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Research article

Laboratory based feeding behaviour of the Chinese mitten crab, *Eriocheir sinensis*, (Crustacea: Decapoda, Brachyura, Varunidae): fish egg consumption

Jessica M. Webster^{1*}, Paul F. Clark² and David Morritt¹

¹*School of Biological Sciences, Royal Holloway University of London, Egham TW20 0EX, United Kingdom*

²*Invertebrates Division, Department of Life Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD*

E-mail: Jessica.Webster.2011@live.rhul.ac.uk (JMW), D.Morritt@rhul.ac.uk (DM), p.clark@nhm.ac.uk (PFC)

** Corresponding author*

Abstract

Dispersal of *Eriocheir sinensis* from its native habitat is a worldwide concern. As one of the most invasive species known, this crab causes significant disruption to foreign ecosystems. In particular, populations in the United Kingdom (UK) are increasing in number and *E. sinensis* has been reported from many river catchments (www.mittencrabs.org.uk). The ecological implications of this invasion are not fully understood. One aspect of concern lies in the potential for mitten crabs to predate fish eggs which, if realistic, could contribute to the decline of riverine populations. In this study, 100 mitten crabs from the River Thames were used in experimental feeding trials to 1) investigate foraging ability on a variety of fish eggs and 2) establish whether crab size affected foraging potential. Eggs ranged from 1-6 millimetres (mm) in diameter from one of four species of marine and freshwater fish; zebrafish, lumpfish, Pacific salmon and trout. Predation by crabs varied with egg type; crabs were capable of foraging 1mm zebrafish eggs, but the majority consumed eggs 2-6mm in diameter. The most attractive eggs were apparently lumpfish, where the median proportion consumed was 100%. Crab size did not appear to govern foraging potential, though variation was observed in the size range of juvenile crabs consuming the different eggs with the largest, salmon, being consumed by crabs of the broadest size range. *E. sinensis* does have the potential to predate on a range of fish eggs, and the results are used to infer the risk presented to specific groups of UK fish stocks.

Key words: *Eriocheir sinensis*, Chinese mitten crab, invasive brachyuran, foraging, fish eggs, carapace size

Introduction

The Chinese mitten crab, *Eriocheir sinensis* (H. Milne Edwards, 1853), is a highly invasive decapod, having successfully colonised numerous countries outside its native range, resulting in a wide global distribution that extends across a number of continents from Asia to NE Europe and USA. Although the specific site of the first mitten crab found in the Thames is unclear, Battersea Power Station (Anon 1936a, b) or Lots Road Power Station (Harold 1936), it was certainly captured in Nine Elms/Chelsea Reach in 1935. However, the next Thames report was not until 1976 (Ingle and Andrews 1976) followed by a series of papers recording establishment of the mitten crab in this watershed (Andrews et al. 1981; Ingle 1986; Attrill and Thomas 1996; PF Clark and Rainbow 1997; PF Clark et al. 1998; Gilbey et al. 2008). Mitten crabs are catadromous, exhibiting a high degree of euryhalinity that enables migration between marine and freshwater environments. Such a life history enables *E. sinensis* to maintain a broad distribution in freshwater for ca. 3–5 years before moving downstream to higher salinities for breeding. As the Thames mitten crab population continues to increase in number and disperse westward to Oxford, consideration should be given to establishing the threat this species poses to native flora and fauna through predation, disease, competition and habitat disturbance.

One issue of particular concern is the possible consumption of fish eggs by mitten crabs and the potential reduction of fish stocks. This may be problematic for species permanently resident in upstream rivers and also those that migrate into freshwater to breed, such as salmon (*Salmo salar* Linnaeus, 1758). In the Thames, smelt (*Osmerus eperlanus* Linnaeus, 1758) is an example of a species migrating from the lower estuary to breed in freshwater. According to Colclough et al. (2002), smelt migrate upstream from south of Gravesend to spawn above Battersea in March and April. Eggs are shed on stones, water plants, submerged bushes, grass and other solid structures, but never on mud (Belyanina 1969). Smelt eggs could therefore potentially be eaten by mitten crabs. Whilst a number of studies have looked into the dietary intake of *E. sinensis* and concluded a low ratio of ingested fish material in comparison to aquatic flora and invertebrates (Rudnick and Resh 2005; Czerniejewski et al. 2010), few have sought to directly investigate the ability of *E. sinensis* to predate fish eggs, and the implications this could have for fish stocks spawning in freshwater. The Global Invasive Species Database hints at the lack of supporting data on this topic by claiming that the risk of predation by *E. sinensis* on fish eggs is ‘presumably low’ (IUCN/SSC Invasive Species Specialist Group 2009).

One study which did attempt to address this topic was conducted in California, in which the predation rate of salmonid eggs and larvae by Chinese mitten crabs was assessed (Culver 2005). Although the results provide some preliminary evidence that *E. sinensis* can predate fish eggs, the data were somewhat limited. Low numbers of crabs were used and eggs from only one genus of fish (*Oncorhynchus*) were included in the assessment, neglecting the potential for crabs to consume eggs from other genera and of a variety of sizes. Furthermore, only carapace width was used as a measure of crab size, overlooking the possible importance of chela width as a determinant of egg consumption. This may have been particularly significant in the study of Culver (2005) due to the incorporation of both adult and juvenile crabs; studies exploring the relative growth of brachyurans (Hartnoll 1982) have observed changes in growth patterns with maturity and suggest a single parameter of size may not be sufficient when comparing crabs of varying maturity, at least without established correlations. Thus there is a lack of a strong dataset to support or refute the potential for *E. sinensis* to predate fish eggs. This is especially concerning in light of the fact that an effective method of controlling this species has not yet been determined, with recent efforts turning towards the prospect of human consumption as a means of limiting the population (PF Clark et al. 2009). At present, the Thames population is continuing to increase in size (PF Clark 2011) and disperse around England and Wales. However, the recent report by Yeomans and J. Clark (2015) of mitten crab fragments in the River Clyde, Scotland are of concern as this species could have a detrimental effect on life cycle of wild salmon and trout populations.

The key aims of this study were to determine the ability of mitten crabs to consume eggs from a range of fish species, to establish whether the size of crabs had any effect on their foraging behaviour and, by extension, to infer the potential risk mitten crabs pose to native fish in the UK.

Methods

Crab collection and maintenance

All crabs used in the study were collected from the banks of the tidal River Thames at either Richmond or Chelsea, and held in the Marine Aquarium at Royal Holloway University of London (RHUL). The crabs were collected from the foreshore at low tide. Crabs were hand-picked before being placed into damp containers and stored within a cool box during transportation to RHUL where they were maintained in large holding tanks, containing aerated, de-chlorinated tap water at 12 ± 1 °C and a 12:12 L:D light regime.

Feeding trials

Feeding trials were carried out from July - October 2013. In total, 100 crabs were incorporated into the study, being dispersed unevenly across 8 individual trial periods. 31 crabs were given zebrafish eggs across three trials, 23 were given lumpfish across 2 trials, 29 were given pacific salmon across 2 trials and 16 were given trout eggs in the final trial. Variations in the number of crabs included in each trial were solely determined by crab availability. Each trial operated over a four day period. On day one, crabs were separated into individual experimental tanks ($10.7 \times 22.5 \times 18\text{cm}$) or individual beakers ($8 \times 12\text{cm}$), based on their size. For each animal, gender, standard carapace width (the distance between the posterior spines on either side of the carapace), chela width and length of the dactylus were recorded. All size measurements were measured to the nearest 0.1 mm using vernier scale callipers. The absence of chelae was recorded. The sex of crabs was distinguished by morphological differences in the width of the abdomen; males are characterised by a narrow v-shaped abdomen, whilst females possess a wider, u-shaped abdomen. Any asymmetry in the width of chelae on each crab was standardised by using the wider chela for the size measurement, and the dactylus of the same chela. The experimental containers were all filled with approximately 3250 ml of dechlorinated tap water, or 750 ml for beakers (water was changed between each trial), and provided with a source of aeration.

