Prey preferences of juvenile whelk *Neptunea arthritica* (Gastropoda: Buccinidae) in Hakodate Bay, Hokkaido, Japan

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**Abstract:** Juvenile Japanese Neptune whelk *Neptunea arthritica* preys on small gastropods in the field. Although the most common prey is *Homalopoma sangarense*, its density is lower than those of other prey species (e.g., *Barleeia angustata*, *Reticunassa fratercula*, and *Cantharidus japonicus*) in the field. To clarify whether *N. arthritica* juveniles show an “actual” or “apparent” preference for *H. sangarense*, we conducted a single-prey feeding experiment. Although *N. arthritica* attacked *H. sangarense* earlier and more frequently than *B. angustata* and *C. japonicus*, there was no difference in attack frequency and latency between *H. sangarense* and *R. fratercula*. Attacks on *H. sangarense* failed more frequently than on the other species, and the handling time for *H. sangarense* was significantly longer compared to the other three species. The large difference in handling time (over 10-fold difference) could be caused by the presence of a thick calcareous operculum on *H. sangarense*. Eventually, *N. arthritica* consumed more individuals of *R. fratercula* than of *H. sangarense* in the experiment. These results indicate that *N. arthritica* juveniles exhibit both “actual” and “apparent” preferences for *H. sangarense*. The “actual preference” of *N. arthritica* juveniles may reflect the past species compositions of small gastropods, because *H. sangarense* has been previously reported as the dominant species at the study site.

**Key words:** attack latency, handling time, *Homalopoma sangarense*, *Neptunea arthritica*, prey preference

**Introduction**

The Japanese Neptune whelk *Neptunea arthritica* (Bernardi, 1857) belongs to the family Buccinidae and is a common carnivorous gastropod in intertidal and subtidal areas of Hokkaido, Japan (Fujinaga & Nakao 1999, Yamakami & Wada 2021a). This species is commercially important in inshore fisheries in Hokkaido (Hoshikawa 2003, Fujinaga 2005), and further knowledge on its foraging behavior is needed for appropriate management and conservation. The species' prey utilization in the field has been quantitatively described in two populations (Fujinaga & Nakao 1999, Yamakami & Wada 2021a). However, no studies have examined prey species preferences in an experimental setting.

Yamakami & Wada (2021a) reported that prey species utilization of this species in Hakodate Bay in southern Hokkaido, Japan, varies around the size of 30–40 mm in shell height: small whelks (<30 mm in shell height) prey mainly on small gastropods while large whelks (>40 mm in shell height) prey on large mollusks. The most common prey species of small whelk was *Homalopoma sangarense* (Schrenck, 1861) (73% in the frequency of observations of foraging whelks [<30 mm] in the field), and the species was also observed to prey on other species, such as *Barleeia angustata* (Pilsbry, 1901) (1.9%), *Reticunassa fratercula* (Dunker, 1860) (6.8%), and *Cantharidus japonicus* (A. Adams, 1853) (<1%) (Yamakami & Wada 2021a). This prey utilization pattern is curious because it does not seem to be efficient according to optimal foraging theory (e.g., Pyke 1984). The most abundant species in the study site throughout the year are *B. angustata* (95% of collected specimens), *Reticunassa fratercula* (1.4%), and *Cantharidus japonicus* (0.8%) (Yamakami & Wada 2021b). The density of *B. angustata* is more than 300 times that of *H. sangarense* (0.3%) in the field (Yamakami...
& Wada 2021b), although B. angustata is smaller than H. sangarense. Body volumes of R. fratercula and C. japonicus do not seem to be substantially different from that of H. sangarense, and densities of the two species are more than three times that of H. sangarense (Yamakami & Wada 2021b). The spatial distributions of the four prey species overlap significantly with the distribution of N. arthritica (Yamakami & Wada 2021a, b). Here, we examine the following two hypotheses for why N. arthritica juveniles prey mainly on H. sangarense: (1) the “actual preference” hypothesis, and (2) the “apparent preference” hypothesis.

