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“Influence of climate change on behavioural traits of *Palaemon elegans*, an invasive species in the Baltic Sea”

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The Baltic Sea is undergoing changes due to climate change, including an increase in its temperature. This may in turn lead to changes in the traits of the species that inhabit it, including non-endemic, invasive species.
Palaemon elegans is a species native to the Atlantic Ocean that has been present in the Baltic Sea since the beginning of this century. Abilities such as high thermal tolerance make it successful in colonising new ecosystems like the brackish waters of this sea. However, less is known about the behavioural traits’ adaptions to these changes. This study aims then to find out how climate change may affect the behaviour of this species. To do so, five behaviours expressed by this species were observed and analysed to see how temperature change, seabed composition and body size influence their expression. The behaviours analysed were aggressiveness, movement frequency, reaction to food stimulus, number of feeding interactions and shelter-seeking.

Analyses were conducted using ten-minute videos with ten specimens of *P. elegans* placed in water tanks and interacting in ecosystems representations with elements typical of the seabed where this species lives, both vegetation and rocks. Student's t-tests in R were then performed to test the significance of possible differences between the behaviours studied and the three parameters that may influence their expression.
The results obtained show that the increase in water temperature might indeed lead to an increase in the frequency of the five behaviours studied except in aggressiveness. On the other hand, it was found that the composition of the ecosystem does not have a significant influence overall, while body size has a major influence on feeding related behaviours.

Therefore,knowing more about changes in the behavior of species susceptible to climate change can be helpful to understand how biodiversity and its distribution will vary in the not so distant and changing future and what consequences it may generate at the ecosystem level.

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Introduction

The Baltic Sea is a basin located near the north of Europe. This sea belongs to the so-called brackish waters. Its location is in the northern part of the European continent. It is very shallow and has little opening to the ocean, which makes the renewal of the water slow and favours pollution problems (Alexander *et al*., 1999). With the rise of research into how climate change and all its consequences can affect different ecosystems, large bodies of water such as the Baltic Sea are also the subject of study as they are susceptible to change.

One of the main changes that has already been demonstrated by several studies regarding sea ecosystems is the increase in its water temperature (Neumann, 2010). This in turn leads to a decrease in ice cover during winter. Temperature increases can also affect the entire hydrological cycle. In the case of the Baltic Sea, it has been seen that higher temperatures lead to lower salinity in the sea. This decrease is mainly caused by increased runoff from the northernmost part of the river, which may suggest an imprint of anthropogenic impact on salinity with consequences both for the entire ecosystem, including its species (Kniebusch *et al*., 2019).

It is precisely the biotic factor one of the most affected by the changes in the ecosystem. The Baltic Sea is considered a basin with a relatively poor amount of fauna. With lower salinity and higher temperatures, there are models explaining the shift of the Baltic Sea to a completely freshwater basin (Stigebrandt & Gustafsson, 2003). This change could lead to shifts in species distribution.

In this sea, another cause of potential biodiversity loss is the so-called dead zones (with high hypoxia rates) due to eutrophication. This process may be caused by residues from human activities on their shores, which encourages microbial activity and the consumption of dissolved oxygen in bottom waters (Diaz & Rosenberg, 2008). Dead zones can cause prey availability to decline, and predators therefore have to feed less, leading to a decrease in size and abundance. This in turn can trigger imbalance processes in the life cycles of many species (Neuenfeldt *et al*., 2020).

One of the most highly represented taxa at prey level are small arthropods. In the Baltic Sea, arthropods are one of the major biotic drivers for the abundance of prey species for fish or birds (Rau *et al*., 2019). Therefore, studies and research on this animal group are of vital importance to assess the state of the ecosystem and how future changes may affect it.

Within this prey group is the subphylum of crustaceans. The Baltic Sea is known for its high number of non-native resident species (Grabowski, 2006). Most of the invasive species in the Baltic Sea come from the Atlantic Ocean. Among introduced species, the Palaemonidae family stands out, present on the Atlantic coasts both on the western side (such as Canada) and on the easternmost side (Europe).

Figure 1 shows an individual of *Palaemon elegans* (Rathke, 1837), a species of shrimp within this family. This species is native to the Atlantic Ocean and the Mediterranean Sea. It mainly inhabits intertidal and vegetated areas with high temperatures (Dalla Via, 1985). During the latter part of the 20th century, this species accidentally and incidentally invaded other large bodies of water across the European and Asian continents. More specifically, in 1950 it was found in the Caspian and Aral Seas (Grabowski, 2006) for the first time and in subsequent decades it was found on the coasts of the Baltic Sea (Lesutienė *et al*., 2014).

Figure 1. *Palaemon elegans* female individual with eggs (Picture: Haagen, 2012).

P. elegans in the Baltic Sea was first found off the Lithuanian coast in 2002 and has gradually been occupying coastal areas further north in this sea including Russian (close to the Kaliningrad enclave (Sudnik & Egorova, 2021), Polish (Grabowski, 2006) and Finnish coasts more recently (Katajisto *et al*., 2013).

This species, being considered invasive in the Baltic Sea, could pose a great threat to other species such as the endemic *Palaemon adspersus*. However, apart from above mentioned environmental changes, other factors to be considered could be the behavioural traits of the species, and how these may determine a response to those environmental changes in the Baltic Sea.

Anthropogenic action in the sea like boat traffic (Pearson, *et al*., 2019) has in part made possible the introduction of species (Liversage *et al*., 2021) such as *P. elegans*. However, climate change could cause both the invasive species and the native species to undergo changes in their distribution and behavioural traits.

Precisely one of the human interests with regard to different shrimp species including Palaemonidae is their increasing use in aquaculture. This practice is more common on the coasts of Southeast Asia due to the much warmer climate (Ahmed, 2013). Due to the temperature difference in the Baltic Sea ecosystem, shrimp aquaculture is smaller and has more limitations (Kautsky *et al*, 2008). But with an increase in sea temperature, many economic activities related to shrimp could perhaps become more frequent and thus represent a further disturbance to the ecosystem. Research into these species’ distribution changes is then important, because ultimately, some of the potential consequences can affect human own interests as a part of the whole that compose the ecosystems.

One of the most novel aspects to consider when assessing the dynamics of species and their status in the ecosystem driven by climate change are the behavioural traits of the species in focus. If global change is combined with the problem of invasion of ecosystems by non-native species, a synergy is generated that negatively affect global biodiversity and human well-being (Chown *et al*., 2007).

Invasive species can adapt in different ways as the ecosystem changes. Regarding climate change, many arthropod invaders may exhibit phenotypic plasticity that makes them more or less advantageous in terms of persistence in the ecosystem (Sgrò *et al*., 2015). Apart from these changes at the phenotypic level, it is known that arthropods can show adaptations at a behavioural level, although many of these mechanisms and their causes leading to behavioural change are not fully understood and research is ongoing.