On day two, following an acclimation period of 24h, crabs were provided with four eggs from one type of fish (Table 1). Eggs were deposited with the crabs for 24h, during which time some of their foraging behaviour was observed and recorded on video camera (See video appendix). As some crabs were placed in beakers, which were smaller than the holding tanks, eggs were deposited in close proximity to crabs in tanks to account for difference in encounter rates with eggs. After 24h the number of eggs consumed by each crab was recorded, and any remaining eggs discarded following dehydration with ethanol. Eggs that were not consumed were counted by eye, occasionally following removal with the aid of a fine sieve (mesh size 20). If eggs appeared half consumed, this was counted as half an egg. Signs of crushed/destroyed eggs were discounted. Following egg counts and the removal of remaining egg material, each crab was provided with a portion of fish flesh (perch) for approximately 12h to determine satiation levels. Foraging behaviour with perch was observed for 30 minutes. Consumption of perch (or lack of) was recorded on the final day. Crabs that had moulted during the trials were also noted, as this may have affected appetite. After each trial all crabs were placed back into their original tanks, and all equipment washed for

subsequent trials. Feeding trials were carried out in the dark, to best replicate the natural benthic habitat. Animals were also provided with debris in the form of shells and pebbles, again to create a similar habitat to that experienced in the wild. Prior to entry into the experimental containers all crabs were starved for approximately one week. A minority of crabs (8) were re-used in a second trial but given different eggs to negate any effects of previous experience with a particular egg type. These crabs were starved for the standardized 1 week period between trials. A control tank was set up for each trial, in which eggs were placed into tanks without crabs to monitor their integrity after the given time period.

Egg selection

The eggs used in this study were largely selected on the basis of their size, with the aim of presenting a variety. Eggs were also chosen to incorporate both marine and freshwater fish species in the study and some groups native to the UK. Due to constraints on egg availability, in the case of Atlantic salmon, a comparable group was used (Pacific salmon). Under the same constraint, some of the eggs (trout and Pacific salmon) contained an added preservative (salt). Eggs from the fish species used here can thus be considered models against which eggs from more relevant species can be compared. The exact species producing salmon and trout eggs were not known. To appreciate the relative size of each egg against the mean chela width of crabs used in this study (6mm), a scale diagram was produced (Figure 6). Relative egg size was calculated by dividing raw egg diameters into 6mm (for example, lumpfish eggs of a 2mm diameter were a third of the size of the average chela width) and scaling up this measurement appropriately to meet the crab chela image size.

Data analysis

All statistical analyses were carried out using the IBM SPSS statistical package (Version 21) and graphs and illustrations produced using Microsoft Word and Microsoft Excel. Normality of data was tested using a Kolmogorov-Smirnov test, and any data that was not normally distributed were analysed using non-parametric statistical tests, namely Spearman's rank correlation, Kruskal-Wallis and Mann-Whitney U tests. To establish a correlation between carapace width and chela width/dactylus length, we used a Spearman's rank correlation test for both male and female crabs. When comparing the number of the different egg types consumed within the trials we used a Kruskal-Wallis statistical test. To test for significant differences in the median proportion of each egg type consumed, we conducted a series of Mann-Whitney U tests. Correlations between the size of eggs and their consumption were

determined using a series of Spearman's rank correlation tests. To establish if there was a difference in male/female consumption and consumption by those in tanks/beakers, a series of Mann-Whitney U tests were used.

Results

Crab size

Carapace width varied considerably among individual crabs, with measurements ranging from 13.8–39.1mm. Similarly, large differences were identified in chela width and dactylus length, with ranges from 3.4–10.5mm and 3.1–12.1mm respectively. Male and female carapace widths were not normally distributed (Kolmogorov-Smirnov Test: $P < 0.05$). Male and female carapace widths were subsequently found to differ significantly (Mann-Whitney: $U = 519$, $P = 0.01$). A strong, statistically significant correlation between carapace width and chela width was identified in both male and female crabs independently (Spearman's rank correlation test: $r = 0.870$, $P < 0.01$; $r = 0.856$, $P < 0.01$ respectively) and when male/female data were pooled (Spearman's rank correlation test: $r = 0.896$, $P < 0.01$; Figure 1). In all three cases as the carapace width increased so did the width of chelae. A highly significant positive correlation was found between carapace width and dactylus length for males and females independently (Spearman's rank correlation test: $r = 0.890$, $P < 0.01$; $r = 0.945$, $P < 0.01$) and combined (Spearman's rank correlation test: $r = 0.901$, $P < 0.01$). There was no significant difference among the mean carapace widths of crabs for each egg type (Kruskal-Wallis: $\chi^2 = 7.09$, d.f. = 3, $P = 0.069$).

Egg consumption

There was considerable variation in the number of given eggs consumed by crabs across the different types within the trials. Overall, every type of egg was ingested by at least some crabs, but when the number of eggs consumed in each treatment were compared, significant differences were observed (Kruskal-Wallis: $\chi^2 = 40.18$, d.f. = 3; $P < 0.001$; Figure 2). Notably more crabs were found to consume none of their eggs in the zebrafish trials than all others, whilst considerably more crabs consumed 2 or more of their eggs in the lumpfish, salmon and trout treatments than in the zebrafish. Figure 3 displays these findings in terms of the median proportion of each egg type consumed. A series of post-hoc Mann-Whitney U tests demonstrated that significantly fewer zebrafish eggs were consumed in comparison to all other egg types ($P < 0.001$ in all cases). A significant difference in consumption was also

observed between Pacific salmon and lumpfish eggs (Mann-Whitney: $U = 157$, $n = 54$ $P = 0.003$) but not between lumpfish and trout eggs (Mann-Whitney $U = 141$, $n = 39$, $P = 0.228$). The two latter egg types were the most readily consumed in these trials. With the exception of zebrafish, in which no crab ate all given eggs, for each egg type there were a number of crabs who consumed all four of their eggs and the portion of fish. These crabs varied in size (Table 3).

There was also an interesting pattern in the size range of crabs consuming each of the four egg types. Crabs consuming the largest eggs, that is, the trout and salmon eggs, presented a broader size range than those consuming the smaller eggs (zebrafish), which were of a consistently narrower size range (Figure 4).

Effect of crab size on egg consumption

Crabs consuming at least one of their eggs varied considerably in size for every egg type. Smaller crabs did not appear confined to foraging smaller eggs (zebrafish and lumpfish), and the same can be said for larger crabs foraging larger eggs (salmon and trout). There was also variation in the number of given eggs consumed by crabs within each trial; many crabs consumed all of their given eggs, whilst others in the same trial and of similar size ate none or only some. In the crabs used in this study (<40mm carapace width), their size does not appear to limit foraging ability.

Zebrafish eggs

Frequency data for the number of eggs consumed was not normally distributed (Kolmogorov-Smirnov: $P < 0.05$) for all crabs. There was no significant correlation between carapace width (hence chelae/dactylus size) and egg consumption (Spearman's rank correlation coefficient = -0.059 , $P > 0.05$; Figure 5A).

Lumpfish eggs

Carapace width and egg consumption were not normally distributed (Kolmogorov-Smirnov Test: $P < 0.05$), and there was a weak, but statistically significant correlation, between carapace width and eggs consumed (Spearman's rank correlation coefficient = -0.475 , $P \leq 0.05$; Figure 5B). The negative coefficient indicates that in some cases the number of eggs consumed decreased as the carapace width increased.

Trout eggs

The number of eggs consumed was not normally distributed (Kolmogorov-Smirnov: $P < 0.05$) and no significant correlation between carapace width and egg consumption was found (Spearman's rank correlation coefficient = 0.421, $P > 0.05$; Figure 5C).

Pacific salmon fish eggs

Number of eggs consumed was not normally distributed (Kolmogorov-Smirnov Test: $P < 0.05$), and there was no statistically significant correlation between carapace width and egg consumption (Spearman's rank correlation coefficient = 0.293, $P > 0.05$; Figure 5D).

Sex ratio

The majority of crabs used in this study were male with only 21 of the one hundred mitten crabs being female. This gives an approximate 1:4 ratio. Of the 21 females, 11 of these were given trout eggs. In this particular trial there was no significant difference in the amount of eggs consumed by males and females (Mann-Whitney: $U = 26.5$, $n = 16$, $P = 0.913$).

Similarly, in the zebrafish egg trial in which 7 females were used alongside 23 males, no significant difference in the amount of eggs consumed was found (Mann-Whitney: $U = 81$, $n = 30$, $P = 1.000$). The predation rates of male and female crabs for salmon and lumpfish eggs were not compared due to the low number of females used in these trials (Table 2).

Variation and controls

Whilst the majority of crabs were in similar physical condition, there was some small variation within this during the study. Of the one hundred crabs, exactly 10% had just one chela, and these individuals were dispersed throughout all treatments. Of this minority, many individuals (60%) did consume eggs, and in the Pacific salmon egg trial, which had the most single-chela animals, no significant difference in egg consumption was found between crabs with one chela and crabs with two (Mann Whitney $U = 30.0$, $n = 26$, $P = 0.762$). One crab possessed no chelae and was thus omitted from data analyses, though interestingly did consume perch (but not eggs). Three male crabs were also observed to moult during the trials, specifically all within the Pacific salmon egg trial. Only one of these individuals attempted to consume eggs, ingesting just one. Moulded crabs were included in analysis of crab size, but were excluded from data analysis on egg consumption, as this may have influenced foraging behaviour. Placing some crabs in beakers appeared to make no difference to egg consumption; no significant difference was found in consumption by crabs in tanks and

beakers ($U = 22.5$, $P < 0.05$). For all egg types the control tanks showed that there was no non-crab egg mortality during treatments.

