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The potential competitive impact of the climate change indicator Montagu's crab (*Xantho hydrophilus* Herbst, 1790) on juvenile edible crab (*Cancer pagurus* Linnaeus, 1758)

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Bachelor of Science in Zoology

Submitted to Swansea University in fulfilment of the requirements for the Degree of MRes Biosciences

Swansea University

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ABSTRACT

Climate change is driving distribution shifts globally, and these shifting species can be considered indicators for the environment. The northward range expansion of Montagu's crab *Xantho hydrophilus*, a shift recently observed along the southeast coast of the UK, has earned this Lusitanian xanthid the climate change indicator tag. *X. hydrophilus* densely populates rocky, boulder-rich shores, in which it likely competes with other intertidal animals. Of those, other crabs occupying an overlapping niche are likely to be *X. hydrophilus*' most significant competitors, including the commercially important edible crab *C. pagurus*. In this study, laboratory experiments testing interference competition for refuge and prey between adult *X. hydrophilus* and juvenile *C. pagurus* were conducted through multiple trial treatments, which incorporated various species, size and density combinations. By running these trials, I sought to test my hypotheses that the more robust *X. hydrophilus* would outcompete, overpower and displace *C. pagurus*. Interspecific concurrence interfered with foraging for both species, however *X. hydrophilus* dominated size-matched *C. pagurus* in agonistic interactions, and were only matched by considerably size-advantaged *C. pagurus*. *X. hydrophilus* were also overwhelmingly dominant at refuge retention and displacement versus *C. pagurus*, yet more tolerant of cohabitation, particularly with conspecifics. In contrast, *C. pagurus* were hyperaggressive versus conspecifics yet more passive and subordinate to *X. hydrophilus*, which was evident in both foraging and refuge trials. This study suggests that *X. hydrophilus* is not only a superior competitor to juvenile *C. pagurus*, but could potentially saturate rocky shore refuge due to high degrees of refuge dependency and conspecific tolerance. This could result in the exclusion of *C. pagurus* from its nursery habitat, culminating in population bottlenecks. However, the poorly understood *X. hydrophilus* requires further research in order to substantiate the conclusions of this study and impel consideration for active population monitoring.

LAY SUMMARY

Climate change is driving global, unpredictable changes to the distributions of many species. As species shift into new habitats and new communities, they can have a profound impact on the native ecosystem by interacting with native species. It is therefore imperative for conservationists to identify the possible changes these shifters could cause, and understanding possible species interactions is an advantageous foundation. In this study, I conducted laboratory experiments to investigate whether two species of crab, both native to the UK, compete for food and refuge. *Xantho hydrophilus*, or Montagu's crab, is largely restricted to southwestern shores, however it has recently been labelled a climate change indicator species due to its apparent north-easterly shift. As ours sears warm, this crab may become progressively more abundant on more northward rocky shores. *Cancer pagurus*, the brown crab or edible crab, is a large and commercially important species predicted to suffer from the impacts of climate change. The intertidal zone is a critical nursery habitat for this crab, as they rely on this area to mature before migrating to deeper water. As refuge and food are limited resources on intertidal rocky shores, juvenile *C. pagurus* are likely and compete with *X. hydrophilus*. To observe interactions between the two, I staged competitive trials in which crabs competed for food or refuge. All trials were done overnight and videorecorded so behaviours and results of conflict could be analysed. The trials were conducted as specific treatments, in which species, size or density of individuals varied, to identify whether outcomes depended on such factors. In foraging trials, interspecific coexistence had a negative impact on the foraging of both species. *X. hydrophilus*' physical dominance was clear, as the vast majority of interactions between size-matched individuals resulted in *C. pagurus* retreat. Considerably size-advantaged *C. pagurus* were much more competitive, but not dominant. In refuge trials, *X. hydrophilus* were dominant, spending more time in refuge than *C. pagurus* and being far more successful at both displacement and retention. Interestingly, *X. hydrophilus* were much more inclined to cohabitate refuge with another crab, particularly those of its own species. In contrast, *C. pagurus* were hyperaggressive when interacting with their own species, whilst most conflicts against *X. hydrophilus* resulted in passive retreat. The results of this study suggest that juvenile *C. pagurus* are subordinate to *X. hydrophilus*. Also, due to being more dependent on refuge and more tolerant of sharing with their own species, *X. hydrophilus* might saturate a rocky habitat's available refuge as they congregate in high densities. This could, amongst other ecological impacts, result in the exclusion of juvenile *C. pagurus* from their nursery habitat, which would have negative consequences for local *C. pagurus* populations. However, due to *X. hydrophilus* being so poorly understood, further research is advised in order to substantiate the conclusions of this study. Future studies should aim to fill the many ecological knowledge gaps on this species and clarify any further ecological impacts the crab may cause if it continues to shift.

Plate 1 Large (55 mm carapace width) adult male *X. hydrophilus*, a climate change indicator species, performing a stereotypical lateral merus display threat with its robust chelae.

UNIVERSITY DECLARATIONS AND STATEMENTS

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed Date 26 / 03 / 2022

This thesis is the result of my own investigations, except where otherwise stated. Where correction services have been used, the extent and nature of the correction is clearly marked in a footnote(s). Other sources are acknowledged by in-text citations giving explicit references. A bibliography is appended.

Signed Date 26 / 03 / 2022

I hereby give consent for my thesis, if accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

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STATEMENT OF EXPENDITURE

Student name: Joseph Peter Dowling

Student number: [redacted]

Project title: The potential competitive impact of the climate change indicator Montagu's crab (*Xantho hydrophilus* Herbst, 1790) on juvenile edible crab (*Cancer pagurus* Linnaeus, 1758)

Category	**Item**	**Description**	**Cost* (£)**
Equipment	Yale CCTV kit (4x cameras)	To record interactions. Quantity: 1	249.00
Equipment	Euro Plastic Storage Boxes	For holding and trial aquaria. Quantity: 10	137.40
Equipment	Food Containers (750 ml, 3 pack)	To segregate crabs in holding aquaria. Quantity: 4	26.40
Consumable	Fine Eco-Sand (15 kg)	For aquaria substrate. Quantity: 2	57.58
Equipment	Plastic Pipe Cutter	To cut barrier pipe. Quantity: 1	14.35
Consumable	Barrier Pipe (2 m)	For sump setup. Quantity: 1	7.69
Consumable	Flexible Hose (1 m)	For sump setup. Quantity: 10	47.88
Equipment	Push-fit Pipe Inserts	For sump setup. Quantity: 20	8.88
Equipment	Push-fit Tank Connectors	For sump setup. Quantity: 10	43.80
Equipment	Push-fit Hose Connectors	For sump setup. Quantity: 10	27.36

Category	Item	Description	Cost* (£)
	Twin Outlet Air Pumps	To aerate aquaria. Quantity: 2	44.26
Consumable	Air Tubing (6 m)	To aerate aquaria. Quantity: 2	10.42
Equipment	3-way Air Control Valves	To aerate aquaria. Quantity: 4	5.38
Equipment	Cylinder Air Stones (2 pack)	To aerate aquaria. Quantity: 3	6.77
Equipment	Fennstone Slate Caves	As refuge resource in competitive trials. Quantity: 4	86.16

TOTAL	733.33

* Included VAT and delivery fees where applicable.

I hereby certify that the above information is true and correct to the best of my knowledge.

Signature (Supervisor)

Signature (Student)

STATEMENT OF CONTRIBUTIONS

Contributor role	**Persons involved**
Conceptualization	JPD, JNG
Data Curation	JPD
Formal Analysis	JPD
Funding Acquisition	
Investigation	JPD
Methodology	JPD
Project Administration	JPD, JNG
Resources	JPD, JNG, TF
Software	
Supervision	JNG
Validation	
Visualisation	JPD
Writing – Original Draft Preparation	JPD
Writing – Review & Editing	JNG

ETHICS APPROVAL

Project Ethics Assessment Confirmation|Cadarnhad o Asesiad Moeseg Prosiect

C

cosethics@swansea.ac.uk
Wed 24/03/2021 16:18
To: DOWLING [redacted]
Cc: John Griffin

This is an automated confirmation email for the following project. The Ethics Assessment status of this project is: APPROVED

Applicant Name: Joseph Dowling
Project Title: Potential competitive exclusion of juvenile edible crab (Cancer pagurus) by Montagu's crab (Xantho hydrophilus), a climate change indicator species.
Project Start Date: 15/02/2021
Project Duration: 6 months
Approval No: SU-Ethics-Student-240321/3702

NOTE: This notice of ethical approval does not cover aspects relating to Health and Safety. Please complete any relevant risk assessments prior to commencing with your project.

Neges awtomataidd yw hon ar gyfer y prosiect canlynol. Statws Asesiad Moeseg y prosiect hwn yw: APPROVED

Enw'r Ymgeisydd: Joseph Dowling
Teitl y Prosiect: Potential competitive exclusion of juvenile edible crab (Cancer pagurus) by Montagu's crab (Xantho hydrophilus), a climate change indicator species.
Dyddiad Dechrau'r Prosiect: 15/02/2021
Hyd y Prosiect: 6 months
Rhif y Gymeradwyaeth: SU-Ethics-Student-240321/3702

SYLWER: Nid yw'r hysbysiad hwn o gymeradwyaeth foesegol yn cynnwys agweddau sy'n ymwneud ag iechyd a Diogelwch. Dylech gwblhau unrhyw asesiadau risg perthnasol cyn dechrau eich prosiect.

H&S AND RISK ASSESSMENT FORMS

SECTION 1: GENERAL ARRANGEMENTS			
Proposed field trip by (group or individual): Individual (+ buddy)		**Status (undergraduate/postgraduate/staff):** Postgraduate (MRes student)	
Department: Biosciences Department (College of Science)		**Name of risk assessor:** Joseph Dowling (ID: [redacted]	
Name Course Leader/Supervisor (if different): Dr. John N Griffin		**Course and course code (if applicable):** MRes thesis	
Is this trip for:			
a. Undergraduates		**a. Teaching Purposes**	
b. Postgraduates	X	**b. Thesis**	X
c. Staff		**c. Dissertation**	
d. Other		**d. Other research project**	
Location: Dale + Aberfelin			
Dates: Late March spring tide, spring tides in April / May	**From:** 45 minutes before low tide	**To:** point of tide turning	

SECTION 2: DETAILED ITINERARY	
Place of Departure: Home address (Ponthirwaun, Ceredigion)	**Destination(s):** - Dale, Pembrokeshire - Aberfelin, Pembrokeshire
Mode of transport/travel arrangements: Personal car	**Dates of stay at accommodation:** N/A
Name, address and telephone number of accommodation: N/A	**Name. address and telephone number of fieldwork base camp (if different):** N/A
Summary of proposed activities: - To collect crabs and prey items (molluscs + macroalgae) for laboratory experiments	
Equipment/techniques to be used: - Measuring callipers, to measure carapace width of crabs - Storage tubs, for storing and transporting crabs and prey - Gloves, for lifting boulders	

SECTION 3: PRE-TRIP PREPARATION AND CHECKS	
Insurance (please specify personal, third party, travel, equipment) arranged with and date: N/A	
Equipment inventory attached?	**No**
List of field workers attached?	**No**
Ratio of staff to students identified to be necessary:	N/A
Health Checks & Vaccinations identified to be necessary (please specify): N/A	
Specific health requirements for individuals available to Course Leader?	**No**
Record of next of kin details for each individual available to Course Leader?	**No**
Record of Foreign Office Advice (to be checked immediately prior to overseas trips): N/A	

SECTION 4: DECLARATION		
The above has been completed to the best of my/our knowledge and is an accurate identification of the known or foreseeable hazards and of the safety controls to be followed		
Risk Assessor	**Signature:** [redacted]	**Date:** 17/03/2021
Worker or course leader	**Signature:**	**Date:**
Supervisor	**Signature:** [redacted]	**Date:** 17/03/2021
Health and Safety Co-ordinator	**Signature:**	**Date:**

Name of Person Undertaking Assessment		Date Conducted:	Field trip/Field work being undertaken					
Joseph Dowling		17/03/2021	MRes crab collection fieldwork					
Ref No	**Hazard under review**	**No & Description of Staff/Students/Others Involved**	**Existing Controls**	**Assessed Level of Risk**			**Further Action Required**	**By (Date) + Review Date**
				L	**M**	**H**		
Physical Hazards (e.g. extreme weather, mountains and cliffs, quarries, excavations, marshes and quicksand, fresh or seawater, etc – specify precisely which apply)								
	Cold and wet weather - hypothermia	1 MRes student, 1 buddy	Consult weather forecast before setting out, plan contingency days in anticipation of bad weather, wear appropriate clothing, bring additional clothing / items to prepare for variable weather conditions and ensure availability to plenty of food and water.	X				
	Tide	1 MRes student, 1 buddy	Consult tide tables, plan work so that it is performed on a falling tide	X				
	Uneven terrain	1 MRes student, 1 buddy	Wear appropriate footwear and avoid walking over visibly uneven / unbalanced terrain where possible.		X			
	Slippery terrain	1 MRes student, 1 buddy	Wear appropriate footwear and avoid walking over wet rock, particularly when covered in wet macroalgae, where possible.		X			
	Deep water	1 MRes student, 1 buddy	Avoid crossing active channels, work on a falling tide, do not enter fast flowing water and do not enter water above knee height.	X				
Biological Hazards (e.g. poisonous animals or plants, aggressive animals, soil (tetanus), freshwater where rats may be endemic (leptospirosis or Weil's disease), dense vegetation (where Lyme disease from sheep ticks could be endemic), insects, hygiene, etc – specify precisely which apply)								
	Aggressive crustaceans	1 MRes student	Wear gloves when exploring crevices and turning boulders and ensure crabs are captures and held safely, with thumb and index finger firmly gripping carapace edges behind the chelal limbs.		X			
	Shelled / spiked animals adhering to rocky surfaces	1 MRes student, 1 buddy	Wear appropriate footwear, wear gloves when exploring crevices and turning boulders and ensure organisms are not being used for fingerhold when turning boulders.		X			
	Cnidarian	1 MRes student, 1 buddy	Wear gloves when exploring crevices and turning boulders and never touch a beached individual.	X				
	Lesser weaver fish	1 MRes student, 1 buddy	Wear appropriate footwear and wear gloves when exploring crevices and turning boulders.	X				
Chemical Hazards (e.g. pesticides, dusts, contaminated soils, chemical brought on the site, biological fixatives, etc – specify precisely which apply)								
Man-made Hazards (e.g. electrical equipment, machinery, transport and vehicles, insecure buildings, slurry and silage pits, power and pipelines, military property – specify precisely which apply)								
Personal safety (e.g. lone working, night working, attack on person or property, cultural difference, poor communication/remoteness etc – specify precisely which apply)								
	Relative remoteness	1 MRes student, 1 buddy	Bring sufficiently charged phone in case of emergency.	X				
Environmental Hazards (e.g. pollution, rubbish, disturbance of ecosystem, etc – specify precisely which apply)								
	Disturbance of ecosystem	1 MRes student, 1 buddy	Minimize unnecessary trampling on sensitive organisms, take care whilst lifting / returning boulders and ensure no plastic / artificial pollution is left on site.	X				
COVID-19 Hazards (specify precisely which apply)								
	Present COVID-19 symptoms before fieldwork	1 MRes student, 1 buddy	Self-isolate for at least 7 days.	X				
	Contact with person presenting COVID-19 symptoms before fieldwork	1 MRes student, 1 buddy	Self-isolate for 14 days.	X				
	Present COVID-19 symptoms during fieldwork	1 MRes student, 1 buddy	Isolate the person, ensure they can return home, call NHS for advice.	X				
	Contact with person presenting COVID-19 symptoms during fieldwork	1 MRes student, 1 buddy	Isolate from the person presenting symptoms, ensure they can return home and follow NHS advice.	X				
	Potential contact with asymptomatic infected person	1 MRes student, 1 buddy	Cover nose and mouth with tissue or elbow when coughing or sneezing, wear appropriate PPE where necessary, minimise contact with public surfaces, minimise exposure to crowded public areas, maintain 2m social distancing, wash hands regularly and thoroughly with soap and water (>60% alcohol hand sanitiser when without hand washing facilities) and wash / sanitise field equipment after use.	X				
Other Hazards (e.g. working in other establishments, manual handling, working in other people's homes, trespassing, noise, change of schedule due to unexpected events -specify precisely which apply)								
	Change of schedule due to unexpected events	1 MRes student, 1 buddy	Consider bad weather or swell as result of bad weather and plan contingency days where necessary.	X				

