



Shrimp habitat selection dependence on flow within *Zostera marina* canopies

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ARTICLE INFO

Keywords:

Palaemon adspersus
Dislodgement
Animal tolerance
Seagrass
Unidirectional flow
Plant density

ABSTRACT

Even though hydrodynamic conditions play an important role in shallow coastal ecosystems such as enhancing primary production by the remobilization of nutrients, they could represent a potential threat to motile benthic animals because they can dislodge them and restrict their movements, thereby impacting their distribution within the ecosystem. Seagrass canopies are critical habitats that shelter many organisms against predators and adverse hydrodynamic conditions, however, they have been declining over time, resulting in seagrass fragmentation and low canopy densities. The shrimp *Palaemon adspersus* is an epifaunal species that thrives in *Zostera marina* seagrass, and therefore can offer insight into the impact canopy fragmentation is having on its behavioral patterns. In a laboratory flume with unidirectional flow, *P. adspersus* individuals were exposed to flow velocities in sand bottoms covered with *Z. marina* canopies, and their distribution studied as a function of both the canopy density and the current velocity. Flow velocities above 3 cm s⁻¹ started to dislodge *P. adspersus* individuals, thereby reducing their tolerance to the flow. However, under flow velocities ranging from 3 cm s⁻¹ to 21 cm s⁻¹, they preferred to shelter within the seagrass canopies with intermediate densities higher than 150 shoots m⁻², compared to bare sand. The patch density at which individuals found patch sheltering decreased linearly as the current velocity increased, indicating that individuals were unable to withstand the velocity of the flow. For current velocities above 21 cm s⁻¹, *P. adspersus* were unable to tolerate the flow velocity, and so were dislodged from the canopy. This study highlights the importance of protecting eelgrass, as the ever-decreasing meadows are making *P. adspersus* even more vulnerable to the high flow rates.

1. Introduction

Benthic organisms, such as shrimps, reside in marine coastal systems but their localization within the habitat and survival depends on three main parameters: the local or synoptic hydrodynamics defined by waves and currents (Foulquier et al., 2020); the structure of the habitat defined by the quality of the seascape (Carrier-Belleau et al., 2021; González-Ortiz et al., 2016); and the biotic relations between individuals, such as predation or competition (Robinson et al., 2013). The development of benthic organisms is under threat from unfavorable environmental conditions caused by either natural or anthropogenic disturbances, such as marine storms (Pérez-Gómez et al., 2021), marine heat waves (Oliver et al., 2019), habitat modification (Hansson et al., 2022), and/or a decrease in water quality (Fettweis et al., 2023).

Therefore, the presence and distribution of fauna, and for some

species their abundance (Riera et al., 2020), in seagrasses highly depend on the architecture of the seagrass canopy and its conditions (Castejón-Silvo et al., 2021). The root system, for example, supports a high number of fauna and prevents the seabed from becoming anoxic, thus resulting in a suitable habitat for the infauna (Fredriksen et al., 2010; Gagnon et al., 2023; Kindeberg et al., 2022). Furthermore, the structure of a seagrass canopy may determine the composition of the species living within and around it, or the distribution of predators and strategies for predation. Seagrass canopies provide valuable nursery habitats (Unsworth et al., 2019) that support commercial fisheries (Stål et al., 2008) as well as habitats, food, and refuge for multiple species (Duarte, 2000). They also serve as a food source for megaherbivores, such as green turtles, dugongs, and manatees, that feed on the seagrass (Beck et al., 2001). Some epifaunal assemblages exhibit a higher abundance at the edge of the canopy, while others prefer to remain in the interior of the

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<https://doi.org/10.1016/j.ecss.2024.108858>

Received 29 November 2023; Received in revised form 3 June 2024; Accepted 22 June 2024

Available online 25 June 2024

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seagrass canopy, displaying a higher diversity and abundance (Källén et al., 2012). For example, the scallop *Argopecten irradians* presents higher densities and growth rates at seagrass edges than in seagrass interiors or on bare soil areas (Bologna and Heck, 1999), whereas the shrimp *Pandalus latirostris* are more abundant in high seagrass densities, regardless of the seagrass species (Yusa et al., 2018). Additionally, while the abundance of juvenile shrimp *P. latirostris* does not depend on the patch size of the seagrass, adult abundance does increase as seagrass patch size decreases as adults frequently migrated between patches during nighttime (Shinomiya et al., 2017). The presence and density of seagrass canopies may also impact the distribution of epifaunal benthic organisms as seagrasses modify the hydrodynamics of coastal areas (Infantes et al., 2012; Luhar et al., 2010; Pujol et al., 2013) by mitigating wave velocity, currents, storms, storm surges and marine heatwaves; all of which are highly dependent on the structure (plant height, density, flexibility, etc.) of the seagrass canopy. Certain level of hydrodynamic conditions such as wave velocity and turbulence are crucial for a good status of the ecosystem as hydrodynamics may reduce the diffusion boundary layer and therefore enhancing the nutrient uptake of seagrass leaves (Fonseca and Kenworthy, 1987). Depending on the flow velocities and turbulence, benthic sessile or mobile organisms can be dislodged from their habitat, which can reduce their locomotion capacity or even compromise their survival (Martinez, 2001). Dislodgement also depends on the organism's size. For instance, for medium-to-large crayfish, the flow velocity needed to dislodge them was between 0.6 m/s and 1 m/s, while for small crayfish, it was 0.3 m/s (Maude and Williams, 1983).