An “actual preference” means that individuals prefer a certain prey species over others when they are offered the same number of individuals of each prey species. Actual preferences are reported among prey species with different defensive responses (e.g., gastropods, Castell & Sweatman 1997) and morphological vulnerabilities (e.g., crabs, Elner & Raffaelli 1980; gastropods, Soto et al. 2004; López et al. 2010; octopuses, Song et al. 2019). For example, the whelk Thais tuberosa (Röding, 1798) prefers the gastropod Turbo brunnneus Röding, 1798, which responds to predation attempts with flight behavior, over juvenile Trochus niloticus Linnaeus, 1767, which exhibits a mucus response (Castell & Sweatman 1997). This preference is consistent with the relative proportions of T. brunnneus and T. niloticus mortality attributed to predation by T. tuberosa in the field (Castell & Sweatman 1997). The drizzling predator Acanthina monodon (Pallas, 1774) prefers the thin-shelled mussel Semimytilus algaeus (Gould, 1850) as prey over the thick-shelled mussel Perumytilus purpuraus (Lamarck, 1819) (Soto et al. 2004). Acanthina monodon also has a higher consumption rate of S. algosus over P. purpuraus in the field unless S. algosus is rare (Soto et al. 2004).

Preferences identified from field observations of predator foraging behavior in intertidal and shallow subtidal zones sometimes differ from the actual preferences described above. This field-based measure of preference is called “apparent preference” (Fairweather & Underwood 1983, Yamamoto 2004). In the field, researchers usually observe intertidal animals at low tide and only get a “snapshot” of predation at that time (Fairweather & Underwood 1983). Yet predator foraging behavior may depend on tidal conditions (Menge 1974, Checon et al. 2020). Prey-handling times also differ among prey species (Fairweather & Underwood 1983, Carroll & Wethey 1990, Creswell & Mclay 1990, Soto et al. 2004, Yamamoto 2004, López et al. 2010, Meirelles & Matthews-Cascon 2016, Song et al. 2019), because prey with more defensive morphologies require longer handling times, which in turn can bias field observations (Fairweather & Underwood 1983). For example, prey-handling time in the whelk Morula marginala (Blainville, 1832) varied from 5 h for the limpet Patelloida latistrigata (Angas, 1865), to 40 h for the tube-worm Galeolaria caespitosa Lamarck, 1818 (Fairweather & Underwood 1983). Although the frequency of M. marginala predation on limpets is roughly equal to that on tube-worms, observations of the latter are more frequent than of the former in the field (Fairweather & Underwood 1983). Even though predators often prefer more vulnerable species in the laboratory, differences in handling time among prey species could result in an “apparent” preference for the species with the longer handling times.

The purpose of this paper is to clarify the behavioral interactions between predatory N. arthritica and four prey gastropods (B. angustata, R. fratercula, C. japonicus, and H. sangarense) by synthesizing prey utilization patterns in the field (Yamakami & Wada 2021a) with gastropod species compositions in the study area (Yamakami & Wada 2021b), and behavioral interactions observed in laboratory experiments.

Materials and Methods

Feeding experiments were conducted in the laboratory from January to June 2020. Juvenile N. arthritica that had not been foraging were collected along with individuals of the four prey gastropods (B. angustata, R. fratercula, C. japonicus, and H. sangarense) at low tide from the intertidal platform in Kattoshi, located on the western coast of Hakodate Bay, southwestern Hokkaido (41°44′N, 140°36′E). Whelks and prey gastropods were brought separately to the laboratory. After measuring shell height (as a proxy for body size), N. arthritica were placed individually into a small, aerated plastic aquarium (15 cm length×10 cm width×11 cm depth, water temperature 15°C, light cycle 24L : 0D, water depth 7 cm) (Fig. 1) and acclimated without food for 24 h. During the acclimation period, prey gastropods were kept in separate tanks without food. The whelks used in the experimental trials ranged in shell height from 10.4 to 34.4 mm (mean±SD: 25.8±5.7 mm).
Prey preferences of Neptunea arthritica

Since sexual maturity size of this species reported so far is 50–70 mm for males and 60–80 mm for females (Fujinaga 1985; Fujinaga et al. 2006; Miranda et al. 2009), individuals used in this study are regarded as juveniles.

