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A taste for aliens: contribution of a novel prey item to native fishes' diet

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Abstract Non-indigenous species (NIS) can alter food web structure and function in many ways. While the predatory and competitive roles of NIS in aquatic environments are commonly studied, their role as a prey item for native predators is often overlooked. As the northern Baltic Sea lacks native crabs, the omnivorous estuarine Harris mud crab (*Rhithropanopeus harrisi*) is a novel invader to the system and provides an opportunity to observe how the species enters the prey field of predatory fish. In fall 2013, 1185 stomachs from 17 fish species were dissected and

analyzed for the presence of *R. harrisi*. Fishermen had previously reported finding crabs mostly in the stomachs of perch (*Perca fluviatilis*), a frequent catch in recreational and commercial fisheries, but our study also found large numbers of crabs in four-horned sculpins (*Myoxocephalus quadricornis*) and small numbers in other species' stomachs (*Rutilus rutilus*, *Leuciscus ide*, *Gymnocephalus cernuus*, and *Blicca bjoerkna*). In the study area occupied by *R. harrisi*, four-horned sculpins were the most frequent predator, with 83% having at least one crab in their stomach. In comparison, 7% of perch and roach had consumed *R. harrisi*. Most crabs eaten were 10–12 mm (carapace width), despite broader size range available (1–26 mm). Predation on *R. harrisi* in this system may be limited by the predators' gape size (i.e., physical feeding restriction). These results highlight the need to understand the role of novel invasive species as prey items for native species, ultimately increase understanding of whether native predators can control NIS populations.

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Introduction

As the impacts of non-indigenous species (NIS) in aquatic environments have drawn increased attention in past years (Carlton and Geller 1993; Simberloff et al. 2013), many studies have concentrated on the top-down predatory impacts of an invader on native prey or their competitive interactions with both native and other introduced species. In reality all species, including NIS, have both predatory and prey roles in food webs, and nearly all NIS are eventually preyed upon by native predators, sometimes leading to reductions in NIS population sizes (Hunt and Yamada 2003; Jensen et al. 2007). One of the most notable marine examples comes from the Chesapeake Bay, USA, in which native blue crabs exert considerable predation pressure on the iconic invasive green crab to the point where there are no green crab populations in the Chesapeake (DeRivera et al. 2005). On the other hand, newly abundant prey items can increase a predators' fitness as shown with native fish predators and an invasive prey (round goby) in the Laurentian Great Lakes, USA (Crane et al. 2015). Sometimes the increased resource leads to an increase in predator populations and results in increased predation on native species as well (Noonburg and Byers 2005). In addition, prey naivety towards invasive predators has been widely studied and reported (e.g., Sih et al. 2010), but far less attention has been given to the naivety of predators, although similar naivety may occur especially towards novel prey (Ward et al. 2010), which may result in low predation pressure on the novel species.

The Harris mud crab, *Rhithropanopeus harrisi* (Gould 1841), invasion in the northern Baltic Sea presents an interesting opportunity to investigate how a novel prey item becomes part of native predators' diets. There are no native crab species in the area (Ojaveer et al. 2006), and therefore predators may be slow or even naive towards adopting this new prey into their diets. *R. harrisi* originates from the Atlantic coast of North America (from Canada to the Gulf of Mexico) and has successfully invaded over 20 countries, including those in Europe, Asia, Central America, and the west coast of North America, making it one of the most successful brachyuran crabs in the world (Roche and Torchin 2007). *R. harrisi* is an integral member of estuarine communities throughout its range, serving as a generalist predator of small

biota, a prey species for numerous vertebrate and invertebrate predators, and a host for several parasite species, including *Loxothylacus panopaei* (Odum and Heald 1972; Williams 1984; Grosholz and Ruiz 1995).

The first observation of *R. harrisi* in the Baltic Sea was made in the 1930s in the Kiel Channel in Germany (Schubert 1936) and later in 1950 in Poland (Demel 1953). In the 2000s, *R. harrisi* began to spread northward, and it was recorded in Lithuania in 2000 (Bacevicius and Gasiunaite 2008), in Finland in the Archipelago Sea in 2009 (Fowler et al. 2013) and in Estonia in 2011 (Kotta and Ojaveer 2012). Since 2009, the range and abundance of *R. harrisi* in the Archipelago Sea has increased rapidly. Currently, the monitoring of *R. harrisi* in the area is largely based on public observations through the Finnish Alien Species Portal (www.vieraslaajit.fi), which reports to the Finnish Biodiversity Information Facility database (FinBIF 2017), with locations and species identifications verified by scientists from the Finnish Environment Institute (SYKE) and the Natural Resources Institute (Luke).

