco), and in weakly oxygenated waters, with a minimum concentration of 1.5 mg·L⁻¹ registered at Ouzej R (upstream of another affluent of the Marchica lagoon). The species demonstrates great plasticity, as evidenced by its ability to tolerate a wide range of organic pollution indicators. Specifically, it can tolerate nitrate concentrations ranging from 0.03 to 53.62 mg· L^{-1} , sulfate concentrations ranging from 34 to 403 mg·L⁻¹, phosphate concentrations ranging from 0.005 to 4.31 mg·L⁻¹ and BOD_5 concentrations ranging from 0.49 to 32.0 mg·L⁻¹. During the study period, *P. acuta* was found in waters with a neutral pH in general, ranging between 6.5 and 8.5, and in water temperatures ranging from 16.9 to 28 °C.

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The mesological parameters of the sites were initially analyzed using standardized principal components. The first two axes F1 and F2 (Figure 2) accounted for 51.6% of the total inertia and held the bulk of the information. Axis F1 (38.9% of total inertia) showed a conductivity gradient that increased from left to right. Axis F2 (12.7% of total inertia) showed water velocity rising from bottom to top and being negatively correlated with depth. The species obviously grew absent when conductivity or water velocity increased.

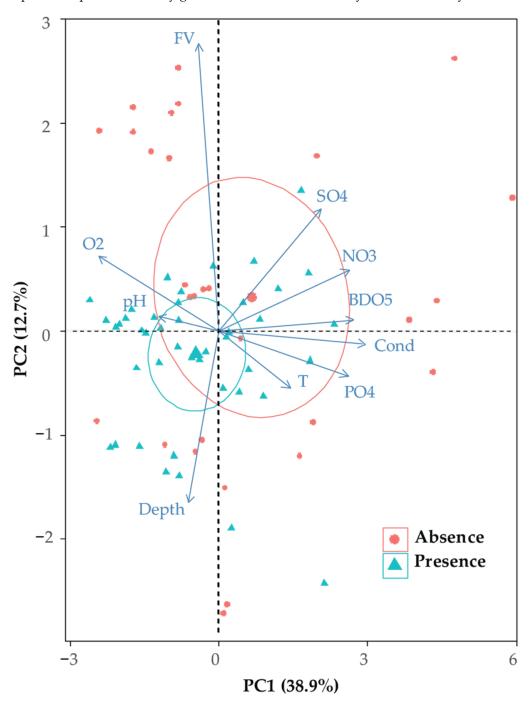


Figure 2. Biplot of the first plane of the principal component analysis of physicochemical parameters (T: temperature, Cond: electrical conductivity, FV: flow velocity, O₂: dissolved oxygen, NO₃: nitrate, SO₄: sulfates, PO₄: orthophosphate, BOD₅: biological oxygen demand and Dep: depth). Circles indicate 95% confidence intervals for the sites colonized by *P. acuta* (blue) and the non-colonized sites (red).

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The analysis of variance (see Figure 3) showed that of the ten mesological variables considered in this study, four had a direct influence on the presence or absence of *P. acuta* and one had an influence on its abundance.

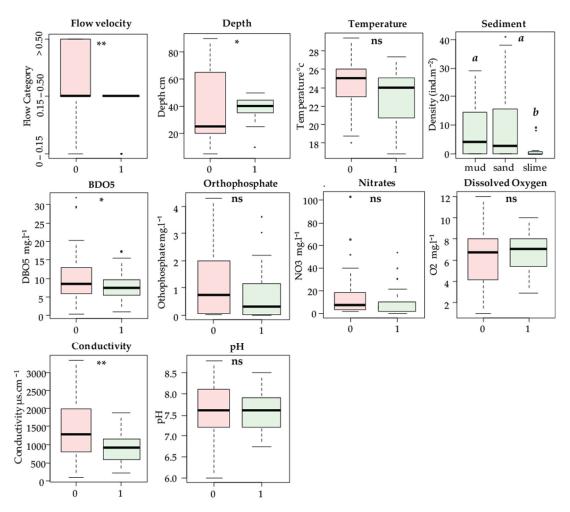


Figure 3. Boxplots of environmental variables classified according to *P. acuta* presence (1)/absence (0) or abundance. The letters above indicate whether there is a significant difference between sites in pairwise post hoc comparisons (ns. not significant. p-values: * ≤ 0.05 ; ** ≤ 0.01).

