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Triggers affecting crayfish burrowing behaviour

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Abstract Surface water inhabiting crayfish are well-known for the impact on their surroundings. This impact has been related to loss of biodiversity and deteriorating water quality for invasive crayfish. Crayfish dig burrows for various reasons like lack of natural shelters, avoiding an upcoming drought, or high crayfish density and this may lead to increased sediment transport and accelerated bank instability. All crayfish are considered to have burrowing capability, but not all species have been observed burrowing. Studies comparing this behaviour among different species in standardized ways are scarce. Crayfish burrowing was investigated under standardized laboratory conditions to reveal differences among species and their sex. All studied species occur in the Netherlands and were the native *Astacus astacus* (Linnaeus, 1758), the Eurasian *Pontastacus leptodactylus* (Eschscholtz, 1823) and the invasive North American *Faxonius virilis* (Hagen, 1870), *F. limosus* (Rafinesque 1817), *Pacifastacus leniusculus* (Dana, 1852), *Procambarus acutus* (Girard 1852), and *P. clarkii* (Girard, 1852). As burrowing triggers were evaluated presence of shelter, increased light intensity, increased water temperature, and increased crayfish density. Results showed species-specific and sometimes sex-specific differences in burrowing behaviour among crayfish. The response to burrowing triggers was also species-specific and no two species reacted identical to all triggers. Absence of shelter was a

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strong driver to burrow for *A. astacus*, *F. limosus* and *F. virilis*, while increased light intensity triggered burrowing behaviour in *P. leptodactylus*, *P. acutus* and *P. clarkii* and lowered activity of *F. limosus*. Burrowing behaviour of *P. clarkii* was mostly influenced by increased water temperature. Significant differences between females and males were observed for *P. leptodactylus*, *P. leniusculus* and *P. acutus* in the shelter, increased density and increased water temperature treatment, respectively. Understanding the triggers that invoke burrowing may help managing populations of these invasive species.

Keywords Density · Invasive species · Light intensity · Shelter · Water temperature

Introduction

Crayfish that inhabit open waters (tertiary and secondary burrowers) are well-known for their impact on the surrounding biotic and abiotic environment (Hobbs 1981). Due to this profound effect on their environment they are regarded as ecosystem engineers (Statzner et al. 2003; Albertson and Daniels 2018). Through their feeding and foraging behaviour, crayfish can have a great negative impact on benthic macroinvertebrate communities (Correia and Anastácio 2008; Souty-Grosset et al. 2016). This may result in less biodiverse communities in places where they occur compared to places where they are absent. The impact of invasive crayfish on the native macroinvertebrate community can be either comparable to (Weber and Traunspurger 2017) or greater (Nystrom et al. 1999) than the impact native crayfish have. Since almost all invasive species are carriers of the crayfish plague, their presence obviously limit the distribution of native species in Europe (Tilmans et al. 2014; Souty-Grosset et al. 2016; Mojžišová et al. 2020, 2022). Crayfish species may also negatively affect emergent, floating or submerged plants by grazing (Nystrom and Strand 1996) and, especially the loss of submerged plants may lead to increased turbidity of the water (Roessink et al. 2017). The relatively substantial individual body size in combination with their behaviour (walking, fighting, foraging) and eventually high population densities may lead to physical disturbance of the sediment that negatively affects water quality (Souty-Grosset et al. 2016; Roessink et al. 2017). Furthermore, the burrows they dig may lead to increased sediment transport in streams (Sanders et al. 2021) and may cause or accelerate river bank instability and erosion (Arce and Diéguez-Uribeondo 2015; Faller et al. 2016; Harvey et al. 2019), collapse of delimiting banks in rice fields (Arce and Diéguez-Uribeondo 2015), and increase the risk of compromised riverbanks in peatland areas (Lemmers et al. 2021). Although all freshwater crayfish species have the ability to burrow (Hobbs 1981; Crandall and De Grave 2017; Florey and Moore 2019), there is also a number of crayfish species that live in permanent water which burrowing may be limited (Berrill and Chenoweth 1982). These observations have been made under different field conditions and studies that compare this burrowing capacity among species under similar conditions are very scarce but see e.g. Burras et al. (1995) and Kouba et al. (2016).

It is generally accepted that burrows function as a means to withstand environmental extremes (e.g. high temperatures) and as a protection against predators, especially during sensitive life history phases (Barbaresi et al. 2004; Stoeckel et al. 2011). But what triggers burrowing behaviour in the different crayfish species? Although burrowing might be a direct result of environmental stress (Correia and Ferreira 1995), triggers for this behaviour seem rather unpredictable (Barbaresi and Gherardi 2006). An important reason for crayfish to excavate is seeking shelter as burrowing appeared to be inversely related to the availability of natural shelters present (Flint 1975; Berrill and Chenoweth 1982; Ilhéu et al. 2003). Burrowing activities can be up to five times higher when there is a lack of protection but depends of the bottom structure (Flint 1975). Crayfish leave shelters for feeding during the night because risk of predation is lower, and this risk increases parallel to increasing light intensities (Flint 1975; Ranta and Lindström 2010). The observed withdrawal of crayfish towards their burrows when light intensities increased (Suzuki et al. 1985; Fernández-De-Miguel and Aréchiga 1992) supports the notion that burrowing and light intensity might be correlated. Increasing light intensity can also act as an early warning signal for an upcoming drought that can have a detrimental effect on crayfish populations (McClain 2013; Kouba et al. 2016). Survival of crayfish outside of water is species dependent (Reynolds et al. 2012), and a link has been observed between drought and burrowing activities (Correia and

