Feeding ecology of the American crab *Rhithropanopeus harrisii* (Crustacea, Decapoda) in the coastal waters of the Baltic Sea*

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Joanna Hegele-Drywa*
Monika Normant

Department of Experimental Ecology
of Marine Organisms,
Institute of Oceanography,
University of Gdańsk,
al. Marszałka Piłsudskiego 46, PL–81–378 Gdynia, Poland;

e-mail: asiahd@ocean.univ.gda.pl

*corresponding author

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Abstract

The feeding ecology of the American crab *Rhithropanopeus harrisii* Gould, 1841 from brackish waters of the Baltic Sea was studied by analyses of the stomach repletion index (SRI) and stomach content with regard to sex, size and habitat (Dead Vistula River and the Gulf of Gdańsk). Neither the sex nor the size of an individual crab had a significant ($P > 0.05$) influence on the SRI or on the diversity of food items found in the stomachs of *R. harrisii.* But the type of food consumed was significantly ($P < 0.05$) dependent on the locality inhabited: the greater the biodiversity of the habitat, the richer the dietary composition. In Baltic coastal waters this species feeds on detritus, and also on animal and plant matter. Remains of Chlorophyta, Amphipoda, Ostracoda, Polychaeta, Gastropoda and Bivalvia were found in the stomachs of the specimens analysed.

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1. Introduction

Since the beginning of the 20th century there has been a significant increase in the number of non-native species turning up in areas well beyond their natural range of distribution (Bax et al. 2003, Occhipinti-Ambrogi & Savini 2003, Thessalou-Legaki et al. 2006). Global in character, this phenomenon has affected the Baltic Sea to a considerable extent, where for the last forty or fifty years, annually increasing numbers of new species of flora and fauna have appeared (Leppäkoski 1984, Leppäkoski & Olenin 2000, Leppäkoski et al. 2002b). On the one hand, this has enhanced the biodiversity of the Baltic, especially its south-eastern part, which is naturally fairly poor in plant and animal species; on the other, it may give rise to a whole range of negative ecological and economic effects (Gollasch & Leppäkoski 1999, Leppäkoski et al. 2002a, Leppäkoski 2004, Streftaris et al. 2005, Gollasch & Rosenthal 2006).

One such non-native species in the Baltic is the American crab *Rhithropanopeus harrisii* Gould, 1841, which arrived in Europe in ballast waters from the Atlantic seaboard of North America (Wolff 1954, Leppäkoski 2005). The species was first recorded by Maitland (1874) in the Netherlands, from where it expanded to Denmark – the waters around Copenhagen (Jensen & Knudsen 2005) – and Germany (Nehring & Leuchs 1999). Since its first appearance in Poland in the 1950s, *R. harrisii* has occurred in the greatest numbers in the Vistula Lagoon (Zalew Wiślany) (Demel 1953, Żmudziński 1957, Rychter 1999) and in the Dead Vistula River (Martwa Wisła) (Michalski 1957, Turoboyski 1973, Janta 1996, Normant et al. 2004). For several years now, increasing numbers of *R. harrisii* have been turning up in the Gulf of Gdańsk (Normant, own observations), in places where earlier it was rare or absent altogether (Żmudziński 1967).

From the moment it arrived in Poland, the American crab aroused the interest of scientists. But studies of this species dealt primarily with its distribution (Demel 1953, Michalski 1957, Żmudziński 1957, 1961, 1967, Czerniejewski & Rybczyk 2008), its biology and ecology (Kujawa 1957, 1963, Filuk & Żmudziński 1965, Ławiński & Pautsch 1969, Pautsch et al. 1969, Turoboyski 1973, Janta 1996, Wiszniewska et al. 1998, Normant et al. 2004), and only to a very small extent with its physiology (Bomirski & Klęk 1974, Rychter 1997, Kidawa et al. 2004, Normant & Gibowicz 2008). Little information is available on the part played by *R. harrisii* in the trophic network of the waters that it inhabits. Studies done so far indicate that in the Dead Vistula *R. harrisii* feeds mainly on animals like ragworms *Hediste (Nereis) diversicolor*, blue mussels *Mytilus edulis,* zebra mussels *Dreissena polymorpha* and hydroids *Cordylophora caspia*, on plants like the green algae *Cladophora* sp. or *Enteromorpha* sp., and on dead organic matter of animal origin (Szudarski 1963, Turoboyski 1973). In the Vistula Lagoon, this crab is a scavenger, feeding on detritus (Demel 1953) or on *D. polymorpha* (Kujawa 1957). In the Odra estuary it feeds mostly on detritus, but algae, animal remains and inorganic material were also found in the gut contents (Czerniejewski & Rybczyk 2008). It is itself a source of food for eels *Anguilla anguilla* and flounder *Platichthys flesus* (Filuk & Żmudziński 1965), and also for cormorants *Phalacrocorax carbo* (Wiszniewska et al. 1998). The biodiversity of Baltic coastal waters is much greater than that of the Dead Vistula or the Vistula Lagoon, so *R. harrisii* may well be involved in numerous trophic interactions with other organisms. In view of this, a comparative study was carried out in an attempt to determine the diet of *R. harrisii* in two ecologically different environments, namely, the Dead Vistula River and the Gulf of Gdańsk. The stomach repletion index and stomach contents were analysed in relation to the sex and size of the individual crabs.