Based on the results of the variance analysis (Figure 3), we inferred that *P. acuta* occurrence was affected by flow velocity, electrical conductivity, depth and BOD5, while sediment impacted its abundance.

The AIC of the best logistic model was 71.554. Based on this model, we concluded that there was a significant correlation between *P. acuta* presence and three environmental factors (conductivity, flow velocity and substrate type) with 95% confidence (Table 1).

Table 1. Final model fit to the study data, n = 74.

	Coeff.	Std. Error	Z	р	95% CI
Conductivity	0.998	0.0007	-3.51	0.0004	[0.996, 0.999]
Flow velocity	0.040	0.877	-3.67	0.0002	[0.005, 0.181]
Sediment/sand	0.357	0.72	-1.43	0.152	[0.079, 1.390]
Sediment/slime	0.031	1.24	-2.80	0.0052	[0.001, 0.273]

The explanatory variables of the ultimate model accounted for 38.39% of the variation in the response variable, as noted by McFadden's pseudo-R2. The predictions were flawed in 13 instances out of a total of 74, equating to a 17.5% misclassification rate.

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The logistic model used in this study was able to forecast the likelihood of *P. acuta* presence (Figure 4). It suggested that the species was more likely to be present when water velocity and electrical conductivity were low. Nevertheless, the chance of the species being present decreased significantly in the presence of slime substrate (25%), whereas it significantly increased when the substrate was muddy (76%) or sandy (63%).

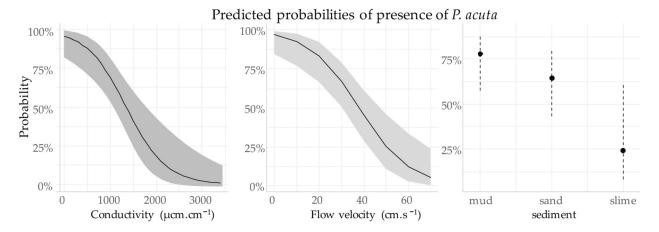


Figure 4. Likelihood of *P. acuta* presence based on the model used in this study with 95% confidence bands.

Figure 4 shows a significant decrease in the probability of the presence of *P. acuta* according to conductivity and flow velocity. *P. acuta* has a 25% chance of inhabiting an environment with a conductivity of 2000 $\mu s \cdot cm^{-1}$ or a flow velocity above 50 cm·s⁻¹.

However, we found a strong interaction between environmental factors; for instance, the probability of the species' presence at a conductivity of 2000 $\mu s \cdot cm^{-1}$ exceeds 80% when the flow velocity is low (Figure 5). The substrate has the same impact on the probability of *P. acuta* presence in relation to the flow speed. The probability is close to 99% for a mud substrate (see Figure 5), compared with 78% (see Figure 4 and Table 2) for a slime substrate, as long as the flow velocity does not exceed 0.15 m·s⁻¹.

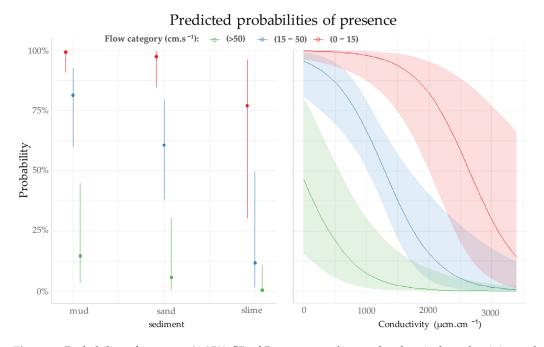


Figure 5. Probability of presence ($\pm 95\%$ CI) of *P. acuta* according to the electrical conductivity and type of sediment for each category of flow velocity.

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Conductivity	Predicted	95% CI	Flow Velocity	Predicted	95% CI	Sediment	Predicted	95% CI
0	0.96	[0.82, 0.99]	0	0.97	[0.85, 0.99]	mud	0.78	[0.57, 0.91]
400	0.90	[0.74, 0.97]	10	0.92	[0.77, 0.98]	sand	0.64	[0.41, 0.83]
900	0.74	[0.58, 0.85]	20	0.83	[0.67, 0.92]	slime	0.24	[0.06, 0.64]
1300	0.53	[0.37, 0.68]	30	0.67	[0.51, 0.79]			
1700	0.31	[0.15, 0.53]	40	0.45	[0.30, 0.62]	-		
2100	0.15	[0.04, 0.40]	50	0.25	[0.11, 0.46]	-		
2500	0.06	[0.01, 0.30]	60	0.12	[0.03, 0.34]	=		
3400	0.01	[0.00, 0.13]	70	0.05	[0.01, 0.24]	-		

Table 2. Likelihood of *P. acuta* presence based on the model used in this study with 95% confidence bands.