Ferreira 1995; Barbaresi et al. 2004). Increase in water temperature is another signal that can be associated with dry periods (Boulton 2003) and higher water temperatures stimulate the activity and metabolism of crayfish (Flint 1975). Furthermore, biological factors like crayfish density may affect burrow use with a higher occupancy rate of burrows at higher *P. clarkii* densities (Ranta and Lindström 2010). Although no relationship seems to exist between burrow density and *P. clarkii* population size (Ilhéu et al. 2003), the number of active burrows has been positively correlated with the population size (Arce and Diéguez-Uribeondo 2015). Burrowing behaviour has also been linked to the reproductive cycle (Romaire and Lutz 1989; Holdich and Black 2007) with earlier burrowing activity in the season by female *P. leniusculus* (Stanton 2004), larger and deeper burrows by female *P. clarkii* (Guo et al. 2020) and, especially females with eggs retreating in burrows (Hasiotis 1995).

Currently, there are several invasive crayfish species with well-established populations in the Netherlands while only one species is native (Lemmers et al. 2021). This offers the opportunity to study burrowing behaviour in a standardized way among different crayfish species. The prime aim of the present study was to investigate crayfish burrowing behaviour and reveal possible differences among seven crayfish species and their sex. The second aim was to identify which triggers invoke this behaviour. In a laboratory experimental set-up, four possible triggers, namely the presence of shelter, increased light intensity, increased water temperature, and increased crayfish density were evaluated for burrowing behaviour in the native species *Astacus astacus* (Linnaeus, 1758), the Eurasian species *Pontastacus leptodactylus* (Eschscholtz, 1823) non-native to the Netherlands, and the invasive North American species *Faxonius virilis* (Hagen, 1870), *Faxonius limosus* (Rafinesque, 1817), *Pacifastacus leniusculus* (Dana, 1852), *Procambarus acutus* (Girard, 1852), and *Procambarus clarkii* (Girard, 1852).

Materials and methods

General set-up burrowing experiment

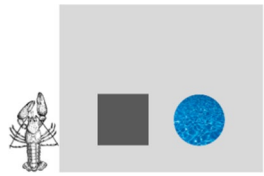
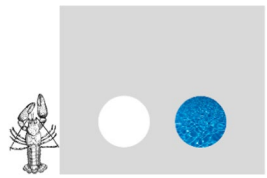
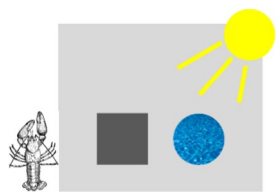
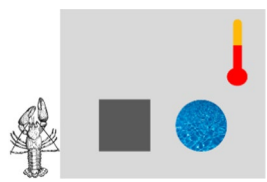
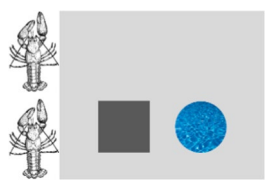
Twelve plastic crates of 60 × 40 × 30 (length × width × height) cm were placed in a water bath (see pictures of Online Resource 1) to ensure a stable and comparable water temperature (18–20 °C). Each crate had an additional PVC wall installed to mimic a bank and to create a visual wall for the crayfish. Two openings in this wall provided access to a PVC pipe (Ø 5.8 cm) with one filled with 25 blue foam blocks of 3–4 cm^3 to provide burrowing opportunities, and the other pipe open to provide a shelter or closed off, depending on the treatment. Copper-free tap water was used to fill the crates until ten centimetres below the top (48 L), minimizing escapes. Aeration via a tube with an air stone was provided in each crate to maintain stable dissolved oxygen levels, while a shade cloth above the creates prevented stress caused by too high artificial light intensity as shown in the pictures of Online Resource 1. Light intensity under the shade cloth but above the crates averaged around 85 µmol m^{-2} s^{-1} (range 74–100 µmol m^{-2} s^{-1}). A day-night regime of 10–14 h was applied.

Each treatment (Table 1) was tested for three successive days. Twelve crates per run were available and in each run six males and six females were deployed. Depending on the availability of animals and time, in principle two runs were performed per species and treatment, giving twelve observations per sex for one treatment. All runs for a species were usually performed within a period of two months. To minimize human impact on crayfish behaviour, the room with the water bath was only accessed by the observers to daily check the well-being of all individuals during a run. After each run, all materials were cleaned with fresh water and the crates were refilled with new water to remove any odour from previous crayfish. In case a crayfish removed at least three blocks (out of 25) from the pipe, this was regarded as burrowing behaviour. In a number of cases, crayfish tried to escape the crate and when this occurred this was recorded as an escape response. The first response (digging or escaping) determined the result for that crayfish for that treatment.