Seagrass ecosystems globally are under threat from density loss and degradation (Waycott et al., 2009). Since 1876, seagrass coverage has been reduced by a third (Waycott et al., 2009). Habitat fragmentation transforms continuous meadows into canopies with interspersed gaps (Barcelona et al., 2021). If plant loss increases the number and area of such gaps, this may result in a network of vegetated patches that are barely interconnected (Robbins and Bell, 1994; Tanner, 2003). The principal causes of seagrass fragmentation are destructive fishing practices, anchoring, and boat moorings, all of which directly contribute to plant loss within seagrass canopies. Additionally, coastal development and overexploitation have been proven to have a major impact on the seafloor (Colomer et al., 2017; Unsworth et al., 2017). Seagrass fragmentation has been found to impact the richness of epifauna. The impact is even more profound in large seagrass beds due to their heterogeneity, with their greater number of niches and microhabitats (Källén et al., 2012). Furthermore, the negative effect on epifaunal diversity is directly related to the increase in seagrass fragmentation (Arponen and Boström, 2012). Boström et al. (2006) suggest that a decrease in seagrass cover of more than 59% may imply functional changes and effects on the associated organisms. For instance, on the dispersal of larval reproductive stages, eggs, and juveniles. Haga clic o pulse aquí para escribir texto. Although fragmented seagrass meadows have been found to support higher densities of decapods than continuous canopies (Eggleston et al., 1998), the response of epifaunal species to habitat fragmentation is not uniform and can depend on various factors such as size, behavior, mobility, dispersal ability, and perception of the patchiness (Boström et al., 2006). In the case of mobile fauna, the predation efficiency may also be affected, and fragmented canopies may have lower densities of organisms due to longer search times for prey (Hovel and Lipcius, 2001). Nevertheless, the loss of seagrass can significantly impact the survival rates of epifaunal species, as these are closely associated with the quality of the canopy.

One example of this is the Baltic prawn, *Palaemon adspersus*, which feeds on filamentous algae and small invertebrates within *Zostera marina* canopies on the Swedish west and south coast (Jephson et al., 2008). *P. adspersus* inhabits mainly *Z. marina* meadows and is an important component in the biomass of the mobile epibenthic fauna (Baden and Pihl, 1984; Berglund, 1980; Persson et al., 2008). The individual characteristics of *P. adspersus* as an epifaunal species make it a suitable model to study the effects of seagrass ecosystem dynamics, because it can offer

insights into the impact canopy fragmentation has on behavioral patterns. Therefore, this study aims to determine the impacts the structural density of *Z. marina* and the hydrodynamic regime have on the behavior of *P. adspersus* by quantifying their tolerance to unidirectional flows, and determining the habitat preference of individual shrimp within *Z. marina* plants under unidirectional flows.

2. Methodology

2.1. Flume set-up

The study was conducted in a hydraulic flume at the Kristineberg Marine Research Station in Sweden. The flume was made of methacrylate and was 800 cm long, 50 cm wide, and 50 cm deep. The test section was 200 cm long, and the mean water working height for all experiments was $H = 10$ cm (Fig. 1). The bottom of the test section was filled with natural sediment taken from the Gullmars Fjord, where the *Z. marina* plants were also collected. The sediment was sieved through a 2 mm mesh size before being placed at the bottom of the test section in order to eliminate residual fauna. The flume was equipped with a motor-run propeller at the end of the flume, which was controlled by an adjustable speed drive to generate mean flow velocities in the range of current velocities naturally found in eelgrass meadow areas (Infantes et al., 2021). Three honeycomb flow stabilizers were placed in front of the test section to transform the turbulent flow from the motor-run flow to unidirectional laminar flow, and a mesh net was placed after the test section to prevent shrimp loss. The seawater used in the experiments had a salinity of $S = 27.65\text{‰}$ and temperature $T = 15 \pm 1$ °C. Therefore, the water density and viscosity were $\rho_w = 1020.36$ kg m⁻³ and $\rho_w = 1.206 \times 10^{-3}$ Pa s⁻¹, respectively.