In recent years, the number of studies on the behaviour of non-human animal species has increased and the development in research of concepts such as personality in vertebrates like fish or even some invertebrates (Pruitt *et al*., 2012) can open up new possibilities to apply more knowledge to environmental changes research. In the case of both *Palaemon* species and other invertebrates, some behavioural traits may be drivers for higher intrusion rates and invasive success (Vázquez & Bas, 2018).

Palaemon elegans is a species of shrimp that is usually found near the seabed, where it feeds on different taxa of animals such as ostracods and different algae (Janas & Baránska, 2008). Because the distribution of algae in the Baltic Sea is expected to change in terms of temperature and salt tolerance (Russell, 2007), the behaviour of these animals may change as they receive different information about these environmental changes in order to adapt to new situations. This is known as environmental sensitivity. Individuals of this species are for example able to sense and react to environmental changes such as changes in toxicity due to heavy metals (Lorenzon *et al*., 2000) or differences in temperature (Ravaux *et al*., 2016) at different life stages. Indeed, with respect to adaptation to changes in the environment, this can occur from the individual to the population level (Minderman *et al*., 2009).

Thus, although the changes studied are mostly expected to be mainly at the level of the group of individuals and therefore at the population level (Guerin & Neil, 2015), studies are also beginning to emerge considering relevant the individual personality (Chapman *et al*., 2013).

It is true that a group's ability to function depends on the characteristics of the individuals who comprise it, the smaller and more cohesive the group, the more significant each member's personality. Vertebrates that gather in groups, like mammals and birds, progressively pick up on social norms (König, 1997).

In the case of invertebrates, a large number of species are found living in aggregations in the pelagic zone (Ritz *et al*., 2011). There are numerous instances, particularly in arthropods, where the group has collective response mechanisms to stimuli in order to respond faster to environmental changes. (Jeanson *et al*., 2012).

But even if there is the same collective response, there is a certain point, where dispersal behaviours that lead groups to disband and animals to resume acting individually may start to occur. (Benton & Bowler, 2012). Individual behaviours are also relevant in terms of traits related to physical attributes such as individual size, physiological changes, for example at the level of organ function such as the heart rate (Morris & Taylor, 1984), reproduction and habitat preference (Evans & Shehadi-Moacdieh, 1988).

Thus, studying animal personality in invertebrates is something that has traditionally constituted a tiny part of behavioural research but could open the door to much more information (Kralj-Fišer & Schuett, 2014).

The seabed of the Baltic Sea is quite diverse in structure from the coastline well into the 40 km offshore (Delpeche-Ellmann, 2018). Masses of seaweed can be found in the northern part of the Baltic Sea, near the Finnish archipelago area, down to a depth of almost 50 metres (Vahteri *et al*., 2000). As it is part of their habitat, specimens of *P. elegans* can be found near the shallow coasts of this part of the Baltic, especially during the summer season, when this shrimp species spends the summer mostly. This species also reproduces during that time of the year (Bilgin *et al*., 2009).

What happens when the algae-filled seabed where *P. elegans* individuals usually take refuge changes to a rock-filled seabed, i.e., without algae? This projected change in the composition of the seabed is driven by the increase in water temperature (Moy & Christie, 2012). Other similar seabed changes that the Baltic Sea is experiencing due to drivers such as eutrophication is the shift from green algae to a seabed with red macroalgae (Rinne *et al*., 2021). Could the behaviour of the shrimp change, could there be new interactions, any difference in reaction or feeding behaviour if any?

Understanding the significance of environmental changes is necessary in order to start responding to these questions. For example, it is known that in shrimp species such as *Artemia franciscana*, even if the food source changes location in an artificial tank, changes in behaviour are detected (Dockery, 2010).

In this instance, the study is focused on specific behavioural characteristics that this species may display in a miniature approximation of many environments that may exist in the Baltic Sea as there is a potential for slow ecological change.

These environment representations consist of the one hand of an algal seabed, where shrimps often find protection and can produce strategies such as polymorphic and colour plasticity and changes in the use of the environment (Duarte *et al*., 2016). On the other hand, there is also an environmental representation of an ecosystem without algae, consisting only of rocks, where shrimps can potentially interact in other ways.

Finally, in order to compare both ecosystem compositions in situ, a representation with both algae and rocks is also studied in order to observe differences in behaviour with both algae and rocks present. This last representation may be the most accurate current representation of the coast where this species breeds in summer, as the water is very shallow and there are both algae and rocks, as seen in Figure 2.

Figure 2. Example of the shallow water seabed where *P. elegans* may inhabit the Baltic Sea coast. Both algae and rocks are present.

Palaemon elegans is a species whose maximum body size does not exceed 5 cm. This characteristic makes it observable to the naked eye and therefore easy to analyse its behavioural traits as an adult.

In this study, five behavioural traits were chosen to generate data collection and comparison. The traits are as follows: a) Aggressiveness, considering a defence interaction between two individuals (López Ruiz de Gauna, 2011), b) amount of movement across two ecosystem representations, c) amount of time in which an individual first reacts to a stimulus, in this case food, d) how many times an individual feeds during specific time periods and e) the number of individuals who spent time sheltered in each environmental simulation within the specified time periods. These five behavioural traits were chosen because they demonstrate key aspects of the adult stage of the species. Feeding, defence and motility.

Therefore, three research questions are posed. The first one is whether the five studied traits regarding the behaviour of this species vary between an environment with algae (plants) and an environment without plants (rocks). The hypothesis is that in an environment without algae covering the seabed, the shrimp individuals would tend to interact and express more visible behaviour (both for feeding reaction, exploration and aggressiveness behaviours).

As already mentioned, in the future there is a potential projection that macroalgae will be covering more seabed areas of the shallow waters of the Baltic Sea. These waters may undergo soil detachment and increased elements dispersal with currents as temperatures rise (Tamelander *et al*., 2017). This change would generate a seabed with sand and rocks, so there would be less space for shelter and therefore a higher level of intraspecific interaction.

The second research question is focused on comparing how a change in temperature can affect the amount of activity that individuals display in a current environmental representation. In this case, the environment representation is a seabed populated only by algae. The hypothesis here is that the higher the temperature, the greater the amount of interaction and activity.

In many cases, an increase in temperature can lead to changes in the behaviour of species. As mentioned above, species invading new ecosystems triggered by climate change may cause species coexistence disrupted (Berglund, 1980), generating advantages and disadvantages to both the invasive species (in this case *Palaemon elegans*) and endemic species (e.g., *Palaemon adspersus*).

