Conspecific interactions as drivers of activity and mortality in a prominent sandy beach amphipod

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ABSTRACT: In harsh habitats, community structure is believed to be controlled primarily by physical factors while biological interactions are considered to be of little relevance. However, evidence of avoidance behaviors between the life stages of some species suggests otherwise. A long-standing hypothesis from sandy beaches suggests that avoidance between adults and juveniles dictates some aspects of their ecology, but this has not been explicitly tested. Here, we used a field survey to document the diel activity of adults and juveniles of the talitrid amphipod *Americorchestia longicornis*. We then used laboratory experiments to assess the influence of adults on the activity of juveniles and to measure juvenile mortality rates in the presence and absence of adults, with and without food. In the field, we found clear differences in the diel activity of adults and juveniles. Adults were active throughout the night but not in daylight, whereas juvenile activity peaked at dusk and dawn. Similar patterns of activity were recorded in laboratory tanks that included both stages. However, when adults were excluded, juveniles shifted towards night activity, suggesting that the pattern of activity observed in the field is a mechanism to avoid larger conspecifics. In separate trials, predation by adults was a significant driver of juvenile mortality, regardless of initial juvenile density and food availability. Altogether, these results suggest that segregation between amphipod life stages is driven by the avoidance of direct interactions, specifically, cannibalism. This likely influences the role played by these amphipods, both as prey and as processors of stranded seaweeds.

KEY WORDS: Temporal avoidance · Sandy beach amphipods · Cannibalism · Atlantic Canada

1. INTRODUCTION

Much of the ecological theory surrounding biological interactions comes from well-known terrestrial and marine ecosystems (see seminal articles by Connell 1978, Schoener 1989, Gurevitch et al. 1992). In comparison, the study of these interactions in transitional semi-terrestrial ecosystems has lagged behind (Tewfik et al. 2016), even though these systems may offer considerable insight into their importance. One

relevant transitional habitat is the sandy beach ecosystem, often perceived as a harsh, physically controlled setting (Schlacher et al. 2015, McLachlan & Defeo 2018) in which the importance of biological interactions is considered negligible in comparison to that of physical factors (Jaramillo et al. 1993). However, a few studies have inferred the occurrence of biological interactions from the examination of field patterns and laboratory manipulations (Croker & Hatfield 1980, Jaramillo et al. 2003, Dugan et al.

2004), the quantification of epibenthic predator effects (Van Tomme et al. 2014), the modelling of interactions among beach consumers (Tewfik et al. 2016) and from the incidence of cannibalism (Kennedy et al. 2000, Duarte et al. 2010, Robinson & Peters 2018). Although limited in number, these studies raise the general question of whether biological interactions can be important in a system at the harsh end of the physical spectrum.

Talitrid amphipods are common in sandy beaches worldwide (Dahl 1952, McLachlan et al. 1981, Schlacher et al. 2008) and are often abundant in cold regions, where sandy beaches have relatively low diversity and trophic complexity (McLachlan & Dorvlo 2005, MacMillan et al. 2017). Amphipods also constitute a central link between upper trophic consumers, such as shorebirds, and the input of primary producers represented by stranded seaweeds (McLachlan et al. 1981, Dugan et al. 2003, Lastra et al. 2008). The wrack subsidy comprising most of their food is not consistently available throughout tides and seasons (Rodil et al. 2015), so sandy beach amphipods are often subjected to variable periods of food shortage. When the input of seaweeds becomes limited, intraguild interactions (defined here as those occurring among species and life stages using a common resource) are expected to operate in this (Duarte et al. 2010) as well as in other coastal habitats (e.g. Armsby & Tisch 2006, Amaral et al. 2009, LeGault & Hunt 2016). For juvenile stages of amphipods in particular, the shortage of food and the incidence of cannibalism may represent an important source of natural mortality (Duarte et al. 2010, Robinson & Peters 2018). Despite this, it remains unclear if or how juvenile amphipods respond to the potential risk of conspecific interactions.

Sandy beach amphipod populations grow rapidly, and juvenile stages often outnumber adults during the warm seasons (Yu & Suh 2006, Pavesi & De Matthaeis 2009). In these circumstances, intraspecific interactions including cannibalism are more likely to occur and interact with shortages of stranded seaweeds. To reduce potential mortality, juvenile amphipods are expected to avoid conspecifics by changing some aspect of their feeding behavior, timing, habitat or diet (see Fallaci et al. 1999, Kennedy et al. 2000, Jaramillo et al. 2003, Scapini & Dugan 2008). In fact, a long-standing hypothesis in sandy beach ecology suggests that temporal or spatial segregation between adults and juveniles helps to avoid negative interactions (e.g. Fallaci et al. 1999, Kennedy et al. 2000, Jaramillo et al. 2003). Interestingly, this hypothesis has not been explicitly (experi-

mentally) tested, and little is known about this process in sandy beach species from cold regions, such as Atlantic Canada. In these regions, a strong seasonality exposes sandy beaches to ice and snow during the winter (Lynn et al. 2023), further limiting the growth of amphipod populations to the warmest months of the year (Dionne & Laverdiere 1972, Knight & Dalrymple 1976, Owens 1976).