The experiments were conducted using eelgrass (*Z. marina*) shoots collected in September 2021 from the Gullmars Fjord. The eelgrass plants had 3 ± 1 leaves shoot⁻¹, a shoot length of 25.5 ± 5.6 cm, a width of 0.4 ± 0.1 cm, and a thickness of 0.045 cm. The plants were kept in laboratory tanks with flow-through seawater from the fjord. To avoid the scouring and uprooting of the seagrass plants, the root was removed, and each shoot was fixed to a wooden stick with a cable tie, and then the stick and cable tie were buried in the sediment. The vegetation patch, L_{patch} , was built by placing 4, 6, 8, 12, 15, 18, 20, 25, 30, or 35 plants into the test section, i.e., corresponding to canopy densities of $n = 50, 74, 100, 120, 150, 180, 200, 250, 300,$ or 350 shoots m⁻². These densities corresponded to the range of shoot densities found in *Z. marina* canopies on the west coast of Sweden (Boström et al., 2014).

The initial flow velocities were measured using an Acoustic Doppler Velocimeter (ADV, Nortek, Vectrino) at a frequency of 25 Hz for 3 min, resulting in 4500 measurements. The temporal mean of the velocity from the 4500 data inputs was used as the characteristic flow velocity for the six experimental hydrodynamic conditions ($U_c = 0, 3, 8, 15, 21,$ and 23 cm s⁻¹), these velocities corresponded with the range of velocities found in the field (Liljebldh and Thomasson, 2001; Pereda-Briones et al., 2018). Vertical profiles of flow velocity were taken longitudinally, 20 cm before and after the patch edge, to avoid signal interference from the eelgrass leaves.

2.2. Shrimp habitat selection and flow tolerance

Adult individuals of *P. adspersus* were used for the experiment trials since they strictly inhabit *Z. marina* areas (Perry et al., 2019). The individuals were kept in laboratory tanks with flow-through seawater from the fjord and fed with raw fish four times a week. A total of 52 individuals were used, and the total body length (TBL), cephalothorax length (CL), and abdomen length (AL) were measured for each individual to characterize their body characteristics. The measurements resulted in $TBL = 5.99$ cm \pm 0.95, $CL = 2.44$ cm \pm 0.46, and $AL = 3.55$ cm \pm 0.65. Once the experiments were completed, the animals were returned to the site from where they had been collected.

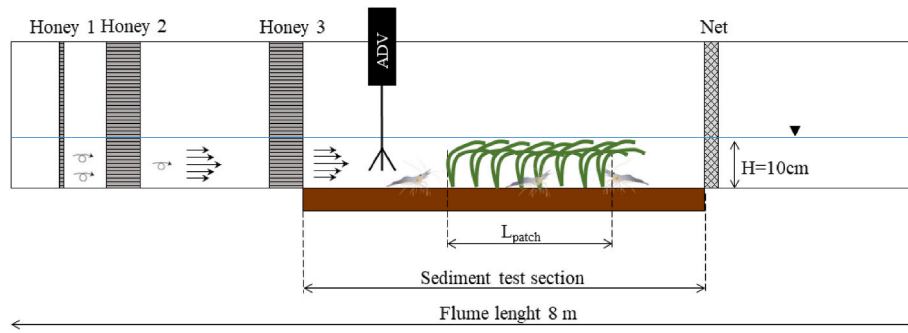


Fig. 1. Lateral view of the experimental set-up. Experiments were conducted in an 800x50 × 50 cm long flume, test section of 200 cm and mean water depth of 10 cm. The vegetated patch, L_{patch} , had dimensions of 40x20 cm. H represents the water level in the flume. An Acoustic Doppler Velocimeter (ADV, Nortek, Vectrino) was vertically mounted to measure the instantaneous velocities at selected vertical heights. Three honeycomb flow stabilizers (HFS1, HFS2, and HFS3) were positioned to obtain a laminar flow, and a net at the end of the test section was needed to avoid shrimp loss.

Each experiment consisted of nine repeated trials, where six mean flow velocities, $U_c = 0, 3, 8, 15, 21$ and 23 cm s^{-1} , corresponding to the Reynolds number of the plant of $Re_p = 0, 117, 303, 522, 746, 843$, were tested (Table 1) and calculated following:

$$Re_p = \frac{U_c * \delta_{fluid} * d_{plant}}{\mu_{fluid}}, \quad (1)$$

where, δ_{fluid} corresponded to the density of the water in the flume, d_{plant} corresponded to the diameter of the plant ($d_{plant} = 0.4 \text{ cm}$) and μ_{fluid} corresponded to the viscosity of the seawater in the flume.

To avoid any interaction between the animals, each experiment was initiated by placing three individuals in the center of the test section with no flow and no light. Under these conditions, the individuals moved randomly throughout the test section. After 40 min of acclimatization in the test section, the water flow was turned on to the lowest velocity for 30 min. A 40-min- acclimation time was determined to be adequate after a pilot test showed that after this time, all shrimps were moving around the flume. The velocities were then gradually increased at 30-min time steps until the highest velocity was reached. The position of each individual shrimp (sand shrimp location or seagrass area location) was located visually by identifying the individuals' localization at sand area or seagrass area three times at 5-min intervals for each flow velocity at 15, 20, and 25 min (Table 1). The seagrass area was considered the area covered by *Z. marina* leaves, while the rest of the test section was considered sand area. Pilot experiments showed that these acclimatization and exposure time intervals were adequate for the experimental set-up. To avoid the shrimps being dragged out of the system when being dislodged, a net was placed at the end of the flume. Concurrently, the tolerance of the shrimp to each flow velocity (i.e., the percentage of shrimp remaining in the test section or being washed out and their substrate preference (either seagrass or sand area) were measured.