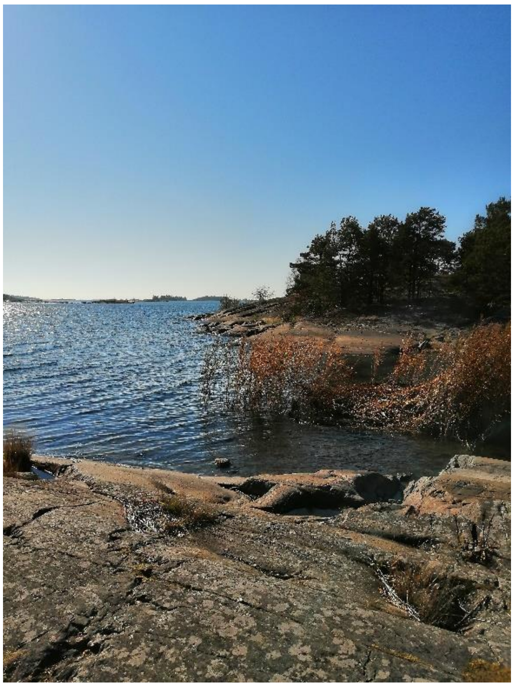
Finally, it is also intended to observe whether there is a difference in the activity of individuals as their body size varies for the two previous research questions. This could assess whether the amount of interaction that individuals can have is influenced by their body size. The hypothesis in this respect is that the larger the individual, the more activity it may have in terms of aggressiveness but less in terms of food intake or movement in the ecosystem for example, as is the case with other species of the genus *Palaemon* (Katre & Reddy, 1977). Size then might determine the expression of certain behaviours, but to what extent?

Materials and Methods

In order to carry out this study, it was necessary to capture *Palaemon elegans* adult specimens. Traps like the one showed on Figure 3 are used to catch them. These traps consist of two plexiglass plates arranged on top of a glass prism which, by varying the opening of the space between the two plates, allow individuals of the desired size to pass through and prevent them from escaping. The traps are attached to a floater which prevents them from sinking and makes them easier to identify and retrieve after the time they are held. These traps are left overnight.

Figure 3. An example of the traps used to capture *P. elegans* specimens.

The area of capture was the shore near the Tvärminne Zoological Station (Figure 4a). The catches were taken on the night of 27-28 May and the traps were placed horizontally along an inlet in the coastline, as seen in Figure 4b. As mentioned above, the breeding of this species takes place around this time (Bilgin *et al*., 2009) so it was to be expected that specimens would be caught. In this case, 29 shrimps were caught. An attempt was also made to capture specimens at the end of September, but no specimens were caught in the traps by that time.



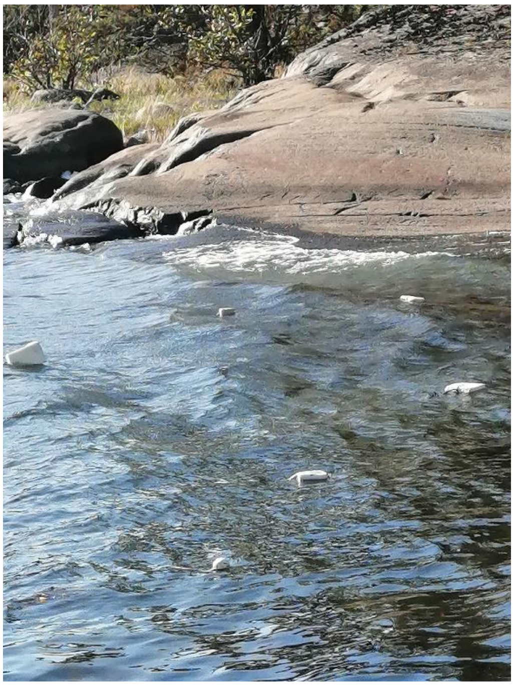


Figure 4a. Coastal trapping area near the Tvärminne zoological station. **Figure 4b**. Disposition of the traps in the water at the time of capture.

After being captured, the individuals were transferred to the Viikki campus at the University of Helsinki to be placed in water tanks. These tanks have 40x30x100cm in size (120L) containing 76L of water. Several of these tanks are split in two to keep enough space to maintain individuals alive. For behavioural studies, individuals were transferred to experimental tanks. One of these experimental tanks can be seen in Figure 5. These tanks were not divided.

Regarding the temperature and salinity conditions in the tanks, it ranged from 8ºC on the first night when the individuals were transferred to almost 15ºC on the days when the experiment took place. Regarding salinity, it was constant in 5 promille of salt concentration.

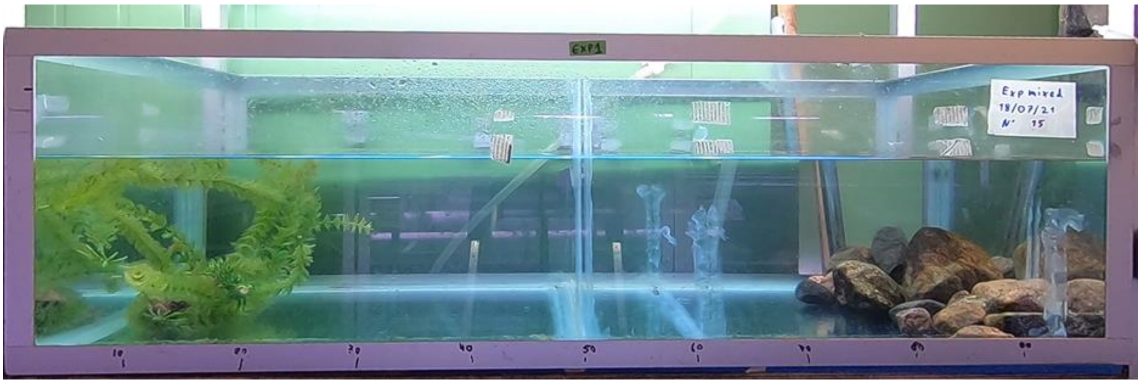


Figure 5. Example of an experimental tank used for the behavioural study. In this case it is the mixed tank, where the two elements used in the study can be observed. On the left side there is vegetation and on the right side there are rocks.

For the behavioural study, 10 individuals were introduced into the experimental tank with each of the three ecosystem representations. The first representation consists in the presence of algae. In this case algae were supplied by artificial vegetation. Two piles of this vegetation are placed on both sides of the aquarium, using approximately 20x30x20 cm. of space, leaving the central part of the tank (around 60 cm.) free as a space for feeding the shrimp.

The second representation involves replacing one of the vegetation bunches at one end of the tank with rocks. This tank is called the mixed tank, showing both elements used for these representations, as shown in Figure 5. Finally, for the third representation, the other pile of vegetation is also removed and replaced by rocks, leaving only rocks in the tank. In these two representations, the same tank spacing was used as in the first simulation described above.

For each of the treatments, twenty 10-minute videos were recorded and used for subsequent analysis. 30 minutes passed between each video. It should be noted that for each performance, the 10 individuals may not be the same.

To find out if there was a difference in the amount of activity in the shrimp at different temperatures, apart from using ten of the twenty replicates with algae on both sides at 15°C, ten replicates with same ecosystem composition at 7°C were recorded for comparison.

Both the capture at the end of May and the recording of the videos were the work of Charlotte Iperburg, an intern in Dr Ulrika Candolin's research group during the summer of 2021.