The talitrid amphipod *Americorchestia longicornis* is an abundant species along sandy beaches of Prince Edward Island (PEI) in Atlantic Canada (MacMillan et al. 2016, 2017) and other temperate shorelines (e.g. Dashtgard & Gingras 2005). Published evidence (Ramus & Forward 2012), laboratory experiments (Lynn et al. 2021) and repeated field observations have shown that adults of this species are active during the night but not during daylight. However, the activity of juveniles has not been examined until now. Nocturnal patterns have been described in other talitrid amphipods elsewhere (Scapini et al. 1992, Kennedy et al. 2000), showing some differences between adult and juvenile distribution and timing, which may represent a potential avoidance mechanism between these stages. In this study, we used a field survey to document the diel patterns of adult and juvenile stages of *A. longicornis* and then laboratory experiments to examine the potential effects of adults on the activity and survival of juvenile amphipods. Our working hypothesis was that adults alter juvenile diel patterns, a response that helps the latter to avoid direct negative interactions. Without disregarding several other potential factors (e.g. food preferences, interactions with upper-level predators or competitors and a variety of physical factors), if our working hypothesis is correct, juvenile mortality rates could be causally linked to cannibalism, regardless of food availability.

2. MATERIALS AND METHODS

2.1. Study area and field survey

This study used the talitrid amphipod *Americorchestia longicornis* (hereafter amphipod) as a model species, given its abundance and widespread distribution along sandy beaches of the north shore of PEI (Fig. 1) and the Atlantic Canada region (MacMillan et al. 2017). Populations of this amphipod have been monitored annually (K. D. Lynn unpubl. data), and repeated observations obtained during those surveys and during experimental manipulations (Lynn et al. 2021) suggest that it is primarily a nocturnal species
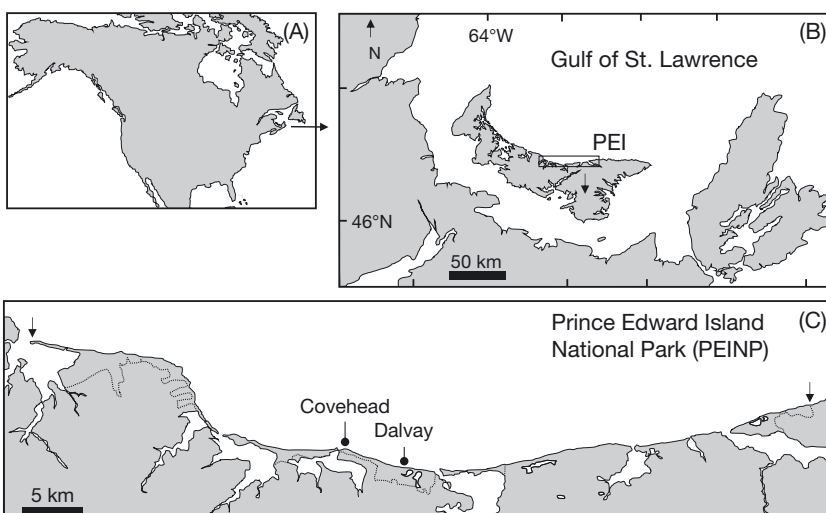
Fig. 1. Maps outlining (A,B) Prince Edward Island in the Atlantic Canada region and (C) the 2 sandy beaches used for amphipod collection and field surveys (Dalvay and Covehead). Arrows and dotted lines in (C) illustrate the boundaries of the Prince Edward Island National Park

feeding on various species of stranded macrophytes (MacMillan & Quijón 2012, Quintanilla-Ahumada et al. 2023). The field survey described below was conducted at Dalvay Beach (46° 25′ 01″ N, 64° 55′ 47″ W; Fig. 1); the collection of specimens for the 2 laboratory experiments was done at that site (Dalvay) and the nearby Covehead Beach (46° 25′ 51″ N, 64° 51′ 28″ W; Fig. 1), taking advantage of the regular collection of amphipods that occurs at those 2 sites as part of the annual monitoring mentioned above. Both sandy beaches are similar in main physical features (mid- to coarse grain sizes, similar slopes and widths), and are located within PEI National Park about 5 km apart from each other. No prominent features (e.g. headlands or river mouths) separate these 2 sites, and both are representative of the narrow sandy beach microtidal systems that are exposed to the waters of the southern Gulf of St. Lawrence and are affected by fairly similar levels of seasonal erosion (MacMillan et al. 2017). Following McLachlan et al. (2018)′s classification, these and other sites in the area can be categorized as 'reflective-type' sandy beaches dominated by 'wave-generated processes'. Stranded seaweed biomass (wrack) is modest (~12 small patches of seaweed per m^2) in comparison to sandy beaches located in the western part of PEI (MacMillan & Quijón 2012).

A field survey was conducted in August 2022 at Dalvay Beach to document the distribution and daily activity (24 h) of adult and juvenile amphipods. Traps consisting of large plastic cups (11 cm diameter, 14 cm height), half-filled with 250 ml of seawater, were buried into the sand with their top edges flush with the surface of the sand. Five of these traps (A−E) were deployed along a transect across the intertidal area: the first trap (A) was placed at the drift line

(high tide), where the burrowing area of the amphipods is normally visible, and the next 4 traps were placed every 3 m downwards towards the low tide level (up to E). Three transects with 5 traps each were established and separated ~50 m apart (i.e. n = 3 replicates per level; 15 traps in total). Starting at noon (12:00 h), traps and transects were open and left undisturbed for 2 h intervals. At the end of that period, traps were carefully retrieved and replaced with new traps, and the procedure was repeated another 11 times until completing 24 h. During the night hours, collection was done with the assistance of infrared lights to avoid disrupting amphipod behavior. Despite tidal variations, the transects consistently covered most of the intertidal area and all the visible areas where amphipods were buried during daylight. At each sampling period, the contents of the traps retrieved (amphipods) were carefully poured into plastic containers, labelled and preserved in 70% ethanol until counting and identification in the laboratory. Identification was conducted using suitable keys for the species of the region (Bousfield 1973, Bromley & Bleakney 1985), and individual amphipods were also categorized as adult males or females (15−25 mm body length; see Bousfield 1973) or juveniles (≤5 mm in body length) based on morphology and size differences. Amphipods in the 5−15 mm body length range were spread across various tidal levels depending on the time.