Discussion

Egg consumption

The risk of mitten crab predation on fish eggs varies among species of fish. Of the four egg types used in this study, zebrafish eggs were apparently the least favoured. This may be related to the small size (~1mm) of these eggs, which likely conferred a low encounter rate and would have been difficult and indeed costly to handle, particularly for larger crabs. This refers to the energetic cost of picking up small eggs, which would require fine muscular control in bringing the dactylus and propodus together firmly around the egg and possibly multiple attempts (which could lead to chela fatigue), for a relatively small calorific return. This selective behaviour has been observed in studies of prey handling in the shore crab, *Carcinus meanus* (Linnaeus, 1758), in which the optimum mussel size, that is, the size at which crabs gain most energy from prey intake whilst accounting for handling time, appeared to increase with crab size (Elner and Hughes 1978). One may therefore expect the crabs consuming zebrafish eggs to be the smallest crabs used, but this was not found to be the case; the zebrafish eggs ingested were done so by intermediately sized crabs (21.3mm-24.6mm Carapace width). Greater consumption rates for bigger eggs (2-6mm) may be a result of the increased ease of handling these eggs, particularly for salmon eggs which could be pierced as opposed to being picked up. This behaviour was observed in the salmon egg trials, with the use of both chelae and mouthparts to penetrate eggs and is reinforced by the fact that crabs appeared to struggle when picking up salmon eggs because occasionally they were dropped (see Video 2 of video appendix). This factor may explain the greater range of carapace widths observed in crabs consuming increasingly bigger eggs. Larger eggs would also likely confer higher nutritional gain for foraging efforts. If egg selection was based on optimal foraging behaviour, it is expected that a greater size range of crab would attempt the bigger eggs; small eggs would only be profitable to small crabs as opposed to larger eggs which would be beneficial to both small and large crabs. It is noteworthy that many of the crabs employed in this study were sub-adults and the largest crab used had a 39.1mm carapace width. The use of this size-range is relevant as crabs of this size spend the majority of their time in the freshwater stretches of rivers where they are most likely to encounter fish eggs. Adult mitten crabs can grow to a carapace width exceeding 84mm (The Natural History Museum 2013)

with a recent specimen from The Wash, Norfolk, UK exceeding 90mm carapace width (PFC, DM pers. obs.). It can be inferred that through the piercing activity observed in our study crabs this large would also be capable of foraging on salmon and possibly trout eggs. Studies incorporating a greater size range of crab including fully grown adults should be undertaken to explore this further.

One factor which may have contributed to the indifference to zebrafish eggs is that they are largely transparent and thus the most difficult eggs to visually locate. It has been established that the compound eyes of crabs enable them to see colour (Lester 2006), and consequently zebrafish eggs may have been harder to find than the other egg types which were brightly coloured. This may have only been of minor significance however, as crabs do not rely solely on vision to detect prey items, and the importance of olfaction as means of locating prey has been suggested in studies of feeding behaviour in other crab species. One such study (Rebach 1996) showed that the rock crab, *Cancer irroratus* (Say, 1817) could detect prey items placed in a simple maze purely using olfactory cues, and when given visually identical shells with and without prey odour, crabs only fed on shells possessing the odour. In the present study, variation in the strength of odour produced by eggs may have, in part, been responsible for the disparity in egg consumption. The significance of colour as a mechanism of prey detection may be even less pronounced in the wild due to the fact that these crabs reside in turbid water. Tactility may play a greater role in the sourcing of prey. Culver (2005) reported that mitten crabs located salmonid larvae more rapidly when they accidentally swam into the legs of crabs. A similar observation has been made for mitten crabs feeding on actively swimming gammarid amphipods (C Mills unpubl. obs.). Whilst fish eggs are static, it can be suggested that the crabs used in our study were more likely to contact the larger eggs through their own movement and the resulting disruption of water.

Variation in egg consumption may potentially be explained by differences in the chemical composition of eggs. Of the four egg types, zebrafish eggs were the only ones not to contain high levels of salt. Salmon and trout eggs both contained added salt as a preservative, and lumpfish, being a marine species, would have produced eggs in a highly saline environment. It can be suggested therefore that the crabs had a preference for particularly salty eggs; decapod crustaceans are known to utilise oesophageal taste receptors to accept or reject food once it enters the oral cavity (Aggio et al. 2012). In the same way, it is possible that the zebrafish eggs contained a chemical which deterred crabs from preying on these. Variation in the nutritional content of eggs may also have contributed to the observed results

and, as discussed, may be implicated with egg size. For example zebrafish eggs of a 1mm diameter would arguably provide crabs with less protein and lipids than the lumpfish, salmon and trout eggs.

Of the remaining three egg types each was consumed to a similar degree, although on average more lumpfish and trout eggs were consumed than salmon eggs. It can be suggested however, that since the salmon eggs were easily the largest eggs (6mm), a similar amount of egg material was actually consumed by crabs predated these. This is supported by the fact that fewer crabs were observed to consume perch flesh after all their eggs in the salmon egg trial than in the lumpfish and trout trials, indicating these crabs were more likely to be satiated following egg consumption. This study suggests therefore that crabs are capable of predated fish eggs of a 1-6mm diameter, and potentially those exceeding this.

The lack of correlation between crab size and egg consumption suggests that the size of crabs was not a major factor affecting the foraging on fish eggs. This is not to say that the size of crabs had no impact whatsoever on their ability to consume eggs, but that on the most part, crabs of a broad size range were capable of handling and ingesting eggs of different diameters. Whilst the statistically significant correlation found between crab size and egg consumption in the crabs consuming lumpfish revealed that the larger crabs consumed fewer eggs than the smaller crabs, the fact that the largest crabs (carapace widths 35.6–36.4mm) still consumed some eggs suggests they do have the ability to predate eggs of this size (2mm). Due to the small number of adults used within the study (Figure 1), it was not possible to accurately determine the impact of maturity on egg consumption. Whilst it appeared, at least on the surface (Figure 2) that adults exhibited similar predation rates to juveniles, this may not be the case in the wild. It is expected that adults will have higher consumption rates than juveniles based on their size and mitten crabs are known to inhibit their feeding activity for several days before and after moulting, which occurs less frequently as crabs develop (Culver 2005). In addition, these crabs become increasingly carnivorous with adulthood (Culver, 2005).

Threats to native fish

The results obtained in this study suggest that small (<40mm) Chinese mitten crabs have the potential to predate a number of types of fish egg. In addition to a considerable overall degree of egg consumption within the trials, many of the crabs who consumed all their given eggs were also observed to consume fish flesh shortly afterwards (within a 30 minute period),

indicating the potential for individuals to exhibit higher predation rates than the trials suggested. As all crabs were starved for the same amount of time, and, as those consuming all of their eggs and perch ranged considerably in size, it is unlikely that these high predation rates are confined to largest crabs used, which may have been expected to consume more prey. The potential applicability of these results does depend on the likelihood of crabs encountering these different types of eggs in the wild, which can be influenced by a number of factors including the upstream migration distance of spawning fish and the timing of life cycle events for both fish species and Chinese mitten crabs.

As mitten crabs spend the majority of their life cycle in freshwater (Herborg et al. 2005), migrating back to high salinities once to reproduce, it can be suggested that the eggs of exclusively fresh water or anadromous species are most threatened by the predation from this crab species. Marine, and particularly estuarine, species of fish do still remain threatened however, by the biggest crabs, and hence quite probably the largest consumers, returning to saline environments to breed. Although the ability of larger mitten crabs (40–80+ mm carapace width) to consume eggs was not identified in this study, it can be inferred from the results that there is a risk of predation. Mitten crabs, in the UK, undergo their breeding migration from late summer (August) to early winter (Morritt et al. 2013) and it is thought that juveniles make an upstream migration into freshwater over March-July (Herborg et al. 2003). How these different stages in the life-cycle of the crab might potentially impact on fish spawning is unclear. For example it is not known to what degree adults feed during their reproductive migration. What is clear, however, is that spawning fish will potentially overlap with intermediate stage, sub-adult crabs (similar to the size range used in the present study) from different cohorts particularly in the freshwater reaches of rivers. Thus it could be argued that there is a persistent predation risk for fish eggs from such crabs and this risk may periodically increase / decrease depending on the crab's life-cycle. Fish such as Atlantic salmon may be at increased risk from predation, as spawning occurs at variable times of the year among different populations (Aas et al. 2011) and is likely, at least in some cases, to overlap with periods of elevated crab presence. Brown trout (*Salmo trutta*) breeding in freshwater may encounter fewer crabs when laying their eggs due the timing of their spawning season, which in native species occurs in winter (Scottish Natural Heritage, 2012).