Home Risk Assessment			
*Grey boxes must be completed by field leader			
College/ PSU	College of Science.	Assessment date	17/03/2021
Location	Home address.	Assessor	Joseph Dowling [redacted]
Activity	Keeping live crabs and mussels, conducting behavioural experiments.	Approved by	Dr. John N Griffin
		Review date (if applicable)	
Associated documents			

Part One: Risk Assessment

What are the hazards?	Who might be harmed?	How could they be harmed?	What are you already doing?	Do you need to do anything else to manage this risk?
COVID-19, contraced via close contact with contagious person(s), or via touching eyes, nose or mouth following contact with a contaminated surface.	Student Household members	Minor illness. Severe illness. Death.	When outside household / at public location… - Maintain social distancing measures at all times. - Minimise contact with public surfaces. - Wash hands regularly and thoroughly with soap and water. - Sanitise (>60% alcohol) hands regularly and thoroughly when without access to hand washing facilities. - Keep unsanitised hands away from eyes, nose and mouth. - Wear appropriate PPE where necessary. If myself or a household member shows symptoms, isolate in accordance with government guidelines.	
Electronics that are exposed to wetness.	Student Household members	Electrocution.	Do not operate electronic equipment with wet hands. Handle wet samples in designated "wet" areas to prevent water contact with electronics and sockets. Ensure all equipment is in service date and has been tested for electrical safety, and has no visible damage.	
Wet / slippery flooring, due to water spillage.	Student Household members	Losing footing and falling, causing anything from minor to severe injury.	Wear appropriate footwear at all times. Dry spillages immediately.	

Actions arising from risk assessment

Actions	Lead	Target Date	Done Yes/No

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INTRODUCTION

Climate change is an ongoing and escalating ecological threat, forcing individualistic responses amongst species and endangering those that fail to either adapt or track their niche (Ash et al., 2017; Pucko et al., 2011). The impacts of climate change are community specific as species distributions may constrict, expand or shift in response (Hawkins et al., 2019; Helmuth et al., 2006; Shoo et al., 2006). Climate-induced shifting can cause species to transcend into ecosystems previously inaccessible due to their climate envelope, which constitutes the climatic boundaries of a species' fundamental niche (Pearson & Dawson, 2003). These shifters can create biotic mismatches as their response to climate change may greatly differ from the other, long-established species native to their extended range (Parmesan, 2006). This can harm the richness and diversity of native ecosystems and destabilise communities as species assemblages change and interaction links collapse (HilleRisLambers et al., 2013; Tepolt & Somero, 2014).

Intertidal species naturally push their thermal boundaries and thus may serve as effective early indicators of climate change-induced stress (Wethey & Woodin, 2008). The intertidal zone is a rich ecosystem that occupies the boundary between terrestrial and marine systems, providing important services such as biogeochemical cycling and protection from tidal erosion (Bishop-Taylor et al., 2019; Hu et al., 2019; Wang et al., 2018). Intertidal ecology is highly variable because communities follow a gradient of environmental pressures perpendicular to the shoreline; this is known as vertical zonation (Chappuis et al., 2014). On rocky shores, zonation is often conspicuous due to the formation of canopy-forming macroalgae; foundation species and ecosystem engineers distributed by species-specific tolerances that ameliorate environmental conditions for sheltered communities (Lalegerie et al., 2020; Scrosati & Ellrich, 2018). Abiotic intertidal pressures include desiccation and excessive saline, thermal and light stress, which are most intense at upper intertidal zones (Quigley et al., 2020). The gradient of community resilience, from the more tolerant upper intertidal to the sensitive lower intertidal, sees intertidal assemblages vary greatly across a small vertical range (Somero, 2002).

Projected climate-induced alterations for many species distributions suggest changes within intertidal communities are inevitable (Wilson et al., 2019). Such changes will

likely include species interactions, which are central to ecological stability and functionality (Bairey et al., 2016; Valiente-Banuet et al., 2014). As intertidal systems are often compact and diverse, communities are often strongly interdependent and resource-driven competitive interactions are common (Dungan, 1986; Wood et al., 2010). Range shifts may destroy or construct interaction links due to species-specific responses to climate change. For example, prey may shift away from its predator's climate envelope, or a species could shift into a novel region and compete with a functionally similar native for limited resources (Bertness et al., 1999; Sorte et al., 2010). This complicates long-established demographic patterns as a species' population may diminish if it shifts into the range of a predator (Harley et al., 2006), or proliferate if it shifts into the range of prey (HilleRisLambers et al., 2013)

Existing work on UK intertidal range shifts is largely focussed on grazers and suspension feeders, specifically northwardly expanding lusitanian (southern) species or northwardly receding boreal (northern) species, with impacts including changes in macroalgal suppression, community diversity and rocky space coverage (Herbert et al., 2003; Hawkins et al., 2008; Mieszkowska et al., 2006; Moore, 2005). Shifted consumers may construct complex interactions in lower trophic levels through top-down force (Bertness & Callaway, 1994; Pallini et al., 1998; Persson, 1991) and / or compete directly with functional analogues (Tallian et al., 2017). However, capacities for behavioural plasticity, niche flexibility or interspecific avoidance could be realised instead (Cimino et al., 2016; Lovari et al., 2013; Tallian et al., 2017). Shifters can also significantly alter dominance hierarchies as sensitive species are prone to displacement by more tolerant or novel species (Gilman et al., 2010). In the event of competitive exclusion, the newly established shifted consumer and its unique behavioural ecology may disorganise a food-web, even if it seems a functional analogue to the previously established consumer (Hawkins et al., 2008).

Predicting a shifting consumer's impact may be more convoluted when concerning an omnivore, as those occupying high trophic levels are key to community functionality due to their foraging activity across trophic levels (Coll & Izraylevich, 1997). A top predator can apply both competitive and predatory pressure on a meso-predator in the form of intraguild predation, in which case cascading effects are dependent on prey availability and the relative strengths of each negative interaction in the system (Eriksson et al., 2011; Navarrete et al., 2000). As omnivores also incorporate

herbivory, their foraging habits and ramifications on the ecosystem can be even more difficult to identify and interpret (Agrawal & Klein, 2000). Range shifts and consequential interactions can be considered threats towards ecosystem function (Walther, 2010), therefore a shifting, generalist omnivore occupying a high trophic level may have profound effects on a community.

Crabs benefit from the locomotory and protective gains provided by carcinization and are key intertidal predators, possessing many trophic linkages across the intertidal-subtidal boundary (Silva et al., 2010; Wolfe et al., 2021). Crabs are considered generalist arthropod predators, exerting significant top-down control across trophic boundaries by consuming both primary and secondary consumers (Edwards et al., 1982; Snyder & Evans, 2006). Crabs facilitate trophic cascades and can even be considered keystone species due to the disproportionate impact they can impose on a community (Boudreau & Worm, 2012). Many crabs are omnivorous and can have profound and complex effects on a community, such as both suppressing and contributing towards herbivory (Lohrer et al., 2000; Wolcott & O'Connor, 1992). Such a generalist nature also ensures most crabs are not subjected to the bottom-up pressure of food scarcity (Meyer & Byers, 2005), and a handful of invasive crabs cause profound ecological and economic concern; impacts include the disruption of native trophic systems (Grosholz et al., 2000), the depletion of commercially important molluscs (DeGraaf & Tyrrell, 2004; Kimbro et al., 2009) and the destructive erosion and subsidence of waterside embankments (Gilbey et al., 2008). Crabs can also be effective, easily observable indicators of ecological change within the intertidal zone due to their impact on ecosystems and ease of sampling (Morgan et al., 2006).

Sympatric crabs avoid niche overlap due to distinct environmental preferences (Lima et al., 2014; Lohrer et al., 2000; Silva et al., 2014), and niche partitioning has also been observed in sympatric species (Arab et al., 2015). However, crabs are often segregated due to direct, agonistic competition for limited resources including food and especially refuge (Navarrete & Castilla, 1990; Orensanz & Gallucci, 1988). Direct, hierarchy-forming conflicts are often dictated by chelal proportions (Lee & Seed, 1992), and size-structured intraguild predation is a common interaction between sympatric crabs (Griffen & Byers, 2006; Rogers et al., 2018). Interaction types and strengths can vary greatly between species, therefore understanding how sympatric crabs interact, both interspecifically and intraspecifically, is an important step towards understanding the

entire community due to their vast trophic linkages (Griffen & Byers, 2009; Griffen & Delaney, 2007; Mascaró & Seed, 2001; Yamada & Boulding, 1996).

In this study, I investigated direct interactions between two crabs native to the southwestern UK; *Cancer pagurus* (Brachyura: Cancridae) and *Xantho hydrophilus* (Brachyura: Xanthidae). Preceding an ontogenetic migration towards deeper water (McKeown et al., 2017), juvenile *C. pagurus* (brown / edible crab) utilise the intertidal zone as a critical nursery habitat, as done by many species due to the abundance of diverse microrefugia and relative scarcity of large predators (Cowan, 1999; Moring, 1986). Rocky microhabitats such as cobble and boulders are considered optimal for juvenile *C. pagurus*, as these provide structurally complex refuge from biotic and abiotic threats (Heraghty, 2013; Robinson & Tully, 2000). *X. hydrophilus* (Montagu's crab), a small yet robust crab wielding large chelae, also occupy these rocky microhabitats in the lower intertidal zone and are thought to be refuge-dependent due to their weak mobility (Hayward et al., 1974; Flores & Paula, 2001; Pallas et al., 2006). These two crabs may interact and compete within the intertidal zone, however interactions between these species have not been investigated prior to this study.

X. hydrophilus is historically considered a lusitanian species (Hayward et al., 1974), and is now labelled a climate-change indicator species due to recent anecdotal reports suggesting a northward range expansion (DWT, 2019). This poorly understood crab may therefore be a viable reference for monitoring intertidal ecological shifts (Siddig et al., 2016), and potentially contribute to ecological change by displacing prey and competitors. The more boreal *C. pagurus* is much more thoroughly studied, possessing substantial commercial value in the UK (FAO, 2018). As a stenohaline osmoconformer, this cancrid is predicted to struggle following impending changes in marine temperature, acidity, salinity and CO_2 concentrations, with potential effects including exoskeleton malformation, failed larval development and a narrowed thermal tolerance breadth (Mangi et al., 2018; Metzger et al., 2007; Weiss et al., 2009; Whiteley et al., 2018). Climate change may therefore be detrimental for *C. pagurus*, a species already threatened by destructive anthropogenic activity including dredging and dumping (Howard, 1982; Jenkins et al., 2001; Öndes et al., 2016). *X. hydrophilus*' sensitivity is unknown, however the xanthid's anticipated range expansion due to climate change implies more resilience.

The objective of this study was to determine whether adult *X. hydrophilus* could outcompete and exclude juvenile *C. pagurus* from the intertidal zone or vice versa. To achieve this, I staged competitive trials under controlled conditions, a practice conducted extensively to analyse direct interactions between sympatric crabs (Jensen et al., 2002; MacDonald et al., 2007; McDonald et al., 2001). These trials were video recorded and later examined to quantify the type and result of each physical interaction and deduce the winner of each resource contest, with win conditions outlined in the methods. In doing so, I tested the following hypotheses:

1. The presence of adult *X. hydrophilus* has a negative impact on equivalently sized juvenile *C. pagurus*' resource use.
2. Adult *X. hydrophilus* dominates equivalently sized juvenile *C. pagurus* in agonistic interactions.

Specific trial treatments sought to reveal whether factors such as competitor species, size and density influence alter both species' competitive ability and the results of each treatment are discussed, along with the established understanding on the ecology of these crabs, to extrapolate on how this specific interaction link may transpire in the intertidal zone.

METHODS

Species sampling

Focal species sampling and laboratory experiments took place from May through August 2021. *X. hydrophilus* and *C. pagurus* were each collected by hand from two rocky intertidal habitats in south-west Wales. *X. hydrophilus* were very abundant at Dale (Pembrokeshire), therefore sampling took place at this site. *C. pagurus* do not populate shores so densely, so sampling for this species took place at both Dale and Aberfelin (Pembrokeshire) to collect enough viable individuals. *X. hydrophilus* are also very abundant at Aberfelin, therefore the crabs are sympatric at both sites. Both sites are fully marine, sheltered and boulder-rich. Crabs were sampled at the lower intertidal, as close as possible to the intertidal-subtidal boundary, by turning boulders.

All crabs were intermoult and lacked any visible external damage, parasitism, disease or epiphyte coverage. All *X. hydrophilus* individuals were of large adult size, at 55mm (± 2 mm) carapace width (hereafter abbreviated to CW), whereas juvenile *C. pagurus* were collected at 55 mm (± 1 mm) and 80 mm (± 2 mm) CW. The smaller size was chosen to size-match *X. hydrophilus* for a 'fair' contest, whilst the larger size tests whether interactions are size-dependent. Only male crabs, identified by their narrow pleons, were collected to prevent sex influencing results. Individuals were only used for a single trial each to avoid pseudo-replication and non-independence in the data.

Tank setups

Crabs were housed in opaque holding tanks (60L x 40W x 40H cm) and segregated individually in opaque, perforated containers (15 x 15 x 8 cm) to prevent captive conflict. Photoperiod regime was controlled (14L : 10D h) whereas seawater conditions were ambient (17 ± 1 °C, 30 ± 1 ppt). Sumps containing air stones ensured continuous aeration and circulation within the holding tanks. Opaque experimental tanks (60 x 40 x 40 cm) possessed the same conditions and sump setups as above, with an additional 1 cm layer of fine sand providing a natural substrate without enabling burial. Experimental tanks possessed 25 cm water depth for all trials bar competitive refuge trials, for which the depth was decreased to 10 cm to emulate low-tide conditions and stimulate refuge use. All tanks were subject to daily partial (25%) water changes, with experimental tanks completely emptied, rinsed and refilled with fresh seawater and sand after each trial to delete residual cues left by previous competitors. Crabs were isolated for a 72 h starvation period prior to use in trials, which standardised satiation and acted as an acclimatisation period.

Competitive foraging trials

X. hydrophilus dietary preference trials (Appendix 1) implied that large (12 – 13 mm CW) *Porcellana platycheles* (Anomura: Porcellanidae) were a preferred prey for this species. As this is also a recognised prey for *C. pagurus* (Amaral et al., 2009; Lawton, 1989), large *P. platycheles* were used as the prey resource throughout foraging trials. These trials were conducted in three distinct treatments: 1) interspecific (n = 16, one

55 mm *X. hydrophilus* and one 55 mm *C. pagurus*), 2) intraspecific (n = 8, two 55 mm *X. hydrophilus* / n = 9, two 55 mm *C. pagurus*) and 3) intersize (n = 12, one 55 mm *X. hydrophilus* and one 80 mm *C. pagurus*). Intraspecific and intersize trials were designed to test whether resource use and the result of interactions are species and / or size dependent for either species, the latter of which being relevant due to the occasional intertidal occurrence of large juvenile *C. pagurus*. Solo trials, consisting of only a single crab and the prey resource, acted as controls for each species' foraging behaviour.