2.2. Adult and juvenile activity in the laboratory

Additional amphipods were collected from Dalvay and Covehead beaches on a weekly basis during the summer months using multiple 20 cm diameter pitfall

traps deployed overnight at the high tide level. These larger traps were half-filled with ~1 l of seawater and buried in the sand as described above. Amphipods collected were transported to the laboratory in large plastic containers with clean damp sand, previously obtained from the same field sites and sieved through 1 mm mesh. Adult and juvenile amphipods were separated and held for 24 h activity trials which were conducted in 2 rectangular acrylic tanks (40 × 26 × 20 cm high) filled with a 5 cm layer of clean sand. These tanks were placed within a large environmental chamber (Controlled Environments Limited) and kept under conditions similar to those recorded at the field sites: 15°C, 90% relative humidity with a 12 h light:12 h dark photoperiod (Lynn et al. 2021). The photoperiod was similar to the one observed in the field sites, and the timing of lights on and off in the laboratory was consistent with the daylight–night conditions in the field sites. One of the tanks held 20 juvenile amphipods (without adults), whereas the second tank held 20 juveniles and 10 adults (shared tank). Both densities were well within the range of densities normally observed in the field (based on past surveys) and used in prior laboratory experiments (MacMillan & Quijón 2012, Lynn et al. 2021). At the top of the sand, standard-size (2.5 g wet weight) fresh blades of *Fucus serratus* (hereafter rockweed), were used as food for the amphipods. This rockweed is one of the most common species of macrophytes found stranded in the study area (MacMillan & Quijón 2012, Quintanilla-Ahumada et al. 2023). Fresh rockweeds were collected by hand from the mid-low intertidal of a rocky shore near the laboratory (Keppoch Beach, Stratford, PEI; 46° 12′ 0″ N, 63° 6′ 55″ W). Fresh rockweed was kept at low temperature in seawater before use in the laboratory trials. Amphipods and rockweeds were held in the conditions described above for 24 h of acclimation before the start of the experiments. Although our system accounted for photoperiod, temperature, food availability and humidity, it did not account for tide variation.

At the beginning of each experiment, sand was moistened with seawater from the study area and the rockweed was replaced. Four 24 h separate (independent) experiments were conducted on non-consecutive days during August, alternating the position of tanks with juveniles and juveniles+adults to avoid potential biases associated with their positions within the chamber. To record amphipod activity in each of these trials, 2 GoPro Hero4 cameras with infrared filters removed were mounted above the tanks and captured images using a ~1 lux (equivalent to ~0.0079 W m^{-2}) infrared light (Cohen et al. 2010). The cameras were programmed to take 1 image min^{-1} (i.e. 1440 photographs over a 24 h experiment) at 12 megapixels with a wide-angle view and low-light mode enabled. Amphipod activity was quantified by counting the number of animals visible in each image (an amphipod above the sand was considered to be active). Juveniles and adults were readily distinguished in the photographs by their size range. New juvenile and adult amphipods were used for each of these 24 h experiments. No incidence of amphipod mortality or molting was recorded in any of the trials.

2.3. Juvenile mortality in the presence and absence of adults and food

Additional amphipods collected with the methodology described above were used to measure juvenile mortality rates resulting from potential interactions with adult amphipods. Either 5 or 10 juvenile amphipods were placed within 16 × 23 × 5 cm high plastic containers which had 1 mm mesh lids on top to allow for air exchange and to maintain high humidity levels. These 2 initial densities (5 or 10 amphipods per container) resembled low and medium densities recorded near or underneath stranded seaweed patches (wrack) in Dalvay and other sandy beaches on the PEI north shore (~10–15 amphipods per sample; MacMillan & Quijón 2012, MacMillan et al. 2017). The containers were kept undisturbed for 24 h of acclimation and then were randomly assigned to one of the 4 treatments summarized in Table 1: presence or absence of adults, in the presence or absence of food (a ~2.5 g wet weight

Table 1. Experimental design to test the influence of food availability (*Fucus serratus*) and cannibalism by adults on mortality rates of juvenile *Americorchestia longicornis* at 2 initial densities

Initial density (no. of juveniles per container)	Food availability	Adult presence	Replication level (no. of trials)
5	+	−	20
	−	−	20
	+	+	16
	−	+	13
10	+	−	15
	−	−	20
	+	+	10
	−	+	10

piece of rockweed). To measure the influence of potential adult–juvenile interactions, a standard number of adult amphipods (5) was added to the corresponding treatments. Replication levels for each treatment at each juvenile initial density was ≥10 in all cases (see Table 1).

All containers (and their corresponding treatments) were randomly placed and maintained within larger (60 × 85 × 12 cm high) plastic trays, with a 3 cm layer of clean damp sand sprayed daily with seawater from the study area to maintain a high level of humidity (~90%; see Duarte et al. 2014). These trials ran for 7 d, maintaining a natural 12 h light:12 h dark cycle and a room temperature of ~15–20°C. The trials were monitored every morning to ensure sand and food conditions remained appropriate and to check the incidence of cannibalism, although dead juvenile amphipods were not removed or replaced. At the end of the trials, mortality rates were estimated from the number of surviving juveniles per container and treatment.

2.4. Data analyses

The field survey was used primarily to document the number of active adult and juvenile amphipods across intertidal levels and during the 24 h period (number of amphipods collected corresponded to active amphipods over the surface of the beach). Data was plotted for visual comparisons among tidal levels (A–E) and time of the daily cycle (24 h). Given that several samples at the E level were lost due to rising tides, we chose to consider only levels A–D, as these offered consistent data over the 24 h period. Although feasibility restricted our survey to 24 h, we acknowledge that a longer period of monitoring (48 h or longer) is often needed to comprehensively document diel patterns.