The first confirmed public observations of *R. harrisi* in fish stomachs in the Archipelago Sea were received in 2011 (Fowler et al. 2013; FinBIF 2017). Since that time, the geographical range and abundance of reports of *R. harrisi* found in fish stomachs has increased along with the increased range of *R. harrisi*. Based on these public observations, *R. harrisi* are most frequently found in the digestive tracts of perch (*Perca fluviatilis* (Linnaeus 1758)) (around 10 observations yearly). *P. fluviatilis* is the most important catch in recreational fisheries (Luonnonvarakeskus 2014) and provides the fourth largest catch (in tonnes) commercially (RKTL 2013) in the study area. Because recreational catches are mainly composed of this single predator, public observations of *R. harrisi* in fish stomachs were likely effort-biased and unlikely to accurately reflect the diversity of predators consuming *R. harrisi* in the Archipelago Sea.

Aiming to investigate which fish species and the proportions of species that consume novel *R. harrisi* in their invasive range in the Archipelago Sea in Finland, we investigated the stomachs of nearly 1200 fish, representing 17 species of commercial and non-commercial significance in the fall of 2013. Furthermore, we aimed to assess the contribution of *R. harrisi* to stomach contents and infer whether

predation was equally distributed across all size classes of *R. harrisii* available in the area.

Methods

Fishing and stomach content analyses

Sample collection was organized simultaneously with the Annual HELCOM Coastal Fish Monitoring effort in the Kaitvesi region. Fish were collected from both the official survey catch (Kaitvesi) and from nine other sites (altogether 10 sites) in the Archipelago Sea, SW Finland (Fig. 1) between September 9 and November 8, 2013. The southernmost location, Nötö, was outside the known range of *R. harrisii*, and since *R. harrisii* were detected neither from the fish stomachs nor from the habitat traps (see below), these data were excluded from further analyses. In Kaitvesi, 45 Nordic Coastal

survey nets (multi mesh size 10–60 mm) were deployed according to HELCOM Coastal Fish Guidelines (HELCOM 2015). Additional fish from the other nine sites were collected with 5–15 bottom gillnets per site (30 m length, 1.5–3 m height, mesh size 30–80 mm). All fish caught were collected and transported to the Turku University of Applied Sciences on ice. They were then measured (total length (TL), mm) and weighed (g), and their digestive tracts were dissected out and carefully visually inspected for contents including *R. harrisii* remains. All identifiable *R. harrisii* were tallied, and individuals with intact carapaces were also measured (carapace width (CW), mm) using calipers. In addition, their contribution to the stomach contents was estimated as a proportion of all stomach contents. The number of nets and the overall sampling effort varied between locations, and therefore the data was pooled for the whole area for further analyses.