The set-up of the experimental tanks for foraging trials is illustrated in Figure 1a. Only one prey resource, tethered to a set location, was offered per trial. This was done to encourage competitive interactions between the two crabs. Crabs were introduced simultaneously, within their opaque containers, at opposite sides of the tank and equally distant from the prey. Crabs were left to acclimatise for 30 min at 19:30:00, with release at 20:00:00 marking trial onset. Foraging trials were done overnight due to preliminary observations suggesting both species to be primarily nocturnal, therefore foraging activity should occur overnight. All trials ceased at 08:00:00 the following day, therefore 12 h total duration. 08:00:00 was chosen as the cessation point due to crabs consistently becoming inactive at approximately this period. All trials were video recorded for their entire duration using Yale CCTV SV-4C-4ABFX-2 cameras assembled directly above the experimental tanks. The camera's infrared night vision should not have influenced the behaviour of either competitor as brachyuran crabs are unable to detect infrared (Cronin, 1986).

Time taken to locate prey and time spent occupying prey were recorded, with wins awarded based on the following conditions:

1. The competitor to first locate the prey resource.
2. The competitor occupying the prey resource until total consumption or satiation, the latter indicated by the occupier dropping the prey resource without being provoked.

All direct interaction were assessed for the specific behaviours involved (defined in Box 1) and the aftermath of said behaviours, with a win awarded to the competitor that forced its opponent to retreat. All trials were analysed for interactions, however trials were discarded from foraging analysis if neither competitor exhibited foraging

behaviour. For the purpose of this study, foraging behaviour was indicated by a competitor clearly engaging with the prey resource. Trials were repeated until eight featuring clear foraging behaviour occurred for each treatment.

Competitive refuge trials

Refuge trials were conducted in three distinct treatments: 1) interspecific (n = 8, two 55 mm *X. hydrophilus* and two 55 mm *C. pagurus*), 2) intraspecific (n = 8 four 55 mm *X. hydrophilus* / n = 8, four 55 mm *C. pagurus*) and 3) interdensity (n = 8, three 55 mm *X. hydrophilus* and one 55 mm *C. pagurus*). Intraspecific and interdensity trials were designed to test whether resource us and the result of interactions are species and / or density dependent for either species, the latter of which being relevant due to the high densities of *X. hydrophilus* observed at collection sites. Solo trials, consisting of only a single crab and the refuge resources, acted as controls for each species' foraging behaviour.

The set-up of the experimental tanks for refuge trials is illustrated in Figure 1b. Two sources of refuge (slate caves) were offered per trial. Cave dimensions (50 x 80 x 50 mm) were only spacious enough to comfortably accommodate a single crab to force interaction if a competitor approached preoccupied refuge (Zhang et al., 2019). A solid sheet blocked crabs from traversing behind and potentially displacing the refuge. Crab introduction and acclimatisation followed the same protocol as for foraging trials. As with foraging trials, refuge trials were done overnight. Naturally, crabs would be active throughout the night then compete for refuge as daylight approaches, therefore 'losers' would be excluded come trial conclusion. All trials ceased at 06:00:00 the following day, therefore 10 h total duration. 06:00:00 was chosen as the cessation point due to no migration to-and-from refuge occurring after this period. All trials were video recorded for their entire duration using the same camera system as for foraging trials.

Time taken occupying and time spent cohabitating refuge were recorded, with wins awarded based on the following conditions:

1. The competitor occupying the refuge resource for the longest period.
2. The competitor(s) occupying the refuge resource at trial cessation.

All direct interactions concerning the refuge resource were assessed for the specific behaviours involved (defined in Box 1) and the aftermath of said behaviours, with a win awarded to the competitor that forced its opponent to retreat.

Statistical analysis

All analyses were conducted in R version 4.0.3. Shapiro-Wilk tests were used to identify non-normality within the data before comparative analyses were performed. To compare competitive resource use, the time spent locating and occupying the prey resource were analysed in foraging trials, whereas the time spent occupying and cohabitating refuge resources were analysed in competitive refuge trials. As a general rule, analysis between species was done via Welch two sample t-tests (or Wilcoxon rank sum as a non-parametric alternative), whilst analysis across treatments was done for each species via ANOVA (or Kruskal-Wallis rank sum) tests, with some variation on this rule based on independent variable count. Tukey HSD post-hoc pairwise comparison followed ANOVA, whilst Dunn's test with Bonferroni correction followed Kruskal-Wallis. The same set of tests were also used to analyse the frequency of defined behaviours when the competitors interacted, as well as the aftermath of said behaviours. Behaviour frequency and result data were converted to proportions prior to analysis. Lastly, binomial proportion tests were used to compare the proportional occurrence of foraging activity in foraging trials, as well as the proportional win rates for resource use and interactions across competitive trials.

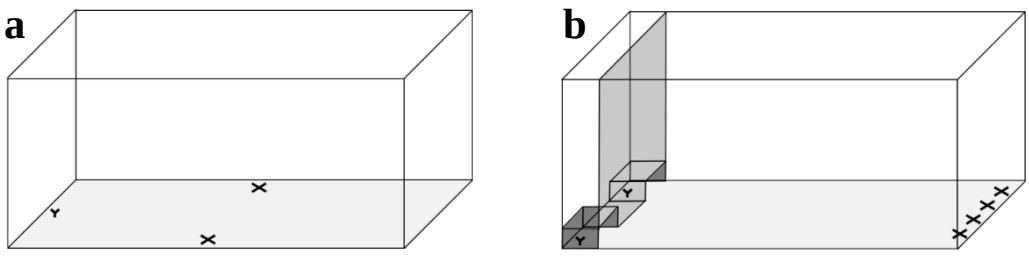

Figure 1 Schematic illustration of the experimental tanks for a) competitive foraging trials, and b) competitive refuge trials. In both diagrams, X represents the locations where competitors were released, whilst Y represents the location of the limited resource

Box 1: Interaction definitions

Many adapted from previous studies by MacDonald et al. (2007), Sciberras & Schembri (2008) and Wright (1968).

Foraging trial interactions:

Passive approach: An approach towards a competitor without intention to interact agonistically.

Assertive approach: An approach towards a competitor with clear intention to interact agonistically, often with merus display and / or attack.

Submission: Medial merus display, body slightly lowered, chelae withdrawn slightly beneath body.

Threat: Lateral merus display (LMD) as defined by Wright (1968), body slightly raised, chelae extended.

Attack: Clear and intended chelal action to physically deter competitor by grasping or striking.

Retaliation: As above but reciprocated in response to an initial chelal attack.

Predation: Prolonged attempt to attack with clear intent to consume opponent.

Retreat: Cessation of interaction by subordinate moving at least one body length away from competitor.

Escape: As above but in event of predation.

Autotomy: Voluntary appendage-loss by the subordinate competitor.

Refuge trial interactions:

Passive approach: An approach towards occupied refuge without intention to interact agonistically.

Assertive approach: An approach towards occupied refuge with clear intention to interact agonistically, often with merus display and / or attack.

Passive defence: Refusal to vacate refuge in response to an approaching competitor without intention to interact agonistically, or a near instantaneous vacation of refuge.

Assertive defence: Refusal to vacate refuge in response to an approaching competitor with clear intention to interact agonistically, often with merus display and / or attack.

Interaction outcomes:

Win / Success: Opposing competitor retreats.

Cohabitation: Prolonged sharing of refuge (only applicable to refuge trials).

Loss / Failure: Competitor retreats.

RESULTS

Competitive resource use

Foraging activity occurred in every solo trial for both species and all *X. hydrophilus* intraspecific trials. However, one *C. pagurus* intraspecific trial, eight interspecific trials and four intersize trials were devoid of foraging activity as neither crab exhibited interest in the prey item throughout. Both *X. hydrophilus* and *C. pagurus* exhibited foraging activity significantly more often in their respective solo and intraspecific trials than during interspecific and intersize trials (Table 1).

Table 1 Output of statistical analyses comparing the occurrence of foraging behaviour across treatments for each species. **Bold** p values indicate statistical significance at alpha 0.05.

Species	Pair	df	X^2	p
	OCCURRENCE OF FORAGING BEHAVIOUR			
Cancer pagurus	Solo – Intraspecific	1	< 0.001	1
	Solo – Interspecific	1	7.573	**0.006**
	Solo – Intersize	1	6.328	**0.012**
	Intraspecific – Interspecific	1	5.531	**0.019**
	Intraspecific – Intersize	1	4.412	**0.036**
	Interspecific – Intersize	1	< 0.001	1
Xantho hydrophilus	Solo – Intraspecific	1		
	Solo – Interspecific	1	11.1	**< 0.001**
	Solo – Intersize	1	6.328	**0.012**
	Intraspecific – Interspecific	1	11.1	**< 0.001**
	Intraspecific – Intersize	1	6.328	**0.012**
	Interspecific – Intersize	1	0.194	0.659

Results for refuge use are presented in Tables 2 – 4. There were no significant differences in time spent locating prey between *X. hydrophilus* and *C. pagurus* in any treatment, however *C. pagurus* took significantly longer to locate prey in the presence of a size-matched heterospecific than when alone (Figure 2a). *C. pagurus*' time spent occupying prey was significantly faster than *X. hydrophilus* in intraspecific, interspecific and intersize trials and did not vary across treatments, whereas *X. hydrophilus* consumed prey faster alone and when paired with a conspecific than when paired with a heterospecific and a larger heterospecific respectively (Figure 2b).

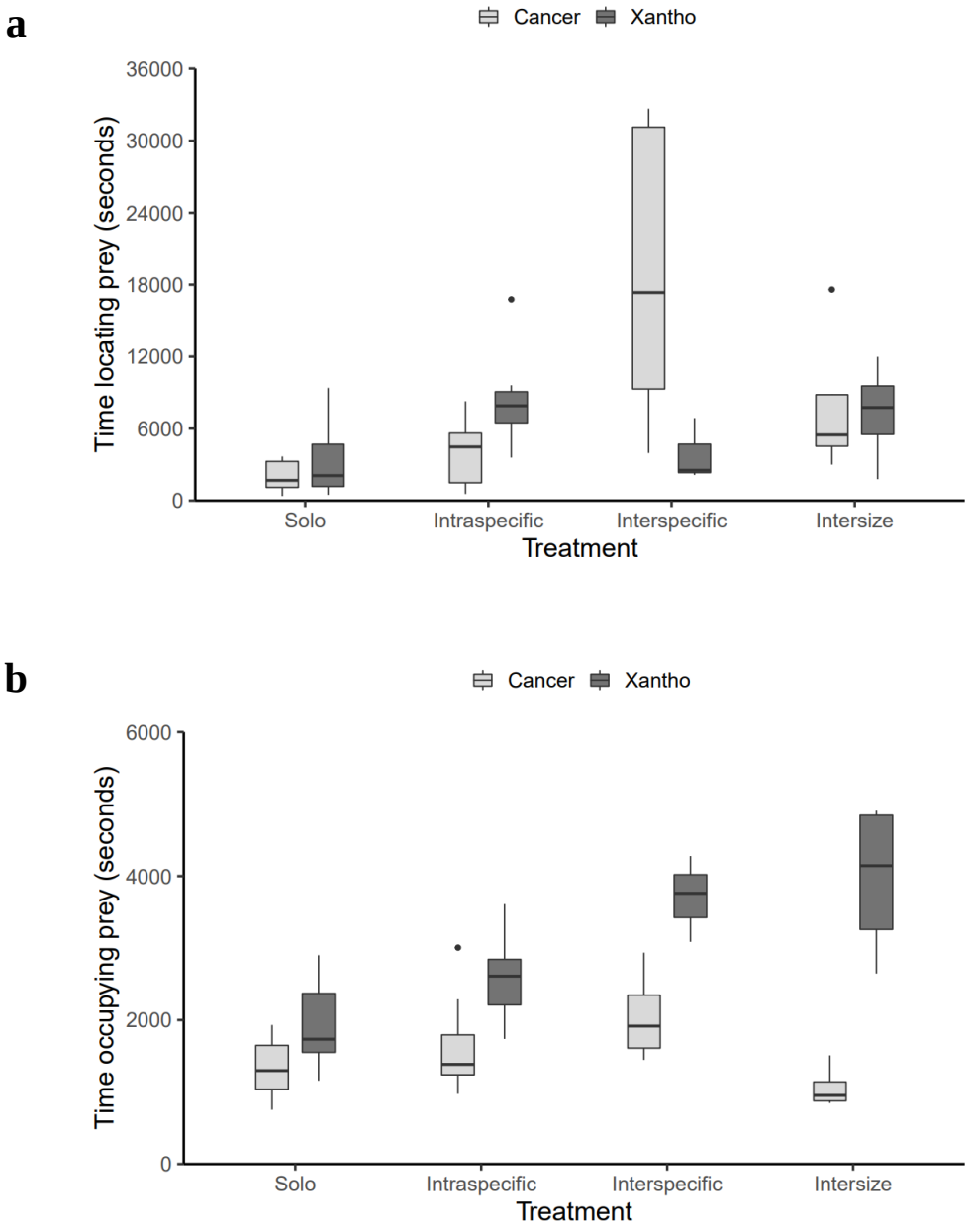

Figure 2 Difference in time spent **a**) locating and **b**) occupying the prey resource between species, within and across competitive foraging treatments. N = 8 per treatment. Boxplots show the data's minimum, lower quartile, median, upper quartile and maximum.

X. hydrophilus occupied refuge for significantly more time than *C. pagurus* in all treatments, and occupation did not change significantly across treatments for either species (Figure 3). *X. hydrophilus* cohabitated refuge for significantly more time than *C. pagurus* in their respective intraspecific trials, with no difference detected for interspecific and interdensity trials (Figure 4a). *X. hydrophilus* did not vary in cohabitation across treatments, however *C. pagurus* cohabitated in both interspecific and interdensity trials significantly more often than during intraspecific trials The three possible interspecific trial cohabitation links differed as the *X. hydrophilus* – *C. pagurus* link cohabitated significantly more than the *C. pagurus* – *C. pagurus* link, however no such significant difference was found in interdensity trials (Figure 4b).

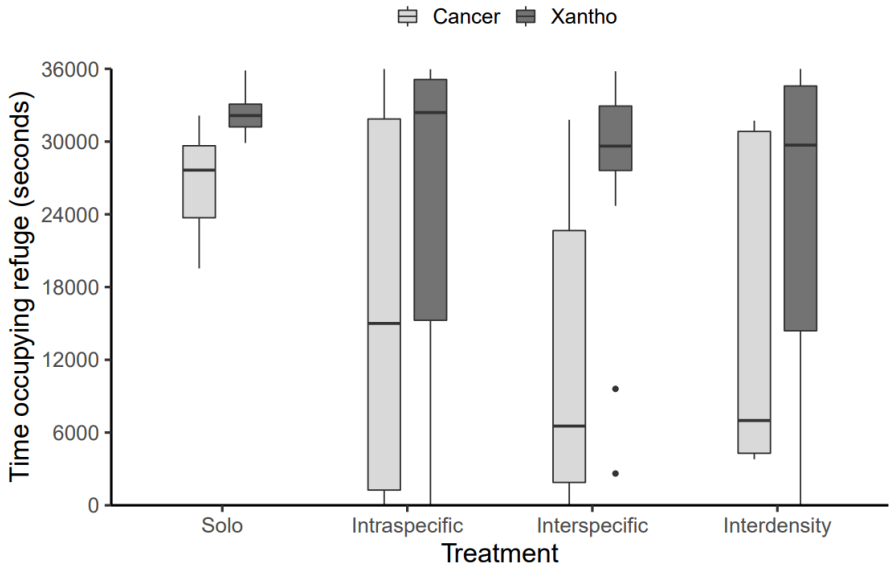

Figure 3 Differences in time spent occupying refuge between species, within and across treatments. N = 8 per treatment. Boxplots show the data's minimum, lower quartile, median, upper quartile and maximum. Outliers are points beyond the minimum and maximum.