Laboratory experiments measuring juvenile and adult activity data were analyzed using generalized additive models for location, scale and shape (GAMLSS; Stasinopoulos & Rigby 2007) available in the 'gamlss' package for R (R Core Team 2017). The proportion of activity (i.e. the proportion of active animals per minute interval) was modelled using a binomial error distribution and a logit link. For the 3 comparisons attempted — (1) juveniles alone vs. adults, (2) juveniles vs. adults when these share a tank, and (3) juveniles alone vs. juveniles in tanks shared with adults — the additive and interactive effects between treatment and time of day (minutes) were included. To adjust the circadian rhythm, the time was fitted non-linearly using P-splines (Eilers et al. 2015). In models in which we included a non-linear interaction between time and treatment, we used a penalized varying coefficient. This function ('pvc' in the 'gamlss' package) allows fitting an interaction where the linear coefficient of an explanatory variable ×1 (i.e. time) is changing smoothly according to another categorical explanatory variable ×2 (i.e. treatment). For model selection, the information-theoretic model comparison and null-hypothesis testing were used (Stephens et al. 2005). Specifically, Akaike's information criterion (AIC; Akaike 1974) and the likelihood ratio test (LRT) were used. In addition, for all models, a pseudo-R^2 was calculated (Nagelkerke 1991). Figures of activity were produced using the 'ggplot2' package (Wickham 2009) for R.

Laboratory experiments measuring juvenile amphipod mortality rates were analyzed separately for each initial density (5 and 10 juveniles per container) using 2-way ANOVAs. These analyses included presence of adults and availability of food and their potential interaction as explanatory variables (see Armsby & Tisch 2006 for a comparison). Due to violation of ANOVA assumptions in the first data set (initial density of 5 juvenile amphipods), the 2-way ANOVA was run on ranked data. All these analyses were conducted in Minitab 21, using a critical significance value (α) of 0.05.

3. RESULTS

3.1. Field survey of adult and juveniles

Adult amphipods showed a clear diel rhythm, with a large proportion (96%) of adult locomotor activity (i.e. number of amphipods collected in the traps) taking place during night hours (Figs. 2 & 3). Regarding variation across intertidal levels, adults were better represented at the traps located high in the intertidal (A and B levels; Fig. 2), whereas juveniles were found in higher numbers at the low part of the intertidal (68% of juveniles were collected at levels C and D; Fig. 2). In relation to temporal variation, most of the adult activity took place between 21:00 and 05:00 h, with highest average values at 23:00 and 01:00 h, and with very little adult activity (~4%) during the daylight hours (09:00–19:00 h; Fig. 3). Juveniles exhibited at least some activity during most of the 24 h period (excluding 15:00 h; Fig. 3), with a main peak of activity at dawn (06:00–07:00 h) and a second, less prominent peak at dusk (21:00 h) (Fig. 3).
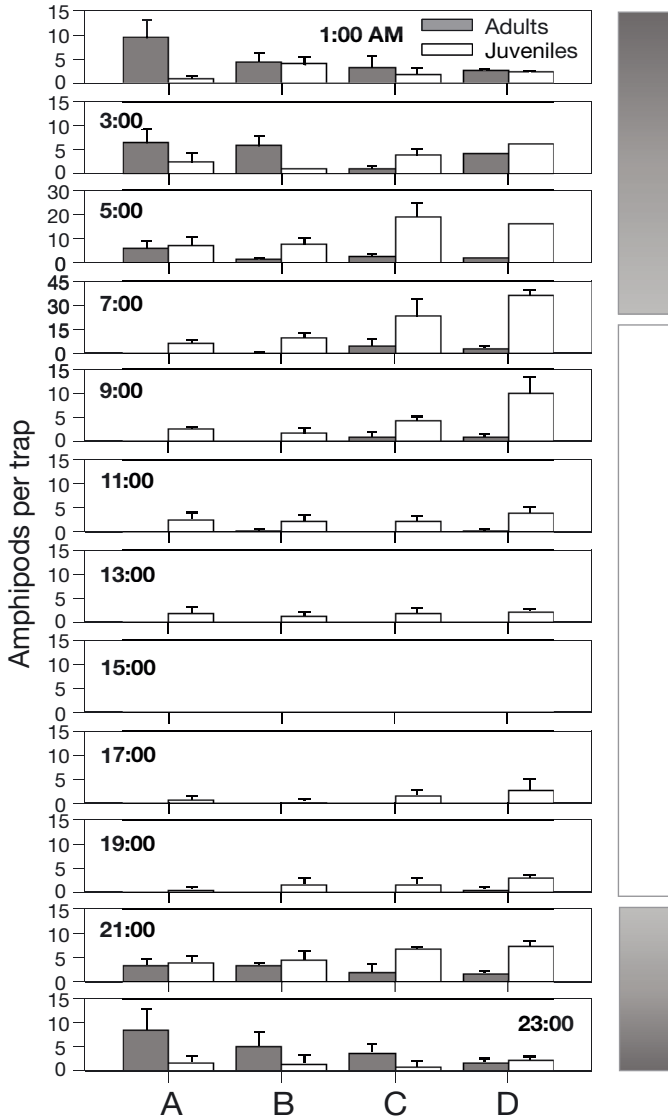
Fig. 2. Mean (+SE) number of amphipods *Americorchestia longicornis* collected in experimental traps placed in the intertidal zone of Dalvay Beach. Values correspond to amounts collected at 2 h intervals at tidal levels A–D (high tide to mid-low tide, respectively)