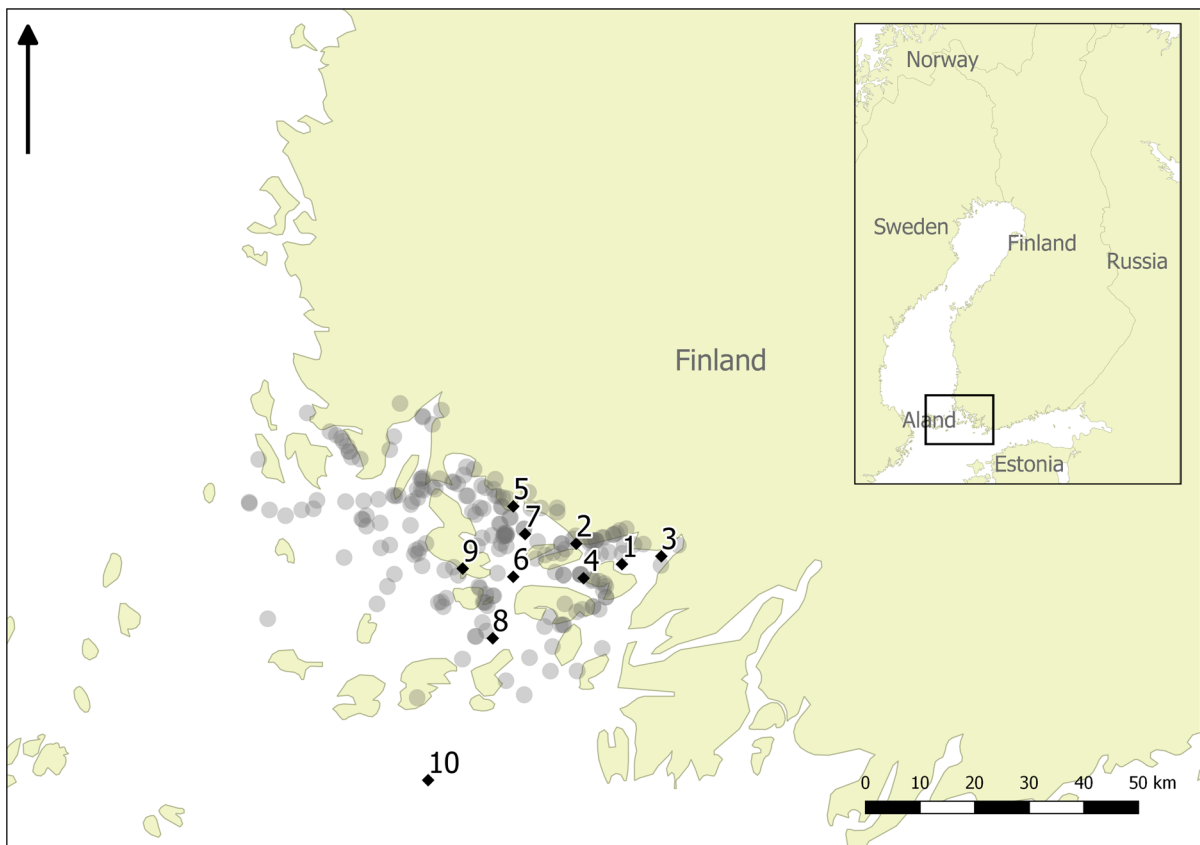


Fig. 1 Map showing the study area overlaid with the range of the *R. harrisii* in Finland in 2013 (grey circles). Exact locations for sampling sites are numbered from 1 to 10. The southernmost

sampling site, Nötö, (10), was excluded from the analyses due to absence of *R. harrisii* in the stomach contents

Available crabs in the area

Habitat traps were deployed at each site using the methods of Fowler et al. (2013) to assess the size range of *R. harrisi* available in the area at the same time that fish sampling occurred. Traps were deployed for a minimum of 4 days, and all *R. harrisi* retrieved from the traps were measured (CW, mm), sexed, and counted. The traps do not provide a reliable estimate of absolute *R. harrisi* density, measure per unit of area, but rather provide information on presence/absence and size distribution. The number of traps as well as the deployment duration varied between the locations. Therefore the data was pooled for further analyses.

Statistical analyses

Due to the small spatial scale, heterogeneity and unbalanced sampling effort in the area, all data over the sampled area were pooled for the analyses. The proportion and sizes of fish feeding on *R. harrisi* were calculated, and their contribution to total predation on *R. harrisi* was calculated as a percentage. Also, the proportion of stomach contents occupied by *R. harrisi* was calculated for each fish species. Furthermore, the relationship between fish size (TL) and the largest crab consumed (CW) was analyzed using Spearman's correlation coefficient and expressed with a linear equation.

All *R. harrisi* found in fish stomachs and habitat trap samples were classified into size classes in 2 mm intervals between 1 and 26 mm, reflecting the size range of *R. harrisi* found in the samples. Selectivity by fish predators towards certain crab size classes was calculated using Manly's selectivity index α (Manly 1974)

$$\alpha_i = \frac{\left(\frac{d_i}{N_i}\right)}{\sum_{i=1}^k \left(\frac{d_i}{N_i}\right)},$$

where i is the *R. harrisi* size class in question, k is the number of available *R. harrisi* size classes, d_i is the proportion that *R. harrisi* size class i is found in a fish stomach and N_i is the proportion of *R. harrisi* size class i found in the habitat traps. Manly's α results in values between 0 and 1, where 0 indicates avoidance (e.g., under-representation of an abundant size class in

fish stomachs) and 1 indicates preference (over-representation of a size class in fish stomachs). If $\alpha > 1/k$ (k = total available size classes), there is predator selection towards that particular size class, and if $\alpha < 1/k$, there is predator avoidance of that particular size class. If $\alpha = 1/k$, there is no predator selection, and the different size classes of *R. harrisi* are consumed proportionally to their availability. The number of size classes in the samples was 13, and therefore the threshold for selection was 0.077.

The fish consuming *R. harrisi* were divided by their species and size (into 2 size classes, smaller and larger than median TL), and selectivity was calculated for each size class within a fish species.

Results

Overall, 1286 fish representing 17 species were caught. Intact fish (1185 individuals) were measured and weighed and their stomachs inspected (Table 1). Of these fish, 450 (35%) had identifiable contents and were included in the detailed stomach content analyses. Remains of *R. harrisi* ($n = 225$) were found in 100 fish stomachs (7% of all fish, 22% of fish with identifiable contents) (Table 2). In some cases ($n = 15$), the number of *R. harrisi* in a stomach could not be determined and was considered to be one individual to avoid over-estimation.