Alongside the timing of breeding events in fish species, the location of spawning sites may be an important factor affecting the risk of crab predation on fish eggs. Whilst Atlantic salmon can migrate as far as 1600km from the sea to spawn, it is thought that the majority

only travel only 160km upstream (Burton and Burton 2002). Anadromous brown trout migrate upstream to lay and fertilize their eggs, and this has been shown to occur at around 100km upstream (Crawford 2001). In the case of resident freshwater brown trout, spawning migration is more limited; tracking studies in European rivers have found individuals to migrate only as far upstream as 28km, with some travelling significantly shorter distances than this (Arnekleiv and Ronnin 2004). Mitten crabs can migrate distances of 1,500km from the sea (PF Clark et al. 1998), and thus it can be inferred that they have the potential to travel as far up rivers as most spawning salmon and trout. Although such impressive distances have only been observed by crabs in their native environment, studies of migrating crabs in British rivers have observed significant increases in upstream movement over time, with distance rising from 16km per year in the early 1990s to 49km per year in the late 1990s (Herborg et al. 2005). Latest records of mitten crab sightings (www.mittencrabs.org) indicate that crabs have been found as far upstream as Didcot in the River Thames, which, using mapped distances on aerial photographs (Harrison 2004) was calculated to be approximately 280km from the entrance to the North Sea at Southend. It is now thought that this upstream migration could reach 500km per year (Bentley 2011), and would not be surprising considering invasive mitten crabs in the River Elbe, Germany, have been noted to progress as far as 700–780km upstream (PF Clark et al. 1998). As this exceeds the length of all UK Rivers, it can be suggested that all freshwater fish spawning sites are potentially accessible to mitten crabs, if distance alone is the only constraint. In practice other topographic factors will also play a role. The recent recovery of Chinese mitten crab remains in the River Clyde, suggests the species is already present in Scotland, where the potential impact on trout and salmon fisheries is of considerable concern (Yeomans and J. Clark 2015). Fish species spawning in freshwater are probably more likely to encounter mitten crabs than marine species due to the reduced surface area of rivers in comparison to the sea and the resulting increase in habitat overlap between fish and crabs. In addition, we do not know the effect of spawning behaviour by mitten crabs on foraging activity; it is quite possible that foraging effort is reduced when breeding.

The spawning strategies and defensive mechanisms employed by fish, especially with regards to site selection, may impact the probability of crabs finding and predated fish eggs. In this study, fish eggs were not hidden from mitten crabs and were instead placed in close proximity to the animals. In the wild crabs are unlikely to encounter eggs as readily, as they are often laid in crevices or within substrates to remain hidden from potential predators. This

may indicate that eggs in the wild are more sheltered from crab predation than the results of this study suggest. Indeed this has been demonstrated when it comes to potential predation of salmon eggs by invasive crayfish, *Pacifastacus leniusculus* (Gladman et al. 2012). Salmonids lay their eggs in nests termed redds, and often in association with gravel and stone substrates. Culver (2005) explored the ability of mitten crabs to forage within a gravel substrate in her study, discovering that juvenile mitten crabs were relatively unlikely to predate hidden (buried) eggs, in contrast to adults who appeared to forage at greater depths within this substrate. More recent research using mitten crabs suggests they burrow to a considerable extent and are subsequently impacting sediment through bioturbation (A. Blight, University of St Andrews, pers. comm.). Such activity suggests crabs are likely to come across buried eggs within a mud substrate. In some European rivers average nest depths in Atlantic salmon have been recorded at 12.9cm (Guadamar et al. 2000), over double the depth at which Gladman et al. (2012) buried eggs within their study. It is thus crucial to establish the maximum and indeed likely depths at which crabs may burrow to and forage in for gravel and mud substrates in the wild to accurately determine the extent to which buried eggs may be protected from crab predation. In the case of lumpfish, females lay their eggs on rocks among sea weed beds (Bañón et al. 2008), a possible habitat for crabs to encounter based on their omnivorous nature. As is common in fish species, male lumpfish guard their eggs once laid and fertilized. Such activity may deter crabs, especially by larger fish species. The possession of sharp claws by crabs may enable them to counter such aggressive interactions. Veldhuizen and Stanish (1999) suggest that mitten crabs may be in reach of the eggs of other nesting fish such as centrarchids, and raise the potentially crucial point that predation rates on fish eggs may be lower in cooler climates where the metabolic rate of crabs will slow (Xiao-Bo et al. 2003).

The results obtained in this study may be used to infer the risk mitten crabs pose to specific groups of native fish. As discussed, the least predated eggs in this study were zebrafish eggs, which may be linked to their small size (1mm). If size is, at least in part, responsible for the low consumption rates observed, it can be suggested that fish species producing eggs of a similar diameter may only be minimally threatened by mitten crab predation. Native British fish in this category include European perch (*Perca fluviatilis* Linnaeus, 1758), whose eggs are ca. 1.28mm in diameter, common rudd (*Scardinius erythrophthalmus* Linnaeus, 1758), ca. 1.33mm in diameter, and bream (*Abramis brama* Linnaeus, 1758) with an estimated egg diameter of 1.64mm (Bonisławska et al. 2001).

European smelt, *Osmerus eperlanus* also belongs to this category, producing eggs of a 1mm diameter (Jones and McCarthy 2014) and spawning in UK Rivers such as the Forth, Thames and Cree. Smelt is considered to be majorly threatened following its decline and disappearance from many British rivers including the Clyde and Almond (Maitland and Lyle 1996). Though our study suggests that crabs may have preference for larger eggs, it is noteworthy that in the wild crabs might not usually come across solitary eggs; many fish species, including perch, lay their eggs in clusters, thus creating the appearance of a larger prey item and most probably increasing encounter rates by crabs. Those native species with a larger diameter of egg that are comparable to the lumpfish, trout and salmon eggs used in this study may be at a higher risk from mitten crab predation. These include pike (*Esox Lucius* Linnaeus, 1758) whose eggs are ca. 2.68mm in diameter, (Bonisławska et al. 2001) brown trout (*Salmo trutta* Linnaeus, 1758), ca. 4.64mm in diameter (Radnak et al. 2006), and Atlantic salmon, whose eggs are comparable to the Pacific salmon eggs used here. All of these are freshwater or anadromous fish, and therefore could be exposed to risk of mitten crab predation. Marine fish that may be at risk include the European plaice, *Pleuronectes platessa* (Linnaeus, 1758), whose eggs are approximately 2mm after spawning and grow to about 7mm prior to hatching (Sussex ICFA) and of which populations are known to spawn in the Irish sea and Bristol channel (Dunn and Pawson 2002). The predation of brown trout and Atlantic salmon eggs by a growing population of mitten crabs in British waters may be of greatest concern, as these are of significant commercial value; reductions in the general population could have significant economic repercussions alongside increasing concerns over the conservation status of these fish in Britain. Rivers including the Dee, Tweed and Tay have already been designated as Special Areas of Conservation (Joint Nature Conservation Committee) due to the importance of resident wildlife, and are known to support high quality populations of Atlantic salmon. Indeed this is not the first study to suggest that salmonid eggs may in particular be at risk from such predation (Culver 2005).

Implications for future research

The results obtained in this study are useful in providing an indication of the potential for mitten crabs to consume fish eggs and a framework for future research. In subsequent studies a wider range of egg types should be incorporated into feeding experiments, including those of native species, which may be particularly valuable in enabling us to conclude accurately the degree to which these species are vulnerable from mitten crab predation. Moreover, incorporation of a broader size range of crabs including fully grown adults may be useful in

determining the size up to which crabs are able to forage the differently sized eggs, if indeed there is a limit. In light of this initial study, and in combination with other research into the negative impacts of mitten crabs on non-native ecosystems, it is crucial that serious consideration is given to controlling the further spread of the Chinese mitten crab, especially in Scotland, and resources are invested in order to facilitate this.