2. Material and methods

The crabs (118 specimens) were collected in the summer months (July–September) of 2005 and 2006 from two areas. 28 females and 44 males were collected from three sampling points in the Gulf of Gdańsk (54°26′37″N, 18°36′13″E; 54°27′52″N, 18°37′90″E; 54°28′59″N, 18°39′71″E) and 26 females and 20 males from one point in the Dead Vistula River (54°20′89″N, 18°47′72″E). Both sampling areas lie in the Polish zone of the Baltic Sea. The animals were immediately frozen at -20°C to halt digestion. In the laboratory the crabs were sexed on the basis of their abdominal structure and number of pleopods (De Man 1892), and their carapace width was measured with slide callipers (± 0.1 mm) (ECOTONE, Poland). Next, the stomach of every specimen was excised and analysed under a stereomicroscope (ECO-VISION – ECOTONE, Poland) at $6.6-45\times$ magnification in order to assess its repletion index (Albertoni et al. 2003) and to determine its content. Repletion was analysed using the five stomach repletion indices (SRIs), where 0 indicates an empty stomach, I a stomach that is 0–25% full, II one that is 25.1–50% full, III one that is 50.1–75% full and IV one that is 75.1–100% full. All the food items in the stomachs were placed in one of the following categories: (1) digested, (2) of plant origin, (3) of animal origin, and (4) detritus. Plant and animal remains were identified to the most precise taxonomic level based on the characters given by Pliński (1980a,b), Jażdżewski & Konopacka (1995) and Kołodziejczyk & Koperski (2000).

The data normal distribution (Gaussian distribution) was validated through the application of the Shapiro-Wilk test at a significance level of 5%.

The differences in the studied parameters between groups of crabs were tested using the Mann-Whitney U-test or the Kolmogorov-Smirnov test at the 5% significance level. The dependence of the SRI and diversity of food items on the locality of occurrence were determined using the comparative proportions test at a significance level of $P < 0.05$. Analyses were carried out using the STATISTICA 6.0 PL program.

3. Results

The carapace width of females from the Gulf of Gdańsk ranged from 3.1 to 16.3 mm (mean 10.5 ± 3.8 mm), those of males from 3.2 to 22.8 mm (mean 10.4 ± 4.0 mm). The corresponding dimensions for animals from the Dead Vistula River were from 8.9 to 19.4 mm (mean 11.5 ± 2.6 mm) (females), and from 9.6 to 21.6 mm (mean 15.0 ± 3.6 mm) (males). The carapace width of males from the Dead Vistula River was significantly greater ($P < 0.05$) than that of males from the Gulf of Gdańsk. In the former area, the most numerously represented width class was 12.1–15.0 mm; in the latter area it was 9.1–12.0 mm.

Neither the sex nor the size of the individual crab had any significant ($P > 0.05$) effect on the stomach repletion index (SRI) in *Rhithropanopeus harrisii*. Statistically significant differences ($P < 0.05$) were found between the SRIs in the crabs from the two areas. In both areas, the greatest number of specimens was found with an SRI of I, and the smallest number with an index of III. In the Gulf of Gdańsk the whole range of SRIs was recorded, but in the Dead Vistula River there was not a single crab with a completely full stomach (Figure 1). The percentages of crabs with SRI categories I and II were statistically different ($P < 0.05$) in the two areas.