Treatments

Five different treatments were tested (Table 1). In the control treatment, the one PVC pipe in the crates was covered with a PVC plate while the other pipe was filled with the blue foam blocks (size approximately 1.5 × 1.5 × 1.5 cm). Crayfish were allowed to burrow

Table 1 Overview of tested treatments. All treatments had a standard water temperature (18–20 °C) and a standard light intensity (85 µmol m^{-2} s^{-1}) and one crayfish per crate unless stated otherwise

Treatment	Description	Schematic representation
Control	One pipe filled with blue foam and the other pipe blocked by a PVC plate	
Shelter	As the Control treatment, but with one additional empty pipe representing a place to shelter	
Increased light intensity	As the Control treatment but light intensity above the crate was increased in two days to an average of 200–280 µmol m^{-2} s^{-1} after 1 run-in day	
Increased water temperature	As the control treatment but temperature of the water in the crate was increased in two day with 3 °C per day (6 °C in total) after 1 run-in day	
Increased crayfish density	As the control treatment but a second crayfish was introduced in the tank. At the start of the experiment, the crayfish were separated from each other for 10 min with a perspex T-structure	

Drawing crayfish by Pearson Scott Foresman

for nearly three days (66 h including, two nights). In the shelter treatment, the pipe with foam was available and from the other pipe the cover was removed to provide a shelter possibility. The increased light intensity treatment started with one day (one night) of acclimatization to the conditions that correspond to the control treatment with only the pipe filled with foam available. All crayfish that showed a response within this one day were removed from the treatment because the response was not triggered by higher light intensity. After this pre-treatment night, the treatment started by increasing the light intensity above the crates during daytime to 200–80 µmol m^{-2} s^{-1} by adapting the emitted intensity of the artificial lamps to the required level. Crayfish were again offered to burrow for three days (two nights). The increased water temperature treatment also started with one day (one night) of acclimatization to the control treatment conditions with again only the pipe filled with foam available. Crayfish that showed a response within this

one day were removed from the treatment because the response was not triggered by higher water temperature. After the pre-treatment, water temperature was gradually increased with 3 °C per day until it reached 26 °C by increasing the temperature of the water bath. For the density treatment, crayfish were individually placed in buckets 24 h before the start of the test to ensure that they were free from odours of other crayfish in their housing tank. Thereafter, they were transferred into the crates under similar conditions as the control treatment. In each container two individuals from the same sex and species were introduced and a divider separated the individuals for the first ten minutes to let them get used to each other's smell, without seeing each other. The divider was removed and both crayfish were free to burrow.

Crayfish

Seven crayfish species were tested over the years (Table 2). Most invasive crayfish were wild-caught by either local fisherman or by the staff. *Faxonius limosus* and *P. clarkii* originated from Hardinxveld-Giessendam (the Netherlands), *F. virilis* from the floodplains of the river Waal near Boven-Leeuwen (the Netherlands), and *P. leniusculus* from the Oude Leij in Tilburg (the Netherlands). *Procambarus acutus* originated from a culture (Harald Groβ, Edelkrebs und Fischzucht, DE) and *P. leptodactylus* frome a commercial supplier (Koidreams, Valburg, NL) while *Astacus astacus* came from an own culture.

Prior to the experiment, crayfish were housed separately to avoid fights and injuries. Three pellets of Trouvit (Skretting, a Nutreco company) were fed to each crayfish twice a week. Each individual got an unique number written with Tipp-Ex on the carapace for individual recognition during the experiment and sex and length of carapace were determined. Due to logistical issues, not all treatments were tested for all species by sex combinations. Control and shelter treatment were performed for all species but both sexes of *F. virilis* could not be tested for increased light intensity and increased water temperature and both sexes of *F. limosus*, *P. acutus* and *P. clarkii* were not tested for density effects. Each crayfish specimen was in principle used in all tests and were given at least seven days between two trials to recover.