Once the videos were recorded, they were analysed. The Behavioural Observation Research Interactive Software (BORIS) was used for the analysis. This software has been developed by the Department of Life Sciences and Systems Biology of the University of Torino. It is used to encode live observations from both video and sound media (Friard & Gamba, 2016).

For the analysis, a maximum number of 10 individuals for all ecosystem representations is considered. These 10 specimens' range in size from less than 1 cm to almost 5 cm. To calculate the difference in behavioural activity with respect to the body size of the individuals, the 10 individuals are divided into two categories regarding the body size. These are small size and large size.

Small size is defined as individuals smaller than 2.5cm (half the maximum size that this species can reach). In this case, 6 individuals are considered small for all treatments (considering that for each treatment the 10 individuals can be replaced, but the size proportion is the same). Individuals between 2.5 and 5 cm in size (the maximum size attainable for this species) are considered large. In this case there are 4 individuals with the same characteristics as for the small size for all treatments. The size of the ten individuals in each treatment was measured using ImageJ program (Schneider *et al*., 2012). The scale used was 9.018 pixels/cm.

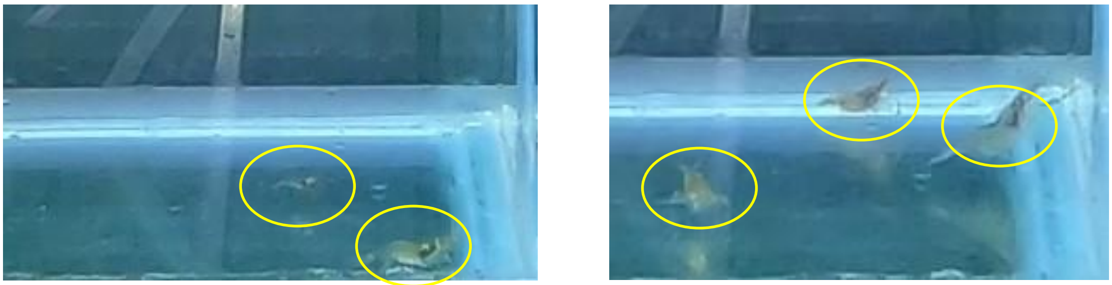


Figure 6. Images taken from the videos used for the study to measure the body size of *P. elegans* individuals in the experimental water tank. **Figure 6a** on the left shows the difference between an individual considered small (top) and one considered large (bottom). **Figure 6b** on the right shows the difference between the size of three individuals considered large. Measured individuals are circled in yellow.

As mentioned above, there are five behavioural traits to be studied. All five are encoded in the BORIS software thus becoming parameters. They are coded and quantified as follows:

a) Regarding aggressiveness, aggressive behaviour is counted when two shrimps interact and one of them attacks the other. This interaction results in the attacked individual recoiling and, in many cases, escaping. In this study, this behaviour is referred to as "Aggressivity".

b) Regarding the movement of shrimp between the two sides of the aquarium where the elements that make up the ecosystemic representation are located, each time an individual crosses from one side with algae or rocks to the other side, crossing the feeding central zone, is quantified. This includes times when the individual stops to feed in the central area of the tank but then does not go back to the same side it came from but ends up crossing to the other side. In this study, this behaviour is referred to as "Border Crossing".

c) The amount of time in which an individual first reacts to the food is quantified with the number of seconds that each of the 10 individuals takes to react to the food the first time they feed. To measure this behaviour, the total number of shrimps reacting to the food for the first time in each video is counted. In this study, this behaviour is referred to as "Food Reaction".

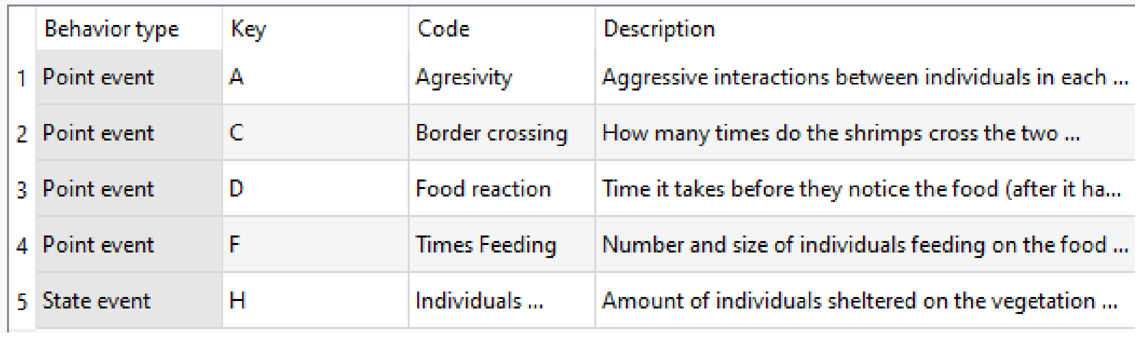
d) Apart from quantifying the first time each individual feeds within 10 minutes of video, it was also quantified the total number of times individuals grouped by size (large and small) and not individually *per se*, feed in 1-minute intervals. In this study, this behaviour is referred to as "Feeding Times".

e) At both ends of the tank, whether there is algae or rocks, shrimp tend to seek shelter, so the number of individuals at each end is quantified at one-minute intervals. For treatments where the same elements are present at both ends, the individuals at both ends are summed to check the proportion of individuals sheltering or interacting at the ends relative to the total in the tank and the treatments are compared (for both sides with vegetation and both sides with rocks). For the vegetation-rock mixed treatment, where each side has different elements, the number of individuals at each one is compared directly in the videos. In this study, this behaviour is referred to as "Individuals Habitat".

For each and every behavioural trait studied, a distinction is made between the number of large and small individuals, as well as the total number of individuals expressing each behaviour. No other abnormal behaviours or events other than those mentioned above are considered because during the viewing of the videos, it was observed that the proportion of other behaviours is negligible. For feeding-related behaviours, the shrimps were fed with defrosted chironomid larvae that are added to the central part of the tank every two minutes.

Regarding the comparison of activity at two different temperatures, for the ten videos with 7ºC in the tank and only vegetation, all the behavioural traits mentioned above were also observed but not analysed (except for the behaviour "Individuals Habitat”).

The five behaviours were coded in the BORIS programme, constructing an ethogram, which is a catalogue of behaviours exhibited by the animal under study (Friard & Gamba, 2016). In this way, it is easier to follow each individual and the behaviours he or she may express during the viewing of the videos. As shown in Figure 7, the behaviours were divided into two types, point events and state events.



	Behavior type	Key	Code	Description
1	Point event	A	Agresivity	Aggressive interactions between individuals in each ...
2	Point event	C	Border crossing	How many times do the shrimps cross the two ...
3	Point event	D	Food reaction	Time it takes before they notice the food (after it ha...
4	Point event	F	Times Feeding	Number and size of individuals feeding on the food ...
5	State event	H	Individuals ...	Amount of individuals sheltered on the vegetation ...