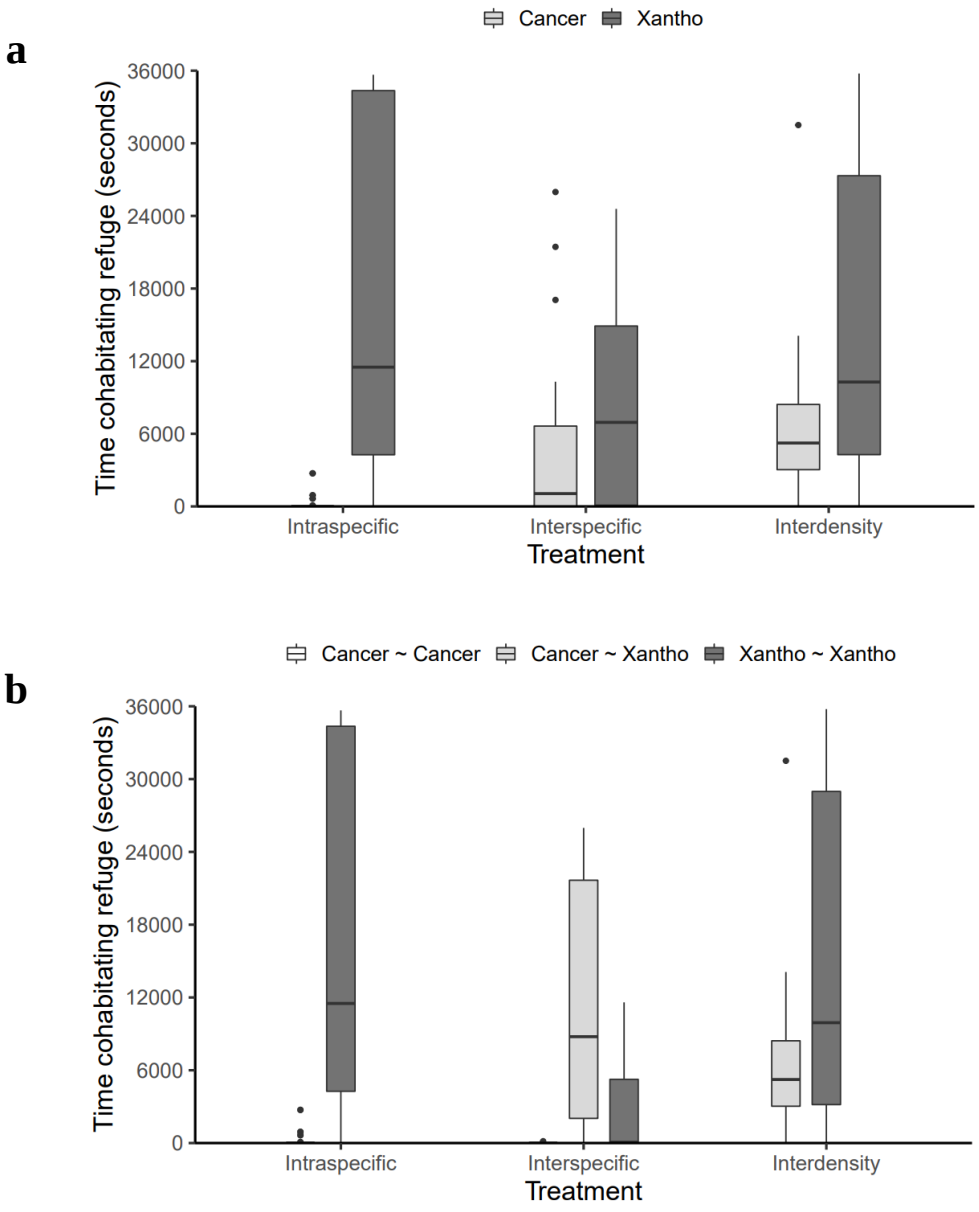

Figure 4 Differences in **a**) time spent cohabitating refuge between species, within and across treatments, and **b**) time spent cohabitation refuge between possible cohabitation links, within and across treatments. N = 8 per treatment. Boxplots show the data's minimum, lower quartile, median, upper quartile and maximum. Outliers are points beyond the minimum and maximum.

Table 2 Mean time (seconds) spent locating prey, occupying prey, occupying refuge and cohabitating refuge for each species and the output of comparative statistical analyses. SD included in parentheses. **Bold** p values indicate statistical significance at alpha 0.05.

Treatment (n)	*Cancer*	*Xantho*	df	t / W	p	*Cancer*	*Xantho*	df	t / W	p
	LOCATING PREY					**OCCUPYING PREY**				
Solo (8)	2009.13 (1291.36)	3435.5 (3270.43)	10	0.217	0.833	1325.25 (417.7)	1899.38 (623.52)	12	2.164	0.051
Intraspecific (8 / 8)	3969.88 (2753.94)	8292.63 (4011.88)	8	1.388	0.205	1633.25 (682.92)	2589.88 (568.71)	14	3.045	**0.009**
Interspecific (8)	18883 (12813.36)	3848 (2631.15)	4	2.643	0.057	2051 (601.99)	3708.67 (597.22)	4	3.789	**0.016**
Intersize (8)	7886 (6583.47)	7319.75 (4271.74)	3	1.176	0.32	1065.5 (304.66)	3960.25 (1098.3)	4	5.08	**0.01**
	OCCUPYING REFUGE					**COHABITATING REFUGE**				
Solo (8)	26682.88 (4186.57)	32324.75 (1787.14)	10	3.506	**0.006**					
Intraspecific (8 / 8)	16627 (15223.52)	25230.53 (12329.73)		700	**0.012**	273.69 (697.71)	16909.25 (14591.17)		932	< **0.001**
Interspecific (8)	11339.69 (10988.07)	28030.38 (9285.52)		230	< **0.001**	5632.81 (8526.99)	8779.25 (8508.52)		159	0.241
Interdensity (8)	15006.13 (13536.34)	25210.13 (11313.54)		144	**0.037**	8333.625 (10363.46)	15202.25 (13235.26)		126	0.199

Table 3 Mean time (seconds) spent cohabitating refuge for each possible cohabitation link and the output of comparative statistical analyses, where *CC* refers to the *C. pagurus – C. pagurus* cohabitation link, *CX* refers to the *C. pagurus – X. hydrophilus* link and *XX* refers to the *X. hydrophilus – X. hydrophilus* link. SD included in parentheses. Post-hoc results are blanked for the interdensity treatment as the test did not require post-hoc analysis. Degrees of freedom (df) are blanked when analyses did not produce such values. **Bold** p values indicate statistical significance at alpha 0.05.

Treatment (n)	*Cancer ~ Cancer*	*Cancer ~ Xantho*	*Xantho ~ Xantho*	df	t / W	F / X^2	p	Pair	Diff. / Z	p
	COHABITATING REFUGE									
Intraspecific (8 / 8)	273.69 (697.71)		16909.25 (14591.17)							
Interspecific (8)	18.75 (53.03)	11234.75 (10576.12)	3158.5 (4851.16)	4		7.918	**0.019**	*CC – CX*	2.813	**0.015**
								CC – XX	1.349	0.532
								CX – XX	1.464	0.429
Interdensity (8)		8333.625 (10363.46)	15615 (14650.7)	4	29		0.35			

T**able 4** Output of statistical analyses comparing the mean time (seconds) spent locating prey, occupying prey, occupying refuge and cohabitating refuge across treatments for each species. Post-hoc results are blanked when analyses were not conducted due to no significance in prior test. **Bold** p values indicate statistical significance at alpha 0.05.

	Test				**Post-hoc**			**Test**				**Post-hoc**		
Species	df	t / W	F / X^2	p	Pair	Diff. / Z	p	df	t / W	F / X^2	p	Pair	Diff. / Z	p
	LOCATING PREY							**OCCUPYING PREY**						
Cancer	3		12.023	**0.007**	Solo – Intra	1.359	1	3		7.333	0.062			
					Solo – Inter	3.307	**0.006**							
					Solo – Intersize	2.080	0.225							
					Intra – Inter	2.115	0.207							
					Intra – Intersize	0.971	1							
					Inter – Intersize	0.912	1							
Xantho	3		2.845	0.065				19		9.926	**< 0.001**	Solo – Intra	690.5	0.233
												Solo – Inter	1809.29	**0.006**
												Solo – Intersize	2060.88	**< 0.001**
												Intra – Inter	1118.79	0.12
												Intra – Intersize	1370.38	**0.023**
												Inter – Intersize	251.58	0.965
	OCCUPYING REFUGE							**COHABITATING REFUGE**						
Cancer	3		4.629	0.201				2		14.343	**< 0.001**	Intra – Inter	2.624	**0.026**
												Intra – Interdensity	3.316	**0.003**
												Inter – Interdensity	1.171	0.725
Xantho	3		0.864	0.834				2		3.733	0.155			

Interactions

Results for foraging trial interactions are presented in Tables 5 – 6. No significant differences were found in the proportion of interactions instigated by *X. hydrophilus* and *C. pagurus* approaches in interspecific foraging trials, however *C. pagurus* instigated significantly more often than *X. hydrophilus* in intersize trials (Figure 5a). The proportion of *X. hydrophilus* instigations was significantly larger in interspecific trials than in intersize trials, whereas the opposite was true for *C. pagurus*.

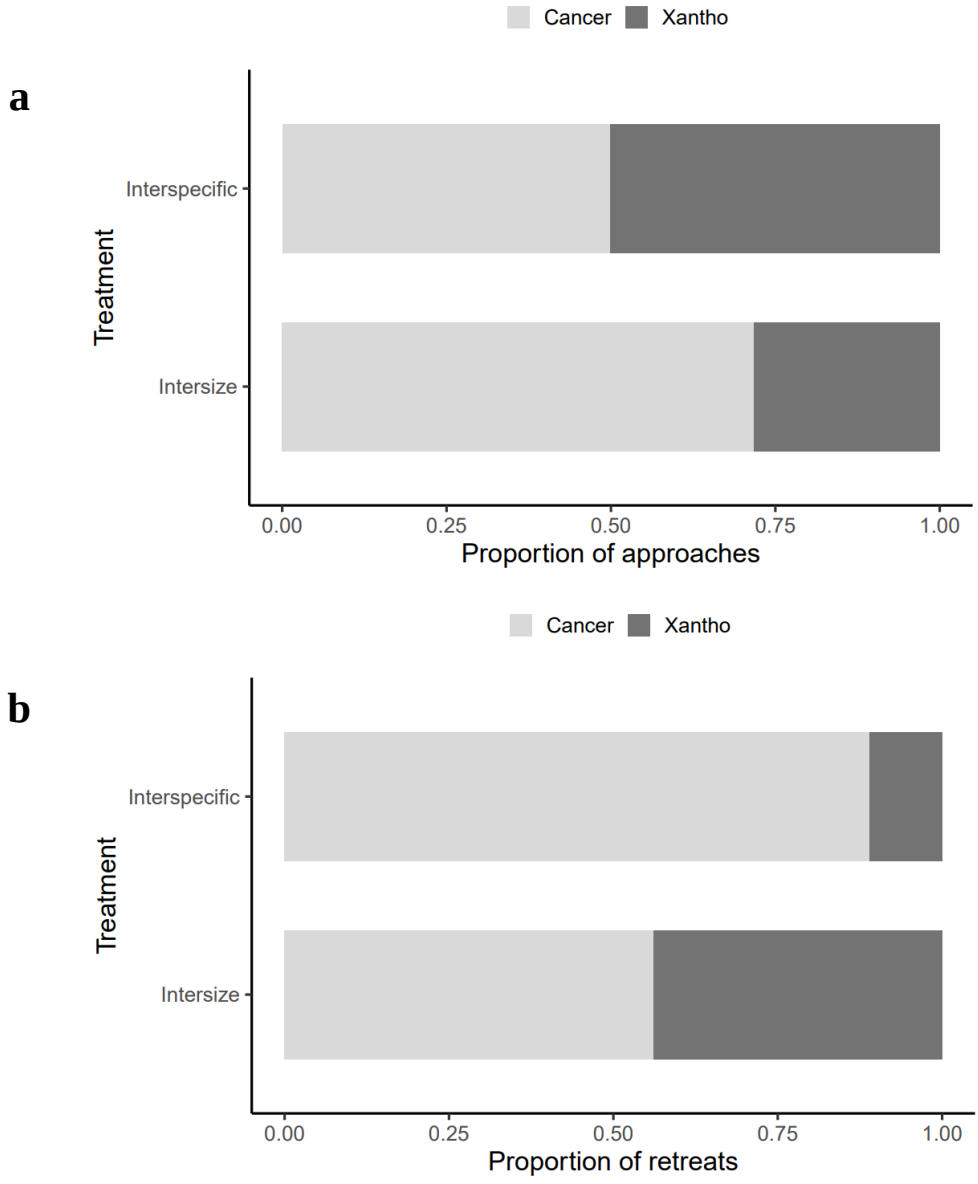

Figure 5 Proportional difference in the number of **a**) approaches and **b**) retreats between species, within and across competitive foraging treatments. N = 8 / n = 9 for *X. hydrophilus* / *C. pagurus* intraspecific trials, n = 16 for interspecific trials and n = 12 for intersize trials.

C. pagurus retreated significantly more than *X. hydrophilus* in interspecific trials, however no such difference occurred in intersize trials (Figure 5b). Across treatments, *X. hydrophilus* retreated significantly more in intersize trials than it did in interspecific trials, whereas the opposite was true for *C. pagurus*.

X. hydrophilus performed LMD threats (see Box 1) significantly more often than both size-matched and size-advantaged *C. pagurus*, and were significantly more successful doing so than size-matched competitors, however there were no such differences in their respective intraspecific trials (Figure 6a; Figure 6b). *X. hydrophilus*' threats per interaction did not vary across treatments, however they were significantly more likely to succeed versus size-matched heterospecific than conspecifics. *C. pagurus* did perform threats significantly more often in intraspecific and intersize trials than in interspecific trials, however, there was no difference in its success rate across treatments.

X. hydrophilus executed chelal attacks significantly more often than *C. pagurus* in interspecific trials, however not in intersize trials nor across their respective intraspecific trials (Figure 7a). Size-matched success rates contrasted greatly, as the xanthid's attacks were 100% successful whilst the cancrid never forced retreat after an attack, and the xanthid was also significantly more likely to succeed than *C. pagurus*' during intersize trials (Figure 7b). *X. hydrophilus* did not execute attacks disproportionately across treatments, however their attacks were more likely to succeed versus size-matched heterospecific than conspecifics. *C. pagurus* attacks were disproportionate in both occurrence and outcome, as conspecifics were attacked significantly more often and successfully than size-matched heterospecifics.

Retaliations were enacted in response to a competitor's attack significantly more often by *X. hydrophilus* than *C. pagurus* in intersize trials, however not in interspecific nor respective intraspecific trials. As with attacks, *X. hydrophilus*' retaliations were 100% effective at forcing retreat in interspecific trials, whilst *C. pagurus*' were 0% effective. Neither *X. hydrophilus* nor *C. pagurus* enacted retaliations disproportionately across treatments, however *C. pagurus*' retaliations were significantly more likely to succeed in intersize trials than in intraspecific trials and interspecific trials.