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References

- Aas O, Klemetsen A, Einum S, Skurdal J. (eds) (2011) Atlantic Salmon Ecology. Wiley-Blackwell, Oxford, UK, 467 pp
- Aggio J, Tieu R, Wei A, Derby, C (2012) Oesophageal chemoreceptors of blue crabs, *Callinectes sapidus*, sense chemical deterrents and can block ingestion of food. *Journal of Experimental Biology* 215: 1700-1710, doi:10.1242/jeb.065854
- Andrews MJ, Aston KFA, Richard DG, Steel JEC (1981) The macrofauna of the Thames Estuary. *London Naturalist* 61:30-61
- Anon (1936a) Exhibitions and notices. October 22nd, 1935. Sir Arthur Smith Woodward LL.D., F.R.S., Vice-President, in the chair. *Proceedings of the Zoological Society of London* 1936 [1935]: 948
- Anon (1936b) No. 387. Abstracts of the Proceeding of the Zoological Society of London. October 22nd, 1935. Sir Arthur Smith Woodward LL.D., F.R.S., Vice-President, in the chair. *Abstracts of the Proceedings of the Zoological Society of London* 1936: 1–15
- Arnekleiv J, Ronning, L (2004) Migratory patterns and return to the catch site of adult brown trout (*Salmo trutta* L.) in a regulated river. *River Research and Applications* 20: 929-942, doi:10.1002/rra.799
- Attrill M, Thomas RM (1996) The current status of the Chinese Mitten Crab, *Eriocheir sinensis* H. Milne Edwards, in the Thames estuary: an increasing population size? pp 9–18. In: Stycznska-Jurewicz E (ed) *Estuarine ecosystems and species*. Proc. of the 2nd International Estuary Symposium held in Gdańsk, October 18-22, 1993 “Crangon” – Issues of the Marine Biology Centre in Gdynia, Gdynia
- Awers. inc, (2013) Nutrition facts. <http://www.red-caviar.com/caviar-nutrition-facts>
- Bañón R, Garazo A, Fernandez A (2008) Note about the presence of the lumpsucker *Cyclopterus lumpus* (Teleostei, Cyclopteridae) in Galician waters (NW Spain). *Journal of Applied Ichthyology* 24: 108-109, doi:10.1111/j.1439-0426.2007.00839.x
- Belyanina TN (1969) Synopsis of biological data on smelt *Osmerus eperlanus* (Linnaeus) 1758. *Fishery Synopsis* 78, FAO, Rome, Italy, v+57pp
- Bentley M (2011) The global spread of the Chinese mitten crab *Eriocheir sinensis*. pp. 107-127. In: Galil BS, Clark PF, Carlton, JT (eds) *In the Wrong Place - Alien Marine Crustaceans: Distribution, Biology and Impacts*, Invading Nature, Springer Series in Invasion Ecology 6, Springer, Dordrecht, Netherlands

- Bonislawska M, Formicki K, Korzelecka-Orkisz A, Winnicki A (2001) Fish egg size variability: biological significance. *Electronic Journal of Polish Agricultural Universities* 4(2). <http://www.ejpau.media.pl/volume4/issue2/fisheries/art-02.html>
- Burton M, Burton R (2002) *International Wildlife Encyclopedia*. (3rd ed) Marshall Cavendish Corporation, New York, USA, 3168 pp
- Clark PF, Rainbow PS (1997) *The Chinese Mitten Crab in the Thames Catchment*. A report for the Environment Agency (Myles Thomas and Willie Yeomans) in three parts. Part 1. A report for the Environment Agency, pp. 1–75 and Part 2 The Appendices to the report for Environment Agency, pp.1-91, with Robbins Roni (NHM), Brian Smith (QMW), Gina Dobson (NHM), Claire Byrne (QMW), Miranda Lowe (NHM) and Ann Morgan (NHM); Part 3. A report on available *Eriocheir sinensis* literature for the Environment Agency, with Roni Robbins (NHM) and Paul Cooper (NHM), pp 1–27
- Clark PF, Mortimer D, Law RJ, Averbs J, Cohen B, Wood D, Rose M, Fernandes A, Rainbow PS (2009) Dioxin and PCB Contamination in Chinese Mitten Crabs: Human Consumption as a Control Mechanism for an Invasive Species. *Environmental Science and Technology* 43: 1624-1629, doi:10.1021/es802935a
- Clark PF, Rainbow PS, Robbins RS, Smith B, Yeomans WE, Thomas, RM, Dobson G (1998) The alien Chinese mitten crab, *Eriocheir sinensis* (Crustacea: Decapoda: Brachyura) in the Thames catchment. *Journal of the Marine Biological Association of the United Kingdom* 78:1215-1221, doi:<http://dx.doi.org/10.1017/S002531540004443X>
- Colclough, S, Gray G, Bark A, Knights B (2002) Fish and fisheries of the tidal Thames: management of the modern resource, research aims and future pressures. *Journal of Fish Biology* 61: 64-73, doi:10.1111/j.1095-8649.2002.tb01762.x
- Crawford S (2001) *Salmonine Introductions to the Laurentian Great Lakes: An Historical Review and Evaluation of Ecological Effects*. Canadian Special Publication of Fisheries and Aquatic Science 132, 205 pp
- Culver CS (2005) *Assessing the potential for Chinese mitten crab predation on eggs and Salmonid larvae*. Final Report for Award # 113323J013 for U.S. Department of Interior Fish and Wildlife Service, Marine Science Institute. University of California, Santa Barbara USA, 13 pp
- Czerniejewski P, Rybczyk A, Wawrzyniak W (2010) Diet of the Chinese mitten crab, *Eriocheir sinensis* H. Milne Edwards, 1853, and the potential effects of the crab on the aquatic community in the river Odra/Oder estuary (N.W.-Poland). *Crustaceana* 83: 195-205, doi:10.1163/001121609X12591347509202

- Dunn M, Pawson M (2002) The stock structure and migrations of plaice populations on the west coast of England and Wales. *Journal of Fish Biology* 61: 360-393, doi:10.1111/j.1095-8649.2002.tb01571.x
- Elliot M (2003) Biological pollutants and biological pollution—an increasing cause for concern. *Marine Pollution Bulletin* 46: 275-280, doi:10.1016/S0025-326X(02)00423-X
- Elner R, Hughes N (1978) Energy maximisation in the diet of the shore crab, *Carcinus maenas*. *Journal of Animal Ecology* 47: 103-106, doi:10.2307/3925
- Gaudemar B, Schroder S, Beall E (2000) Nest placement and egg distribution in Atlantic salmon redds. *Environmental Biology of Fishes* 57: 37-47, doi:10.1023/A:1007562508973
- Gilbey V, Atrill M, Coleman R (2008) Juvenile Chinese mitten crabs (*Eriocheir sinensis*) in the Thames estuary: distribution, movement and possible interactions with the native crab *Carcinus maenas*. *Biological Invasions* 10: 67-77, doi:10.1007/s10530-007-9110-4
- Gladman ZF, Adams, CE, Bean CW, Long J, Yeomans WE (2012) Investigating the threat of non-native North American signal crayfish (*Pacifastacus leniusculus*) to salmon redds. *Aquatic Conservation: Marine and Freshwater Ecosystems* 22: 134-137, doi:10.1002/aqc.1238
- Harrison, I (2004) *The Thames: From Source to Sea*. Collins. Affiliated web address: www.getmapping.com
- Hartnoll RG (1982) Growth, pp. 111–196. In: Abele LG (ed), *Embryology, Morphology and Genetics. The Biology of Crustacea*. Academic Press, New York, USA
- Herborg L, Rushton S, Clare A, Bentley M (2003) Spread of the Chinese mitten crab (*Eriocheir sinensis* H. Milne Edwards) in Continental Europe: analysis of a historical data set. *Hydrobiologia* 503: 21-28, doi: 10.1023/B:HYDR.0000008483.63314.3c
- Herborg L, Rushton S, Clare A, Bentley M (2005) The invasion of the Chinese mitten crab (*Eriocheir sinensis*) in the United Kingdom and its comparison to continental Europe. *Biological Invasions* 7: 959-968, doi:10.1007/s10530-004-2999-y
- Ingle RW (1986) The Chinese mitten crab *Eriocheir sinensis* a contentious immigrant. *London Naturalist* 65: 101-105
- Ingle RW, Andrews MJ (1976) Chinese mitten crab reappears in Britain. *New Scientist* 263: 638

Joint Nature Conservation Committee. Special Areas of Conservation (SAC).

<http://jncc.defra.gov.uk/page-23>

Jones N, McCarty I (2014) Environmentally Friendly Diversification of Aquaculture.