Figure 7. Ethogram with the codes used for the behaviours analysed in the BORIS programme (Friard & Gamba, 2016). Behaviours were divided into point or state events depending on whether their frequency or duration was measured. The key pressed to account for each behavioural expression during the analysis of each video is also shown.

Four of the five behaviours (aggressiveness, border crossing, food reaction and times feeding) were assigned the category of point events, i.e., each time the individual expressed a behaviour, only the time in the video at which the action was performed was noted, not the time the action itself lasted. These actions expressed by the shrimp have a very short duration and what is important to know in the study is to count the number of times the behaviour is expressed.

In the case of the "Individuals habitat" behaviour, when counting the number of shrimps in a given area, a temporal measurement in one-minute intervals was used. During these intervals, it was noted when an individual reached the vegetated/rocky area of the tank and the time spent there until it left that area was counted. At the end of the minute, the remaining shrimps in that area were counted. This is why it was then assigned the state event category, as it was easier to follow the individuals during the analysis and to count more accurately the number of refugee individuals per minute. The length of time they could be sheltered ranged from a few seconds to several minutes in some cases.

Once all the videos are viewed and coded, all the data was entered into an Excel sheet for statistical analysis.

The subsequent statistical analysis was carried out in the RStudio programme. Analyses were carried out on the different behaviours between the different treatments. On the one hand, the difference between the different behaviours with respect to the size of the shrimp within the ecosystemic representations. On the other hand, the difference in the frequency of the behaviours displayed by the individuals between the different treatments. Finally, the difference in the frequency of behaviours at two different temperatures in the vegetation-only treatment was also measured.

To see the differences and compare the different groups, a Student's T-test was used. This statistical test is used to find out the difference between the mean values of each group. Also, it lets to know if the potential differences in means could have happened by chance. To carry out the analyses, RStudio packages *dplyr* (To group and thus manipulate data more efficiently (Whickman *et al*., 2018), *ggpubr* (To create and visualise data more easily with plots) and *pairedData* (To analyse paired data) were used in RStudio.

In performing the Student's t-test for the analyses, the normality of the data produced by BORIS was first checked with the Shapiro-Wilk test. Once this was checked, the test was carried out, taking into account the following hypotheses. The null hypothesis of all analyses is whether there are no significant differences between the two sets of data while the alternative hypothesis is whether there are significant differences between the data. These differences are between individual body sizes (large and small), tank treatments (rock and vegetation) and temperature (7ºC and 15ºC).

If there is indeed a significant difference, it is of interest to know which of the two groups has a greater difference compared to the other. To do this, another T-test is performed, but this time testing the alternative hypothesis that the mean values of one group are higher or lower than those of the other group (both options are tested, considering that only one of them will have a significant value).

Summarised then, the studied behaviours were statistically analysed with respect to possible differences between different traits and preferences of the tested individuals regarding body size, ecosystem structure and different water temperature.

Results

Differences between the size of individuals

The first parameter on which the analyses were carried out was the influence of all behaviours with respect to the body size of the individuals, between small as and large individuals. These results can be seen in Table 1.

Comparing the number of aggressive interactions in terms of size within the same ecosystem shows that there is no significant difference in any case because the resulting p-value is greater than 0.05. This may mean that the size of the individuals does not influence the amount of aggressiveness presented within the same ecosystem (including the case where both ecosystem elements coexist in the same tank, both plants and rocks). Although not significant, it is worth noting that in two out of three treatments (rock only treatment and mixed treatment), individuals considered big showed more slightly amount aggressive interactions while on the vegetation only ecosystem were the small that showed slightly more aggressive interactions.

For the number of times the shrimp cross from one side of the tank to the other (Border crossing), the same analyses were carried out. With respect to specimen size, for the three tested ecosystems, there was a significant difference in both cases, with the p-value resulting from the test being less than 0.05. When checking which of the two sizes has a greater difference with respect to the other, in the three cases it turns out that it is the specimens considered small that cross significantly more between the sides of the tank (for all the three cases the p-value resulted in $p < 0.001$ respectively). This may mean that size can influence the amount of activity the shrimp can have in a given space (in this case along the length of the water tank). In all cases, a smaller size may indicate a greater amount of activity.

About the number of shrimps that react to the larvae and feed for the first time (Food reaction) in the ten-minute videos examined, for the three treatments tested, there was also a significant difference with respect number of individuals reacting and size, with the p-value resulting from the test being less than 0.05.

It was then checked which of the two sizes has a greater difference with respect to the other. In the three cases it turns out that the specimens considered small are those that react most frequently to the food (for all the three cases the p-value resulted in $p < 0.001$ respectively). This may mean that shrimps with size considered small may tend to want to feed more and therefore respond more quickly to food stimuli.

Regarding the number of times the shrimps are fed throughout the videos analysed, the test results for the difference in this behaviour with respect to specimen's size concluded that for the three treatments tested, there was a significant difference with respect the total number of shrimps feeding during the experiment and size, with the p-value resulting from the test being less than 0.05.

In this case it was also checked which of the two sizes has a greater difference with respect to the other. In the three cases it turns out that the specimens considered small are those that feed more frequently than the larger ones (for all the three cases the p-value resulted in $p < 0.001$ respectively). This may mean that shrimps with a size considered small may tend to need to feed more.

About the time individuals spent sheltering at one end of the tank, where the ecosystem elements (rocks and/or vegetation) were located, after each minute of the experiment, the total number of shrimps that were sheltered was counted. With regard to the size of the shrimps, for the two first treatments tested, there was a significant difference in both of them, with the p-value resulting from the test being less than 0.05.

It was checked which of the two sizes has a greater difference with respect to the other. In all cases it turns out that the specimens considered small are those that tend to seek shelter more frequently than large individuals both in rock only tank and vegetation only tank (the p-value associated with the hypothesis that effectively small individuals are in a greater number than large individuals seeking shelter was $p < 0.001$ in the three cases).

An analysis of this behaviour in the mixed tank with vegetation on the left side and rocks on the right side was also carried out. Two different Student's T-tests were performed for each side as each side had a different ecosystem representation. On the left side there was no significant difference between sizes, with the resulting p-value being greater than 0.05. On the right side, however, there was a significant difference. When hypothesised that individuals considered small had a greater tendency to hide in rocks, there was also a significant difference (the p-value associated with the test was $p< 0.001$).

Table 1. Results of T-test analyses performed comparing the difference between large and small individuals in the different ecosystems and the frequency of each of the behaviours analysed. Degrees of freedom for all cases; df. = 19. Significance level of 0.05 to reject the null hypothesis. Legend of the ecosystems represented in the tanks: “Rock-rock” the tank with rocks only, “Veg-veg” the tank with vegetation only and “Veg-Rock” the mixed tank with vegetation on the left side and rocks on the right side.