3.2. Adult and juvenile activity in the laboratory

When adults and juveniles were held together (Fig. 4A), the activity of adults showed a clear circadian pattern, where activity was high during night hours (~19:30–08:00 h; a proportion ≥0.2, or ≥20% of the activity) and low during daylight hours (reaching up to only ~0.1 on average). The juveniles within these shared tanks (Fig. 4A) showed peaks of activity (0.15–0.17) at dusk (~20:00 h) and dawn (~07:30 h), but activity remained low during most of the night (21:00–06:30 h; ≤0.05 of activity) and daylight hours (~0.03–0.08; Fig. 4A). However, in tanks where juvenile amphipods were alone (i.e. without adults), they exhibited a circadian rhythm similar to adults, as described above (Fig. 4B): juvenile activity was high (≥0.2 individuals active) during the night hours (i.e. ~19:30 to ~06:30 h) and very low during daylight (~08:00–19:00 h; ≤0.05 proportional activity). For direct comparison, the patterns displayed by juveniles when placed alone (gray line) and when sharing the tank with adults (yellow line) are presented in Fig. 4C.

The most parsimonious model to explain the probability of juvenile and adult amphipod activity included additive and interactive effects between hour of the day and treatment (Table 2). The assessment of whether patterns of activity were different was based on LRTs for each of the comparisons explored (1–3). All non-linear interactions were significant (p < 0.0001) and models explained (1) 54.1% of the variation of juveniles alone versus adults (LRT with 20.2 df = 1264), (2) 64.4% of the variation of juveniles versus adults when sharing a tank (LRT with 24 df = 4523) and (3) 77.7% of the variation in the comparison juveniles alone versus juveniles together with adults (LRT with 29 df = 7879.5) (Table 2).
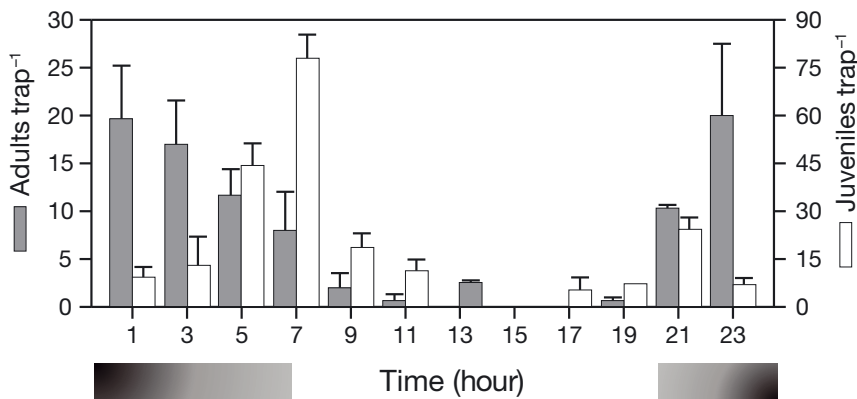

Fig. 3. Mean (+SE) number of amphipods *Americorchestia longicornis* collected in traps placed at intertidal transects in Dalvay Beach. Plots correspond to amphipods collected at 2 h intervals (tidal levels A–D combined) over 24 h
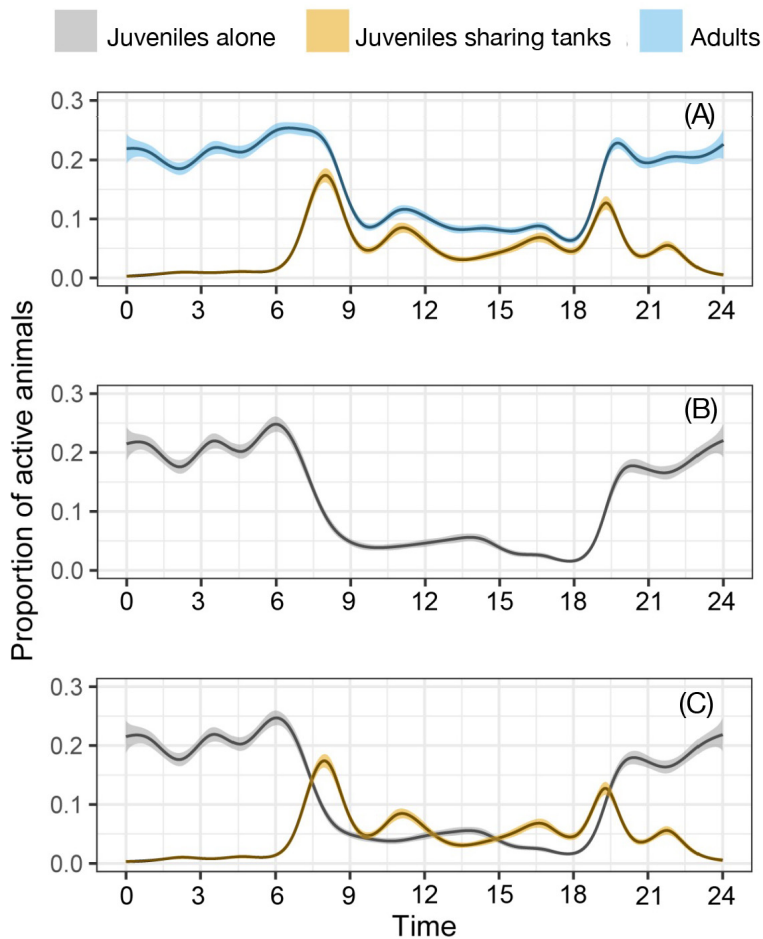
Fig. 4. Mean (± 95% confidence interval) proportion of active amphipods *Americorchestia longicornis* over a 24 h period. (A) Juveniles and adult stages held together in the tanks. (B) Juveniles held without adults in the tanks. (C) Juveniles held alone versus juveniles sharing tanks with adults