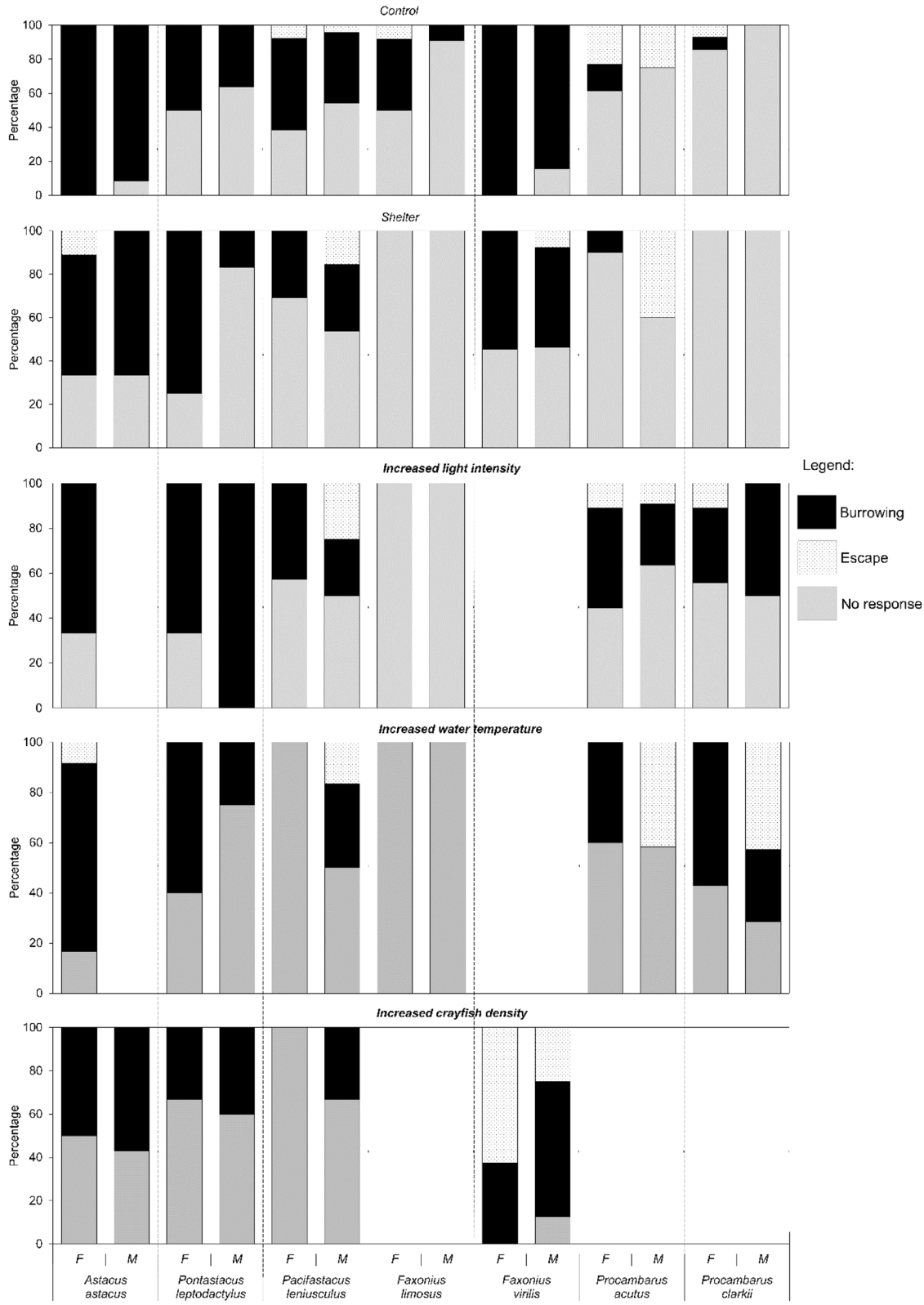
Data analysis

Both the water temperature and light intensity treatment had an one day run-in period using the standard conditions from the control experiment. Specimens that showed a response during this first day and night were removed from the treatment. As a consequence, a lower number of replicates for that treatment was available for statistical testing and for some species the number of observations became lower than a-priori anticipated. Density treatment was always performed at the end of the series of tests. This was done to avoid damages that may arise when specimens fight with each other, so we ensured that all other tested treatments were performed with intact animals.

The number of times that burrowing, escaping and no responses occurred were determined per treatment and per species and sex. Fisher's exact tests in SPSS (Field 2013) were applied to test whether the observed responses (burrowing, escaping or no response) of a single species (females and males separately and taken together) in a specific treatment significantly differed from the control treatment. Adjusted standardized residuals were evaluated to discover which observed response deviated from

Table 2 Overview of the seven species, their origin, period of testing (month and year), and available number of specimens (*n*) for the experiment

Species	English name	Origin	Period of testing	*n*
Astacus astacus	Noble crayfish	Europe	06–2015	24
Pontastacus leptodactylus	Narrow-clawed crayfish	Eurasia	05–2015	23
Pacifastacus leniusculus	Signal crayfish	North America	09–2016 till 01–2017	50
Faxonius limosus	Spiny-cheek crayfish	North America	04–2013	23
Faxonius virilis	Virile crayfish	North America	04–2016	24
Procambarus acutus	White river crayfish	North America	04–2013	21
Procambarus clarkii	Red swamp crayfish	North America	04–2013	22



◂**Fig. 1** Relative distribution of responses for all treatments for the tested seven species separated by sex. No bar means not tested, except for male *A. astacus*, that responded already in the acclimatization period of the increased light intensity and increased water temperature treatment. F = females, M = males

the expectation. A p value ≤ 0.05 indicated a significant difference while a value between 0.05 and 0.10 was regarded as indicating a trend. Fisher's exact test was also used to statistically evaluate the differences between sexes per species in the different treatments and to evaluate differences between species.

Results

Figure 1 shows a summary of the obtained results and the raw data counts can be found in Online Resource 2.

Sex-specific response behaviour

In a number of cases, the response of females to a treatment differed significantly from males (Fig. 1, Table 3). Significantly ($p \leq 0.05$) less *P. leptodactylus* males burrowed in the shelter treatment, less *P. acutus* males in the increased water temperature treatment and more *P. leniusculus* males burrowed in the increased crayfish density treatment. There was a trend ($0.05 < p \leq 0.10$) in more *P. acutus* females showing no response in the shelter treatment and less *P. leniusculus* females showing a response in the increased water temperature treatment.

Species-specific response behaviour

Astacus astacus was an active burrower (95% of the specimen) in the control treatment (Fig. 1), and burrowing activity was significantly (Table 4) lower in the shelter treatment. All males responded during the acclimatization period for both the increased light intensity and increased water temperature treatment. Increased light intensity resulted in a trend with fewer females burrowing compared to the control treatment. Increased water temperature did not lead to significant changes in females. Increased crayfish density significantly lowered burrowing activity in this species.

A quarter of the specimens of *F. limosus* burrowed in the control treatment (Fig. 1). In the shelter, increased light intensity, and increased water temperature treatment, all specimen showed no response and the difference with the control treatment was significant (Table 4) except for the increased water temperature treatment due to the lower number of observations in this treatment. These differences were mainly due to changes in the behaviour of the females.

Faxonius virilis actively burrowed in the control treatment (Fig. 1) and offering shelter significantly (Table 4) reduced the number of burrowing specimens. In the increased crayfish density treatment, significantly more specimens tried to escape the experimental setting.

Approximately half of *P. leniusculus* specimens burrowed in the control treatment (Fig. 1) and the shelter and increased light intensity treatment did not result in significant changes in behaviour. In the increased water temperature and increased crayfish density treatments, one third of the males and none of the females burrowed and the difference of the latter with the control treatment were significant (Table 4).