Conservation aquaculture rearing techniques for the European smelt *Osmerus eperlanus*. Seafare.

http://www.google.co.uk/url?url=http://www.seafareproject.eu/index.php/download_file/view/16/72/&rct=j&frm=1&q=&esrc=s&sa=U&ei=3NRGVJqBLuSC7gb-o4D4Ag&ved=0CBkQFjAA&sig2=VeppzWfI9cfesW0NtJbLGg&usg=AFQjCNE1-s6mFch8NBSGEtRaURXbEjIZgA

Lester P (2006) Visual communication: Images with messages. (4th ed) Thomas Wadsworth, Belmont, USA. viii+450 pp

Maitland P, Lyle A (1996) The smelt *Osmerus eperlanus* in Scotland. Freshwater Forum 6: 57-68

Mitten crab recording project (2013) <http://mittencrabs.org.uk>

Morritt D, Mills H, Hind K, Clifton-Dey D, Clark P (2013) Monitoring downstream migrations of *Eriocheir sinensis* H. Milne Edwards, 1853 (Crustacea: Brachyura: Grapsoidea: Varunidae) in the River Thames using capture data from a water abstraction intake. Management of Biological Invasions 4: 139-147, doi:<http://dx.doi.org/10.3391/mbi.2013.4.2.07>

National Institute of Biology (2011) <http://www.nib.si/eng/index.php/storitve-in-oprema/test-toksinosti-na-zarodkih-rib-cebric.html>

Natural History Museum:

<http://www.nhm.ac.uk/nature-online/species-of-the-day/biodiversity/alien-species/eriocheir-sinensis/>

Rebach S (1996) Role of prey odour in food recognition by rock crabs *Cancer irroratus* Say. Journal of Chemical Ecology 22: 2197-2207

Rudnick D, Resh V (2005) Stable isotopes, mesocosms and gut content analysis demonstrate trophic differences in two invasive decapod Crustacea. Freshwater Biology 50: 1323-1336, doi: 10.1007/BF02029540

Scottish Natural Heritage (2012) <http://www.snh.gov.uk/about-scotlands-nature/species/fish/freshwater-fish/trout/>

Sussex Inshore Fisheries and Conservation Authority.

http://www.sussex-ifca.gov.uk/index.php?option=com_content&view=article&id=73&Itemid=169

- The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN) (2009) *Eriocheir sinensis*. <http://www.issg.org/database/species/ecology.asp?si=38>
- Veldhuizen T, Stanish S (1999) Overview of the life history, distribution, abundance, and impacts of the Chinese mitten crab, *Eriocheir sinensis*. Report prepared for the US Fish and Wildlife Service. California Department of Water Resources Environmental Studies Office, Interagency Program. Sacramento, California, USA, 26 pp
- Wen X, Chen L, Ai C, Zhou Z (2003) Effects of temperature and body weight on fasting metabolism of the juvenile *Eriocheir sinensis*. *Acta Hydrobiologica Sinica* 27: 361-364
- Yeomans WE, Clark J (2015) A Chinese mitten crab *Eriocheir sinensis* from the River Clyde: the first record of this invasive, non-native species in Scotland? *JMBA, Marine Biodiversity Records* [In Press]

Tables

Table 1. The different types of eggs used in the study. Egg diameters were measured using a ruler, except for the zebrafish embryos which were too small to accurately measure in this way; size data were obtained from the National Institute of Biology (2011).

Egg type	Approximate diameter (mm)	Colour	Preservative	Source
Zebrafish	1	Virtually transparent	None	Royal Holloway laboratory breeding culture
Lumpfish (<i>Cyclopterus lumpus</i>)	2	Black or red (both used in alternate trials)	None	Independent fishmonger
Trout	4	Red	Salt	Online supplier (Amazon.co.uk)
Pacific salmon (<i>Oncorhynchus</i>)	6	Orange	Salt	Waitrose supermarket

Table 2. The proportion of males and females used within each trial alongside their sizes and egg consumption. Data excludes three male crabs that moulted during the trials and one that possessed no chelae.

Trial	Egg type	No. of males	Mean crab size (mm)	Size range (mm)	% Males	Mean proportion of eggs consumed	No. of females	Mean crab size (mm)	Size range (mm)	% females	Mean proportion of eggs consumed
1	Zebrafish	11	24.14	12.40	100	0	0	-	-	0	-
2	Zebrafish	6	24.53	7.80	100	0.17	0	-	-	0	-
3	Pacific salmon	14	24.65	21.70	100	1.43	0	-	-	0	-
4	Pacific salmon	12	24.16	17.5	100	2.33	0	-	-	0	-
5	Lumpfish	12	26.73	19.5	100	2.71	0	-	-	0	-
6	Lumpfish	8	19.93	9.6	72.73	3.50	3	18.33	2.70	27.27	3.33
7	Zebrafish	7	18.89	10.8	50	0.86	7	20.43	23.30	50	0.29
8	Trout	5	18.96	9.3	31.25	2.20	11	21.73	20.60	68.75	2.18

Table 3. The size of all crabs consuming all of their eggs and fish flesh for each egg type. Red values represent females, black represent males, and those underlined represent adults.

Egg type	Egg diameter (mm)	Raw number of crabs	Percentage of crabs consuming all eggs + perch (%)	Carapace width of highlighted crabs (mm)							
Zebrafish	1	31	0	-							
Lumpfish	2	23	30.4	28.1	27.4	24.9	17.5	18.3	18.7	18.5	
Pacific salmon	6	26	15.4	28.1	28.0	33.8	27.4				
Trout	4	16	58.3	25.9	23.1	19.2	17.6	14.6	<u>31.9</u>	<u>35.2</u>	

Captions

Figure 1. Correlation of carapace width and chela width for male and female mitten crabs ($P < 0.01$, Spearman's correlation coefficient = 0.896). Starred data points represent adults, all others represent juveniles.

Figure 2. Percentage of crabs consuming the different number of given eggs. The number of eggs consumed by crabs for each of the given egg types. A. zebrafish eggs, B. Lumpfish eggs, C. Pacific salmon eggs, D. trout eggs. J: juvenile A: Adult. Percentage of crabs is used instead of raw number due to the disparity in the number of crabs given the different fish eggs. The number in brackets is the raw number of crabs given each egg type.

Figure 3. The median proportion of each egg type consumed by male and female mitten crabs, alongside the size of each egg (Kruskal-Wallis independent samples test: $P < 0.05$) ZF: zebrafish, LF: lumpfish, T: trout, PS: Pacific salmon, ED: Egg diameter, MPC: Median proportion consumed. Letters above bars denote the statistical differences between proportions of consumed eggs.

Figure 4. Size range of crabs consuming each egg type against the size of each egg. Crab size ranges = 8.8mm (zebrafish), 19.6mm (lumpfish), 20.6mm (trout) and 21.7mm (Pacific salmon).

Figure 5. Carapace width against number of eggs consumed for each of the four egg types, arranged in order of increasing egg size A. zebrafish embryo, B. lumpfish roe, C. trout roe, D. salmon roe. The only significant correlation between egg consumption and carapace width was for crabs consuming Lumpfish eggs (Spearman's rank correlation test: $P \leq 0.05$).

Figure 6. The relative size of fish eggs against the mean width of a chela. The approximate sizes of eggs were obtained by dividing egg sizes into 6 (the mean chela width of crabs used in this study) and using the scale to correlate these to the image size of chela (13mm). Of the crabs with a 6mm chela width the average carapace width was 22.1mm. Image obtained from <http://www.padil.gov.au/pests-and-diseases/Pest/Main/136524/8988>.