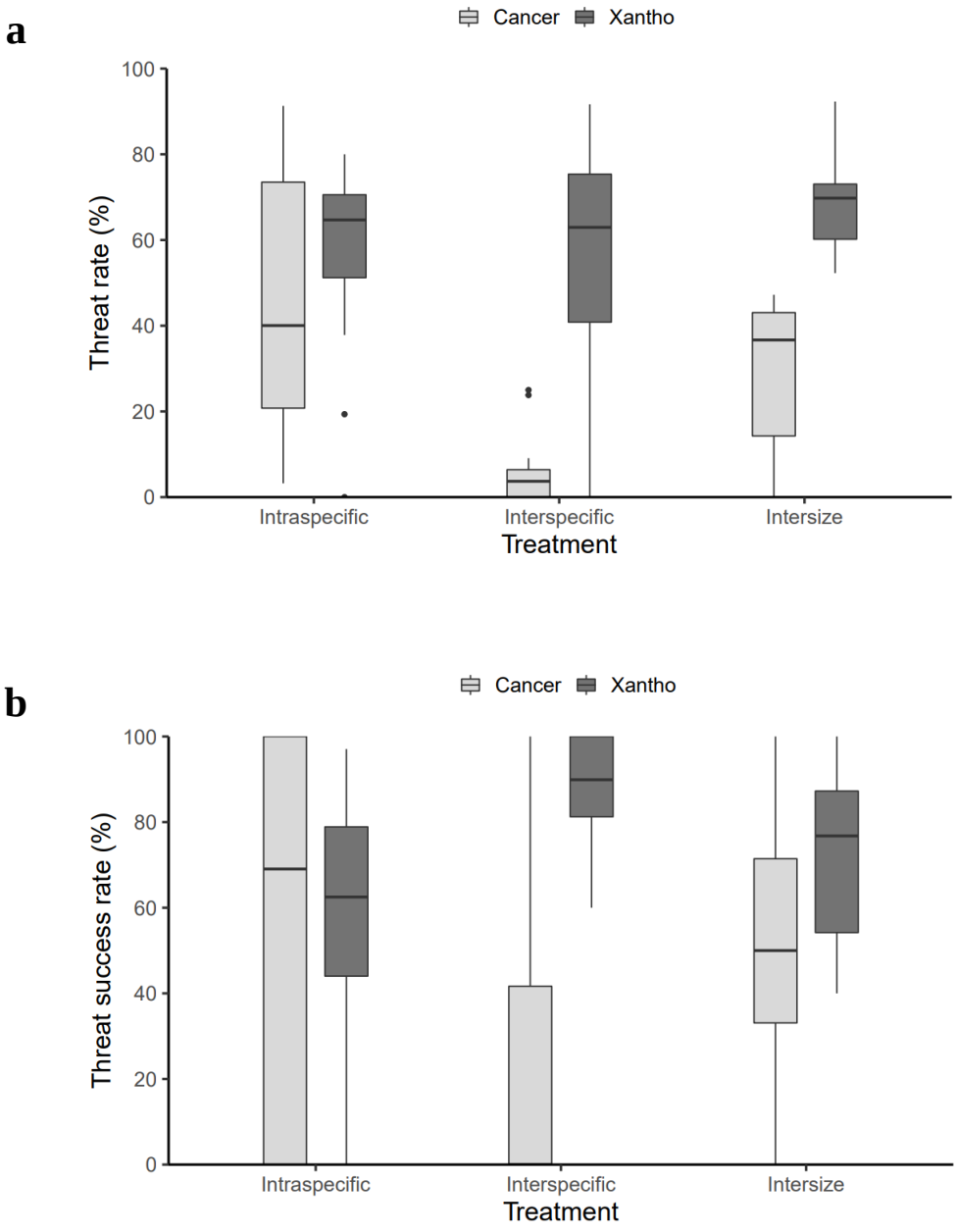

Figure 6 Differences in **a**) threat rate and **b**) threat success rate between species, within and across competitive foraging treatments. N = 8 / n = 9 for *X. hydrophilus* / *C. pagurus* intraspecific trials, n = 16 for interspecific trials and n = 12 for intersize trials. Boxplots show the data's minimum, lower quartile, median, upper quartile and maximum. Outliers are points beyond the minimum and maximum.

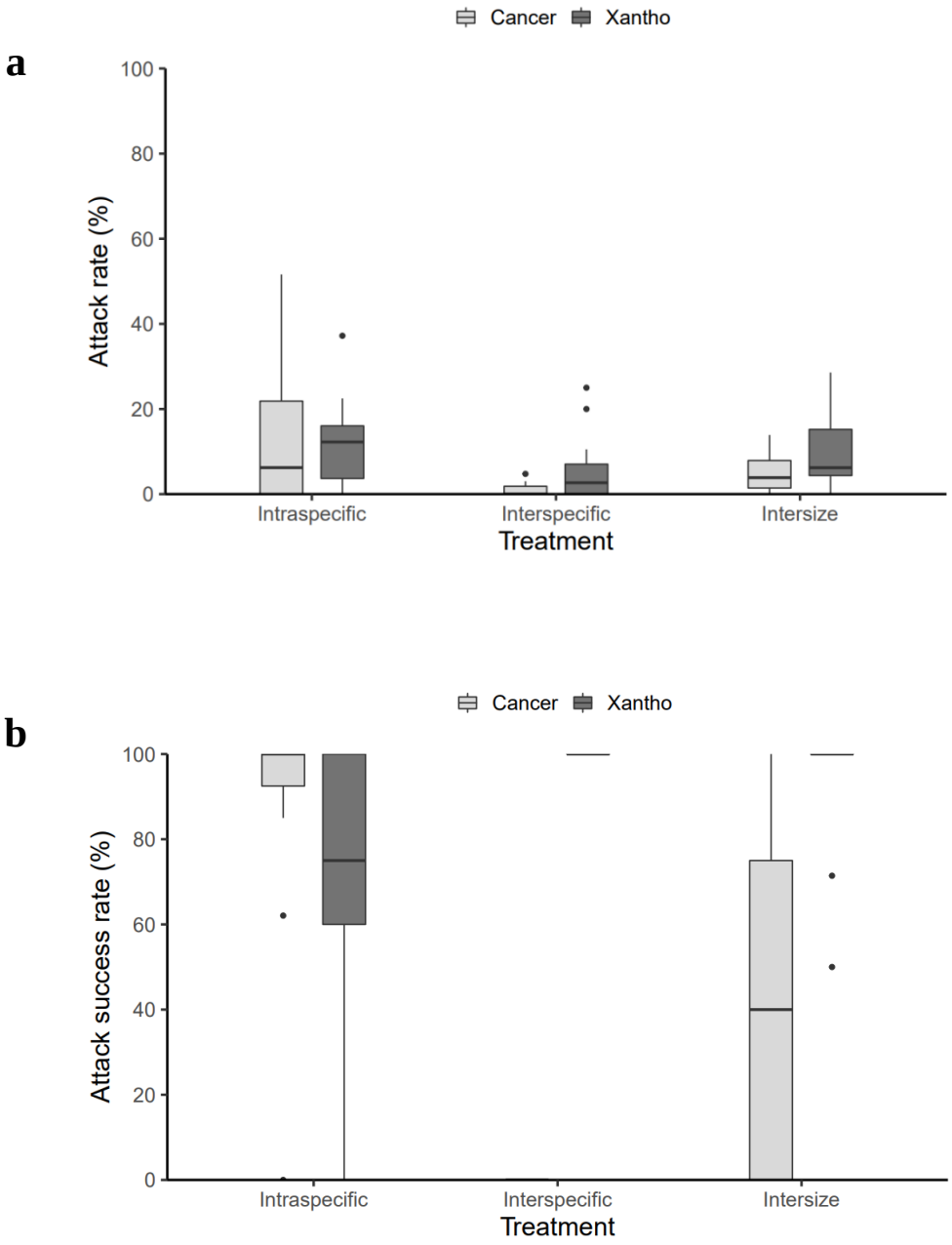

Figure 7 Differences in **a**) attack rate and **b**) attack success rate between species, within and across competitive foraging treatments. N = 8 / n = 9 for *X. hydrophilus* / *C. pagurus* intraspecific trials, n = 16 for interspecific trials and n = 12 for intersize trials. Boxplots show the data's minimum, lower quartile, median, upper quartile and maximum. Outliers are points beyond the minimum and maximum.

Results for refuge trial interactions are presented in Tables 7 – 12 and illustrated in Figure 8. Generally, passive interactions between *X. hydrophilus* conspecifics were less likely to result in success, yet significantly less likely to result in failure, than for *C. pagurus* in equivalent intraspecific trials. This is because the vast majority of *X. hydrophilus*' passive interactions resulted in cohabitation, whereas this outcome was scarce for *C. pagurus*. Assertive interaction outcomes were more similar between species, with cohabitation rare and totally absent for *X. hydrophilus* and *C. pagurus* respectively.

X. hydrophilus' success rates were significantly higher than *C. pagurus*' across all four forms of interaction in interspecific trials, whilst failure rates were significantly lower. Cohabitation was more common for the xanthid in passive interactions, however neither species exhibited cohabitation following an assertive interaction. Considering specific interaction links, *X. hydrophilus* were generally more successful, slightly more likely to cohabitate and less likely to fail versus heterospecifics than conspecifics. Indeed, when assertive, *X. hydrophilus* was 100% successful at refuge displacement and retention versus *C. pagurus*. *C. pagurus*' interaction link dynamics were largely the opposite, although conspecific cohabitation rates were surprisingly high considering the rarity of this outcome in intraspecific trials.

Interdensity trial interactions followed a very similar general trend to interspecific trials, however results lacked statistical significance in comparison. This is likely because less interspecific interaction occurred in interdensity trials due to the lower abundance of *C. pagurus*, thus limiting statistical power. Comparing results across treatments, *X. hydrophilus* were more successful across all four interaction types in interspecific and interdensity trials than intraspecific trials. In contrast, *C. pagurus* were generally more successful in intraspecific trials than interspecific and interdensity trials.

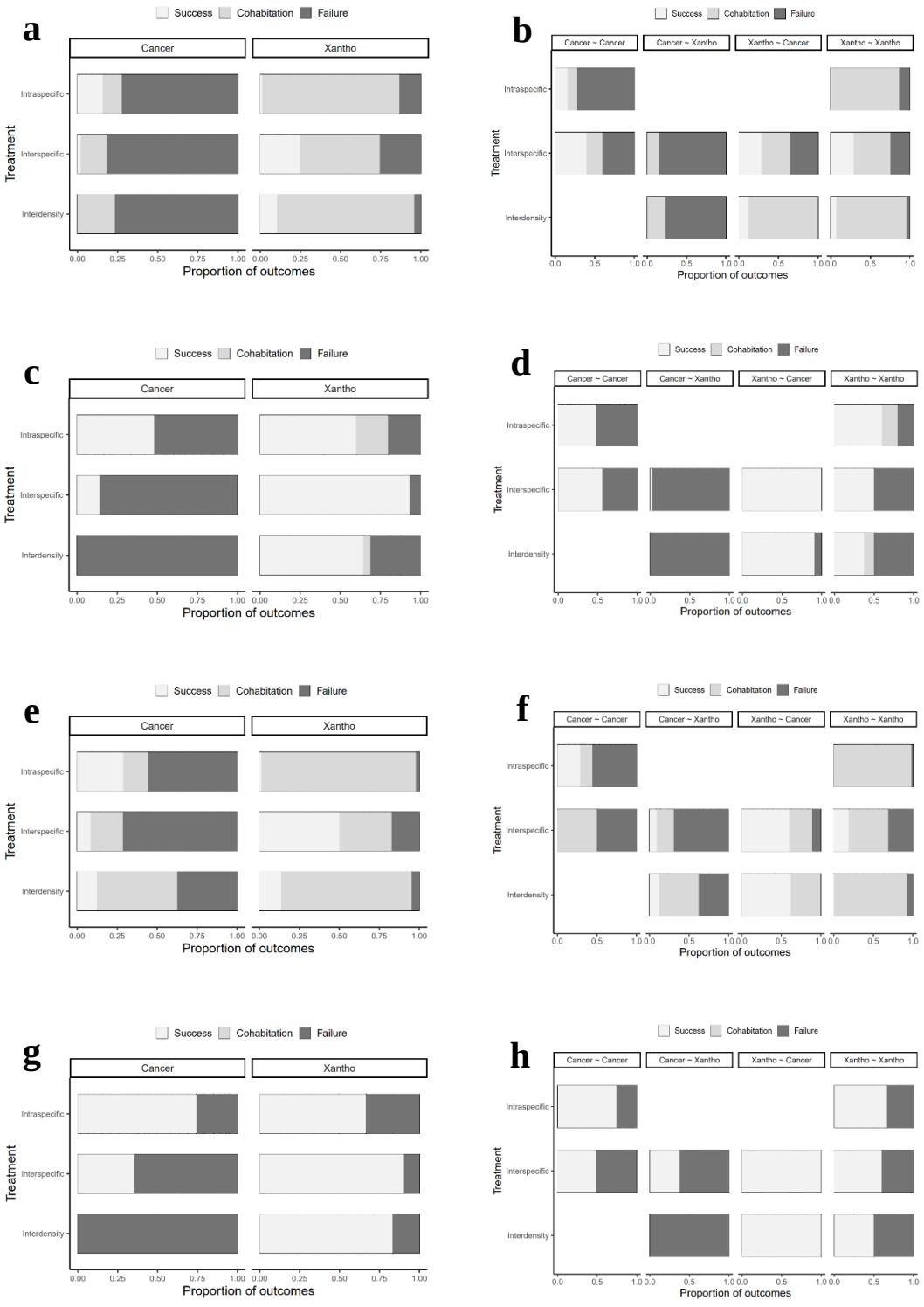

Figure 8 Proportional differences in the refuge interaction outcomes of **a – b**) passive approach, **c – d**) assertive approach, **e – f**) passive defence and **g – h**) assertive defence, between species (left column) and between all possible interaction links (right) within and across treatments. N = 8 per treatment. For all individual column headings, the species whose name is present (or first for interaction links) is the one committing the interaction versus an opponent.

Table 5 Mean proportion (%) of approaches, retreats, threats, attacks and retaliations occurring per interaction for each species, plus the mean success rate (%) of threats, attacks and retaliations per interaction for each species, and the output of comparative statistical analyses. SD included in parentheses. Degrees of freedom (df) are blanked when analyses did not produce such values. *Italicised* values represent mean frequency per trial. **Bold** p values indicate statistical significance at alpha 0.05.