A total of 678 *R. harrisi* were collected from the habitat traps deployed at the fishing sites. The majority of *R. harrisi* ($n = 389$) were caught in the western part of the sampling area (inner archipelago) and the least ($n = 46$) in the southern sites (outer archipelago) (Table 2). Sizes of *R. harrisi* varied between 1.4 and 25.9 mm ($\bar{X} = 10.83$ mm, SD 5.56 mm).

Based on the inspected stomachs, the most *R. harrisi* ($n = 146$) were eaten by four-horned sculpins (*Myoxocephalus quadricornis* (Linnaeus, 1758)). Their predation constituted 65% of all *R. harrisi* found in fish stomachs in this study. Excluding *M. quadricornis* caught from the site which had no *R. harrisi* in the habitat traps (the southernmost location, Nötö), 40 of 48 (83%) fish had at least one *R. harrisi* present in the stomach contents. The mean size (TL) of *M. quadricornis* that had consumed crabs was 210 mm (SD 23; range 180–290 mm), and the mean size present in the catch was 217 mm (SD 34; range

Table 1 All fish caught that were intact enough to be measured

Species	# of fish	Mean TL (mm)	Max TL (mm)	Min TL (mm)
<i>Perca fluviatilis</i>	538	189	310	71
<i>Rutilus rutilus</i>	208	232	302	105
<i>Sander lucioperca</i>	171	250	535	101
<i>Myoxocephalus quadricornis</i>	102	217	298	168
<i>Blicca bjoerkna</i>	50	162	231	100
<i>Abramis brama</i>	38	320	480	155
<i>Gymnocephalus cernuus</i>	23	137	190	106
<i>Coregonus lavaretus</i>	14	385	450	283
<i>Esox lucius</i>	11	624	890	435
<i>Alburnus alburnus</i>	8	111	121	102
<i>Platichthys flesus</i>	6	218	256	191
<i>Clupea harengus membras</i>	4	241	275	212
<i>Leuciscus ide</i>	3	303	388	251
<i>Scardinius erythrophthalmus</i>	3	179	250	130
<i>Osmerus eperlanus</i>	2	176	186	165
<i>Scophthalmus maximus</i>	2	194	202	185
<i>Tinca tinca</i>	2	410	434	385
Total	1185			

168–298 mm) (Fig. 2a). The average number of *R. harrisii* present in *M. quadricornis* stomachs was 3.7 (SD 2.6), although a maximum of 13 was found in one stomach (TL 229 mm). The contribution of *R. harrisii* to the stomach contents of *M. quadricornis* was, on average, 85.3% when they were present in the stomachs.

Perch (*Perca fluviatilis*) were the most numerous fish in the catch across all sampling locations. Of 538 perch caught, 41 (7.6%) had at least one *R. harrisii* in the stomach contents. The total number of *R. harrisii* eaten by *P. fluviatilis* was 56. The contribution of *P. fluviatilis* to all *R. harrisii* found in the fish stomachs represented about 26%. The mean size (TL) of *P. fluviatilis* that had eaten *R. harrisii* was 209 mm (SD 41; range 120–300 mm), which was larger than the mean size of *P. fluviatilis* in the catch, 189 mm (SD 51; range 71–310) (Fig. 2b). *P. fluviatilis* larger than 200 mm TL (likely targeted by the recreational and commercial fisheries) consumed 70% of *R. harrisii* found in all *P. fluviatilis* stomachs. The average number of *R. harrisii* present in *P. fluviatilis* stomachs was 1.5 (SD 0.85), with a maximum of four (TL 225 mm). When *R. harrisii* was present in the *P. fluviatilis* stomachs, they accounted for 87.6% of stomach contents.

A total of 209 roach (*Rutilus rutilus* (Linnaeus, 1758)) were caught, of which 15 (7.2%) had eaten *R. harrisii*. Only two *R. harrisii* (both 2 mm carapace width) were recovered from the stomachs intact enough to be tallied and measured. Therefore, the estimated number of *R. harrisii* eaten by *R. rutilus* was 15 individuals, which contributed about 7% to all *R. harrisii* found in fish stomachs. The mean size (TL) of *R. rutilus* that had consumed *R. harrisii* was 261 mm (SD 20; range 228–290 mm). In addition, whole specimens or remains of five *R. harrisii* were found in the stomachs of one ide (*Leuciscus ide*, (Linnaeus, 1758)), two ruffes (*Gymnocephalus cernuus*, (Linnaeus, 1758)) and two white breams (*Blicca bjoerkna*, (Linnaeus, 1758)). Altogether their predation contributed 2% to the *R. harrisii* found in fish stomachs in this study.