Figures

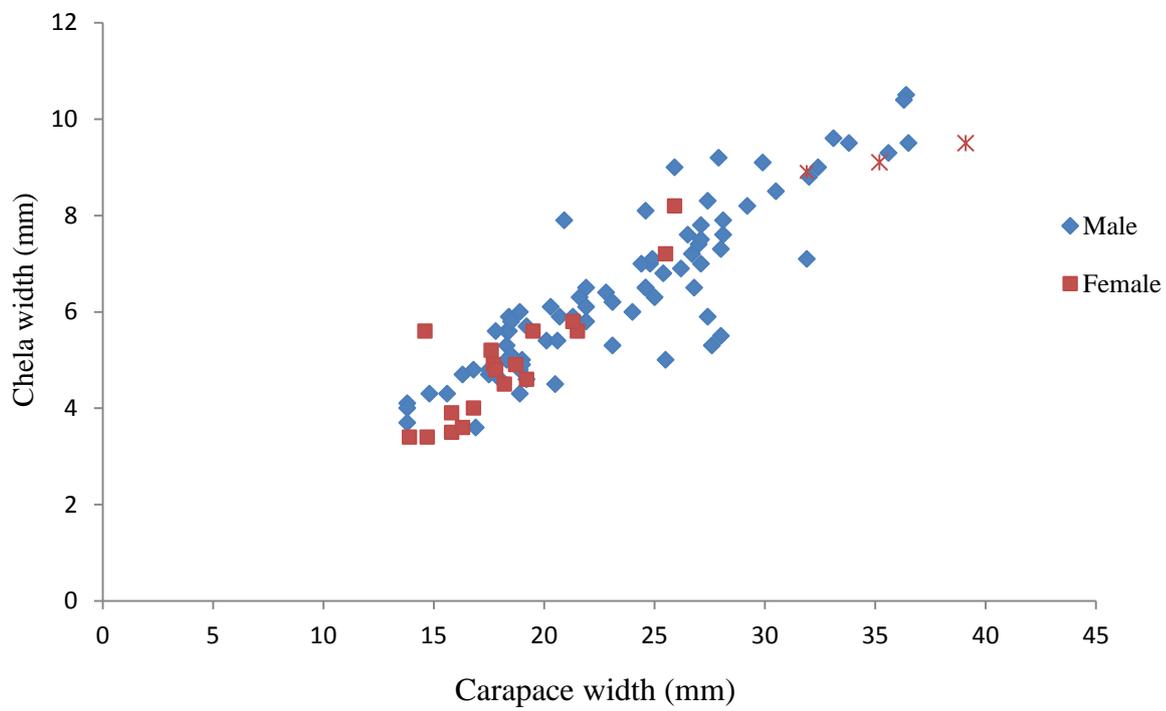


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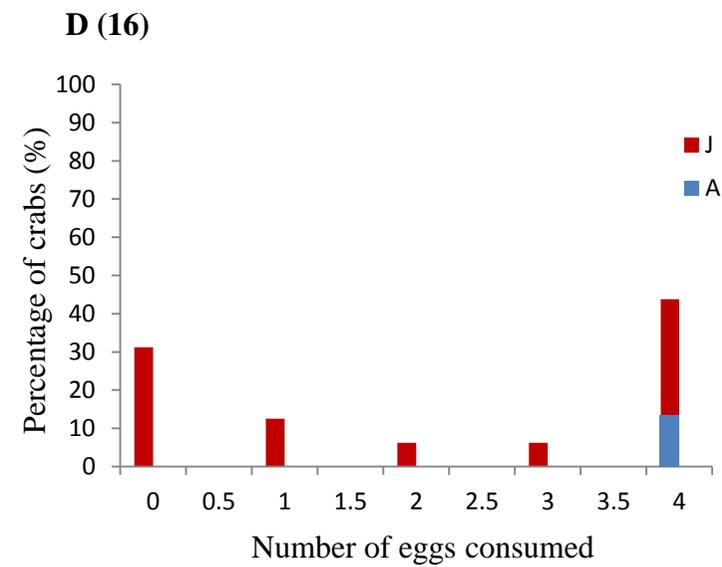
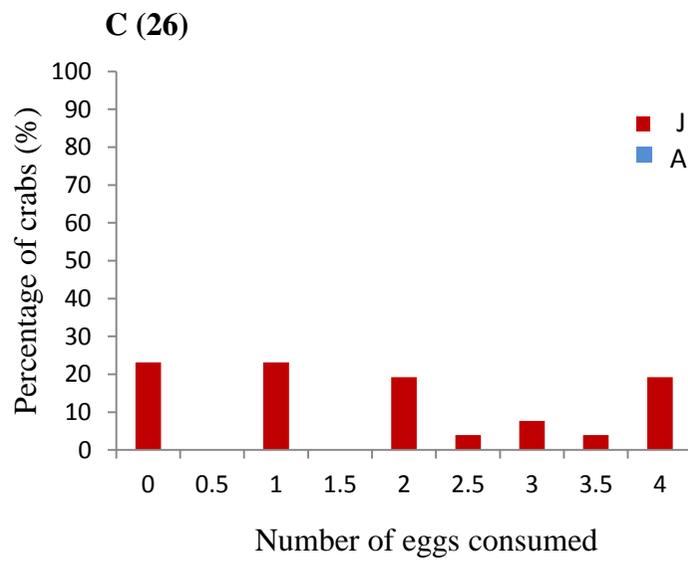
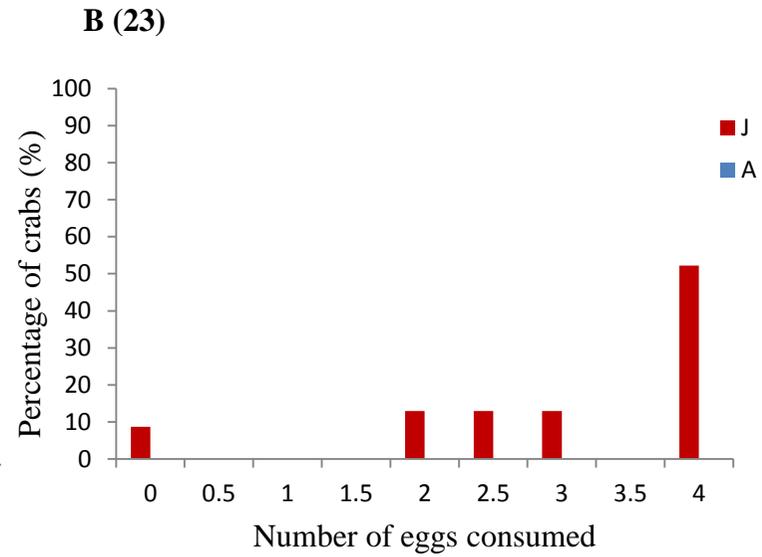
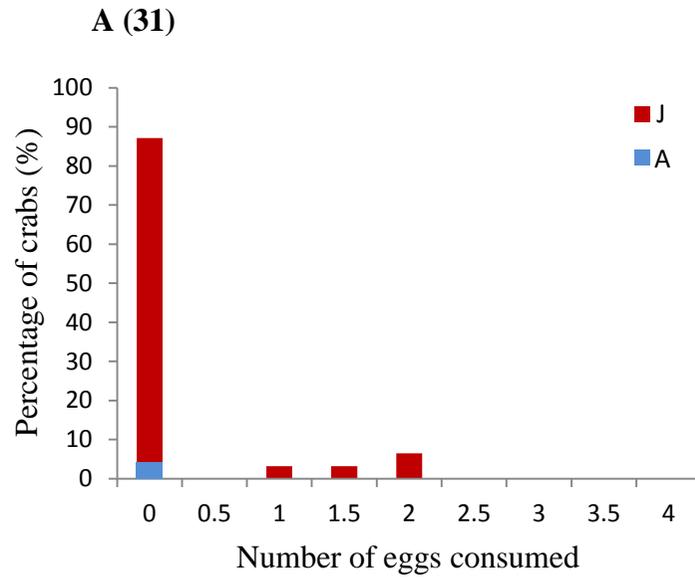


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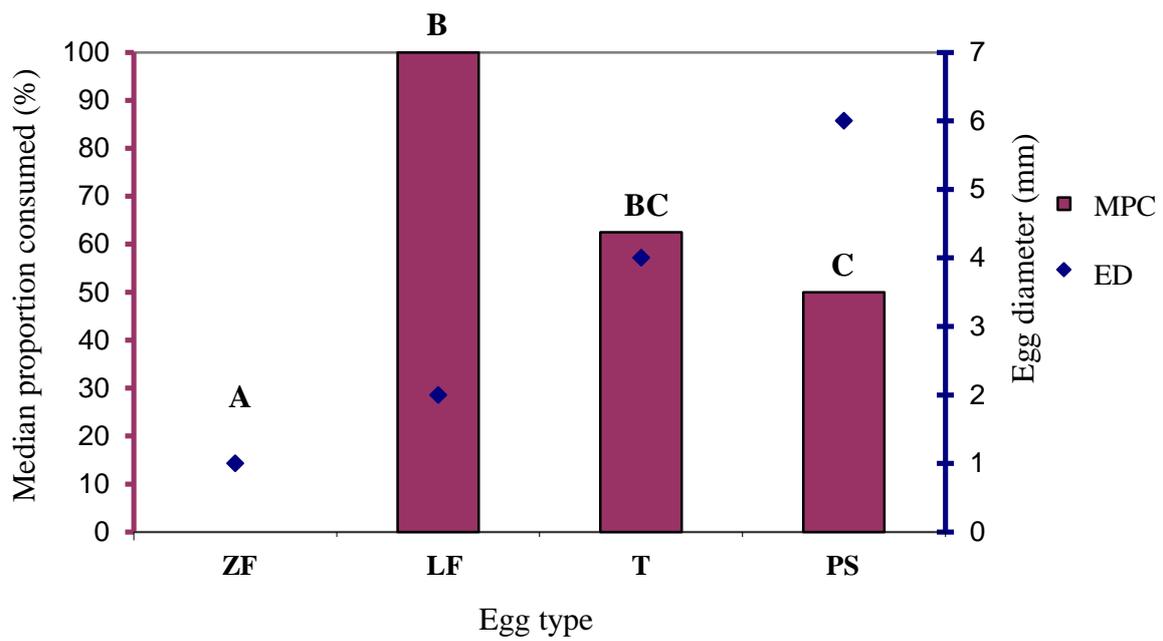