Behaviour	Ecosystem	T-statistic	P-value	Significant difference
Aggressivity	Rock-rock	-1.487	0.154	No
	Veg-Veg	1.39	0.181	No
	Veg-Rock	2.017	0.058	No
Border crossing	Rock-rock	-7.336	< 0.001	Yes
	Veg-Veg	-9.367	< 0.001	Yes
	Veg-Rock	-8.776	< 0.001	Yes
Food reaction	Rock-rock	-5.446	< 0.001	Yes
	Veg-Veg	-10.878	< 0.001	Yes
	Veg-Rock	-4.613	< 0.001	Yes
Times feeding	Rock-rock	-8.171	< 0.001	Yes
	Veg-Veg	-13.536	< 0.001	Yes
	Veg-Rock	-8.386	< 0.001	Yes
Individuals sheltered in the habitat	Rock-rock	-7.289	< 0.001	Yes
	Veg-Veg	-3.689	< 0.001	Yes
	Veg-Rock (Veg Left)	-1.701	0.105	No
	Veg-Rock (Rock Right)	-4.367	< 0.001	Yes

Differences between ecosystem composition

Table 2 shows the results of the comparison analysis between the different ecosystem composition, comparing the water tanks with only vegetation and only rock with the behaviours studied.

For all behaviours, there was no significant difference. This may mean that the number of aggressive interactions, border crossing frequency, food reaction, times of feeding and time sheltered may not vary with respect to the composition of the ecosystem for both rocks and vegetation.

Although the difference was small, it can be noted that for each behaviour, the difference with respect to this analysis varies for each one. In the case of the number of aggressive interactions and shrimp reacting to food, the difference is negligible. In the case of crossing behaviour between tank ends, the difference is balanced towards the rocky tank while for the number of shrimps feeding and shrimp seeking shelter, the difference is balanced towards the vegetated tank.

In the analysis of the sheltering behaviour however, a further test was carried out to check the preference of individual shrimp to find refuge on one of the two sides of the tank, as can be seen in Table 3. Thus, an attempt was made to test one of the hypotheses mentioned above. That was whether the shrimp preferred to find refuge in plants rather than rocks. To do this, shrimp that spent time sheltering in the mixed tank with both ecosystem elements (plants and rocks) were counted.

It turned to be there was also a significant difference between the sides, with the left side with plants being the preferred side, with a p-value resulting from the hypothesis of a greater difference in the number of shrimps sheltering on this side compared to the other of 0. 022.This may mean that shrimps prefer to hide in vegetation rather than rocks.

Table 2. Results of T-test analyses performed comparing the difference between vegetated and rock ecosystems and the frequency of each of the behaviours analysed in each treatment. Degrees of freedom for all cases; df. = 19. Significance level of 0.05 to reject the null hypothesis. All tests were carried out comparing the vegetation-only tank and the rock-only tank.

Behaviour	T-statistic	P-value	Significant difference
Aggressivity	0.076	0.941	No
Border crossing	2.048	0.055	No
Food reaction	0.134	0.895	No
Times feeding	-1.345	0.194	No
Individuals sheltered in the habitat	-1.244	0.229	No

Table 3. Results of T-test analyses performed comparing the difference between left vegetated side and right rock side on the mixed tank regarding sheltering time of individuals. Degrees of freedom for all cases; df. = 19. Significance level of 0.05 to reject the null hypothesis. All tests were carried out comparing the time shrimps spent on each of the sides (in 1-minute intervals) in the only vegetated tank.

Ecosystems	T-statistic	P-value	Significant difference
Between tank sides in Veg-Rock	2.156	0.044	Yes

Differences between temperature

The tank with only vegetation was analysed but with different temperatures (both 7ºC and 15ºC) to compare the possible differences with regard the different behaviours studied. The results of these analyses are presented in Table 4.

There was a significant difference when comparing the same ecosystem at different temperatures in the case of aggressivity. The tank with the highest number of shrimps presenting these interactions the one with the temperature at 15ºC. The p-value of the hypothesis where this tank is effectively considered to have greater aggressiveness than the one at 7ºC was $p < 0.001$. This may mean that the higher the temperature, the more aggressive interactions there are.

There was also a significant difference when comparing the same ecosystem at different temperatures in the case of border crossing behaviour. The tank with the highest number of shrimps crossing between the two corners is the one with the temperature at 15ºC. The p-value of the hypothesis where this tank is effectively considered to have a higher mean activity than the one at 7ºC was $p < 0.001$. This may mean that the higher the temperature, the more frequency of movement from side to side of the tank there can be.

In food reaction behaviour, there was a significant difference too. The tank with the highest number of shrimps reacting for the first time to food is the one with the temperature at 15ºC. The p-value of the hypothesis where this tank is effectively considered to have a higher number of shrimps reacting to food than the one at 7ºC, resulted $p < 0.001$. Thus, the higher the temperature, the more shrimp tend to react more frequently to the stimulus eaten for the first time.

At different temperatures, the frequency with which individuals feed also makes a significant difference when analysed. The tank with the highest number of shrimps feeding interactions is the one with the temperature at 15ºC. The p-value of the hypothesis where this tank is effectively considered to have a higher amount of feeding frequency than the 7ºC resulted $p < 0.001$. This may mean that the higher the temperature, the higher the number of shrimps feeding.

For the behaviour of the number of shrimps taking refuge in the rocky or vegetated area of the tanks, there was no significant difference when comparing the two temperatures, as the p-values associated with the test are greater than 0.05. This may mean that the number of shrimps sheltered may not vary with respect to the temperature of the tank.

Table 4. Results of T-test analyses performed comparing the difference between temperature and the frequency of each of the behaviours analysed in each treatment. Degrees of freedom for all cases df = 9. Significance level of 0.05 to reject the null hypothesis. All tests were carried out comparing the vegetation-only tank at 7ºC and at 15ºC.

Behaviour	T-statistic	P-value	Significant difference
Aggressivity	7.821	< 0.001	Yes
Border crossing	-5.214	< 0.001	Yes
Food reaction	4.191	< 0.001	Yes

Times feeding	11.106	< 0.001	Yes
Individuals sheltered in the habitat	0.125	0.903	No

Discussion

The findings of the analyses show that different conclusions can be drawn from the various behaviours studied. differences within them were examined in relation to the two different specimen sizes, three different tank treatments, and the two different temperatures studied.

With respect to specimen size, aggressiveness is the only behaviour where no significant difference was found in any of the treatments. Even so, both for the rock-only ecosystem and the mixed rock-vegetation ecosystem, the individuals considered to be large showed a slighter number of aggressive interactions.