Each *N. arthritica* individual was randomly assigned to one of the four prey species (*B. angustata*, *R. fratercula*, *C. japonicus*, *H. sangarense*). Each whelk was offered ten live individuals of the prey species (body sizes: *B. angustata*, 2.59±0.30 mm in shell height, *n*=520; *R. fratercula*, 8.32±1.6 mm in shell height, *n*=490; *C. japonicus*, 5.97±0.93 mm in shell width, *n*=510; *H. sangarense*, 6.28±1.56 mm in shell width, *n*=490). Predator feeding behavior were recorded for 72 h by time-lapse video at 2-min intervals. No whelks died during the experiment and all showed activity (e.g., crawling, siphon movement) during the experiment.

We also conducted trials with similar procedures under no predation, where ten individuals of a prey species were kept for 72 h in the aquarium with a juvenile whelk, but the whelk was contained in a perforated zipper bag to prevent it from attacking prey. Ten trials were conducted for each prey species; prey mortality was zero in all trials except for one individual *B. angustata*. All *N. arthritica* and surviving prey were released at the study site after each trial.

From each video, we recorded the following data: (1) whether whelks attacked a prey individual, (2) the latency of the first attack, (3) the outcome of each attack (successful or unsuccessful), (4) contact time of each attack (handling time), and (5) the number of prey consumed during the 72-h observation period. “Attack” was defined as contacting the prey with the foot (Fig. 2). Attacks were deemed successful if they ended with prey consumption, and unsuccessful if the prey remained alive after the whelk moved away from the prey. After successful attack, we confirmed empty shell of the prey. Whether the prey remained alive or not was confirmed by the victim’s behavior in the subsequent video. If a whelk consumed a same prey individual discontinuously (and it did not attack other prey between feeding bouts), we classified it as one case of a successful attack and the handling time was taken as the total time for all bouts. In such cases (four cases in all cases), it was unknown whether the prey remained alive after the first attack. If the video recording ended while an instance of predation was in progress, the attack was deemed successful if the prey had died by the end of recording. Although many attacks were successful, five individuals of...
attacked *H. sangarense* was intact and crawled again. We did not include those five cases in the analysis because the outcome of such attack event was unknown.

The five parameters listed above were compared among experiments with different prey species. The effect of whelk size on attack occurrence was analyzed by using a generalized linear model with a binomial error distribution and a logit link. The latency of first attack was analyzed by using Cox’s proportional hazard model with prey species and whelk size as explanatory variables, and month as a random factor. For individuals that did not attack during the experimental period, the latency to first attack was recorded as 72 h (censored data). The handling time was also analyzed by using Cox’s proportional hazard model with prey species and whelk size as explanatory variables, and whelk ID and month as a random factor. The duration of attacks that ended in failure and those that were interrupted by the end of the video recording were included as censored data of handling time. All statistical analyses were carried out using R version 4.0.2 (R Core Team 2020). We used the R package “coxme” (Therneau 2020) to analyze the latency of first attack and the handling times.