To gain knowledge of the *P. adspersus* substrate selection (seagrass or sand) a non-dimensional model was set up using the Buckingham pi-

Table 1
Summary of the experimental conditions tested.

Run	N (shoots)	n (shoots m^{-2})	U_c (cm s^{-1})	Re
R1	4	50	0.0–23	0.0–843
R2	6	75	0.0–23	0.0–843
R3	8	100	0.0–23	0.0–843
R4	12	120	0.0–23	0.0–843
R5	15	150	0.0–23	0.0–843
R6	18	180	0.0–23	0.0–843
R7	20	200	0.0–23	0.0–843
R8	25	250	0.0–23	0.0–843
R9	30	300	0.0–23	0.0–843
R10	35	350	0.0–23	0.0–843

theorem (Evans, 1972). This theorem defined the non-dimensional key parameters that best correlated the dependent variables (shrimp position) with the non-dimensional parameters characterizing the system, Reynolds number and plant density. Therefore, the non-dimensional model (Eq. (1)) can be expressed following:

$$\frac{N_{seagrass}}{N_{sand}} = f(ad, Re) \quad (2)$$

where $\frac{N_{seagrass}}{N_{sand}}$ represents the ratio between the number of shrimp found in the seagrass area ($N_{seagrass}$) versus the number found in the sand area (N_{sand}), Re_p is the plant Reynolds number and ad is the volume fraction of the vegetation over the total volume, where $a = Nd/A$ (Nepf et al., 1997) is the frontal area of the canopy per unit volume, N is the total number of plants, A is the total bed area occupied by the plants, and d is the stem plant diameter of the *Z. marina* plants.

3. Results

The tolerance to the flow of *P. adspersus* was found to follow two different regimes depending on the mean flow velocity, and therefore the plant Reynolds number. Up to plant Reynolds numbers of $Re_p = 117$, corresponding to a flow velocity of $U_c = 3 \text{ cm s}^{-1}$, flow tolerance remained constant at 100 %. Therefore, all individuals were able to remain in the test section, swimming or staying still in the sediment (Fig. 2). However, for hydrodynamic regimes with plant Reynolds numbers higher than 117.19, shrimp flow tolerance decreased following a linear decay with Re_p (% flow tolerance = $-0.078 * Re_p + 110.84$, with $R^2 = 0.99$ and $p\text{-value} < 0.01$) (Fig. 2).

For both regimes ($Re_p < 117$ and $Re > 117$), two substratum selection behaviors were determined. Within the vegetated eelgrass area, the percentage of *P. adspersus* individuals increased with seagrass density, following a non-linear trend (Fig. 3a and b). In contrast, for the sandy area, the percentage of individuals decreased as the density of nearby seagrass increased (Fig. 3a and b). For low plant Reynolds numbers and canopy densities of $< 300 \text{ shoots m}^{-2}$, the percentage of individuals in the sand was greater than in the seagrass (Fig. 3a). However, for canopy densities $> 300 \text{ shoots m}^{-2}$, the percentage of individuals was greater in the seagrass than in the sand. For canopy densities of $300 \text{ shoots m}^{-2}$ and low flow velocities, the percentage of individuals in the sand was close to that found in the seagrass (Fig. 3a). For higher flow velocities ($U_c = 21 \text{ cm s}^{-1}$), the percentage of individuals in both the sand and the seagrass was lower (Fig. 3b) than for low flow velocities (Fig. 3a). However, as found in the low flow velocities, for low canopy densities ($< 150 \text{ shoots m}^{-2}$), the percentage of individuals in the sand was greater than in the seagrass (Fig. 3b). In contrast, for denser canopies, the percentage of individuals in the sand was lower than in the seagrass.