Treatment (n) *Mean frequency per trial*	*Cancer*	*Xantho*	df	t / W	p	*Cancer*	*Xantho*	df	t / W	p
	APPROACH					**RETREAT**				
Interspecific (16)	49.85 (28.25)	50.15 (28.35)	30	0.031	0.976	88.92 (11.78)	11.08 (11.78)		0	< **0.001**
13.03	*12.19*	*13.88*				*22.75*	*3.31*			
Intersize (12)	71.66 (28.21)	28.35 (28.21)		20.5	**0.003**	56.12 (27.05)	43.88 (27.05)	22	1.108	0.28
21.21	*31.58*	*10.83*				*20.67*	*21.75*			
	Occurrence					**Success**				
	THREAT									
Intraspecific (8 / 9)	44.57 (30.2)	56.95 (21.85)		170.5	0.369	56.33 (44.16)	56.51 (28.95)		147.5	0.662
35 / 33.67	*16.83*	*17.5*								
Interspecific (16)	5.88 (7.79)	54.78 (29.94)		225.5	< **0.001**	27.58 (39.56)	87.97 (12.29)		23	**0.003**
16.13	*1.38*	*14.75*								
Intersize (12)	29.91 (17.2)	68.37 (11.34)		144	< **0.001**	48.91 (31.11)	70.92 (21.32)	17	1.869	0.079
42.83	*14.92*	*27.92*								
	ATTACK									
Intraspecific (8 / 9)	14.27 (17.58)	11.73 (9.84)		155	0.714	86.1 (30.88)	67.17 (35.84)		101	0.072
7.63 / 11.56	*5.78*	*3.81*								
Interspecific (16)	0.92 (1.53)	5.26 (7.57)		176	**0.048**	0 (0)	100 (0)			
1.5	*0.31*	*1.19*								
Intersize (12)	4.92 (4.67)	10.23 (9.34)	20	1.512	0.146	39.44 (43.04)	92.14 (17.32)		14	**0.007**
6.33	*2.42*	*3.92*								
	RETALIATION									
Intraspecific (8 / 9)	13.92 (29.22)	29.12 (14.41)		101	0.072	21.91 (20.55)	27.78 (44.01)		15	0.836
2.62 / 4	*2*	*1.31*								
Interspecific (16)	17.04 (33.35)	20 (44.72)		20.5	0.802	0 (0)	100 (0)			
0.25	*0.19*	*0.06*								
Intersize (12)	8.86 (20.09)	46.8 (38.51)		73	**0.015**	87.5 (17.68)	71.43 (39.34)		8	0.872
1.75	*0.58*	*1.17*								

T**able 6** Output of statistical analyses comparing the mean proportion of approaches, retreats, threats, attacks and retaliations occurring per interaction for each species, plus the mean success rate of threats, attacks and retaliations per interaction for each species, across treatments. Degrees of freedom (df) are blanked when analyses did not produce such values. Post-hoc results are blanked when analyses were not conducted due to no significance in prior test. **Bold** p values indicate statistical significance at alpha 0.05.

	Test				**Post-hoc**			**Test**				**Post-hoc**		
Species	df	t / W	F / X^2	p	Pair	Diff. / Z	p	df	t / W	F / X^2	p	Pair	Diff. / Z	p
	APPROACH							**RETREAT**						
Cancer		53		**0.043**					162.5		**0.002**			
Xantho		140		**0.043**					29.5		**0.002**			
	Occurrence							**Success**						
	THREAT													
Cancer	2		19.383	**< 0.001**	Intra – Inter	4.262	**< 0.001**	2		3.083	0.214			
					Intra – Intersize	0.856	1							
					Inter – Intersize	2.999	**0.008**							
Xantho	2		1.402	0.496				2		7.512	**0.002**	Intra – Inter	0.444	**0.001**
												Intra – Intersize	0.208	0.204
												Inter – Intersize	0.236	0.139
	ATTACK													
Cancer	2		9.066	**0.011**	Intra – Inter	2.867	**0.012**	2		12.341	**0.002**	Intra – Inter	3.359	**0.003**
					Intra – Intersize	0.414	1					Intra – Intersize	2.215	0.08
					Inter – Intersize	2.175	0.089					Inter – Intersize	1.463	0.43
Xantho	2		5.251	0.072				2		11.555	**0.003**	Intra – Inter	3.215	**0.004**
												Intra – Intersize	2.357	0.055
												Inter – Intersize	0.878	1
	RETALIATION													
Cancer	2		0.407	0.816				2		13.09	**0.01**	Intra – Inter	0.405	0.274
												Intra – Intersize	0.904	**0.038**
												Inter – Intersize	1.309	**0.009**
Xantho	2		2.907	0.234				2		4.583	0.101			

T**able 7** Mean success, cohabitation and failure rates (%) for each species' passive and assertive approach attempts and the output of comparative statistical analyses. SD included in parentheses. Degrees of freedom (df) are blanked when analyses did not produce such values. *Italicised* values represent mean frequency per trial. **Bold** p values indicate statistical significance at alpha 0.05.

Treatment (n) *Mean frequency per trial*	Result	*Cancer*	*Xantho*	df	t / W	p	*Cancer*	*Xantho*	df	t / W	p
		PASSIVE APPROACH					**ASSERTIVE APPROACH**				
Intraspecific (8 / 8)	Success	15.83 (32.66) *0.16*	1.39 (5.89) *0.03*		143.5	0.097	48.15 (42.53) *0.75*	60 (54.77) *0.13*		48.5	0.653
	Cohabitation	11.83 (30.67) *0.13*	85.32 (33.28) *1.03*		318	< **0.001**	0 (0) *0*	20 (44.72) *0.03*		51	0.083
	Failure	72.34 (40.52) *1.25*	13.29 (32.22) *0.13*		64	< **0.001**	51.85 (42.53) *1.34*	20 (44.72) *0.03*		24.5	0.151
Interspecific (8)	Success	2.17 (4.94) *0.19*	24.78 (30.68) *0.69*		126.5	**0.01**	14.03 (29.35) *0.25*	93.5 (14.15) *1.25*		114	< **0.001**
	Cohabitation	15.75 (21.53) *0.75*	49.85 (41.25) *1.44*		120	**0.045**	0 (0) *0*	0 (0) *0*			
	Failure	82.08 (20.49) *3.75*	25.37 (26.46) *0.94*		11	< **0.001**	85.97 (29.35) *1*	6.5 (14.15) *0.19*		6	< **0.001**
Interdensity (8)	Success	0 (0) *0*	10.26 (19.88) *0.13*		40	0.288	0 (0) *0*	64.58 (44.04) *0.42*		21	0.062
	Cohabitation	23.33 (32.49) *0.63*	85.89 (22.41) *0.96*		60	**0.004**	0 (0) *0*	4.17 (11.79) *0.04*		13.5	0.683
	Failure	76.67 (32.49) *1*	3.85 (13.87) *0.13*		1.5	< **0.001**	100 (0) *1.38*	31.25 (45.81) *0.13*		3	0.055

T**able 8** Mean success, cohabitation and failure rates (%) for each species' passive and assertive defence attempts and the output of comparative statistical analyses. SD included in parentheses. Degrees of freedom (df) are blanked when analyses did not produce such values. *Italicised* values represent mean frequency per trial. **Bold** p values indicate statistical significance at alpha 0.05.

Treatment (n)	Result	*Cancer*	*Xantho*	df	t / W	p	*Cancer*	*Xantho*	df	t / W	p
Mean frequency per trial		**PASSIVE DEFENCE**					**ASSERTIVE DEFENCE**				
Intraspecific (8 / 8)	Success	28.89 (41.05)	1.39 (5.89)		85.5	**0.013**	74.19 (34.72)	66.67 (51.64)		60	0.863
		0.22	*0.03*				*2.41*	*0.13*			
	Cohabitation	15.55 (29.86)	96.53 (11.98)		259	**< 0.001**	0 (0)	0 (0)			
		0.13	*1.25*				*0*	*0*			
	Failure	55.56 (49.87)	2.08 (6.43)		60	**0.001**	25.81 (34.72)	33.33 (51.64)		54	0.863
		0.34	*0.06*				*0.56*	*0.09*			
Interspecific (8)	Success	8.41 (18.38)	50.19 (34.12)		132	**0.002**	35.71 (33.92)	90.48 (27.51)		91	**< 0.001**
		0.38	*1.75*				*0.81*	*3.75*			
	Cohabitation	20.23 (34.65)	32.72 (28.19)		97	0.257	0 (0)	0 (0)			
		0.63	*1.56*				*0*	*0*			
	Failure	71.36 (36.88)	17.09 (30.75)		21	**0.002**	64.29 (33.92)	9.52 (27.51)		7	**< 0.001**
		1.38	*0.38*				*0.63*	*0.13*			
Interdensity (8)	Success	12.5 (35)	13.81 (23.27)		29	0.946	0 (0)	83.33 (35.64)		15	0.052
		0.13	*0.25*				*0*	*0.75*			
	Cohabitation	50 (40.83)	81.43 (26.79)		40.5	0.159	0 (0)	0 (0)			
		0.5	*1.17*				*0*	*0*			
	Failure	37.5 (47.87)	4.76 (12.11)		16	0.093	100 (0)	16.67 (35.64)		1	0.052
		0.38	*0.08*				*0.63*	*0.13*			

T**able 9** Mean success, cohabitation and failure rates (%) for *C. pagurus*' approach and defence attempts versus conspecific and heterospecific competitors, and the output of comparative statistical analyses. SD included in parentheses. Degrees of freedom (df) are blanked when analyses did not produce such values. *Italicised* values represent mean frequency per trial. **Bold** p values indicate statistical significance at alpha 0.05.

Treatment (n) *Mean frequency per trial*	Result	Conspecific	Heterospecific	df	t / W	p	Conspecific	Heterospecific	df	t / W	p
		PASSIVE APPROACH					**ASSERTIVE APPROACH**				
Interspecific (8)	Success	40 (54.78) *0.13*	0.71 (2.67) *0.06*		22.5	0.08	55.56 (38.49) *0.19*	2.5 (7.91) *0.06*		0	**0.003**
	Cohabitation	20 (44.72) *0.06*	14.52 (20.75) *0.69*		40	0.63	0 (0) *0*	0 (0) *0*			
	Failure	40 (54.77) *0.25*	84.77 (20.38) *3.5*		49	0.185	44.44 (38.49) *0.25*	97.5 (7.91) *1.63*		30	**0.003**
		PASSIVE DEFENCE					**ASSERTIVE DEFENCE**				
Interspecific (8)	Success	0 (0) *0*	9.25 (19.15) *0.38*		13	0.481	48.33 (45.8) *0.5*	37.5 (25) *0.31*		7	0.526
	Cohabitation	50 (70.71) *0.06*	21.25 (35.1) *0.56*		7.5	0.631	0 (0) *0*	0 (0) *0*			
	Failure	50 (70.71) *0.06*	69.5 (37.15) *1.31*		12	0.73	51.67 (45.8) *0.25*	62.5 (25) *0.38*		13	0.526

T**able 10** Mean success, cohabitation and failure rates (%) for *X. hydrophilus*' approach and defence attempts versus conspecific and heterospecific competitors, and the output of comparative statistical analyses. SD included in parentheses. Degrees of freedom (df) are blanked when analyses did not produce such values. *Italicised* values represent mean frequency per trial. **Bold** p values indicate statistical significance at alpha 0.05.

Treatment (n)	Result	Conspecific	Heterospecific	df	t / W	p	Conspecific	Heterospecific	df	t / W	p
Mean frequency per trial		**PASSIVE APPROACH**					**ASSERTIVE APPROACH**				
Interspecific (8)	Success	29.17 (45.21)	28.44 (32.22)		39	0.794	50 (57.74)	100 (0)		30	**0.027**
		0.19	*0.5*				*0.13*	*1.13*			
	Cohabitation	46.66 (45.18)	36.64 (42.95)		31.5	0.688	0 (0)	0 (0)			
		0.88	*0.56*				*0*	*0*			
	Failure	24.17 (35.93)	34.92 (42.17)		41	0.646	50 (57.74)	0 (0)		10	**0.027**
		0.25	*0.69*				*0.19*	*0*			
Interdensity (8)	Success	6.94 (16.6)	12.5 (25)		26.5	0.722	37.5 (47.87)	91.67 (20.41)		20	0.07
		0.08	*0.04*				*0.13*	*0.29*			
	Cohabitation	88.89 (20.52)	87.5 (25)		23.5	1	12.5	0 (0)		9	0.307
		0.79	*0.17*				*0.04*	*0*			
	Failure	4.17 (14.43)	0 (0)		22	0.665	50 (57.74)	8.33 (20.41)		7	0.236
		0.13	*0*				*0.08*	*0.04*			
		PASSIVE DEFENCE					**ASSERTIVE DEFENCE**				
Interspecific (8)	Success	18.75 (37.2)	60.52 (32.03)		70.5	**0.026**	60 (54.77)	100 (0)		45.5	**0.024**
		0.13	*1.63*				*0.25*	*3.5*			
	Cohabitation	50 (46.29)	28.87 (34.42)		34	0.412	0 (0)	0 (0)			
		0.88	*0.69*				*0*	*0*			
	Failure	31.25 (45.81)	10.61 (20.1)		36	0.451	40 (54.77)	0 (0)		19.5	**0.024**
		0.19	*0.19*				*0.13*	*0*			
Interdensity (8)	Success	0 (0)	62 (41.47)		49.5	**0.001**	50 (57.74)	100 (0)		15	0.128
		0	*0.25*				*0.21*	*0.54*			
	Cohabitation	92.42 (17.26)	38 (41.47)		7	**0.009**	0 (0)	0 (0)			
		0.96	*0.21*				*0*	*0*			
	Failure	7.58 (17.26)	0 ()		22.5	0.376	50 (57.74)	0 (0)		5	0.128
		0.08	*0*				*0.13*	*0*			

T**able 11** Output of statistical analyses comparing the mean success, cohabitation and failure rates (%) for each species' passive and assertive approach attempts across treatments. Post-hoc results are blanked when analyses were not conducted due to no significance in prior test. **Bold** p values indicate statistical significance at alpha 0.05.

		Test			**Post-hoc**			**Test**			**Post-hoc**		
Spec.	Result	df	F / X^2	p	Pair	Diff. / Z	p	df	F / X^2	p	Pair	Diff. / Z	p
		PASSIVE APPROACH						**ASSERTIVE APPROACH**					
Can.	Success	2	1.795	0.408				2	7.787	**0.02**	Intra – Inter	2.24	0.075
											Intra – Interdensity	2.17	0.09
											Inter – Interdensity	0.797	1
	Cohabit.	2	2.151	0.341									
	Failure	2	0.229	0.989				2	7/787	**0.02**	Intra – Inter	2.24	0.075
											Intra – Interdensity	2.17	0.09
											Inter – Interdensity	0.797	1
Xan.	Success	2	10.923	**< 0.001**	Intra – Inter	3.303	**0.003**	2	2.612	0.271			
					Intra – Interdensity	1.221	0.667						
					Inter – Interdensity	2.001	0.136						
	Cohabit.	2	8.581	**0.014**	Intra – Inter	2.77	**0.017**	2	1.902	0.386			
					Intra – Interdensity	0.232	1						
					Inter – Interdensity	2.382	0.052						
	Failure	2	8.45	**0.015**	Intra – Inter	2.175	0.089	2	1.243	0.537			
					Intra – Interdensity	2.175	1						
					Inter – Interdensity	2.823	**0.014**						

T**able 12** Output of statistical analyses comparing the mean success, cohabitation and failure rates (%) for each species' passive and assertive defence attempts across treatments. Post-hoc results are blanked when analyses were not conducted due to no significance in prior test. **Bold** p values indicate statistical significance at alpha 0.05.

Spec.	Result	Test			Post-hoc			Test			Post-hoc		
		df	F / X^2	p	Pair	Diff. / Z	p	df	F / X^2	p	Pair	Diff. / Z	p
		PASSIVE DEFENCE						**ASSERTIVE DEFENCE**					
Can.	Success	2	1.186	0.553				2	9.27	**0.01**	Intra – Inter	2.358	0.055
											Intra – Interdensity	2.279	0.068
											Inter – Interdensity	0.813	1
	Cohabit.	2	3.418	0.181									
	Failure	2	1.702	0.427				2	9.27	**0.01**	Intra – Inter	2.358	0.055
											Intra – Interdensity	2.279	0.068
											Inter – Interdensity	0.813	1
Xan.	Success	2	22.204	**< 0.001**	Intra – Inter	4.659	**< 0.001**	2	1.188	0.552			
					Intra – Interdensity	1.406	0.479						
					Inter – Interdensity	3.068	**0.007**						
	Cohabit.	2	26.732	**< 0.001**	Intra – Inter	5.082	**< 0.001**						
					Intra – Interdensity	1.366	0.516						
					Inter – Interdensity	3.503	**0.001**						
	Failure	2	3.788	0.151				2	1.188	0.552			

Competitive and interactive wins.