Around 40–50% of *P. leptodactylus* burrowed in the control treatment (Fig. 1) and in the shelter treatment only males burrowed significantly less (Table 4). In the increased light intensity treatment, significantly more specimens burrowed which was due to the males. No significant differences were observed due to the increased water temperature or increased crayfish density.

Roughly 10% of *P. acutus* specimens burrowed in the control treatment (Fig. 1) and this did not significantly (Table 4) change in the shelter treatment despite the trend in response between females and males. In the increased light intensity and increased water temperature treatment, more specimens showed a response but this was not significant.

Less than 5% of the *P. clarkii* specimens burrowed in the control treatment (Fig. 1) and a similar pattern was observed for the shelter treatment which was not significantly (Table 4) different from the control treatment. Both increased light intensity and increased water temperature significantly reduced the number of specimens without a response in favour of more burrowing or males trying to escape.

Table 3 Results of Fisher's exact test (Chi-square, *p* value, degree of freedom, total observations) to evaluate the significance of sex per species

Treatment	Fisher's Test	*A. astacus*	*P. leptodactylus*	*P. leniusculus*	*F. limosus*	*F. virilis*	*P. acutus*	*P. clarkii*
Control	χ2	1.043	0.436	1.387	4.346	1.846	1.143	1.210
	p	1.000	0.407	0.531	0.104	0.482	0.803	1.000
	df	1	1	2	2	1	2	2
	n	24	23	50	23	24	21	22
Shelter	χ2	1.423	***8.224***	1.938	Constant	0.938	**4.090**	Constant
	p	0.796	***0.006***	0.580		1.000	**0.095**	
	df	2	***1***	2		2	**2**	
	n	21	***24***	26	24	24	**15**	14
Increased light availability	χ2	N.D	2.250	1.869	Constant	N.A	1.044	0.938
	p		0.333	0.608			0.807	1.000
	df		1	2			2	2
	n		9	15	21		20	15
Increased water temperature	χ2	N.D	1.400	*4.550*	Constant	N.A	***8.507***	3.497
	p		0.280	**0.070**			***0.009***	0.257
	df		1	**2**			***2***	2
	n		14	**13**	9		***22***	14
Increased crayfish density	χ2	0.133	0.105	***4.800***	N.A	2.630	N.A	N.A
	p	1.000	1.000	***0.047***		0.315		
	df	1	1	***1***		2		
	n	26	22	***24***		16		

N.A.: not tested at all, N.D.: no data available because all specimens from one sex escaped during the acclimatization period, Constant: no variability in response due to the exact same response by females and males

Significant ($p \leq 0.05$) differences between females and males are in bold and italic and trends ($0.05 < p \leq 0.10$) in bold only

Differences in response behaviour among species

The species tested in the treatments showed significantly different behaviour (Table 5). *Astacus astacus* and *F. virilis* burrowed significantly more in the control treatment while only a small fraction of *F. limosus* and both *Procambarus* species burrowed. A similar pattern was observed in the shelter treatment. In the increased light and increased water temperature treatment, *P. leptodactylus* burried more frequently than the other tested species *F. limosus*, *P. leniusculus* and both *Procambarus* species. *Pacifastacus leniusculus* burrowed less than *P. leptodactylus*, *F. virilis* and *A. astacus* while *F. virilis* more frequently escaped.

Roughly 50% of *A. astacus* and *P. leptodactylus* dug in all treatments (Fig. 1) which is in contrast with the lack of burrowing in a number of treatments for *F. limosus, P. acutus* and *P. clarkii. Procambarus acutus* and *P. clarkii* and male *P. leniusculus* more frequently escaped than the other species. Half of the *F. virilis* specimens showed this escape behaviour in the density experiment. Both *Procambarus* species were triggered to burrow by increased light intensity and especially increased water temperature. The increased water temperature treatment resulted in the highest response of *P. clarkii* to stimuli. Increased light intensity also triggered male *P. leptodactylus* to dig. The increased crayfish density treatment triggered *F. virilis* to escape, a response that was not observed for the other species.

Discussion

In this laboratory study, crayfish were placed in an artificial environment with one pipe filled with pieces of foam to study their burrowing behaviour. Pipes of comparable diameter have been successfully used as shelters in other experiments with tertiary crayfish (Gherardi and Daniels 2003; Payette and McGaw 2003; Stanton 2004; Barbaresi and Gherardi 2006)

Table 4 Results of Fisher's exact test (Chi-square, *p* value, degree of freedom, number of observations) to evaluate the significance of observed difference in behaviour between the treatment and control