To determine the canopy density threshold at which the percentage

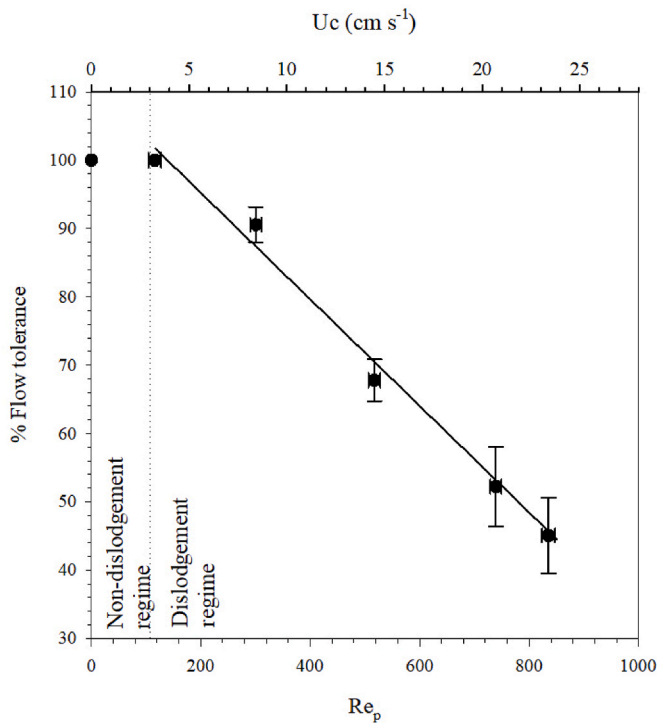


Fig. 2. Flow tolerance of shrimp to flow (in %) averaged for all experimental runs (densities) tested versus experimental plant Reynolds numbers (bottom axis) and versus tested flow velocities, U_c (top axis). Error bars are the standard error, $n = 10$.

of individual shrimp in the seagrass is the same as that in the sand, the relation between the canopy density threshold versus flow velocity was calculated (Fig. 4a). The relationship between canopy density threshold and U_c was found to be non-linear. At low current velocities ($U_c < 3.3 \text{ cm s}^{-1}$), the threshold for what percentage of individuals in the seagrass was equal to that in the sand, remained constant with U_c . In contrast, for current velocities $3.3 \text{ cm s}^{-1} < U_c < 20.7 \text{ cm s}^{-1}$, the canopy density threshold decreased linearly with U_c . For $U_c > 20.7 \text{ cm s}^{-1}$, the threshold remained constant with U_c . Within the seagrass, and

especially for high flow velocities, shrimp were observed to stay mainly behind plant stems (Fig. 4b).

Considering the non-dimensional model Eq. (1), two behaviors were determined by establishing the dependence of $N_{seagrass}/N_{sand}$ on ad and Re_p , based on the following equation $ad \cdot Re_p^{1.5}$ (Fig. 5). For $ad \cdot Re_p^{1.5} < 9$, $N_{seagrass}/N_{sand}$ remained constant with $ad \cdot Re_p^{1.5}$ at a value of $N_{seagrass}/N_{sand} = 0.22$, while for $ad \cdot Re_p^{1.5} > 9$, $N_{seagrass}/N_{sand}$ followed a power trend expressed by: $N_{seagrass}/N_{sand} = 2.6 \times 10^{-3} \cdot (ad^{1.76} \cdot Re_p^{2.64})$ (Fig. 5). The first regime, where $N_{seagrass}/N_{sand}$ remained constant, corresponded to all the cases where $Re_p < 117.2$, the case of $Re_p = 117.2$ and some of the $Re_p = 303.4$ cases, corresponding to $U_c = 3.3$ and 8.4 cm s^{-1} (left part of Fig. 4). In contrast, the second regime, corresponded to the cases from Re_p in the range of $303.4\text{--}746.2$, corresponding to U_c range between 8.4 and 20.7 cm s^{-1} (right part of Fig. 5). The threshold between both regimes defined the plant density for which the $N_{seagrass}/N_{sand}$ shifted from being constant to depend on ad and Re_p . The threshold was found at $ad \cdot Re^{1.5} = 9$.

From the model equation, the minimum plant density to observe a seagrass substratum preference by the individuals of *P. adspersus* could be calculated as:

$$ad \cdot Re_p^{1.5} = 9 \tag{2}$$

which, by defining $ad = nd^2$, where n is the plant density and d is the diameter of the plant stem, resulted in the following equation:

$$nd^2 \cdot Re_p^{1.5} = 9 \tag{3}$$

Therefore, the minimum plant density that defined shrimp habitat preference depended on both the Re_p , and the plant diameter d , according to:

$$n = \frac{9}{Re_p^{1.5} d^2} = \frac{9 \mu_w^{1.5}}{d^{3.5} \delta_w^{1.5} U_c^{1.5}} \tag{4}$$

4. Discussion

This study demonstrates that the habitat selection of *P. adspersus* depends on both the hydrodynamic regime and the structural characteristics of seagrass canopies. These results provide new insights into the behavior of *P. adspersus* over a range of unidirectional flow conditions and structural characteristics of meadows.