### Results

During the experiment period, significantly more whelks in tanks with *R. fratercula* and *H. sangarense* attacked prey than in those in tanks with *B. angustata* and *C. japonicus* (Fisher’s exact test with Bonferroni correction, *R. fratercula* [H. sangarense] vs. *B. angustata* [C. japonicus], all *P*<0.001, Fig. 3a). Most whelks (>87%) attacked *R. fratercula* (44 of 49 individuals) or *H. sangarense* (43 of 49 individuals), whereas only a few (<16%) attacked *B. angustata* (8 of 52 individuals) or *C. japonicus* (6 of 51 individuals). There was no significant difference in attack frequency between *R. fratercula* and *H. sangarense*, or between *B. angustata* and *C. japonicus* (Fisher’s exact test with Bonferroni correction; *R. fratercula* vs. *H. sangarense*, *B. angustata* vs. *C. japonicus*, both *P*=1.00). The preference pattern was consistent throughout the experimental period (Fig. S1). The latency of first attack for *H. sangarense* was similar to that for *R. fratercula*, but significantly shorter than for *B. angustata* and *C. japonicus* (Cox’s proportional hazard model: *R. fratercula*, *z*=0.44, *P*=0.660; *B. angustata*,

![Fig. 3. Differences in the attacking behavior of *Neptunea arthritica* for four prey species: *Barleeia angustata* (BA), *Reticunassa fratercula* (RF), *Cantharidus japonicus* (CJ), and *Homalopoma sangarense* (HS). (a) Relative proportions of individuals that attacked prey (black) or did not attack (white). (b) Kaplan–Meier survival curves of the latency to first attack. In panel (a), columns that do not share lowercase letters are significantly different as determined by using Fisher’s exact test with a Bonferroni correction (*P*<0.001).](https://example.com/fic3.png)

Table 1. Summary of Cox’s proportional hazard model for latency to first attack by *Neptunea arthritica* on different prey species. The first three rows show comparisons between *Homalopoma sangarense* (HS) and one of *Barleeia angustata* (BA), *Reticunassa fratercula* (RF), or *Cantharidus japonicus* (CJ). Bold text indicates statistical significance (*P*<0.05).

|                   | Estimate | SE  | z     | *P*   |
|-------------------|----------|-----|-------|-------|
| Prey: HS vs. BA   | −2.723   | 0.400| −6.81 | <0.001|
| Prey: HS vs. RF   | 0.096    | 0.219| 0.44  | 0.660 |
| Prey: HS vs. CJ   | −3.037   | 0.445| −6.82 | <0.001|
| Whelk Size        | 0.037    | 0.016| 2.26  | 0.024 |


Prey preferences of *Neptunea arthritica*

The effects of whelk size on attack occurrence differed between *B. angustata* and the other three prey species (Table 2, see Fig. S2 for raw data). A significant negative effect of whelk size on attack frequency was found for *B. angustata*, meaning that smaller juveniles attacked *B. angustata* more frequently (GLM with a binomial error distribution, \( z = -2.42, P = 0.016 \), Table 2). By contrast, positive but non-significant effects of whelk size on attack frequently were found for the three other prey species (GLM with binomial distribution: *R. fratercula*, \( z = 1.82, P = 0.069 \); *C. japonicus*, \( z = 1.58, P = 0.114 \); *H. sangarense*, \( z = 1.26, P = 0.206 \), Table 2).

Prey handling time was significantly longer for *H. sangarense* than for the three other prey species (Cox’s proportional hazard model: *B. angustata*, \( z = 7.01, P < 0.001 \); *R. fratercula*, \( z = 6.23, P < 0.001 \); *C. japonicus*, \( z = 6.51, P < 0.001 \); Fig. 4, Table 3). The mean (±SD) handling time

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### Table 2. Summary of logistic regression analysis for the effect of whelk size on whether whelks did or did not attack each prey species (a–d). Bold text indicates statistical significance (\( P < 0.05 \)).

|                | Estimate | SE  | z       | P     |
|----------------|----------|-----|---------|-------|
| (a) *Barleeia angustata* |          |     |         |       |
| Intercept      | 14.496   | 6.075| 2.386   | 0.017 |
| Whelk size     | -0.986   | 0.408| -2.415  | 0.016 |
| (b) *Reticunassa fratercula* |         |     |         |       |
| Intercept      | -10.667  | 6.076| -1.756  | 0.079 |
| Whelk size     | 0.800    | 0.440| 1.817   | 0.069 |
| (c) *Cantharidus japonicus* |        |     |         |       |
| Intercept      | -5.840   | 2.603| -2.244  | 0.025 |
| Whelk size     | 0.153    | 0.097| 1.580   | 0.114 |
| (d) *Homalopoma sangarense* |         |     |         |       |
| Intercept      | -0.099   | 1.602| -0.062  | 0.951 |
| Whelk size     | 0.098    | 0.077| 1.263   | 0.206 |