Win results are presented in Table 13. Foraging winners were identified by two conditions:

1. The competitor to first locate the prey resource.
2. The competitor occupying the prey resource until total consumption or satiation, the latter indicated by the occupier dropping the prey resource without being provoked.

In all cases, the first to locate was also the consumer, hence the same statistically insignificant results for proportional differences in win rate for both conditions, in both treatments. There were also there were no significant differences in win rates across treatments for *X. hydrophilus* nor *C. pagurus*.

1. Refuge winners were also identified by two conditions, both suggesting superior resistance versus displacement: The competitor occupying the refuge resource for the longest period.
2. The competitor(s) occupying the refuge resource at trial cessation.

X. hydrophilus occupied the refuge for the longest duration in every trial across interspecific and interdensity trials, therefore this species accumulated every win for the occupation length condition. For occupation at cessation, *X. hydrophilus* winners were statistically significantly more numerous than *C. pagurus* in both treatments. Across treatments, occupation length win rates were identical, whilst occupation at cessation wins did not vary significantly for *X. hydrophilus* nor *C. pagurus*. Interactive winners, applicable for both sets of competitive trials (only heterospecific interactions are considered from refuge trials here), were identified as the competitor which forced the opponent to retreat after an interaction. In competitive foraging trials, *X. hydrophilus* accumulated 87.3% of the interactive wins in interspecific trials. This was significantly more than *C. pagurus*, however the two species were much more evenly matching in intersize trials, with the larger cancrid claiming 51.3% of wins. *X. hydrophilus* was dominant in both competitive refuge treatments, claiming 89.3% and 96.4% of wins in interspecific and interdensity trials, respectively. Across treatments, *C. pagurus* was significantly more successful in intersize foraging trials than interspecific trials, whilst no difference was identified in refuge trials.

Table 13 Tallied wins for each species and the output of comparative statistical analyses. Test results are blanked when analyses were not conducted due to identical tallies. **Bold** p values indicate statistical significance at alpha 0.05.

Treatment (n)	*Cancer*	*Xantho*	df	X^2	p	*Cancer*	*Xantho*	df	X^2	p	*Cancer*	*Xantho*	df	X^2	p
	OBTAINED PREY					**CONSUMED PREY**					**FORAGING TRIAL INTERACTIONS**				
Interspecific (8)	5	3	1	0.25	0.617	5	3	1	0.25	0.617	53	364	1	460.91	**< 0.001**
Intersize (8)	4	4				4	4				261	248	1	0.566	**0.452**
	TIME OCCUPYING REFUGE					**OCCUPYING REFUGE AT CESSATION**					**REGUFE TRIAL INTERACTIONS**				
Interspecific (8)	0	8	1	12.25	**< 0.001**	6	14	1	4.9	**0.027**	13	108	1	146.05	**< 0.001**
Interdensity (8)	0	8	1	12.25	**< 0.001**	2	21	1	28.174	**< 0.001**	1	27	1	44.463	**< 0.001**

DISCUSSION

Table 14 Summarised findings for this study including the hypotheses (see Introduction for full statements) and the key results for each. **Bold** conclusions indicate statistical significance at alpha 0.05.

Hypothesis	Trial type	Predicted result	Observed result	Conclusion
H1	Foraging	Decreased prey consumption by *Cancer* in interspecific trials vs solo and intraspecific trials.	Decreased vs both.	**Supported**.
		Xantho dominant at consuming prey in interspecific trials.	No clear dominance.	Not supported.
	Refuge	Decreased refuge occupation by *Cancer* in interspecific trials vs solo and intraspecific trials.	No significant decrease.	Not supported.
		Xantho dominant at occupying refuge in interspecific trials.	Dominance by *Xantho*.	**Supported**.
		Xantho dominant at occupying refuge at trial cessation in interspecific trials.	Dominance by *Xantho*.	**Supported**.
H2	Foraging	*Xantho* dominant at forcing retreat in interspecific trial interactions.	Dominance by *Xantho*.	**Supported**.
	Refuge	*Xantho* dominant at forcing retreat in interspecific trial interactions.	Dominance by *Xantho*.	**Supported**.

As *Xantho hydrophilus* expands its UK range and increases in abundance, it could pose a competitive threat to species whose niche overlaps the xanthid's own, such as *C. pagurus*. And yet, no studies investigating its competitive ability have been conducted. Previously, competitive trials under controlled conditions have highlighted species-specific, hierarchy-forming interactions within crab communities and provided insight into the possible impacts of invasive crabs (Jensen et al., 2002; MacDonald et al., 2007 McDonald et al., 2001). Here, I present findings from both competitive foraging and competitive refuge trials between the climate change indicator *X. hydrophilus* and juvenile *C. pagurus*, in which the xanthid proved competitively dominant when competing for refuge and interacting agonistically (Table 14), yet curiously tolerant of conspecifics sharing refuge. Considering these results and the available scientific literature, I discuss the ecology of the poorly understood *X. hydrophilus* and its possible impact as its distribution shifts in response to climate change.

Competitive foraging

Both *X. hydrophilus* and *C. pagurus* were far more reluctant to engage in foraging activity when competing interspecifically than when alone or competing intraspecifically. This implies that the immediate presence of *X. hydrophilus* or its chemical cues may negatively affect *C. pagurus*' foraging in the intertidal zone, and vice versa. Though detrimental for both, *C. pagurus* may be more adversely affected by this interaction due to the much higher density of established *X. hydrophilus* populations (pers. obs.). Decreased foraging rate could facilitate emigration (Iribarne et al., 1995), potentially into an unfavourable habitat, which may increase mortality rates amongst juvenile *C. pagurus*.

Surprisingly, no physical contests concerning the prey resource occurred. Dominant crabs, such as *C. maenas*, have been observed actively wrestling food away from other species with great success (MacDonald et al., 2007). Furthermore, Jensen et al. (2002) imply that a subordinate species may learn to avoid conflict and thus be reluctant to challenge for prey. However, in the present study, the agonistically dominant *X. hydrophilus* did not challenge *C. pagurus*. This could be partly due to *X. hydrophilus*' apparent reluctance to forage in captivity (Hayward et al., 1974), and partly due to the limitations of the experimental tanks being designed to maximise interactions rather than replicate intertidal conditions. Non-experimental observations of captive *X. hydrophilus*, provided a far more naturalistic habitat, saw the crab respond to olfactory cues to approach and obtain food, before swiftly returning to refuge to consume it (pers. obs.). Robust xanthids such as *Eriphia smithii* are known to retreat into refuge with prey to reduce vulnerability (Seed & Lee, 1995). This may also be done by *X. hydrophilus* due to their relatively weak mobility, therefore they may not have exhibited entirely natural behaviours during the totally unconcealed competitive foraging trials and dietary preference trials. Additionally, due to the importance of olfactory cues for foraging crabs (Kaiser et al., 1993; Salierno et al., 2003), damaged prey items as used by McDonald et al. (2001) and Rossong et al. (2011) may have been a better choice to elicit active foraging responses than live *P. platycheles*. Analysing activity and foraging patterns (Reid & Naylor, 1989; Spilmont et al., 2015) and undertaking *in situ* studies, perhaps utilising mesocosms, are likely key to understanding and comparing these species' foraging dynamics.

C. pagurus generally consumed prey quicker than *X. hydrophilus*. This could be an adaptation to minimise the chance of kleptoparasitism (Chakravarti & Cotton, 2014), or alternatively be due to the associated effects of chelal morphology and dietary preference. Crabs can be assigned to 'guilds' based on their foraging behaviour, which is largely influenced by morphology (Seed & Hughes, 1995). Lightly built forms (most portunids and grapsids), can be considered part of a more dextrous guild whereas heavy builds (most cancrids and xanthids) conform to a more robust guild. By sacrificing dexterity and versatility in favour of crushing strength and mechanical advantage (MA), robust crabs are often preferential or specialist durophages, exploiting prey largely invulnerable to dextrous crabs (Freire et al., 1996; Seed & Hughes, 1995; Yamada & Boulding, 1998). Consistent with this, *C. pagurus* is a prolific predator of durable prey (Lawton, 1989; Lawton & Hughes, 1985; Mascaró & Seed, 2001), and *X. hydrophilus* has also been noted to consume bivalves, decapods and echinoderms (Hayward et al., 1974; Muntz et al., 1965; Puljas & Morton, 2019). Considering the above, it is surprising that dietary preference trials imply *X. hydrophilus* to be largely herbivorous, supporting the stomach content analysis by Hayward et al. (1974). This species in heterochelous, wielding molariform chelae of great size in relation to carapace width; supposedly indicative of high MA (Vermeij, 1977). The master chela also possesses a dactylar tooth on the master chela which is thought to significantly increase MA (Bisker & Castagna, 1987). However, Puljas & Morton (2019) report *X. hydrophilus* (here referred to as *Lophozozymous incisus*, likely an erroneous citation for the homonymous *X. incisus*, as identified by González (2016) in a separate study) to only possess an MA of 0.24, which is inferior to the lighter-built portunids *Necora puber* and *C. maenas*, and far inferior to *C. pagurus* and superficially similarly xanthids (Lee & Seed, 1992; Seed & Hughes, 1995). Although MA is not entirely indicative of crushing force as mechanical leverage, intricate variation in dentition and internal musculature are also important factors (Abele et al., 1981; Vermeij, 1977; Warner et al., 2009), a relatively weak crushing force could partly explain *X. hydrophilus*' reluctance to consume durable prey in preference trials, particularly as there was no secure refuge provided for the crabs to repeatedly load prey. Perhaps the large chelae wielded by male *X. hydrophilus* are not at all influenced by diet; instead an adaptation for male-male combat, display and courtship in addition to basic functions (Hartnoll, 1974). This omnivorous crab may be a plastic generalist, a trait commonly associated with more dextrous crabs which could imply a broad

trophic influence (Cannicci et al., 2007; Yamada & Boulding, 1998). Further morphometric study on the chelae, mouthparts, gastric mill and foregut, along with physiological studies concerning enzyme activity and more thorough observations on dietary preference, are necessary to confidently define the foraging habits of this species (Brousseau & Baglivo, 2005; Creswell & Marsden, 1990; Griffen & Mosblack. 2011; Johnston & Freeman, 2005). However, if herbivory contributes to as much of *X. hydrophilus*' diet as currently suggested, it is unlikely that it poses a significant competitive threat to the foraging activity of the prolific predator *C. pagurus*.

Competitive refuge use

The results from the competitive refuge trials suggest many interesting differences between *X. hydrophilus* and *C. pagurus*' refuge use. The xanthid occupied refuge for longer than the cancrid across treatments; this may suggest a greater degree of refuge dependence. Refuge dependency has been identified in crabs with weak mobility and burial capabilities, as poor proficiencies in these traits render crabs vulnerable if caught unconcealed (Jensen et al., 2002). Likely due to their robust build and short legs, *X. hydrophilus* does seem relatively sedentary in comparison to *C. pagurus*, the latter itself known to be sedentary compared to *C. maenas* (Mascaró & Seed, 2001). Hayward et al. (1974) suggest foraging activity by *X. hydrophilus* likely occurs within its refuge, consuming macroalgal debris swept under boulders by hydrodynamic action. Boulders and cobble provide a structurally complex habitat and effectively act as nutrient accumulation sites by capturing detrital debris, attracting algal settlement and providing refuge for prey species (Abele, 1974). Gregarious *P. platycheles*, the chosen prey resource for foraging trials, accumulate in high densities on sheltered shores under lower-intertidal boulders and cobble (Pallas et al., 2006; Smaldon, 1972). By foraging here, *X. hydrophilus* could maximise its refuge use and nullify its vulnerability. Boulders are also considered a preferred habitat for juvenile *C. pagurus* (Heraghty, 2013), so this is likely an area of direct competition between the two species.

X. hydrophilus displays a far greater degree of intraspecific cohabitation than *C. pagurus*; this could be indicative of high conspecific tolerance. This tolerance is thought to be driving *Hemigrapsus sanguineus*' success as an invasive species in North America by facilitating the grapsid's dominance for limited refuge whilst displacing

the intraspecifically agonistic *C. maenas* and *C. irroratus* (Hobbs et al., 2017). Although impossible to confirm without dedicated observational studies and field surveys, this could be a driving force behind *X. hydrophilus*' range shift and the very high densities observed during sampling. In contrast, and akin to *C. maenas* and *C. irroratus*, *C. pagurus* were often agonistic towards conspecifics and heterospecifics alike, with very little intraspecific cohabitation occurring. The relatively frequent interspecific cohabitation between the two species implies *X. hydrophilus* does not always attempt to actively exclude *C. pagurus*, however such high densities may result in refuge saturation and the passive exclusion of competitors. Field-based studies, ideally considering additional competitors, are necessary to determine whether possible refuge saturation by *X. hydrophilus* could have a genuine negative impact on *C. pagurus*' refuge use; alternatively, though unlikely, the presence of *X. hydrophilus* might facilitate the survival of juvenile *C. pagurus*.

Agonistic interactions

Considering both sets of trials, *X. hydrophilus* dominates equivalently sized *C. pagurus* in agonistic interactions, including those concerning refuge. This asymmetrical competition could partly be due to intercohort dynamics. Juvenile *Acanthocyclus* spp. have been observed cohabitating refuge with congeners despite great niche overlap, whereas adults compete aggressively and often at the expense of the species welding lighter chelae (Navarrete & Castilla, 1990), perhaps due to adult territoriality. This trait may be an important factor, as many studies have observed adults of smaller species to be competitively superior versus size-matched juveniles of larger species (Jensen et al., 2002; McDonald et a., 2001; Steinberg & Epifanio, 2011; Van den Brink & Hutting, 2017). This could explain *X. hydrophilus*' increased aggression compared to *C. pagurus*, evident by the proportional difference in their agonistic behaviours performed.

Intercohort competition favours mature individuals, however size advantage can shift the balance of competition. Van den Brink & Hutting (2017) found a 10 mm size advantage large enough for juvenile *C. maenas* to match adult *H. takanoi* in foraging trials. Larger body size tends to present an advantage for direct interference (Alatalo & Moreno, 1987; Persson, 1985; Robertson, 1996), however the competitive

disadvantage of a size deficit can be offset through physical and behavioural traits (Martin & Ghalambor, 2014). In crabs, species-specific traits can override size differences and shift the balance of competition in favour of a smaller species, assuming the size difference is not great. Lee & Seed (1992) regard chelal size and meral spread to be more important than body size for determining agonistic dominance, and Brown et al. (2005) found the robust and aggressive xanthid *Menippe adina* outcompeted two larger, yet less robust and aggressive, mud crabs for refuge. These factors could explain the intersize foraging trial results, as despite the 25 mm CW advantage, *C. pagurus* still possessed less robust chelae than *X. hydrophilus*. Furthermore, although *C. pagurus* were much more aggressive during intersize trials than during interspecific trials, they were still less aggressive than *X. hydrophilus*. Although *C. pagurus*' agonistic success rate was much higher in intersize trials than interspecific trials, the larger cancrid failed to dominate the robust xanthid and still had less success when performing threats and attacks. The synergistic effect of maturity, greater aggression and more robust chelae likely drive *X. hydrophilus*' dominance in size-matched interactions and competitiveness in intersize interactions.