Species	Shelter				Increased light intensity				Increased water temperature				Increased crayfish density			
	$\chi 2$	*p*	*df*	*n*	$\chi 2$	*p*	*df*	*n*	$\chi 2$	*p*	*df*	*n*	$\chi 2$	*p*	*df*	*n*
A. astacus	***7.887***	***0.009***	***2***	***45***									***11.435***	***< 0.001***	***1***	***50***
F	***5.972***	***0.021***	***2***	***21***	**4.500**	**0.098**	**1**	**18**	2.976	0.217	2	24	***8.000***	***0.007***	***1***	***24***
M	2.403	0.158	1	24	N.D				N.D				**3.914**	**0.060**	**1**	**26**
P. leptodactylus	0.260	0.552	1	47	***5.420***	***0.024***	***1***	***32***	0.149	0.481	1	37	0.237	0.428	1	45
F	1.623	0.200	1	24	0.268	0.554	1	15	0.220	0.485	1	22	0.686	0.340	1	24
M	1.168	0.275	1	23	***6.491***	***0.017***	***1***	***17***	0.170	0.593	1	15	0.029	0.608	1	21
P. leniusculus	2.213	0.379	2	76	1.740	0.401	2	65	**4.877**	**0.071**	**2**	**63**	***9.058***	***0.007***	***2***	***74***
F	3.184	0.216	2	39	0.907	0.797	2	33	***8.018***	***0.013***	***2***	***33***	***13.282***	***< 0.001***	***2***	***38***
M	1.616	0.594	2	37	2.932	0.268	2	32	1.607	0.590	2	30	0.864	0.814	2	36
F. limosus	***8.562***	***0.004***	***2***	***47***	***7.586***	***0.014***	***2***	***44***	3.216	0.188	2	32	N.A			
F	***7.738***	***0.014***	***2***	***24***	***7.181***	***0.023***	***2***	***23***	4.129	0.150	2	18	N.A			
M	1.140	0.478	1	23	1.339	0.524	1	21	0.294	0.786	1	14	N.A			
F. virilis	***10.127***	***0.003***	***2***	***48***	N.A				N.A				***12.788***	***< 0.001***	***2***	***40***
F	***6.471***	***0.018***	***1***	***22***	N.A				N.A				***9.330***	***0.005***	***1***	***19***
M	**4.246**	**0.097**	**2**	**26**	N.A				N.A				3.179	0.236	2	21
P. acutus	0.862	0.854	2	36	4.210	0.127	2	41	0.729	0.824	2	43	N.A			
F	2.742	0.405	2	23	2.229	0.432	2	22	3.207	0.244	2	23	N.A			
M	0.325	0.510	1	13	2.701	0.404	2	19	0.586	0.392	2	20	N.A			
P. clarkii	1.262	1.000	2	36	***7.553***	***0.014***	***2***	***37***	***11.920***	***0.001***	***2***	***36***	N.A			
F	1.023	1.000	2	20	3.024	0.366	2	23	***5.927***	***0.025***	***2***	***21***	N.A			
M	Constant				**5.091**	**0.055**	**1**	**14**	***7.645***	***0.007***	***2***	***15***	N.A			

F females, *M* males, *N.A.* not tested at all, *N.D.* no data available because all specimens from one sex escaped during the acclimatization period constant: exactly the same response in treatment and control

Treatments that significantly ($p \leq 0.05$) deviated from control are in bold and italic and trends ($0.05 < p \leq 0.10$) in bold only

and match sizes of occupied burrows in field observations (Souty-Grosset et al. 2014). The number of burrows dug by crayfish has been related to type and composition of the sediment (Stanton 2004; Emery-Butcher et al. 2023). The foam used in this study does not resemble natural sediments at all, and may therefore have affected the burrowing behaviour of the tested species. However, all species showed to be able to remove the foam from the pipe and occupy the pipe in at least one of the treatments and, therefore, the general set-up is regarded suitable as a means to study burrowing behaviour in a standardized way. The various species were tested in spring/early summer in different years, except for *P. leniusculus* that was tested in autumn/early winter. Since activity of *P. leniusculus* shows a seasonal cycle with low activity in winter (Flint 1977), their burrowing activity in the present study might be underestimated for the spring/early season.

Burrowing behaviour has also been linked to the reproductive cycle (Romaire and Lutz 1989; Holdich and Black 2007) and especially to females with eggs retreating in burrows (Hasiotis 1995). To avoid bias in the results due to a few gravid females, these specimens were excluded from the experiment. The different runs for each species were performed within a relatively short period of time and by that excluding seasonal variation. The advantage of this approach is that significant differences among treatments are indeed due to the applied triggers and thus shed light on how each species responds to the triggers applied. The responses, however, may change over the seasons and repeating the experiments in other seasons may reveal the consistency in response to the triggers.

Table 5 Results of Fisher's exact tests to evaluate differences in response among species to the treatments

Treatment	Fisher's exact test				Behaviour	Species						
	$\chi 2$	*p*	*df*	*n*		*A. astacus*	*P. leptodactylus*	*P. leniusculus*	*F. limosus*	*F. virilis*	*P. acutus*	*P. clarkii*
Control	86.836	< 0.001	12	187	Burrow	***5.1***	-0.4	0.2	***-2.2***	***4.7***	***−3.7***	***−4.3***
					Escape	−1.2	−1.2	0.2	−0.2	−1.2	***4***	−0.2
					No Response	***−4.6***	0.9	−0.3	***2.3***	***−4.1***	1.9	***4.3***
Shelter	45.319	< 0.001	12	148	Burrow	***3.4***	1.8	0	***−3.5***	***2.3***	***−2.1***	***−2.6***
					Escape	0.2	−1.1	1	−1.1	0	1.9	−0.8
					No Response	***−3.4***	−1.3	−0.5	***3.9***	***−2.2***	1.2	***2.9***
Increased light intensity	29.734	< 0.001	8	80	Burrow		***3.8***	0.1	***−3.7***		0.3	0.7
					Escape	N.T	−0.8	1.3	−1.4	N.T	0.8	0.1
					No Response		***−3.3***	−0.7	***4.2***		−0.7	−0.7
Increased water temperature	16.48	0.017	8	72	Burrow		***2.2***	−1	−1.9		−1	1.6
					Escape	N.T	−1.6	−0.6	−1.2	N.T	1.7	1.1
					No Response		−1	1.3	***2.6***		−0.2	***−2.2***
Increased crayfish density	37.024	< 0.001	6	88	Burrow	1.9	−0.3	***−2.6***		1		
					Escape	−1.8	−1.6	−1.7	N.T	***5.8***	N.T	N.T
					No Response	−0.9	1.1	***3.4***		***−4.2***		