Unlike the sex and size of individuals ($P > 0.05$), the locality of occurrence did have a significant ($P < 0.05$) influence on the diversity of food items in the stomachs of *R. harrisii*. 50 and 72.7% of the specimens from the Gulf of Gdańsk and the Dead Vistula River respectively had stomachs containing only digested matter. In 45% of crabs with full stomachs from the Gulf of Gdańsk the food items were identified as belonging to one of three categories (plant matter, animal matter, detritus), and in 14.3% they were from two categories; in only one single crab were all three categories found. In the case of the crabs from the Dead Vistula River, 44% had food items from one category in their stomachs, and only one individual had items from two. Animal remains were found in 39% of crabs from the Gulf of Gdańsk with full stomachs, whereas plant remains were found in 34% of replete crabs. Animal and plant remains were identified in 15 and 21% respectively of crabs from the Dead Vistula River. Detritus was found in 34% of crabs from the Gulf of Gdańsk and in 15% from the Dead Vistula

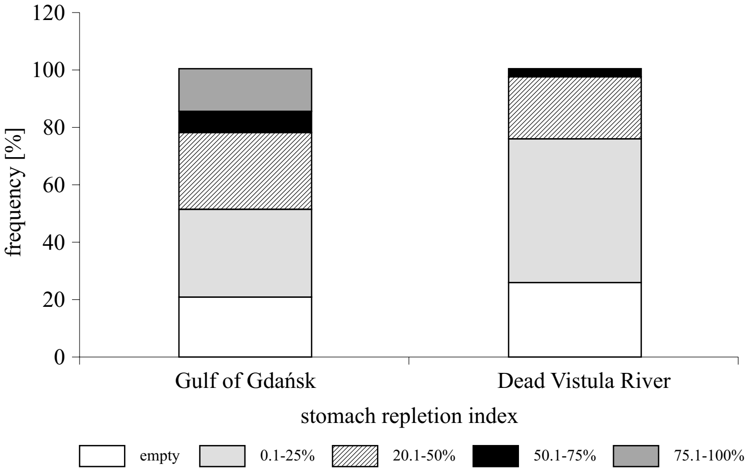

Figure 1. Frequency of crabs with different stomach repletion indices (SRI) collected in the Gulf of Gdańsk (n = 72) and the Dead Vistula River (n = 46)

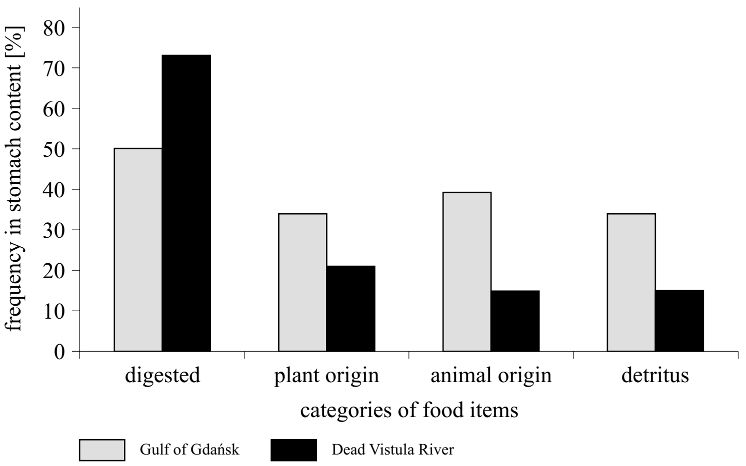

Figure 2. Frequency of different categories of food items in the stomachs of crabs from the Gulf of Gdańsk (n = 56) and the Dead Vistula River (n = 34)

River (Figure 2). Only the percentages of crabs with digested matter in their stomachs differed significantly ($P < 0.05$) in the two areas.

Among plant matter, Chlorophyta remains were found in the largest number of crabs from the Gulf of Gdańsk and the Dead Vistula River – 14 and 5 respectively (Figure 3). Among the animal remains found in crabs from the Gulf of Gdańsk five different taxonomic groups were recorded: Polychaeta, Amphipoda, Ostracoda, Bivalvia, Gastropoda. The most frequent were Amphipoda fragments, which appeared in 10 specimens.