The mean carapace width (CW) of *R. harrisii* eaten by the two most significant predators was approximately 11.6 ± 2.46 mm for *P. fluviatilis* and 12.1 ± 2.54 mm for *M. quadricornis*, and majority of *R. harrisii* found from the stomachs were between 9 and 14 mm CW (Fig. 3). Based on the habitat trap catch, available *R. harrisii* in the area spanned a much larger size range from 1 to 26 mm (Fig. 3). Manly's selectivity index showed fish preference towards certain size classes. Small *P. fluviatilis* (smaller than

Table 2 The number of *R. harrisi* in the traps, fish catch by four main species, number of fish caught with *R. harrisi* in their stomachs and number of *R. harrisi* in fish stomachs at each site. Site 10, Nötö, was excluded from the analyses and total amounts due to an absence of *R. harrisi* in fish stomachs and in habitat traps

Site	Location	Crabs in traps	<i>Perca fluviatilis</i>		<i>Rutilus rutilus</i>		<i>Sander lucioperca</i>		<i>Myoxocephalus quadricornis</i>		Other species ^a			
			Catch w. crabs	# of crabs	Catch w. crabs	# of crabs	Catch w. crabs	# of crabs	Catch w. crabs	# of crabs	Catch w. crabs	# of crabs		
1	Kaitvesi	351	401	31	47	54	2	2	127	87	4	4		
2	Kuusistonsalmi	29	1	1	1	4	1	1	1	10				
3	Paimionlahti	1	5			23		6		6				
4	Parainen	8	19	1	2	17	1	1	21	4				
5	Naantali	128	15	2	2	7	2	2	4	5				
6	Vepsä	91	71	4	4	45	2	2	10	13	12	38		
7	Ruissalo	24	9	1	1	22	7	7	1	7	1	1		
8	Seili	25	6	1	1	25				16	11	25		
9	Maisaari	21	11	1	2	12		1		19	18	83		
10	Nötö									54		29		
	Totalexcl. Nötö)	678	538	41	59	209	15	15	171	48	41	146	137	5

^aSee Table 1 for the full list of species

Fig. 2 Number of individual fish in 2 mm increment size distributions (TL: Total length in mm) of **a** *Perca fluviatilis* and **b** *Myoxocephalus quadricornis* from the survey (dark grey) and the ones with *R. harrisii* in their stomachs (light grey)

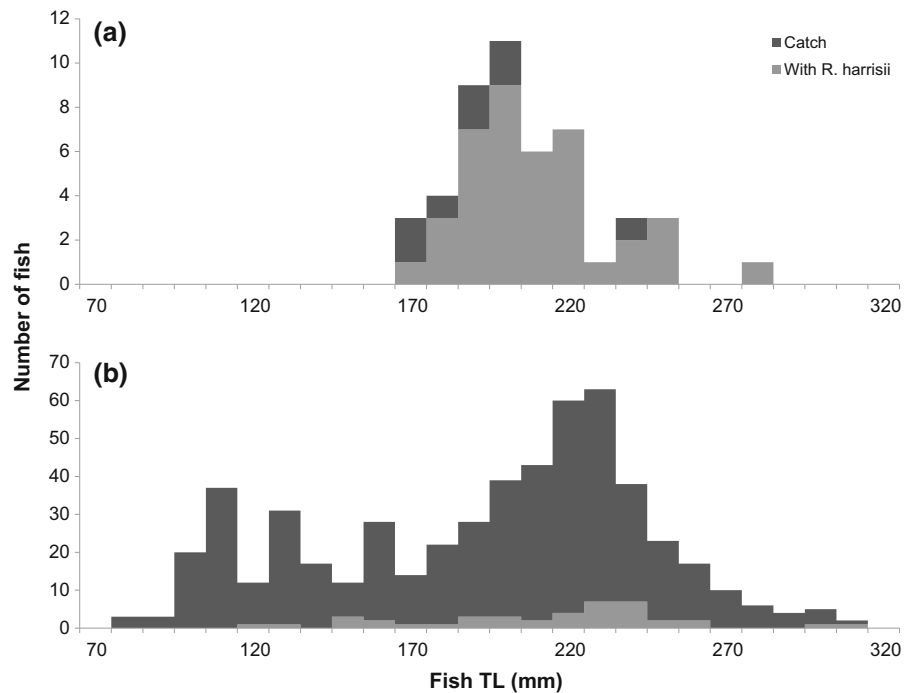
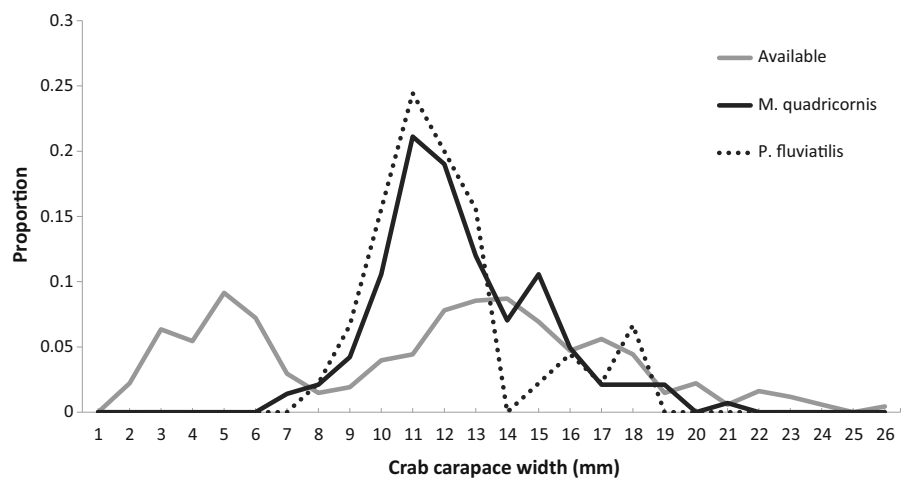