Potential implications for *C. pagurus*

Rocky intertidal microhabitats, such as boulders, enhance structural complexity and provide vital refuge for vulnerable species. This environment is an essential nursery habitat for juvenile *C. pagurus* prior to an ontogenetic shift for subtidal regions (McKeown et al., 2017). However, rocky habitats such as cobble and boulders are also the preferred habitats for *X. hydrophilus* (Flores & Paula, 2001; Flores & Paula, 2002; pers. obs). Unlike *C. pagurus*, the xanthid does not undergo an ontogenetic habitat shift; adults and juveniles both inhabit lower intertidal and upper subtidal rocky microhabitats alike (Pallas et al., 2006). Therefore, adult *X. hydrophilus* are likely to actively compete with juvenile *C. pagurus*.

Crab population densities are largely determined by the impacts of ontogenetic emigration, density-dependent emigration and interference competition for refuge; nursery refuge exclusion could therefore have a bottleneck impact on *C. pagurus* populations due to the enhanced risks of negative interactions including intracohort competition, intercohort cannibalism, and interspecific interactions such as intraguild

predation by other crabs (Iribarne et al., 1994; Juanario & Navarrete, 2013; Marshall et al., 2005; Moksnes, 2004; Moksnes et al., 1998; Van den Brink & Hutting, 2017). *C. pagurus* are intense intersize cannibals (Amaral et al., 2009), as observed in preliminary dietary preference trials, and adult *C. pagurus* are known to migrate up the shore for high-tide foraging (Karlsson & Christiansen, 1996). As juvenile *C. pagurus* rely on refuge to avoid predation, exclusion by *X. hydrophilus* may indirectly drive intercohort cannibalism in *C. pagurus*. *X. hydrophilus*' prolonged, defensive refuge occupation and robust chelae, the latter trait known to provide effective defence versus larger *C. pagurus* (Lawton, 1989), may suggest a relative invulnerability against intraguild predation. Dedicated predator resistance studies incorporating a multitude of potential predators may provide insight on natural controls for *X. hydrophilus* populations.

It is unknown whether *X. hydrophilus* cannibalises, however the sympatry of adults and juveniles suggests it does not. This could drive high populations densities and might even be indicative of gregariousness, which can drive refuge saturation (Amaral et al., 2009; Jensen et al., 2002). This could also drive cooperative behaviours, such as group defence, and while such behaviours may not significantly benefit a subordinate competitor (Behringer & Hart, 2017), they could amplify dominion for a dominant competitor. However, at present, it is impossible to confirm whether facilitative intraspecific behaviours such as gregariousness or cooperation occur in this species. Further study including female and juvenile *X. hydrophilus* are essential to determine the species' overall vulnerability to predation and competition, as these groups do not possess the size nor relative chelal robustness as adult males, as well as broaden our knowledge on this species' intraspecific dynamics.

Considering the importance of refuge for small crabs and the largely opportunistic, availability-dependent diets of most species, interference competition for refuge is considered a more significant limiting factor than exploitative competition for food (Orensanz & Gallucci, 1988). High levels of conspecific tolerance and refuge dependence may be facilitating refuge saturation by *X. hydrophilus* on rocky shores. In addition, the xanthid's robust chelae and apparent aggression drive asymmetrical competitive dominance in interactions with size-matched *C. pagurus*. As a result, *X. hydrophilus*' establishment in novel sites might exclude juvenile *C. pagurus* from refuge within their nursery habitats, rendering the juveniles more prone to predatory

and competitive pressure. Avoidance behaviour by *C. pagurus* may also be detrimental for growth due to decreased foraging activity (Shepard et al., 2021). Furthermore, as *X. hydrophilus* do not undergo an ontogenetic habitat shift, *C. pagurus* may not benefit from seasonal reprieve.

The impact of saturation-forced exclusion could be habitat and community specific, and *X. hydrophilus* populations may self-regulate by driving self-detrimental habitat alteration or exceeding carrying capacity (Griffen et al., 2015; Toscano & Griffen, 2013). Otherwise, shifting *X. hydrophilus* may have a role in bottlenecking *C. pagurus* populations by excluding juveniles from refuge, which could even result in total habitat exclusion (Brown et al., 2005). Density manipulation and subsequent surveys across sites may shed light on whether *X. hydrophilus* have a significant impact on diversity, community assemblage and ecological stability (Behringer & Hart, 2017).

Further research and long-term surveys across a variety of sites are necessary to judge whether the discussed phenomena are occurring. This study provides insight into direct interactions between the two focal crab species, and offers ecological discussion, however interpretation of results should include consideration for the experimental conditions. Such conditions can provide false differences and mask true differences due to species-specific preferences having species-specific behavioural consequences in response to the simplistic habitat provided (Mascaró & Seed, 2001). The results cannot be interpreted as 100% analogous to what occurs under true intertidal conditions; however, they can serve as a foundation for further studies. As well as further competitive studies, it would be greatly beneficial to build a greater ecological understanding of *X. hydrophilus*, as factors such as settlement dynamics, larval development, and mating systems remain poorly understood for this climate change indicator species.

CONCLUSION

Although it is impossible to interpret a controlled experiment as a true representation of the intertidal zone, its results can provide critical insight and serve as the foundation for further study. Here I present substantial ecological information on *Xantho hydrophilus*, a climate change indicator species poorly represented in published literature, and its potential role as a competitor versus *Cancer pagurus*. As an omnivore, this crab could have impacts across trophic levels. It densely populates rocky intertidal habitats and, as a refuge-dependent, conspecific tolerant crab wielding large chelae, has the potential to claim and saturate available refuge when established. This might have negative implications for sympatric species, including juveniles of the commercially valuable *C. pagurus*, as the progressively northward shifting xanthid might overwhelm community resistance through sheer abundance. Though their foraging preferences may not substantially overlap, competitive trials suggest that *X. hydrophilus* could directly exclude size-matched *C. pagurus* from refuge through aggressive interference, with the results of agonistic interaction analyses indicative of asymmetrical competition in favour of the xanthid. *X. hydrophilus* may also indirectly exclude *C. pagurus* through refuge saturation. Ultimately, the xanthid's establishment could bottleneck *C. pagurus* populations; one of potentially many interaction-specific ecological changes that could occur as it shifts further. It may therefore be prudent to consider long-term and large-scale monitoring of *X. hydrophilus*' populations and to assess its impact across its historical range, recently expanded range, and just beyond the northerly limits of its expanded range in order to gauge whether the crab is driving progressive ecological change through shifting. However, at our current level of ecological understanding regarding *X. hydrophilus*, remarks on its impact are speculatory. Further studies are necessary to substantiate the conclusions of this study.

APPENDIX 1

X. hydrophilus dietary preference trials

Due to the scarcity of information regarding the behaviour and ecology of *X. hydrophilus*, dietary preference trials were conducted prior to competitive trials to identify an animal prey that both species readily consume, thus minimising preference bias and identifying a source for natural competition between the focal species. Ten different animal species were selected for use in preference trials, as well as four macroalgal species as Hayward et al. (1974) speculated the crab to be largely herbivorous following gut content analysis. Identifying herbivorous preferences could shed light on the ecology and behaviour of this species (Wolcott & O'Connor, 1992), and set a foundation for future study. Most potential food items were collected by hand from Dale (Pembrokeshire) and selected based on their high relative abundance and sympatry with *X. hydrophilus* around the low intertidal – shallow subtidal boundary, within the *Fucus serratus* subzone and *Laminaria* zone (Evans, 1949). The exception to this rule was *Mytilus edulis*, which were collected from Llangrannog (Ceredigion) and selected due to being preferred prey for *C. pagurus* (Griffin et al., 2008). Only items lacking any visible external damage, parasitism or disease were collected. Animals and macroalgae were kept in holding tanks under the same conditions as formerly described for focal crab species and were kept for 24 h before use.

All animal preference trials were multi-choice in terms of prey size to test for size selectivity. Size categories were defined according to commonly observed size-ranges at the collection site. Methods of measurement, done with callipers, were species-specific due to morphological diversity; shell height for gastropods, shell length for mussels, disk diameter for brittlestars and carapace width for crabs. All four gastropod species were grouped into a single trial for practical convenience due to their similar morphologies, therefore multi-choice for species as well as size. Though also morphologically similar, crabs were separated into species-specific trials to prevent combat or predation occurring between prey. Gastropods were tethered due to their ability to scale aquarium sides, as practiced in previous studies (Bourdeau & O'Connor, 2003). Eight animals were offered per trial in all aside from the porcelain crab trials, for which only six individuals were provided due to limited size-variation whilst sampling. All animal preference trials lasted 48 h, with inspection periods

occurring every 12 h. The species and size category of consumed prey were tallied for analysis. Constant prey availability was maintained by replacing damaged and entirely consumed prey during inspection periods. Further multi-choice trials would have been conducted if *X. hydrophilus* showed preference for multiple species, however such trials were not necessary.

After the removal of all epiphytes, macroalgae were rinsed, blotted dry and weighed before use in macroalgal preference trials. These trials were conducted in two treatments: no-choice and multi-choice. During no-choice trials, 10g of a single macroalgae species was presented to a single *X. hydrophilus* per trial. These no-choice trials were used to identify palatable macroalgae to include in the final multi-choice trials. During multi-choice trials, 5 g of each of the three preferred macroalgae (15 g total) were presented concurrently to a single *X. hydrophilus* per trial. Each macroalgal trial lasted 48 h. At cessation, the remaining macroalgae was blotted dry and weighed. For each trial, equivalent macroalgae (in terms of species and weight) were left concurrently *without* a crab and then weighed to act as a control. The difference in mass (g) between control and trial macroalgae weights were calculated to determine how much (if any) was consumed.

X. hydrophilus' foraging preferences were analysed using ANOVA tests for comparing consumption within no-choice and multi-choice trials, and Welch two sample t-tests for comparing consumption across the trial types. Non-parametric alternatives (Kruskal-Wallis rank sum tests, Wilcoxon rank sum tests), were used when Shapiro-Wilk tests identified non-normality. Tukey HSD post-hoc pairwise comparison followed ANOVA, whilst Dunn's test with Bonferroni correction followed Kruskal-Wallis.

Only three of the ten animal species presented to *X. hydrophilus* were consumed (Table 16). Only a single *M. edulis* was consumed, which is not indicative of preference, and subsequent video observations suggest cannibalism was the likely cause of mortality amongst small juvenile *C. pagurus*. As *P. platycheles* are suspension-feeders and non-cannibalistic (Amaral et al., 2009), *X. hydrophilus* was certain to be the consumer, therefore this was considered the preferred prey animal. There was no difference amongst *P. platycheles* size categories ($X^2 = 4.527$, df = 2, p = 0.104), however 12 – 14 mm CW *P. platycheles* were chosen for use in competitive foraging trials due to

being consumed most often. There was no significant difference in the consumption of individual macroalgae species between no choice and multi-choice trials (Table 15). *X. hydrophilus* exhibited clear preference for *Saccharina latissima* in both no choice and multi-choice treatments (Figure 9); significantly more so than *Chrondus crispus* and *Fucus serratus* in no choice and multi-choice trials respectively (Table 17).

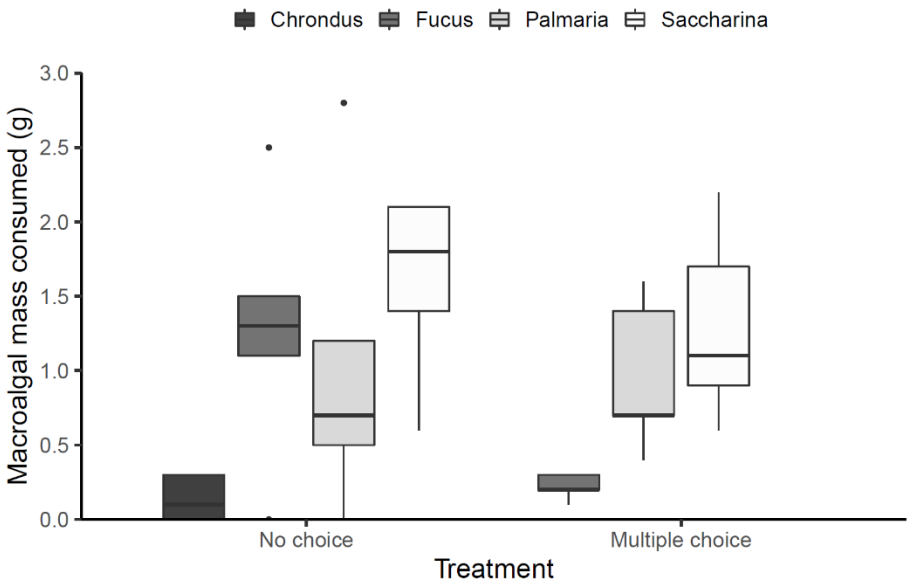

Figure 9 Differences in species-specific macroalgal consumption (g) by *X. hydrophilus*, within and across treatments. N = 5 per species in no choice trials and n = 5 for multiple choice trials. Boxplots show the data's minimum, lower quartile, median, upper quartile and maximum. Outliers are points beyond the minimum and maximum.

T**able 15** Mean macroalgal mass (g) consumed per macroalgal preference trial and the output of comparative statistical analyses across treatments. SD included in parentheses. Test results are blanked for *C. crispus* due to its exclusion from multi-choice trials. **Bold** p values indicate statistical significance at alpha 0.05.

Species	No choice	Multi-choice	df	t / W	p
C. crispus	0.14 (0.152)				
F. serratus	1.28 (0.896)	0.22 (0.084)	4	2.635	0.057
P. palmata	1.04 (1.074)	0.96 (0.513)	6	0.15	0.886
S. latissima	1.6 (0.629)	1.3 (0.644)	8	0.745	0.48

T**able 16** Mean prey consumed per animal preference trial and individual trial group characteristics including details on species, size and quantity provided. SD included in parentheses.

Trial group	Prey species offered	Size categories offered (mm)	Offered per trial	Consumed per trial
Gastropod	*Steromphala cineraria*	16 – 20	1	0
		22 – 26	1	0
	Tritia reticulata	16 – 20	1	0
		22 – 26	1	0
	Littorina littorea	22 – 26	1	0
		28 – 32	1	0
	Ocenebra erinaceus	22 – 26	1	0
		28 – 32	1	0
Mussel	*Mytilus edulis*	10 – 14	2	0
		16 – 18	2	0
		22 – 26	2	0
		28 – 32	2	0.2 (0.48)
Brittlestar	*Ophiothrix fragilis*	6 – 8	2	0
		10 – 12	2	0
		14 – 16	2	0
		18 – 20	2	0
Porcelain crab	*Porcellana platycheles*	6 – 7	2	0
		9 – 10	2	0.4 (0.55)
		12 – 13	2	1 (1)
Velvet crab	*Necora puber*	10 – 15	2	0
		20 – 25	2	0
		30 – 35	2	0
		40 – 45	2	0
Risso's crab	*Xantho pilipes*	10 – 15	2	0
		20 – 25	2	0
		30 – 35	2	0
		40 – 45	2	0
Edible crab	*Cancer pagurus*	10 – 15	2	0.6 (0.55)
		20 – 25	2	0.2 (0.48)
		30 – 35	2	0.2 (0.48)
		40 – 45	2	0

T**able 17** Output of statistical analyses comparing macroalgal mass (g) consumed within treatments. **Bold** p values indicate statistical significance at alpha 0.05.

Treatment	Test results			Post-hoc results		
	df	F / X^2	p	Pair	Diff. / Z	p
No choice	3	3.311	**0.047**	*C. crispus – F. serratus*	1.14	0.13
				C. crispus – P. palmata	0.9	0.289
				C. crispus – S. latissima	1.46	**0.384**
				F. serratus – P. palmata	0.24	0.96
				F. serratus – S. latissima	0.32	0.912
				P. palmata – S. latissima	0.56	0.666
Multi-choice	2	6.677	**0.011**	*F. serratus – P. palmata*	0.74	0.073
				F. serratus – S. latissima	1.08	**0.01**
				P. palmata – S. latissima	0.34	0.512

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