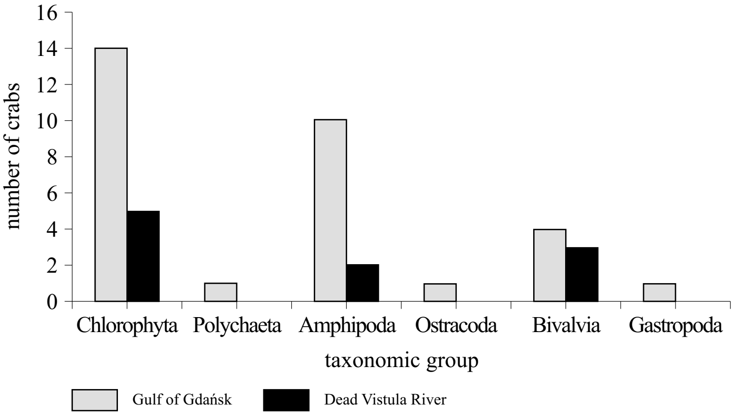

Figure 3. Frequency of occurrence of different plant and animal food items in the stomachs of crabs from the Gulf of Gdańsk (n = 27) and the Dead Vistula River (n = 9)

In crabs from the Dead Vistula River only two taxonomic groups were found: Amphipoda and Bivalvia; the latter was the most numerous and was recorded in 3 specimens.

4. Discussion

The dietary composition of Decapoda in their natural environment is frequently determined directly from an analysis of their stomach contents, even though identification of the food remains is difficult as they are very finely comminuted. This is due to the structure and function of the mouthparts and the gastric mill in this order of animals (Hill 1976, Williams 1981, Grabda (ed.) 1985, Choy 1986, Chande & Mgaya 2004).

From studies done so far of *Rhithropanopeus harrisii* from different regions, it can be inferred that the species is omnivorous, feeding as it does on detritus, as well as on animal and plant matter (Mordukhay-Boltovskoy 1952, Szudarski 1963). But as in other Decapoda (Hill 1976, Ryer 1987, Parslow-Williams et al. 2002), the frequency of feeding and the quality of the food ingested depend not only on the locality inhabited by an individual, but also on the diurnal cycle of activity and foraging (Takahashi & Kawaguchi 2001, Turra & Denadai 2003). In the literature there does not appear to be any endorsement of the above statements applying directly to feeding patterns in *R. harrisii.* The environments from which the crabs for the present investigation were taken – the Gulf of Gdańsk and the Dead Vistula River – differ in their abiotic factors (temperature, salinity, type of bottom), as well as in the availability and diversity of species of flora and fauna that are potential food items for *R. harrisii* (Kruk-Dowgiałło

1994, Żmudziński 1997, Pliński 1999, Osowiecki 2000, Janas et al. 2004, Janas 2005, Łysiak-Pastuszak et al. 2006, Kruk-Dowgiałło & Szaniawska 2008, own observations). Confirmation of the better trophic conditions for *R. harrisii* in the Gulf of Gdańsk is the presence there of specimens with full stomachs; crabs in this condition were not caught in the Dead Vistula River. Interestingly, the individuals from the Gulf of Gdańsk were smaller in size, and the rate of consumption in these smaller crabs may have been limited by the availability of prey in the vulnerable size classes (Kneib & Weeks 1990, Cotton et al. 2004). On the other hand, smaller, younger specimens have a faster rate of metabolism and consumption than larger, older individuals (Bridges & Brand 1980, Emmerson 1985, Schmidt-Nielsen 1997, Łapucki et al. 2005). Large individuals of *R. harrisii*, which have the greatest chance of capturing prey, do not in fact forage for prey if they have sufficient energy reserves (Kidawa et al. 2004). In addition, fewer individuals from the Gulf of Gdańsk had digested matter in their stomachs; more had undigested plant and animal remains. These latter belonged to six different classes of flora and invertebrate fauna, whereas in the crabs from the Dead Vistula River the undigested food remains were from three classes.