Fig. 3 The proportions of sizes of *R. harrisii* (carapace width in mm) available in the area (Available) (N = 678), and the sizes of *R. harrisii* found in the stomachs of *Myoxocephalus quadricornis* (N = 146) and *Perca fluviatilis* (N = 59)



the median TL 222) showed no preference, but larger *P. fluviatilis* preferred 12 mm CW *R. harrisii* (Fig. 4a). Small *M. quadricornis* preferred 12–14 mm CW *R. harrisii*, and larger individuals preferred larger (14–16 mm CW) *R. harrisii* (Fig. 4b). In both species, larger fish consumed larger *R. harrisii* (*P. fluviatilis*, $y = 0.0388x + 5.5976$, $R^2 = 0.466$, $p = 0.002$; *M. quadricornis*, $y = 0.0527x + 0.5038$, $R^2 = 0.415$, $p < 0.0001$). Both male and female *R. harrisii* were consumed more or less equally across all

fish stomachs (37% males, 46% females). The sex could not be determined for approximately 17% of the crabs (in most cases, juveniles < 4 mm CW).

Discussion

Some native predators can take advantage of a novel species introducing an alternative food source, and in some cases predators can control the populations of

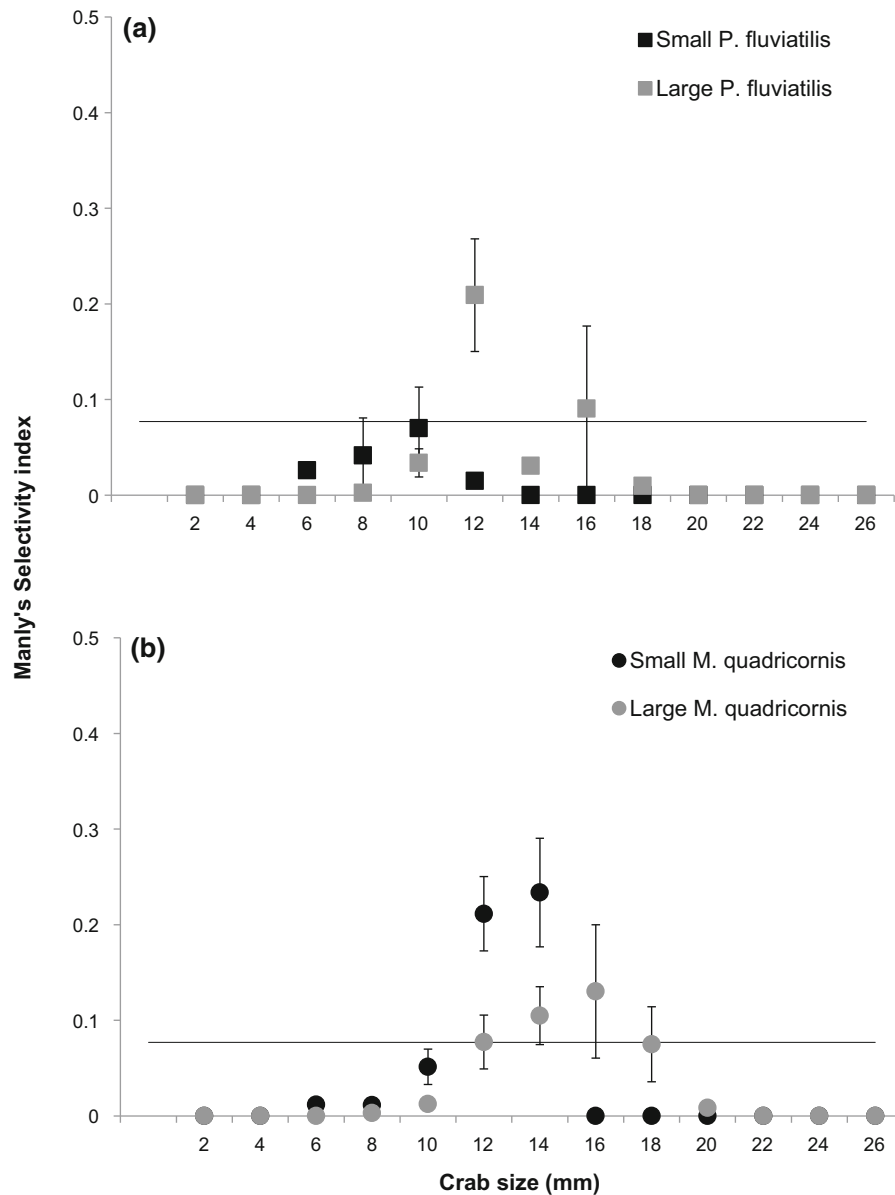


Fig. 4 Manly's selectivity index of two main fish predators towards *R. harrisii* by carapace width (mm) for small and large **a** *Perca fluviatilis* and **b** *Myoxocephalus quadricornis*. Size classes were determined based on the median total length of fish that had eaten crabs (i.e., 222 mm for *P. fluviatilis* and 211 mm

for *M. quadricornis*). The black solid line indicates the threshold value ($1/k$) for selection (0.077). Values above the line indicate selection towards the *R. harrisii* carapace size, and values below the line indicate selection against the size. The error bars indicate 1 SE

these invasive species (Hunt and Yamada 2003; Jensen et al. 2007). Considering the increase in both range and abundance of the introduced Harris mud crab, *R. harrisii*, in the Archipelago Sea of Finland over the past decade, the fish predation pressure seems inadequate to control their population growth. The results here show that at least a few native fish (*M.*

quadricornis, *P. fluviatilis*, *G. cernuus* and some cyprinids) consume these novel prey items, although the prevalence of *R. harrisii* in fish stomachs varied greatly among fish species. Furthermore, predation pressure, especially on the larger *R. harrisii*, may be limited by predator size since larger fish tended to target larger crabs.