4. Discussion

Since its introduction into Morocco in 1972, probably via the Aquarium/ornamental plant trade or by migratory birds, the North American P. acuta has become the most widespread invasive mollusk in Morocco [24], where the species appears to be highly euryceous and can thrive in various habitats, including degraded ones. The habitats of this species vary widely, from large permanent streams at high and low altitudes to reservoirs, natural and managed springs, and small temporary tributaries, as long as they are connected to a permanent source or underground water. It can also be found in human-made structures, such as irrigation canals and cement tanks used for water retention. Its southernmost record is presently in the Laayoune-Sakia El Hamra region, where it seems to adapt easily and to have low requirements in terms of habitat quality. In Morocco, the species has been found in freshwaters with high levels of organic matter and low dissolved oxygen levels. Specimens have been found in the waters of the Selouan and Za Rivers—some of the most polluted rivers in eastern Morocco [38]. This result is congruent with the literature on P. acuta in which it is considered a globally invasive species living in all kinds of freshwater environments, including altered habitats [18,39,40]. Once established, P. acuta can adapt to a wide range of habitat conditions including highly polluted freshwaters [40]. It is highly tolerant to elevated temperature and often abundant in reservoirs affected by thermal waters from heat and power plants [41,42]. Its high capacity to tolerate great variability in abiotic factors and to successfully withstand extreme physical and chemical parameter values might be key to its biological success [43–45]. *Physella acuta* can survive in unstable, heated freshwater environments and colonize environmentally toxic habitats inaccessible to other snail species thanks to its high resistance to pollution [46,47]. It can stand anaerobic conditions for prolonged periods because snails are pulmonates and can use atmospheric oxygen [48]. One of the most important traits of P. acuta is its huge evolutionary potential which allows it to adapt to new environmental conditions [49]. P. acuta has remarkable reproductive plasticity and a greater foraging ability than native species. This feature might contribute to its invasion success and allow it to displace native gastropods and become the dominant species over very short periods of time [50–52].

Among the environmental parameters explaining the current distribution of *P. acuta* in Morocco, our models highlighted that flow velocity and conductivity were the two main limiting factors (alongside other factors) explaining its distribution. Its low tolerance to flow velocity explains why it can invade flowing water ecosystems only in summer, after water levels and flow rates have decreased and when the current velocity slows down. This phenomenon is particularly noticeable in the Moulouya, Za and Melloulou Rivers [28,29,37]. This finding is congruent with those of previous studies on the sensitivity of *P. acuta* to flow velocity [53,54]. It is indeed known to inhabit standing water ecosystems such as wetlands, ponds, lakes and downstream stretches of rivers [18]. Its current distribution may be strongly enlarged by the impact of climate change in Morocco because climate change is impacting the water discharge of streams and rivers worldwide [55].

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This is particularly true in North African countries which are particularly impacted by anthropogenic activities, and Morocco is a good example. The country currently faces a crisis due to climate change and the overexploitation of its resources in freshwaters. The country extends latitudinally through five different bioclimatic zones [56], which results in a declining rainfall gradient from north to south and a longitudinal gradient influenced by the Atlas Mountains. Precipitation trends in Morocco are highly variable. However, projections from the USIAD indicate a significant decrease in average annual rainfall across the country from 10–20% to as much as 30% in the Saharan region [57]. The construction of hydraulic facilities has increased considerably since the 1990s to compensate for this scarce rainfall, and several surface water mobilization structures have been built on watercourses in catchment basins, mainly in the northern part of the country [58]. The National Water Strategy of Morocco has already planned the construction of about 60 large dams by 2030 in addition the 150 existing ones and also 1000 small dams for the development and transfer of raw water resources from the north to the south and for the safeguarding of hydraulic infrastructures. Moreover, there are already 13 water transfer systems between watersheds that may promote the dispersion of *P. acuta* between hydrosystems [59]. As a consequence, the distribution of *P. acuta* in Morocco may strongly increase over the next few decades.