3.3. Juvenile mortality in presence and absence of adults and food

At low initial densities (5 juveniles per container), juvenile mortality rates were significantly higher in the presence of adults compared to controls, i.e. those without adults (2-way ANOVA, $F_{1,62} = 33.084$, p < 0.001; Table 3, Fig. 5A). However, the presence of food did not significantly affect mortality rates (2-way ANOVA, $F_{1,62} = 0.646$, p = 0.404). In the presence of adults, juvenile mortality rates were at least 3 times higher than in the absence of adults, regardless of food availability (Fig. 5A, Table 3). No significant interaction was found between these factors (2-way ANOVA, $F_{1,62} = 2.141$, p = 0.147). At high initial densities (10 juveniles per container), juvenile mortality levels were consistently higher, and both food availability and cannibalism significantly affected mortality rates (2-way ANOVA, $F_{1,47} = 8.751$, p = 0.005 and $F_{1,47} = 36.728$, p < 0.001, respectively; Table 3). However, no significant interaction between factors was detected (2-way ANOVA, $F_{1,47} = 0.505$, p = 0.481). Mean juvenile mortality rates were higher in the absence of food and in the presence of adult amphipods (Fig. 5B, Table 3). Remains of juvenile amphipods were observed in the tanks containing adult amphipods but not in those lacking adults. Although we did not

Table 2. Model selection for the proportion of active amphipods *Americorchestia longicornis* in response to additive and interactive (non-linear) effects of treatment and time of the experiment (minutes). Models (GAMLSS with binomial error distribution) are sorted by increasing Akaike's information criterion (AIC) values. ΔAIC: AIC differences between i^{th} model and the best model; R^2: generalized (pseudo) R^2 (in percentage); pb: P-splines; pvc: penalized verifying coefficients

Condition (comparisons)	Model	Formula	df	AIC	ΔAIC	R^2
(1) Juveniles alone vs. adults	M0	Treatment + pb(Time) + pvc(Time × Treatment)	42	61175	–	54.1
	M1	Treatment + pb(Time)	22	62399	1224	50.6
	M2	pb(Time)	21	63258	2083	48.1
	M3	Treatment	2	73762	12587	4.5
(2) Juveniles vs. adults (both sharing tanks)	M4	Treatment + pb(Time) + pvc(Time × Treatment)	46	55884	–	64.4
	M5	Treatment + pb(Time)	22	60359	4475	53.8
	M6	Treatment	2	64158	8274	42.3
	M7	pb(Time)	21	69692	13808	20.6
(3) Juveniles alone vs. juveniles (with adults)	M8	Treatment + pb(Time) + pvc(Time × Treatment)	50	32576	–	77.7
	M9	Treatment + pb(Time)	21	40398	7822	55.7
	M10	Treatment	2	44808	12231	33.7
	M11	pb(Time)	20	45054	12478	34.9

quantify these remains, they were more abundant in the tanks with initial densities of 10 juvenile amphipods.

Table 3. Summary of 2-way ANOVAs assessing the influence of food availability, cannibalism and their interaction on the mortality rates of juvenile *Americorchestia longicornis* at 2 initial densities. SV: Source of variation; Adj. MS: Adjusted mean squares. Significant p-values (p < 0.05) are in **bold**

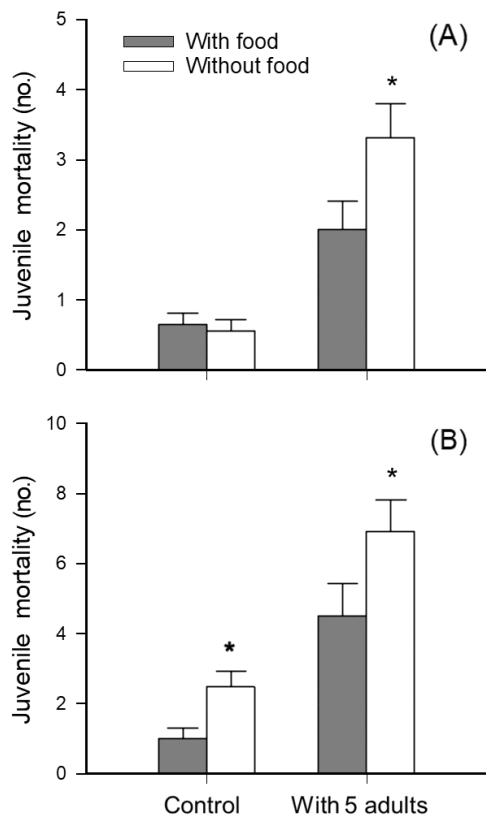| Initial density (no. of juveniles)	SV	df	Adj. MS	p
5	Food (F)	1	160.2	0.404
	Cannibalism (C)	1	7563.5	**<0.001**
	F × C	1	490.1	0.147
	Error	62	227.0	
10	F	1	45.364	**0.005**
	C	1	190.387	**<0.001**
	F × C	1	2.616	0.481
	Error	47	5.184	

Fig. 5. Mean (+SE) juvenile amphipod *Americorchestia longicornis* mortality rates after 7 d trials using initial densities of (A) 5 and (B) 10 juveniles. Asterisks denote significant differences (p < 0.05) between food treatments. Asterisks are not presented for the 'presence of adults' treatment, but presence–absence differences were significant in both analyses