Based on the stomach contents of nearly 1200 fish caught in the coastal monitoring effort, *M. quadricornis* were the main consumers of *R. harrisii*. This may be explained by the fact that sculpins are benthic generalist predators (Savolainen 1975; Timola 1986) and therefore likely to adopt new benthic items into their diet. They are also ambush predators, capable of crushing hard shelled organisms and commonly feed on slow moving invertebrates, such as the benthic isopod *Saduria entomon* (Leonardsson et al. 1988). Due to their feeding behavior, they would be very likely to encounter *R. harrisii* and feed on them. They also do not seem particularly selective based on previous diet studies (e.g., Savolainen 1975; Timola 1986) and the presence of non-prey items in their stomachs (e.g., small rocks found in this study).

Perca fluviatilis, which have previously been reported to feed on *R. harrisii* in the area (Fowler et al. 2013; FinBIF 2017), consumed fewer *R. harrisii* than *M. quadricornis*. However, although only about 8% of *P. fluviatilis* at sites with *R. harrisii* present had consumed them, the overall consumption may be significant due to the high abundance of *P. fluviatilis* in the area, reflected by a recreational catch of 308 tonnes in 2013 (Luonnonvarakeskus 2014). The overall contribution of *P. fluviatilis* to *R. harrisii* predation in this study was about 30%, despite this fish species being the most abundant in the catch. There may be a couple of reasons why *P. fluviatilis* did not consume as many *R. harrisii* as *M. quadricornis*: (1) they are not entirely benthic feeders and would not likely come across *R. harrisii* buried in the substrate and (2) *P. fluviatilis* are visual predators that may not detect *R. harrisii* which are often effectively hiding in structured habitat. In addition, the size range of perch capable of feeding effectively on *R. harrisii* may be limited in the area. Most *R. harrisii* (about 70%) were consumed by larger *P. fluviatilis* (> 200 mm TL), which is the size at which they begin to be targeted by recreational and commercial fisheries (Setälä et al. 2003), and the catch-per-unit-effort of large (> 250 mm TL) *P. fluviatilis* has showed a decline in a part of the study area over the past decade (Heikinheimo et al. 2013). Furthermore, perch tend to switch to fish prey when they grow larger (e.g., Lappalainen et al. 2001).