The range of expansion of P. acuta may be restricted by the rising salinity of freshwaters due to climate change. Our study shows that P. acuta is sensitive to electrical conductivity above $400~\mu s.cm^{-1}$. This confirms the results of previous experimental studies that highlighted the sensitivity of pulmonate gastropoda to salinity, especially of P. acuta [60]. In freshwaters, the concentration of dissolved ions can increase through evaporation, especially in semi-arid and arid regions and regions with seasonally hot dry climates [61]. This trend is expected to increase due to climate change and the reduction in available surface water volumes [57]. Several processes can contribute to salinization in arid and semi-arid areas. For instance, irrigation leaves salt residues behind after evaporation, and groundwater levels rise following vegetation removal. All of this brings salt ions from weathering geological sources toward the soil surface [62]. This can be expected in Morocco where the water management strategy will increase groundwater pumping and promote evaporation in dams and irrigation channels. The resulting potential rising conductivity may restrict the range of expansion of P. acuta if conductivity reaches the threshold of $400~\mu s.cm^{-1}$ highlighted in our study.

Molluscan invasions can lead to fauna homogenization, extirpation of vulnerable endemic species and alterations in the biotic composition of the invaded ecosystems, as in the case of *P. acuta*. This invasive species can cause several negative impacts on the invaded freshwater ecosystems [13,63,64]. In addition to *P. acuta*, five other alien and notorious invasive snails can be found in the freshwaters of Morocco, i.e., the seminole rams-horn *Helisoma duryi* (Wetherby, 1879), the New Zealand mudsnail *Potamopyrgus antipodarum* (J.E. Gray, 1843), the North American freshwater limpet *Ferrissia californica* (Tryon 1863), the Malayan livebearing snail *Melanoides tuberculata* (O.F. Müller, 1774) and the Fountain bladder snail *Physa fontinalis* (Linnaeus, 1758). Worse still, many invasive species have been recorded recently to be present in the freshwater ecosystems of Morocco, including fish, annelids, mollusks and arthropods, leading to the formation of new communities in the area through diverse unknown interactions with unpredictable damage [24,65–68].

In 2023, we have seen huge gaps between the number of known alien species and the number of studies devoted to examining their impacts in the freshwater ecosystems in Morocco and how management strategies against biological invasion are still lacking [24]. Even worse, except for the ruddy-headedduck *Oxyura jamaicensis* (Gmelin, 1789), there is no eradication program to eliminate or stop the spread of exotic species in Morocco. Management plans for the control or eradication of invasive alien species, such as *P. acuta* and other notorious snails, must be implemented and are urgently needed.

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5. Conclusions

The bladder snail is one of the most widespread freshwater exotic species in Morocco, and the fact that its spread has gone undetected is linked to the lack of studies on alien species. The results of this study once again demonstrate the adaptability of *P. acuta* and identify current velocity (among others) as the primary factor hindering its spread in North Africa. As a result of ongoing anthropogenic changes in natural habitats and climate patterns (irregular and scarce rainfall), the lotic ecosystems of Morocco are expected to experience a decrease in their flow rate and velocity. This could lead to significant expansion of the dispersal range of invasive species such as *P. acuta*. However, climate change may also lead to an increase in conductivity that may limit its range of expansion. Further studies on the impact of salinization in Morocco are required to better predict the range of expansion of *P. acuta*.

Although the relationship between *P. acuta* populations and environmental factors is well documented in the invaded areas of the North Palearctic regions, our understanding of how environmental factors influence *P. acuta* populations in the freshwaters of North Africa is limited. This study represents an important step toward a better understanding of the invasion process of *P. acuta* and its population dynamics in response to environmental factors and climate change in Morocco and North Africa as a whole.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/w16060803/s1, Table S1: Values of abundance of Physella acuta and physico-chemical parameters recorded at each site.

Author Contributions: Conceptualization, methodology, software, formal analysis, investigation, resources, data curation and writing—original draft preparation, Y.M., A.F.T. and P.G.; writing—review and editing, visualization and supervision, C.P. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data presented in this study are available upon request from the corresponding author. Site locations are available in Taybi et al. 2023 [24] and GBIF (https://www.gbif.org, (assessed on 10 October 2023)).

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Conflicts of Interest: The authors declare no conflicts of interest.

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