4. DISCUSSION

Strong species interactions are often deemed of little relevance in communities of low diversity or in those associated with the harsh end of the physical spectrum (Bennett et al. 2015, Schlacher et al. 2015, McLachlan & Defeo 2018). However, these characteristics do not necessarily prevent strong intraspecific interactions (see Pereira et al. 2017), with possible implications for community structure (Dugan et al. 2004). Our examination of amphipods in the field identified strong differences in the timing of the activity of adults and juveniles, and a further examination in the laboratory mirrored the patterns observed in the field. This was not unexpected, considering the plasticity that different life stages of amphipods exhibit in response to a myriad of physical and biological factors (see Brown 1996, Scapini 2014). Interestingly, though, when adults were artificially excluded from the experimental tanks, we detected a striking shift in the activity of juveniles toward the night hours, the time slot that, until now, was observed in adults only. These results provide strong support for our working hypothesis and indicate that adults do alter juvenile activity patterns. Furthermore, when assessing the potential influence of adults on juveniles, we found that when adults were present, remains of juvenile amphipods were readily found and a significant increase (3×) in juvenile mortality was quantified, regardless of food availability. We link that outcome to conspecific predation (cannibalism). Given that we controlled for most other physical and biological factors, we argue that the patterns of juvenile avoidance of adults observed in the field and in shared tanks in the laboratory are a mechanism to minimize cannibalism.

4.1. Segregation in the field

Spatial and temporal segregation as a mechanism to avoid the harm of negative interactions between species or life stages has been proposed before in marine soft-bottoms (e.g. Peterson & Andre 1980) and in sandy beaches in particular (Croker & Hatfield 1980, Jaramillo et al. 2003, Dugan et al. 2004). Some studies have explained segregation between species and stages as a response to abiotic factors, including desiccation and heat stress (e.g. Scapini et al. 1992, Poulin & Latham 2002). According to Morritt (1987), juvenile amphipods are more susceptible to desiccation than adults due to the faster rate of evaporative water loss they endure. This may partially

explain one aspect of our results: the spatial distribution of juveniles when aggregating in large numbers towards low tide levels. Similarly, Scapini et al. (1992) found that displaced juveniles of a different talitrid (the amphipod *Talitrus saltator*) were often unable to return to a wet zone of the beach over relatively long distances, a capacity that adults do have. While those physiological constraints cannot be ignored, they do not necessarily explain the decline in juvenile activity when adult activity peaked, i.e. during the night hours. The nocturnal pattern of activity in adult amphipods has already been reported several times for this (*Americorchestia longicornis*; Lynn et al. 2021) and other sandy beach species elsewhere (e.g. Luarte et al. 2016, Duarte et al. 2023).

An alternative explanation for spatial and temporal segregation is the role of interactions among species or, in the case studied here, between life stages of the same species. We argue that these constitute a more plausible explanation than abiotic factors for the differences observed among tide levels and, in particular, for the differences observed between diel patterns. Kennedy et al. (2000), working with another talitrid species in South America (the amphipod *Orchestoidea tuberculata*), reached a similar conclusion. Those authors described different locomotor activity rhythms in adult and juvenile stages of that species and attributed the difference to avoidance behaviors aimed at preventing negative interactions. The same authors found peaks of juvenile activity at hours following the sunset (Kennedy et al. 2000), a result also obtained by Jaramillo et al. (2003) and in the present study.

4.2. Temporal segregation in the laboratory

Until now, conclusions regarding the mechanisms of segregation (the timing of locomotor and feeding activity) have been inferences from field data rather than the outcome of experiments. Our laboratory mesocosm results showed that juveniles display significantly different diel patterns of activity depending on the presence or absence of adult conspecifics. Avoiding predation by conspecifics is a plausible explanation for such a behavioral change, even though there may be other interactions operating simultaneously (Fallaci et al. 1999, Jaramillo et al. 2003, Beermann et al. 2018). Prior studies conducted on sandy beaches in Europe, North America and South America have suggested or demonstrated interference competition (Defeo et al. 1997, Dugan et

al. 2004) or 'damaging encounter' competition (Van Tomme et al. 2012) as possible causes of spatial segregation. These cannot be disregarded, even though we are confident (as the results discussed below show) that direct predation among conspecifics (cannibalism) is a clear driver of juvenile mortality and the main cause behind the striking change in behavior reported here.

When adults and juveniles were held together in tanks, adult activity remained nocturnal, whereas juvenile activity was lower and peaked only at dusk and dawn. This mirrors what has been observed in the field for other sandy beach amphipods (e.g. Kennedy et al. 2000, Jaramillo et al. 2003, Luarte et al. 2016) and related sandy beach species such as oniscoid isopods (*Tylus spinulosus*; Duarte et al. 2019) and even insects (Duarte et al. 2023). The 'release' from adults that juvenile *A. longicornis* experienced in our laboratory trials resulted in a remarkable shift of their activity towards the night hours (see the side-by-side comparison in Fig. 4C). Juvenile amphipods must forage extensively to fulfill the high nutrient requirements imposed by growth (Scapini et al. 1992), so we can speculate that they would naturally achieve an optimal pattern of foraging at night. However, in nature, they must weigh the risk of cannibalism as greater than the benefits they receive from seeking and gathering food, and this likely constrains their time of maximal activity. If this is the case, deviating from an optimal feeding pattern by temporarily or spatially avoiding adults seems a plausible explanation. Juvenile amphipods rely primarily on visual detection (Miranda 2020), although chemical cues and physical contact may also alert them to the presence of adults (Scapini et al. 1989). Such differences represent an interesting venue of research for further studies on interactions. Regardless, potential segregation between juvenile and adult populations across (tide-related) or along sandy beaches (potentially related to grain size or other physical features) is also plausible in these systems (see Defeo & McLachlan 2005 for analyses at multiple spatial scales). The examination of those patterns is well beyond the scope of this study but is a venue for further studies in this and other sandy beaches, in this region and elsewhere.