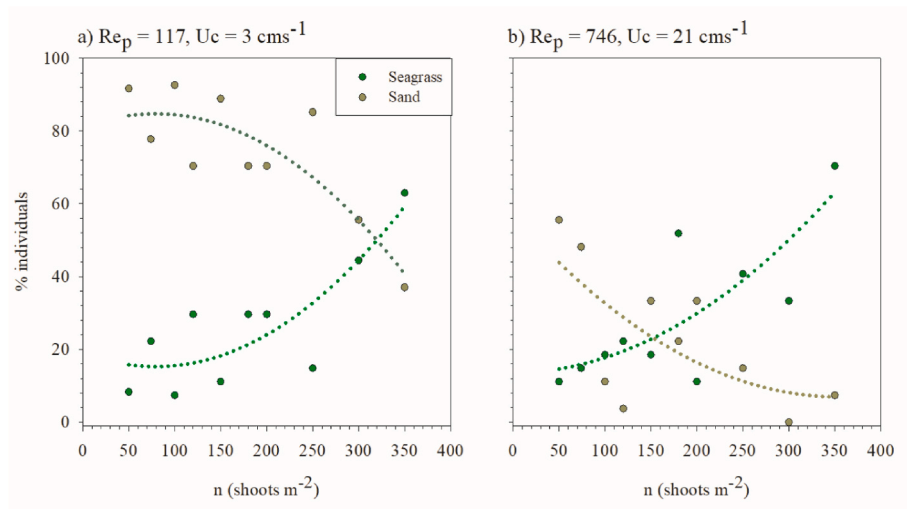


Fig. 3. Substratum selection by shrimp under two flow velocities and ten plant densities. Percentage of shrimp in the sand (brown circles) and in the seagrass (green circles) of a) Reynolds number, $Re_p = 117$ and flow velocity, $U_c = 3 \text{ cm s}^{-1}$; and b) Reynolds number, $Re_p = 746$ and flow velocity, $U_c = 21 \text{ cm s}^{-1}$. Dashed lines have been plotted to aid visualization of the percentage of individuals' tendencies. For those cases where the sum of the percentage of individuals in the seagrass plus that in the sand is below 100%, the percentage of individuals left correspond to those washed out and trapped by the net at the end of the flume. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

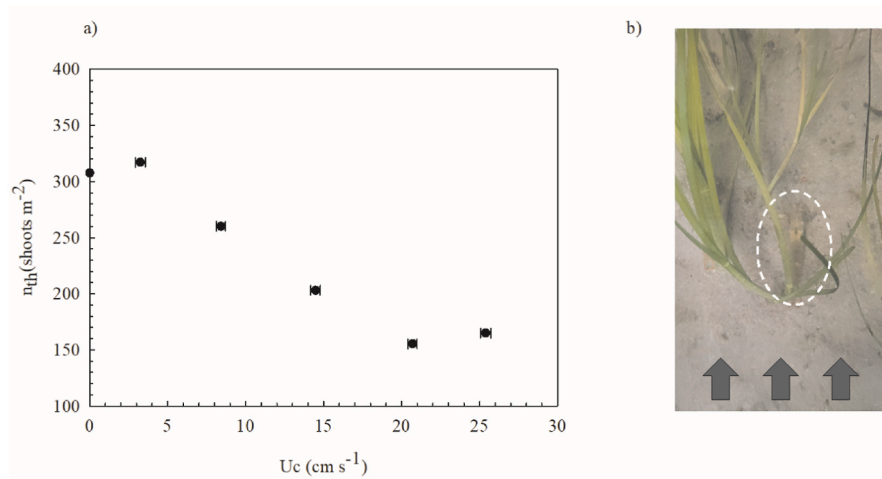


Fig. 4. a) Canopy density threshold (n_{th} , in shoots m^{-2}) versus U_c (in $cm\ s^{-1}$). The canopy density threshold represents the canopy density for what the % individual shrimp in the sand is equal to the % individuals in the seagrass (as shown in Fig. 3). b) *Palaemon adspersus* sheltering behind an eelgrass shoot. Arrows indicate the flow direction and the white lines encircle the location of *P. adspersus*.

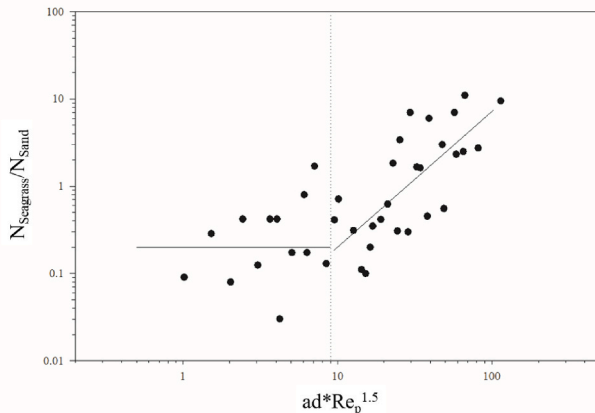


Fig. 5. Non-dimensional model for the ratio of shrimp in the seagrass ($N_{seagrass}$) and the individuals in the sand area (N_{sand}) as $N_{seagrass}/N_{sand}$. Vertical dashed line represents the threshold of $ad*Re_p^{1.5}$. Horizontal solid line at $N_{seagrass}/N_{sand} = 0.22$ represents that for $ad*Re_p^{1.5} < 9$, $N_{seagrass}/N_{sand}$ remained constant. For $ad*Re_p^{1.5} > 9$, a power tendency was found: $N_{seagrass}/N_{sand} = 2.6 \cdot 10^{-3*} (ad^{1.76} * Re^{2.64})$, with $R^2 = 0.57$ and 99% of confidence.