This study did not indicate the existence of feeding selectivity in *R. harrisii* from the Gulf of Gdańsk, because the numbers of individuals feeding on plant or animal matter, or detritus, were similar. The choice of food to be consumed depends not only on its availability in the environment, but also on its assimilability sensu lato. It has been reported that crustaceans frequently select small and medium-sized high-energy food items from which the nutrients are readily assimilated (Morales & Antezana 1983, Juanes 1992, Kennish & Williams 1997). It is important that the energy value of the food compensates for the energy expended by the animal in foraging for it. Crabs belong to the mobile benthic fauna, but they mostly crawl about on the bottom, and sudden movements are not in their nature: they are not good hunters. They therefore tend to feed on sessile organisms, macrophytes or detritus (Bourdeau & O'Connor 2003). Crabs are particularly fond of mussels and snails, the shells of which they crush with their pincers (Elner 1978, Hughes & Seed 1981, Flimlin & Beal 1993). Evidence for *R. harrisii* feeding on mussels is supplied by a few shell fragments, which could have entered the stomach attached to the soft tissue (e.g. adductor muscle) consumed (Hill 1976). The small proportion of mussel remains found in the stomachs of crabs from the Gulf of Gdańsk could be due to the fact that softer-bodied prey like mussels or polychaetes require considerably less time to be digested than harder prey items like crustaceans (Parslow-Williams et al. 2002). Hence, the presence of an item in the gut contents can be taken as positive evidence of ingestion, but its absence cannot be taken as evidence that the item does not occur in the diet (Kneib & Weeks 1990). Interestingly, the stomachs of crabs from both the Dead Vistula River and the Gulf of Gdańsk contained carapace fragments from amphipods, which apparently move much faster than the crabs. On the other hand, there are large numbers of gammarids in some parts of the Gulf of Gdańsk (among the mussel beds, for instance), which improves the chances of a predator capturing them. *R. harrisii* probably finds dead organisms with the aid of its very well developed chemoreceptor sense (Kidawa et al. 2004). Even though a diet of crustaceans has a fairly low energy value, it does nonetheless supply consumers with the essential minerals and calcium. *R. harrisii* is omnivorous, a feeding strategy that is optimal since a mixed diet provides for the best growth (Buck et al. 2003). By feeding on animal matter, crabs obtain the necessary proteins and fats (Takeuchi & Murakami 2007), and the plant matter they ingest supplies important nutrients (O'Brien 1994, Dahdouh-Guebas et al. 1999).

Interestingly, even though male crabs are usually more active and more aggressive than females, and though their pincers are more massive, the SRIs suggest that the foraging frequency is similar in the two sexes (Lee 1995, Takahashi & Kawaguchi 2001, Barki et al. 2003). This observation may be due to the fact that this investigation was carried out on crabs caught in summer, i.e. at a time of year when the high temperature of the water governs feeding intensity and growth (Turoboyski 1973). In this season, too, reproduction in *R. harrisii* is intensified, which suggests that females should have a fairly low SRI, since they consume less food during the breeding period (Ruiz-Tagle et al. 2002). In any case, ovigerous females bury themselves in the bottom and spend more time grooming their eggs than feeding (Turoboyski 1973, Sumpton & Smith 1990). Nevertheless, to produce eggs females require a lot of energy, which they probably acquire in their food and then save up for the breeding season (Ruiz-Tagle et al. 2002).

Studies of *R. harrisii* in the Gulf of Gdańsk done to date suggest that it does not have many natural enemies in these waters. The crab was not found either in the stomachs of benthic fish from the Gulf of Gdańsk or in the diet of cormorants (Ostrowski 1997, Wandzel 2003, Bzoma & Meissner 2005, Złoch et al. 2005, Karlson et al. 2007). It can itself, however, affect the existence of the benthic flora and fauna ubiquitous in the Gulf of Gdańsk, e.g. Chlorophyta, Amphipoda, Ostracoda, Polychaeta, Gastropoda and Bivalvia species (Wiktor 1990, Osowiecki 1998, 2000, Jęczmień & Szaniawska 2000a,b, Kruk-Dowgiałło & Szaniawska 2008). In view of the ever-increasing numbers of *R. harrisii* in the Gulf of Gdańsk over the last few years (Normant & Gibowicz 2008, Hegele-Drywa et al., in preparation), this situation may have serious ecological consequences. The present investigation is the first on the feeding ecology of *R. harrisii* in Baltic coastal waters. Stomach contents often reflect the availability of food in the environment rather than an animal's preferences. That is why laboratory studies are now in progress to try to discover the feeding preferences of *R. harrisii* and the rate at which it consumes food. From the results it should be possible to assess the potential effect of the American crab on the benthic communities that it inhabits.

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