This result makes sense, because this shrimp species may present a lower level of aggressiveness as the number of individuals in a defined area (in this case the tank) increases (Hernández-Castro, 2007). Individuals of this species in nature tend to monopolise tangible ecosystem elements such as rocks or algae in a certain area. The population density of these tanks is considered high. It was not observed that the shrimps tended to be aggressive in defending these elements (Rodríguez-Coello, 2008). The individuals in the study tended to be more aggressive when feeding in the central part of the tank, so the aggressiveness was therefore determined more by the food stimulus than by territoriality. Similarly, between different ecosystem representations there was no significant difference in aggressiveness. this could have been because the amount of food given to the shrimps in the study was the same for all treatments.

In the case of the number of times the shrimp crossed from one side of the tank to the other, with respect to body size, a significant difference was obtained for all treatments, with the individuals considered small showing the greatest amount of movement. This behaviour was studied to test whether the level of activity and movement through a given area (the tank length) might depend on the composition of the ecosystem, rather than the body size of the individuals as such. However, in terms of difference between the amount of movement across the tank between treatments, there was no significant difference.

This can mean two things. On the one hand, the larger individuals tend to displace the smaller ones from where they are, in an aggressive or non-aggressive way, so small individuals would tend to move around more than the larger individuals (Evans & Shehadi-Moacdieh, 1988). On the other hand, the fact that there is no significant difference between ecosystems may mean that shrimp movement preferences do not depend on ecosystem composition. In nature, this species tends to move over long distances between deeper and more coastal areas following its migration pattern (Gruszka & Więcaszek, 2011). Thus, movements over a short distance may be mainly the result of territoriality in the ecosystem regardless of its composition. Another reason for their mobility is also the search of food (López Ruiz de Gauna, 2011).

The result is identical for the two behaviours concerning the feeding of the specimens in relation to their body size. For the behaviour of first reaction time to the food stimulus, small individuals reacted more frequently than large individuals. Similarly, for the number of times individuals fed during the study time, it was also the small individuals that fed more often. Both differences were significant.

Smaller individuals tend to have less variation in feeding while larger ones can feed on more animal and plant food sources more frequently (Lesutienė *et al*., 2014). This factor might be the reason why smaller individuals eat more and react more to food. Larger individuals do not pay as much attention to food and therefore may tend to feed less. Smaller individuals, however, may take more opportunities to feed, as larger individuals tend to be more aggressive when approached, so the more times smaller individuals attempt to feed, the more likely they are to succeed.

It is known that the body size of this species can vary with respect to the amount of food available, among other factors like the water salinity level. In the Baltic Sea, individuals of this species have been found to be smaller in length than in other places where they are distributed, including their native areas such as the Atlantic ocean (Bilgin & Samsun, 2006). This smaller size of individuals means that the reproduction process in the Baltic is changing towards one where females lay fewer but larger eggs. This adaption factor is considered to be responsible for the large colonisation of this species in the Baltic, so that smaller individuals may be more successful in this particular ecosystem (Janas & Mańkucka, 2010).

With regard to the difference between these two feeding related behaviours with respect to the type of ecosystem represented in the tank, it was found that in neither case was there a significant difference. Ecosystem composition therefore does not appear to be a key factor in the feeding behaviour of this species. In the wild, this shrimp species prefers to feed on animal prey over algae, although algae also constitute part of their diet (Persson *et al*., 2008). Therefore, the source of food origin may be more relevant than the composition of the ecosystem.

Analyses of the behaviour of individuals sheltered in the rocky and/or vegetated areas of the tank also gave different results with respect to differences between specimen size and tank treatment. With respect to body size, there were significant differences in the rock-only and vegetation-only tanks. For both cases, individuals considered small remained sheltered for longer than larger individuals.

Regarding this fact, it seems logical considering the aggressiveness traits of this population. Smaller individuals are not as aggressive as larger ones and therefore in many cases tend to hide quickly after feeding or move further around the tank to reach vegetated or rocky edges more frequently. Larger individuals tend to wander more in the bare centre of the tank, in many cases remaining motionless.

In the Baltic Sea, shrimp species are hardly found in non-vegetated areas. In particular, *P. elegans* tends to feel more secure in vegetated areas than in bare or rocky areas (Grabowski, 2006). However, even if there is no vegetated area, shrimp will tend to seek shelter anywhere over being in a bare area to hide.

To then compare the *in-situ* preference of the studied individuals for vegetation or rocks as shelter, this behaviour was analysed in the mixed tank with a vegetated area on the left side of the tank and a rocky area on the right side of the tank. Each of the edges separately regarding size differences was analysed first and then tank as a whole regarding ecosystem preference.

On the left vegetated side, there was no significant difference between sizes, being more normal for large and small individuals to spend almost equally more time in this area. On the rocky right side, there was a significant difference. Small individuals spent more time in this area than large individuals.

Regarding ecosystem preference in the mixed tank as a whole, there was a significant difference when comparing them, with the side with vegetation (left side) having the highest number of shrimp sheltering compared to the side with rocks.

To test whether this preference occurred only when shrimp were exposed to both types of sheltering elements in the same area, the difference between the number of shrimps sheltering in both the vegetation tank alone and the tank with rock only was also analysed. The difference between these two tanks with respect to this behaviour was found to be non-significant. That is, the number of shrimps seeking shelter was similar for both cases. This may mean that shrimp of this species tend to seek refuge in anything other than a bare surface, be it rocks or vegetation, but that when exposed to both elements at the same time, they tend to prefer to seek refuge in vegetation. This also corresponds to the fact that part of the diet of this species is algae (Janas & Baranska, 2008) and that, as mentioned above, this species tends to shelter more frequently in vegetated areas (Grabowski, 2006).

Then, according to the hypotheses set out at the beginning of the study, with regard to body size, it can indeed be seen that it influences the expression of most behaviours, with small individuals tending to be more active than large ones. In several species of this genus, with respect to food intake and sheltering, smaller individuals tend to be more active, so this is not an unreasonable result (Katre & Reddy, 1977). What is striking is the result regarding aggressive interactions, because normally larger individuals tend to be more aggressive (Evans & Shehadi-Moacdieh), but here neither of the two sizes differed markedly.

However, body size and aggressiveness do have much more influence in terms of other type of behaviours, like the reproductive ones, not studied in this case. Female *Palaemon elegans* may be more aggressive the larger they are, and for example the variation in the number of eggs may also be subject to the size of the parent (Janas & Mankucka, 2010). A possible limitation of the study in terms of the influence of body size on the five behaviours in question could be that it does not take into account the sex of the individuals. Thus, perhaps the aggressiveness studied when comparing known gender individuals, could have turned out differently.

Regarding the composition of the ecosystem, a research question had also been posed, in which a higher amount of shrimp activity was predicted in a rocky scenario compared to a vegetated representation. This hypothesis, however, did not prove to be satisfactory after analyses, because in no case was there a significant difference in the level of expression of any of the behaviours.

This may mean that shrimps have the same level of activity in a seabed consisting only of rocks or vegetation. By being able to maintain this activity in different ecosystem compositions, it is easier for their spatial variation and colonisation capacity to be greater and therefore advantageous. As it is considered invasive in several locations such as the Baltic Sea, it is not surprising that this advantage is one of the reasons for its potential colonisation success (Al-Khafaji *et al*., 2016).