4.3. Direct interactions as a likely cause of segregation

Interactions among conspecifics, where larger individuals have the advantage of size and are often

superior competitors and consumers, are common among crustaceans (Van Olst et al. 1975, Moksnes 2004, Gehrels et al. 2016, Tummon Flynn et al. 2020). Cannibalism in particular can be a major structuring force in crustacean populations and it is known to operate in the life histories of several talitrid amphipods (Luppi et al. 2001, Christie & Kfvelin 2004, Duarte et al. 2010). Yet this is the first study to document adult *A. longicornis* causing direct mortality in juvenile conspecifics. Until now, this species had been described as an herbivore across its distributional range, with a preference for stranded fucoid algae in this study area (MacMillan & Quijón 2012, Quintanilla-Ahumada et al. 2023) and blue-green algae, bacteria and diatoms in other coastal regions (Hargrave 1970, Brenner et al. 1976). Our results suggest that the consumption of conspecifics should not be ignored among the spectrum of food choices available to this species. Moreover, strong effects of cannibalism were measured at 2 naturally occurring densities in the presence and absence of *Fucus serratus*, a main food source for this species (MacMillan & Quijón 2012). The increase in density associated with the addition of 5 adults in the tanks with juveniles may be perceived as a potential bias (assuming density-dependent effects linked with food availability). However, repeated field and laboratory observations (MacMillan & Quijón 2012, Lynn et al. 2021) indicate that densities much higher than those used here have had little influence on the incidence of mortality. In the field, a combination of physical factors (e.g. Defeo & McLachlan 2005), seaweed availability (e.g. MacMillan et al. 2016), interactions among species (e.g. Croker & Hatfield 1980) and with upper-level predators (e.g. Dugan et al. 2003) can easily obscure the potential role of conspecific interactions. However, the striking changes detected in the laboratory when adults were either present or absent, and the finding of juvenile remains in tanks containing adults, can be interpreted as strong evidence that cannibalism was, in fact, the main cause behind the rise in juvenile mortality rates quantified here.

The strong influence of cannibalism in cold regions such as Atlantic Canada is likely accentuated by the short warm season (Lynn et al. 2023) in which the rapid growth of amphipod populations occurs (Dionne & Laverdiere 1972, Pavesi & De Matthaeis 2009). During this period, the supply of seaweed wrack varies widely depending on weather and tidal cycles (e.g. Kim 1992, Bustamante et al. 1995, Polis & Hurd 1996, Schlacher et al. 2008), a scenario that is likely to favor adult–juvenile interactions, as demonstrated by treatments in which juvenile mortality was significantly higher in the presence than in the absence of adults. Similar conclusions were reported for *O. tuberculata*, for which juvenile mortality was also found to increase when adults were present and food (algae) was scarce (Duarte et al. 2010). To our surprise, there was no interaction between cannibalism and food availability, even though food availability is normally an important limiting factor for amphipod growth (Elmgren et al. 2001, Wenngren & Ólafsson 2002). In our 7 d experiments, the lack of food was harmful to juveniles only at high initial densities, with an increase in mortality rates roughly proportional to the increase in juvenile density. The increase in juvenile mortality in the absence of conspecific predators suggests that at least some mortality may be caused by factors beyond cannibalism, such as starvation. As suggested by Duarte et al. (2010), predation within and between size classes may interact with food shortage, and so the role of these interactions between factors should not be disregarded.

4.4. Implications

The strong influence of adults over juvenile activity patterns and mortality rates suggests that negative intraspecific interactions play an important role in the dynamics of amphipod populations. As has been the case for other species, further studies should explore the spatial patterns of activity of *A. longicornis* across different sandy beaches to build a more integrative model of the interactions between the life stages of this species. Similarly, these experimental findings now need to be linked to data on the seasonal abundance of amphipods and stranded seaweed availability. Such information would allow us to infer when cannibalism is potentially more intense and, therefore, when avoidance behaviors between life stages are more likely to operate. Gaining insight into the potential interactions taking place in sandy beach systems is critical for an understanding of how they indirectly affect the role played by amphipods in the trophic web and in the processing of seaweed wrack in this region (Brenner et al. 1976, Chow 2020) as well as other coastlines elsewhere (Dugan et al. 2003, Spiller et al. 2010).

In the study of cannibalism as the causative factor behind the alteration of juvenile activity patterns, *F. serratus* was the logical choice as a proxy for food availability (Quintanilla-Ahumada et al. 2023). However, this seaweed is far from being the only macrophyte species contributing to the wrack in this

(MacMillan & Quijón 2012) and other temperate and cold sandy beaches (see review by Hyndes et al. 2022). This is not a trivial point, considering that amphipods are known to actively seek food choices based on algal nutritive value, morphology and palatability (Duarte et al. 2010, 2014, Pelletier et al. 2011, Poore & Gallagher 2013), and at times other factors (Quintanilla-Ahumada et al. 2023). Whether the quantity (biomass) or quality (species composition) of stranded seaweeds plays a role in ameliorating the effects of cannibalism and avoidance mechanisms in juvenile amphipods is intriguing and merits further study. Along the same lines, the growing use of experiments alongside field observations is critical in ecology (e.g. Underwood 1990, Walker & Schlacher 2011), as they help to answer relevant questions such as the ones addressed here on life-stage segregation and its underlying causes. These experiments also provide unambiguous support to long-standing hypotheses that have motivated a growing number of studies in sandy beach systems worldwide but have, surprisingly, not been explicitly tested.

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