As prey, *R. harrisii* offer little, in terms of energetics, to the predator; they have hard shells and relatively small amounts of muscle mass

(Wiszniewska et al. 1998). Slow moving benthic predators, such as *M. quadricornis*, may obtain enough to justify feeding on the crabs, but quick-moving and efficient predators, such as *P. fluviatilis*, can obtain better quality prey and may only occasionally feed on *R. harrisii* that they encounter. This may explain, at least partly, why the prevalence of *R. harrisii* in *M. quadricornis* stomachs was so much higher than in other predatory fish.

Both perch (*P. fluviatilis*) and four-horned sculpins (*M. quadricornis*) had consumed mostly 10–12 mm carapace width (CW) *R. harrisii* despite the much broader size range of crabs available in the area. Larger fish, however, showed preference for slightly larger *R. harrisii* (12–16 mm CW). The upper size limit of the preferred prey of each fish species is likely a result of the physical restriction in feeding (gape size) and behavior (larger *P. fluviatilis* switch to fish prey; Lappalainen et al. 2001). In general, larger fish ate larger crabs likely due to this constraint. However, while larger *R. harrisii* (> 18 mm CW) were present in the habitat traps, sometimes in great quantities, they were not found with any frequency in fish stomachs in the study area. Also, *P. fluviatilis* and *M. quadricornis* do not grow much larger than the largest fish in our sample (303 and 285 mm TL, respectively), and large individuals are quite rare in the study area (HELCOM 2006). The largest *R. harrisii* individuals (especially > 19 mm CW), therefore, may benefit from a predation refuge from fish due to their size.

Roach (*Rutilus rutilus*) and other cyprinid fish may consume more *R. harrisii* than is reflected by our data. The cyprinid feeding structure, i.e., the pharyngeal jaw apparatus (Winfield and Nelson 1991), grinds prey into an unidentifiable state, and therefore *R. harrisii* remains may have gone unnoticed. Based on the *R. harrisii* collected from the fish stomachs, cyprinids preferentially feed on the smallest *R. harrisii* (2 mm CW), which are abundant in the system. The degree of predation pressure by cyprinids on small *R. harrisii* cannot be estimated from our data, but it could be high due to the large abundance of cyprinids in the area (Heikinheimo et al. 2013; Kääriä et al. 2013; Vielma et al. 2013). Genetic analyses of fish stomach contents could be useful in future evaluation of *R. harrisii* contribution to fish stomach contents for species such as *R. rutilus*.

Although extensive, our sampling data is temporally limited; the survey was conducted in the fall of

only 1 year. The coastal fish assemblages exhibit seasonal patterns, and some species migrate between deep and shallow waters (Mustamäki et al. 2015). For example, the temperature preference of *M. quadricornis* is around 10 °C, and therefore their range potentially overlaps with *R. harrisii* only when water temperatures are around that preference (e.g., Kottelat and Freyhof 2007). The surface water temperatures were below 12 °C at the time of sampling, indicating that this study probably accurately reflects or very slightly underestimates the predation of *M. quadricornis* on *R. harrisii*. *P. fluviatilis* is more abundant in preferred *R. harrisii* habitats, i.e., vegetated shallow areas, year-round, but they feed on *R. harrisii* to a lesser degree. In addition, their tendency to switch to fish prey at larger sizes may further decrease overall predation, especially on large *R. harrisii*. Furthermore, there are probably more fish species present in the area capable of preying on *R. harrisii*, especially other species foraging on the benthos. *R. harrisii* remains have been found in burbot (*Lota lota* (Oken, 1817)), pikeperch (*Sander lucioperca* (Linnaeus, 1758)) and whitefish (*Coregonus lavaretus* (Linnaeus, 1758)) stomachs in the area (Fowler et al. 2013; FinBIF 2017). However, although both *S. lucioperca* and *C. lavaretus* were caught in this study, no *R. harrisii* were detected in their stomachs.

Finally, we know very little about the different foraging strategies and diet switching abilities of many fish species present in the area. Both the diet switching aspect and feeding abilities of predators contribute to how novel prey organisms are adopted into native predator diets and how effective native predators can become in controlling the populations of invasive prey.

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