4.1. Effect of flow velocity on shrimp flow tolerance

Shrimp capacity to remain in the area against the current was constant up to a flow velocity of $U_c = 3\ cm\ s^{-1}$, which corresponds to a plant Reynolds number, $Re_p = 117$. For greater velocities ($U_c = 8\ cm\ s^{-1}$), the shrimps were dislodged. The swimming velocity of *Palaemon serratus* was found to be $\sim 4.5\ cm\ s^{-1}$ (Oliveira et al., 2012). Assuming a similar swimming velocity for *P. adspersus*, flow velocities above their swimming velocity can wash individuals out of the system. Thus, their niche was compromised as the individuals were not able to withstand the hydrodynamic conditions in the system. In addition to the mean flow velocity, two hydrodynamical parts can be distinguished in the seagrass leaves, a blade like part which correspond to part of the plant which moves freely with the flow and the stem like part which corresponds to the stiffer part of the leaves (Barcelona et al., 2023). The turbulence produced by stiffer part of the plant can also dislodge the shrimp. A relationship between the plant Reynolds number and the vortex shedding created by the turbulent flow induced by the stem wake was determined. Nepf et al. (1997) found that a vortex shedding regime is produced at $Re = 100$ for rigid cylinders. Other authors established a

range of Reynolds numbers between 60 and 200 to develop vortex shedding (Gerrard, 1978; Kiya et al., 1980). However, since *Z. marina* seagrass plants have flexible leaves, their deflection prevents the penetration of sweep events and produces the ejection of within-turbulence to the upper part of the meadow (Houseago et al., 2022) counteracting the vortex shedding created by the stem and so may act as a protective habitat for shrimp.

4.2. Effect of plant density on shrimp habitat selection

This study has demonstrated that the habitat selection as a response to hydrodynamic conditions of *P. adspersus* in absence of predators depends on the plant density within the seagrass canopies, particularly for low flow velocities ($< 3\ cm\ s^{-1}$). At low velocities, shrimp were located the sand area to the seagrass area, albeit except for seagrass densities above 300 shoots per m^2 . However, for velocities above $3\ cm\ s^{-1}$, shrimp moved from the sand area to the seagrass area, possibly due to the need for protection against the current. As the current velocity increased, the transition from bare sand to seagrass areas occurred at lower canopy densities. This indicates that the structural density of the *Z. marina* canopy played a crucial role in the dislodgment of the shrimp within a patch. Thus, at high canopy densities (above 150 shoots per m^2), shrimp selected seagrass areas to sand areas. Conversely, for the same flow velocity, they selected sandy areas to seagrass areas. Hence, their preference changed according to the canopy density. For low flow velocities, where $Re_p = 117$, the canopy density where this change was observed was 300 shoots m^{-2} , whereas for high current velocities with $Re_p = 746$ it was 150 shoots m^{-2} .

However, the effect of canopy density itself in attracting faunal organisms depends on the faunal species (Arponen and Boström, 2012). Edgar and Robertson (1992) found a decrease in the abundance of mobile fauna bed for sparse patches of seagrass. Another important factor that determines habitat selection according to seagrass density is the life stage and body size of the organism (Shinomiya et al., 2017). Shinomiya et al. (2017) studied the distribution of *Pandalus latirostris* (Hokkai shrimp), which inhabits *Z. marina* and *Zostera caespitosa* seagrass patches. While they found a uniform distribution of juveniles, an increase in adult numbers was observed on small vegetation patches. Juveniles tend to avoid leaving the seagrass patch due to their low ability to escape and the high risk of predation outside the patch, whereas adults tend to patrol bare spaces at night and use small patches for hiding. However, *Pandalus latirostris* is larger than *P. adspersus*; the length of *P. latirostris* can reach up to 12 cm (Shinomiya et al., 2017),

whereas the *P. adspersus* adults used in this study had a body length of $5.99 \text{ cm} \pm 0.95 \text{ cm}$. Therefore, the fact that *P. adspersus* individuals are smaller in size may explain why they prefer dense seagrass areas when the environmental hydrodynamic conditions are not favorable for their development.