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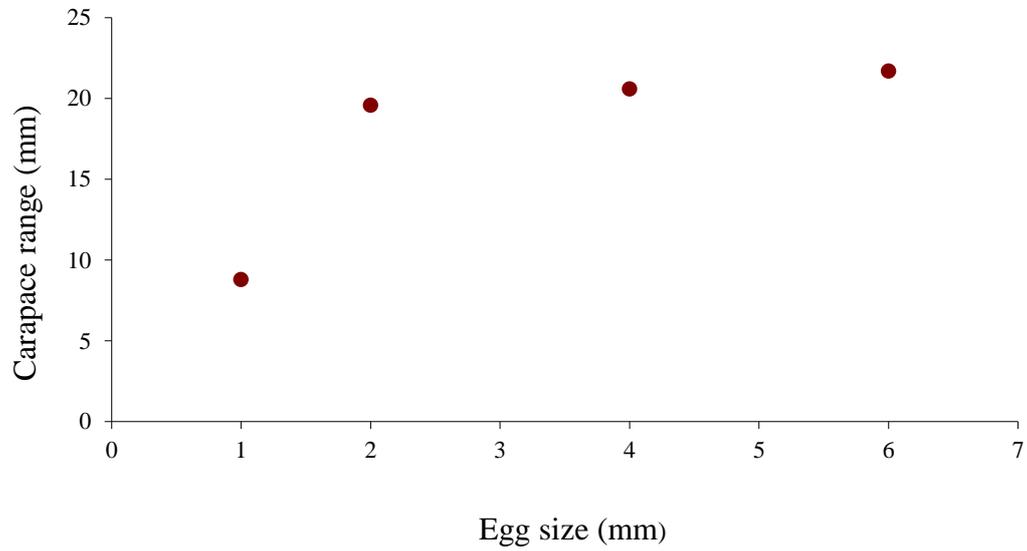


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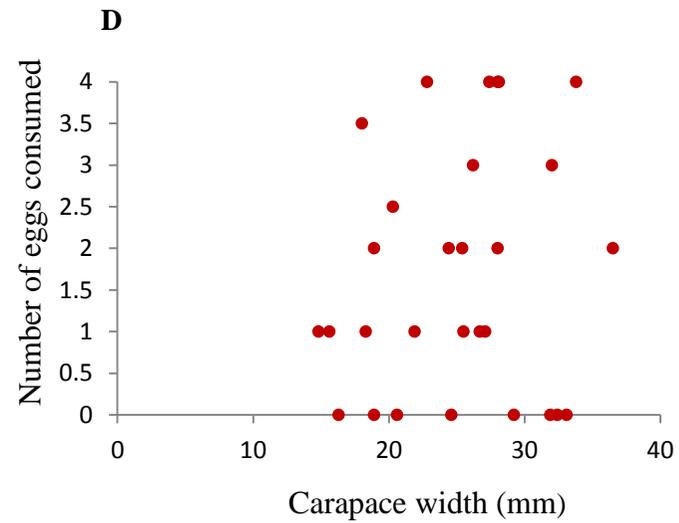
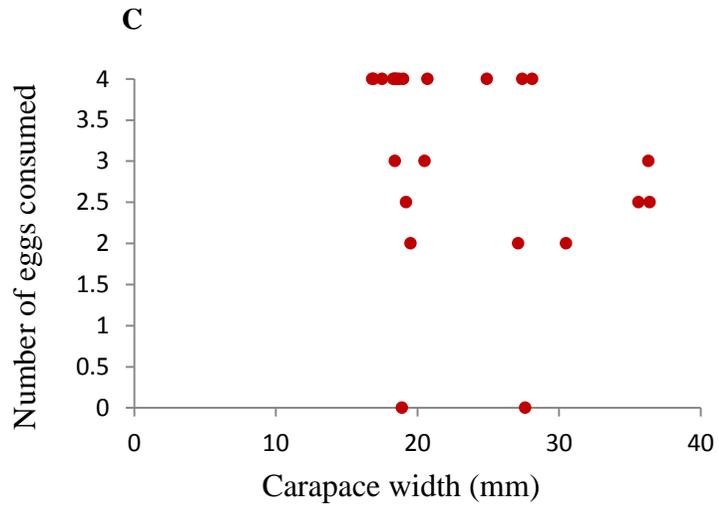
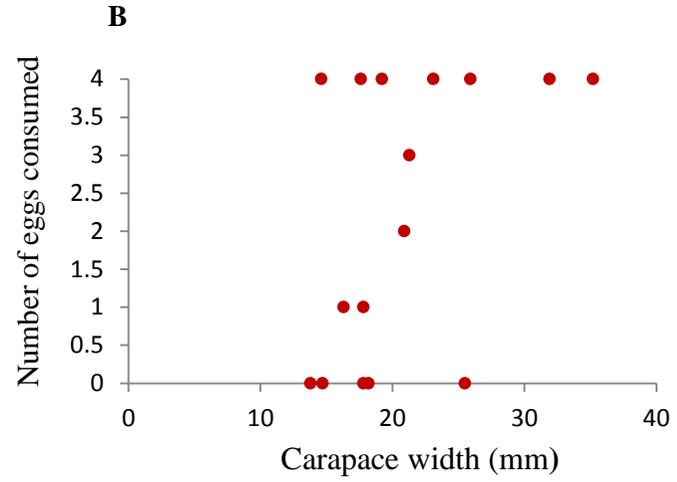
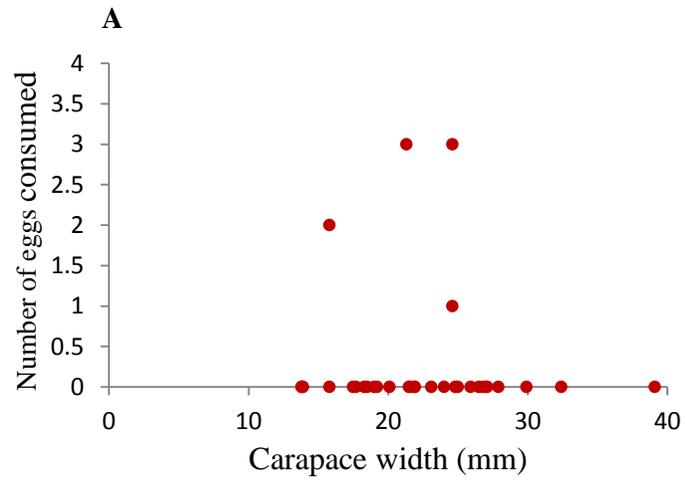


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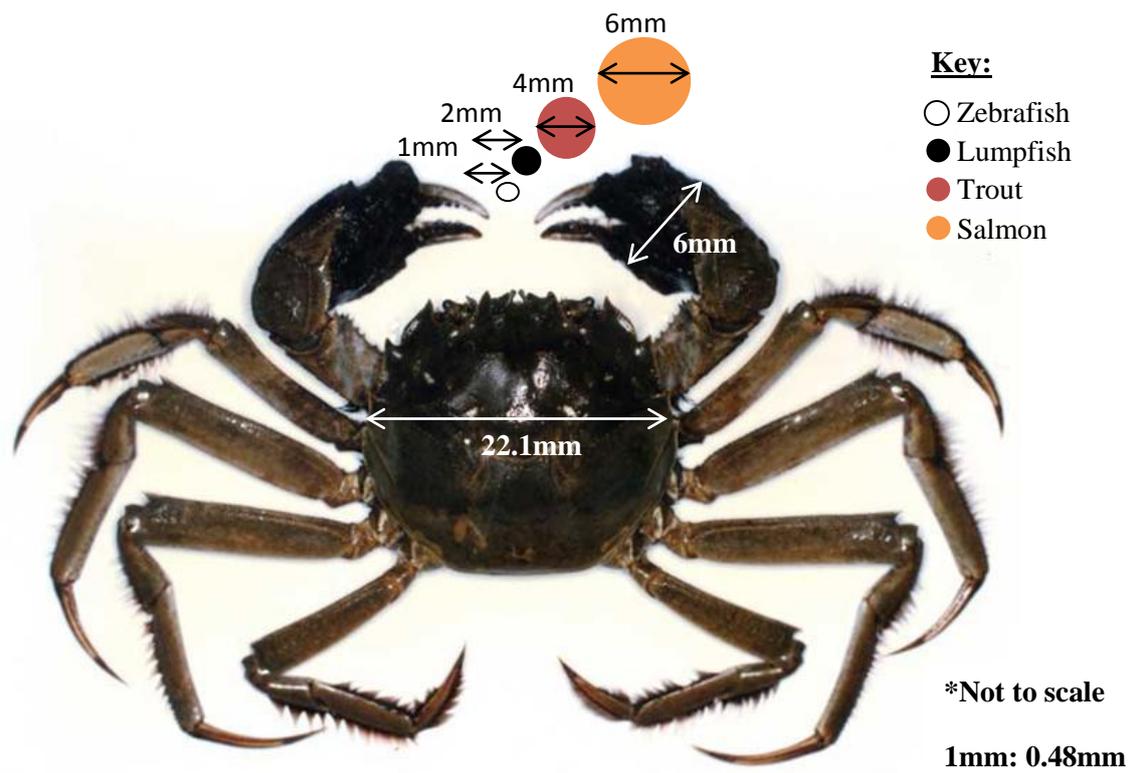


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