Would it then have been interesting to compare the activity level of the mixed aquarium with each of the other two treatments to see if the shrimp are more or less active? The answer is that with the result obtained and knowing that normally the seabeds that this species inhabits near the shore have both rocks and vegetation (Bilgin *et al*., 2008), perhaps there would not have been a relevant significance either, as this species is active in both elements.

Apart from comparing the differences in the chosen behaviours with respect to the size of the specimens and the ecosystems represented, these behaviours were also analysed by comparing two scenarios with different temperatures. The results of the analyses under these conditions were almost unanimous. For four of the five behaviours, there was a significant difference when comparing the frequency of the behaviour was expressed between tanks fully vegetated at 7ºC and at 15ºC. These behaviours that shared this result were aggressiveness, movement throughout the tank, reaction to food and number of times feeding. In all cases, the difference was in favour of a greater expression of the behaviours in the 15ºC tank individuals.

The only behaviour where there was no significant difference between tanks at different temperatures was the time shrimps remained sheltered at the ends of the tank. In this single instance, it is possible to state that shrimps tend to hide in vegetation at a similar frequency regardless of temperature. It seems then that temperature affects physiological processes and general activity level (Morris & Taylor, 1985), as with all other behaviours, which measure feeding parameters, interactions or movement. As this is a resting or almost motionless behaviour, temperature might not be a determining factor in this case and therefore other factors play a part.

These results show that individuals of this species tend to be more active at higher temperatures. Therefore, the hypothesis that the higher the temperature, the higher the shrimp’s activity, was resolved with a satisfactory outcome. This species' life processes, such as moulting, occur more frequently at higher temperatures. (Nugegoda & Rainbow, 1987). This species has a fairly high survival rate with respect to temperature, mainly due to seasonal changes. Thus, *P. elegans* can be exposed to very cold temperatures (almost 2°C) and be able to survive (Janas & Spicer, 2008) as well as almost 30°C in some extreme cases (Madeira *et al*., 2015).

Although the temperature range is high, the level of activity at different temperatures is not the same. On the one hand, at cold temperatures almost only the smaller individuals are able to survive so most of the individuals tend to migrate to areas with warmer water, so they can obtain a greater variety of food and a higher survival rate. The optimum temperature for larval development and proper organ function even in adults in this species is 20°C, which is high compared to other species inhabiting similar waters (Rochanaburanon & Williamson, 1976).

Conclusion

In the future, when the temperature of the Baltic Sea is predicted to rise (Siegel *et al*., 2006), the ecosystem, including both biotic and abiotic components, may change. Some species that have recently managed to colonise this sea and are currently classified as invasive species may vary their behaviour with changes in the ecosystem, in turn generating potential behavioural variation in other endemic species at the same or different trophic level (Falk-Petersen *et al*., 2007).

Palaemon elegans was found in this sea for the first time in the early years of this century, and its spawning and presence in this area is becoming more and more common. This means that it successfully has been able to adapt. This adaptability and colonization might be attributed to the fact that the Baltic Sea is an ecosystem that is being impacted by climate change in a variety of ways. This study has tried to demonstrate that some of the behaviours that this species expresses with respect to feeding, mobility and defensive interactions in the form of aggression or sheltering may be affected by changes in the ecosystem they inhabit.

Indeed, temperature change influence has been the highlight of the results of this study. Traditionally, this species prefers to inhabit warmer waters than Baltic Sea. As this sea increases in temperature, it was expected that the amount of activity would vary, but the difference in this study in a step from 7ºC to 15ºC was quite a lot. Likewise, it should be noted that at low temperatures, this species shows a high amount of activity (Janas & Spicer, 2010) compared to other species. In this case at 7ºC the behavioural expression was rather low, almost null.

Then, one of the key elements for greater adaptation to changes in the ecosystem is to have a high thermal tolerance. *P. elegans* is characterised by this, and although other species of the same genus may possess even greater tolerance, a large but moderate thermal tolerance makes it more sensitive to future changes as well, reflected in possible physiological adaptations in its life cycle (Ravaux *et al*., 2016).

True, this study has proved the species' ability to persist in the Baltic Sea throughout time. However, some limitations can be considered in this study which, if addressed, would have complemented the information obtained in the results. On the one hand, apart from temperature, a change in the salinity of the Baltic Sea waters is expected. An experiment comparing these behaviours in tanks with different salinity would have been interesting, as it is known that many physiological functions of this species are salinity dependent (Nugegoda & Rainbow, 1989).

On the other hand, several studies highlight the strategy and changes of reproductive behaviour in species of this genus in relation to changes in the ecosystem (Szaniawska & Łapińska, 2006). In this study, no reproductive behaviour was analysed due to the impossibility of identifying the sex of individuals and the lack of individuals showing any reproductive interactions. Perhaps working with a larger number of individuals during the breeding season could provide more data on this type of behaviours.

It should not be forgotten that this invasive species shares a niche in the Baltic Sea with another endemic species, *Palaemon adspersus*. A next step in this study could also be to analyse all the behaviours studied under the same circumstances for specimens of the native species in order to compare the behavioural response to ecosystem changes with those obtained with *Palaemon elegans*. This would be useful to see under which environmental conditions one or another species has a greater adaptive advantage, as demonstrated with the potential shift in salinity, which affects one species more than another depending on how this parameter varies (Cavraro *et al*., 2022).

The environmental impact that species currently considered invasive can cause is negative in the areas they colonise, generating consequences that affect native species. However, when that area undergoes changes, this can pose an adaptive challenge to the species inhabiting the ecosystem, including invasive species. In the face of these changes, the invasive species may find it even easier to live in the invaded area or, on the contrary, they may turn the tables and the native species may be more prepared (Mainka & Howard, 2010). However, in many cases, colonising species often have greater physiological capacities such as thermal tolerance than endemic species (Ravaux *et al*., 2016).

Understanding a species' behavioural features in the face of these changes, on the other hand, is part of behavioural ecology, a field that, because to technological advances, is becoming increasingly relevant to global climate change research. Studying possible behavioural changes in invertebrates is becoming easier and in fact is crucial to understanding the future of ecosystems, as many of them are an important ecosystem component.

Palaemon elegans is just a small part of the whole that is the Baltic Sea ecosystem. Although it is a relatively new species in this ecosystem, it is nowadays considered part of it, because this species interacts with other species (Jakubavičiūtė & Candolin, 2021). Long-term projections indicate that this ecosystem will be populated by many more species from other ecosystems (Holopainen *et al*., 2016). Even other species of the genus *Palaemon* have arrived in the last decade in the Baltic Sea as *Palaemon macrodactylus* (Janas & Tutak, 2014). This will then lead to further changes, adaptations and interactions, and it is necessary to understand each piece of this changing environmental puzzle in order to comprehend and complete it.

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