Test results (Chi-square, *p* value, degree of freedom, total observations) are given as well as the standardized residuals. Significant standardized residuals are in bold and italic. Positive values indicate more frequently observed and negative values less frequently observed

N.T. species not tested

Crayfish use refuge and burrows to be protected against predators, to withstand environmental extremes or for reproduction (Hobbs 1981; Barbaresi et al. 2004; Stoeckel et al. 2011). Excavating burrows by crayfish seem to be inversely linked to the availability of natural shelters present (Berrill and Chenoweth 1982; Ilhéu et al. 2003). When no shelter was present in our experiment, certain species show active burrowing behaviour (*A. astacus*, *F. virilis, P. leptodactylus*), while others show hardly any burrowing activity (*P. clarkii*, male *F. limosus*), limited burrowing activity (female *F. limosus*, *P. leniusculus*) or only limited escape behaviour (*P. acutus*). In permanent water with similar environmental laboratory conditions, the examined crayfish species thus differ in their burrowing response. Our laboratory findings therefore, support the field observations that among crayfish that live in open water some species burrow and others not depending on the prevailing conditions (Berrill and Chenoweth 1982). This burrowing capability seems, however, to be flexible since *P. leniusculus*, which is considered a non-burrowing species, heavily burrowed outside its native range in the banks of a river in the UK (Guan 1994) and also showed burrowing behaviour in our study. Similarly, Kaestner (1991) and Statzner et al. (2000) mention that *F. limosus* does not burrow while other sources e.g. Holdich and Black (2007) state this species is a notorious burrower. Even among genetically uniform specimens, behavioural plasticity in burrowing has been observed (Linzmaier et al. 2018).

The present study observed that there were significant differences in burrowing activity between females and males from the same species, with, for example, less *P. leptodactylus* males burrowing compared to females when a shelter was present. Significant differences between sexes were also found for *P. acutus* in the increased water temperature treatment and for *P. leniusculus* for the increased density treatment. Especially during sensitive life history phases, use of shelters by crayfish is of great importance (Barbaresi et al. 2004; Stoeckel et al. 2011). For example, *P. clarkii* maternal females showed a much stronger shelter competition and use than conspecific males or non-maternal females (Figler et al. 2001; Haubrock et al. 2019) and such shelter-related aggression seems to be quite common in decapods (Figler et al. 1998). In addition, Haubrock et al. (2019) observed no differences between males and females in burrow activity prior to mating and Berrill and Chenoweth (1982) also found no differences between sexes. On the other hand, the study of Guo et al. (2020) indicated that there were differences between female and male *P. clarkii* in shelter use also outside the reproductive period. In the present study, in which no gravid females were used, most treatment and species combinations did not show sex-specific responses and thus supports the lack of differences in burrowing behaviour between males and females.

Crayfish use natural refuges besides burrows to seek shelter and the presence of natural shelters seem to reduce burrowing activity (Flint 1975; Ilhéu et al. 2003; Groza et al. 2016). The observations in the present study showed that the presence of a shelter indeed reduced burrowing behaviour in *A. astacus*, *F. limosus*, and *F. virilis.* Interestingly, the presence or absence of a shelter did not lead to a change in their behaviour of *P. leniusculus*, *P. leptodactylus*, *P. acutus* and *P. clarkii*. Remarkably, for *F. limosus*, lack of shelter was the only environmental stressor that triggered burrowing behaviour. According to the results of the present study, the response to shelter availability is likely to be species-specific.

Crayfish species vary in their ability to survive out of water (Reynolds et al. 2012; Kouba et al. 2016) and one way to deal with desiccation is excavating burrows (Hobbs 1981; Peay and Dunn 2014). A decrease in water level may induce burrowing activity as observed in *P. clarkii* by Correia and Ferreira (1995) and both increasing water temperature and increasing light availability may act as early warning signals for upcoming lower water levels (Boulton 2003). The burrowing behaviour of *P. clarkii* has been related to drought avoidance (Hobbs 1981), and in the present study *P. clarkii* was the only species that increased burrowing activity to both drought indicators. The response of *P. clarkii* was stronger to the water temperature increase than the light intensity increase with more specimens burrowing at higher water temperatures. *Pontastacus leptodactylus* also increased burrowing activity at increased light intensity but not with higher water temperatures which is in line with the observation by Valido et al. (2021). Interestingly, both drought triggers caused a total lack of response in *F. limosus*. This species generally occurs in all types of water bodies but prefers warmer, slow-flowing and standing waters and is very tolerant to a variety of environmental stressors and this high tolerance

towards eutrophic conditions and water temperature may explain the observed lack of response (Todorov et al. 2020). Crayfish are in general night-active and search more actively for shelter (Flint 1975, 1977) and occupy more shelters during day compared to the night (Ranta and Lindström 2010; Thomas et al. 2016). Furthermore, increased artificial light during the night increased the time *P. leniusculus* spent in the shelter (Thomas et al. 2016). Nevertheless, this study clearly indicate that the responses to drought triggers are species-specific.