4.3. Shrimp habitat selection threshold

The non-dimensional model for the ratio of $N_{\text{seagrass}}/N_{\text{sand}}$ indicated that the ratio between the shrimp individuals found in the seagrass versus those found in the sand remained constant ($=0.22$) for $\text{ad} \cdot \text{Re}^{1.5} < 9$. Low values of $\text{ad} \cdot \text{Re}^{1.5} < 9$ apply to both low seagrass densities and low flow velocities, indicating that the shrimps were able to move freely through both the seagrass and sand habitats under these conditions, with a clear selection for sandy areas over seagrass areas. However, when threatened by hydrodynamic conditions, they moved to seagrass areas where they felt more protected against the current velocity. Thus, as flow velocities increase, shrimp exhibits a clear preference for occupying a vegetated patch. On the other hand, the threshold at $\text{ad} \cdot \text{Re}_p^{1.5} = 9$ means that the minimum plant density required for the *P. adspersus* survival and tolerance to the flow can be compromised under certain hydrodynamic conditions. Therefore, this study has demonstrated that the habitat selection of shrimp not only depends on the structure of the seagrass meadow, but also on the hydrodynamics within the canopy. This observation agrees with Tanner (2003), who demonstrated that passively dispersed seagrass epifauna were affected by the shape and orientation of the seagrass patches under currents. These results support the seasonal variation on abundance of associated benthic communities, Włodarska-Kawalczyk et al. (2014) found a decrease in the abundance of microbenthic fauna during late fall and early spring when the macrophyte vegetation were least developed and the hydrodynamic episodes such as storms are stronger. This aligns with this study where lower plant densities and higher hydrodynamic conditions are disfavored for the associated fauna, such as the shrimps.

4.4. Ecological implications

Palaemon adspersus is predominantly found in vegetated bottoms with eelgrass (Baden and Pihl, 1984), unlike *Palaemon elegans* which is found in both vegetated and unvegetated bottoms (Berglund, 1985). In this study, we observed that *P. adspersus* under laboratory conditions selected unvegetated bottoms at low flow velocities ($< 3 \text{ cm s}^{-1}$) or at densities below 250 shoots m^2 . This behavior may be attributed to the absence of predators in the flume and the resulting fact that the shrimp did not need to seek shelter. However, our results clearly indicate that at high flow velocities, eelgrass plays a crucial role as a hold-fast for *P. adspersus*, preventing it from being transported by the flow. These results suggest that in calm weather, low plant densities do not offer protection to *P. adspersus*, and so it shows no interest in such environments in absence of predators, therefore shrimps can move freely in the surroundings of the seagrass patches. In contrast, during high-energy weather conditions, *P. adspersus* seeks shelter in eelgrass meadows of higher densities as lower densities do not provide adequate protection. These findings are of great significance as disappearing seagrass meadows are becoming less dense under human pressures (Marbà et al., 2005; McCloskey and Unsworth, 2015), thereby rendering the meadows less suitable as shelter for some species. Therefore, it is crucial to consider the impact human activities have on the density of seagrass meadows, and the consequent effects on the organisms that rely on them for shelter.

In addition, the abundance of species of the whole ecosystem may be altered by the dislodgment of *P. adspersus* for higher flows. That is, if individuals of *P. adspersus*, which can act as grazers, decreases the epiphyte community may increase as a result of the decrease in their consumption. (Jiménez-Ramos et al., 2019). This process may imply an overproduction of epiphytes resulting in eutrophic waters that may

finally induce a seagrass loss (Walker and McComb, 1992). Moreover, seagrass densities and hydrodynamic conditions, especially current velocity, influence the levels of dissolved oxygen. Higher current velocities and sparse or non-vegetated meadows imply a more variable oxygen flux (Hume et al., 2011). This can impact on the eutrophication, Schmidt et al. (2017) found a decrease in species richness of mobile fishes and invertebrates under eutrophication conditions.

5. Conclusions

The current study has determined that the distribution of the epifaunal shrimp *P. adspersus* depends on both the structural characteristics of the seagrass *Z. marina* canopies (densities between 50 and $350 \text{ shoots m}^{-2}$) and the current velocity in the system. *P. adspersus* shrimp can tolerate flow velocities up to 3 cm s^{-1} . However, flow velocities above 3 cm s^{-1} caused the dislodgement of shrimp individuals and reduced their tolerance to the flow. This threshold in the current velocity may be close to the maximum velocity tolerated by *P. adspersus* individuals.

Furthermore, while shrimp preferred the sand near the vegetation patch for low flow velocities below 3 cm s^{-1} , for greater flow velocities they moved to the vegetation to seek protection behind plant stems. The density of the canopy shrimp required for sheltering, decreased as the current velocity increased. However, current velocities above 21 cm s^{-1} produced shrimp dislodgement regardless of the canopy density, meaning that they could not withstand such flow velocities.

CRedit authorship contribution statement

Aina Barcelona: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Teresa Serra:** Writing – review & editing, Methodology, Investigation, Funding acquisition. **Jordi Colomer:** Writing – review & editing, Investigation. **Eduardo Infantes:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Teresa Serra reports financial support was provided by Spain Ministry of Science and Innovation. Eduardo Infantes reports financial support was provided by Swedish Research Council. Aina Barcelona reports financial support was provided by Government of Catalonia Agency for Administration of University and Research Grants. Aina Barcelona reports financial support was provided by University of Girona. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

This research was funded the Swedish Research Council (FORMAS) Dnr:2019–01192 and by the Ministry of Science and Innovation through the Grant Number PID 2021-1238600B-100. Aina Barcelona was funded by the pre-doctoral grant 2020 FI SDUR 00043 from the “Generalitat de Catalunya” and by the mobility grant MOB2021 from the University of Girona. Thanks to Susanne Pihl Baden for her comments on the manuscript.

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