The density treatment in this study could only be applied to a limited number of species and gave interesting results. The response to this treatment seems also species-specific with *A. astacus* and *P. leniusculus* showing less burrowing, *P. leptodactylus* having no change in behaviour and *F. virilis* showing a larger proportion of specimens trying to escape. Studies have indicated that the number of burrows is uncorrelated with crayfish density (Guan 1994; Ilhéu et al. 2003; Haubrock et al. 2019) and this seems to contradict the results from this study except for *P. leptodactylus*. Unlike in field conditions where multiple opportunities are present, there was only one place where the animals could dig a burrow in the present study. The lower burrowing activity of *A. astacus* and *P. leniusculus* could possibly be due to specimens interacting more with the other specimen present in the experimental arena than seeking shelter. Support for this hypothesis comes from observations that differences in levels of aggression determine access to limited shelter together with fighting constituting a high proportion of total interactions in equally sized pairs (Vorburger and Ribi 1999). An alternative explanation for the unoccupied shelters could be that the dominant crayfish prevented the subordinate one from using it. This was also observed by Gherardi and Daniels (2004) in an interspecies shelter occupancy experiment where the dominant *P. clarkii* did not use the shelter after evicting subordinate *P. acutus acutus* from it. Unfortunately, no video recordings have been made in the present study to verify this.

Implications

The results of the present experiments indicate that the tested species showed a different burrowing response to the triggers they were exposed to. These species-specific responses are very relevant for managing crayfish populations and the problems they cause. Like in many countries in Europe (e.g. Kouba et al. 2014; Souty-Grosset et al. 2016), the Netherlands has to deal with several invasive crayfish species (Lemmers et al. 2021; van Kuijk et al. 2021). The presence of these burrowing animals may increase the risk of bank erosion (Harvey et al. 2019) resulting in concerns of dike collapses in peatland areas in the Netherlands (Lemmers et al. 2021). High burrow density by *P. leniusculus* had led to considerable damage of river banks in the UK (Guan 1994) and burrowing activity by *P. clarkii* in rice field dikes in Portugal resulted in leakages and finally the collapse of these delimiting banks (Fonseca et al. 1997; Holdich 1999). The most widespread invasive crayfish species in the Netherlands are *F. limosus* and *P. clarkii* (van Kuijk et al. 2021). The present study showed that *F. limosus* greatly lowers burrowing activity when natural shelters are present. The Netherlands has an extensive and complex network of ditches and canals to discharge excess water (Verdonschot et al. 2011). The sediment in those ditches and canals frequently consists of fine material and thus ideal for crayfish to burrow (Correia and Ferreira 1995; Barbaresi et al. 2004). Intense management of these systems through frequent dredging and yearly thoroughly cleaning of the vegetation in the water ways has resulted in a homogeneous underwater environment. The lack of shelters in those environments is probably one of the most important triggers for *F. limosus* to burrow. Changing the way of managing water courses and creating a more heterogeneous environment with more variability in natural shelters might help to refrain *F. limosus* from burrowing.

The lack of shelters does not seem to be an important trigger to burrow for the other widespread species *P. clarkii* in the Netherlands as demonstrated in the control treatment of the present experiment. Although the species did not burrow in ephemeral waters in Portugal, it did make use of boulders and complex microhabitats in the wild to shelter (Aquiloni et al. 2005). It might be valuable to investigate if adding complex habitats in otherwise homogeneous environments may lower burrowing intensity of this species. In the present study, *P. clarkii* clearly responded to the increased water temperature which is in line with studies indicating that crayfish demonstrated greater burrowing activity with higher water temperatures (Flint 1977;

Guan and Wiles 1997; Bubb et al. 2002; Stanton 2004). Although Ilhéu et al. (2003) found no relationship between total burrow density and *P. clarkii* population size, the number of active burrows has been positively correlated with the density of *P. clarkii* (Arce and Diéguez-Uribeondo 2015). Interestingly, *P. clarkii* seems to be an inefficient user of its burrows as Barbaresi et al. (2004) found that individuals stayed on average 6 h in a burrow and once abandoned, they started excavating a new burrow instead of reoccupying the old one in areas with dense *P. clarkii* populations. The inefficient use of burrows in combination with warmer summers due to climate change may lead to large amounts of removed bank sediments and possibly to collapses of dikes. For water managers, more insight is needed in how to prevent such massive burrowing. More knowledge on how to reduce burrowing activity as well as more knowledge of factors governing *P. clarkii* population dynamics are essential for a proper managing these invaders.

Conclusion

In conclusion, the present experiment shows that burrowing behaviour among freshwater crayfish is species-specific and for some species sex specific. This study also shed light on how crayfish will alter their burrowing behaviour in response to climate change. Droughts are likely to increase in certain areas in the world, and our results show that early warning signals of drought increase burrowing behaviour for certain species. The response to burrowing triggers is species-specific with lack of shelter as a strong driver to burrow for *A. astacus*, *F. limosus* and *F. virilis*, while increased light intensity triggers burrowing behaviour in *P. leptodactylus*, *P. acutus* and *P. clarkii* and lowered activity of *F. limosus*. Increased water temperature was the most important trigger for *P. clarkii* to burrow. The presence of a conspecific reduced burrowing activity in *A. astacus* and *P. leniusculus* and triggered *F. virilis* to escape. Testing in a field situation whether more complex habitats indeed result in lower burrowing activity together with more knowledge on the causes of the species-specific responses and population dynamics may help managing populations of these invasive species.

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Data availability The data underlying this study are included in the published article and can be found in Online Resource 2.

Declarations

Conflict of interest All authors declare to have no competing interests.

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