### Table 3. Summary of Cox’s proportional hazard model for prey handling time by *Neptunea arthritica* on different prey species. The first three rows show comparisons between *Homalopoma sangarense* (HS) and one of *Barleeia angustata* (BA), *Reticunassa fratercula* (RF), or *Cantharidus japonicus* (CJ). Bold text indicates statistical significance (\( P < 0.05 \)).

|                | Estimate | SE  | z      | P     |
|----------------|----------|-----|--------|-------|
| Prey: HS vs. BA | 7.643    | 1.091| 7.01   | <0.001|
| Prey: HS vs. RF | 6.460    | 1.036| 6.23   | <0.001|
| Prey: HS vs. CJ | 7.184    | 1.104| 6.51   | <0.001|
| Whelk size     | 0.043    | 0.015| 2.78   | 0.0054|

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**Fig. 4.** Kaplan–Meier survival curves of handling times by juvenile *Neptunea arthritica* of four prey species: (a) *Barleeia angustata*, (b) *Reticunassa fratercula*, (c) *Cantharidus japonicus*, and (d) *Homalopoma sangarense*. Curves shows the proportion of individuals that were still engaged in an attack over time. Crosses (+) indicate censoring, including that due to unsuccessful attacks and the end of the experiment.

**Fig. 5.** Proportions of outcomes of all attack events (successful (black) or unsuccessful (white)) for each prey species: *Barleeia angustata* (BA), *Reticunassa fratercula* (RF), *Cantharidus japonicus* (CJ), and *Homalopoma sangarense* (HS). These data include attacks in which the observation was censored but prey were already killed. The proportion of successful attacks was higher for RF than in HS (Fisher’s exact test, \( P < 0.001 \)).
was 24.7 ± 10.7 h for *H. sangarense*, whereas those for *R. fratercula*, *B. angustata*, and *C. japonicus* were 2.1 ± 1.9, 1.6 ± 0.6, and 1.3 ± 0.6 h, respectively. A total of 299 attacks by 101 individuals were categorized into successful attacks (i.e., the prey died) and unsuccessful attacks (i.e., the prey survived), with the exception of five attacks where the outcome was unknown due to censoring (i.e., the observation period ended) prior to consumption (Fig. 5). The frequency of successful attacks was significantly lower for *H. sangarense* than for *R. fratercula* (Fisher’s exact test: *P* < 0.001, Fig. 5). Although the sample size was small, all attacks succeeded for *B. angustata* (*n* = 27) and *C. japonicus* (*n* = 9). As a result, whelks offered *R. fratercula* consumed the highest mean number of prey over 72 h was 3.31 ± 1.95 individuals, as compared to 1.43 ± 0.82 *H. sangarense*, 0.63 ± 1.8 *B. angustata* and 0.18 ± 0.52 *C. japonicus*.

**Discussion**

Our feeding experiments revealed differences in *N. arthritica* foraging behavior by prey species in each of the five measured parameters: attack frequency, latency to first attack, handling time, frequency of successful attacks, and the number of prey consumed. Data partly support both the “actual” and “apparent preference” hypotheses for explaining prey utilization patterns by *N. arthritica* juveniles in the field.

Juvenile whelk exhibited preferences for different prey species through differences in attack frequency and the latency to first attack. In fact, whelks attacked *H. sangarense* both earlier and at a higher frequency than *B. angustata* and *C. japonicus*. Despite the lack of alternative prey species in each tank, most *N. arthritica* did not attack either *B. angustata* or *C. japonicus*. These results support the “actual preference” hypothesis and would explain the low utilization of these two species despite their high availability in the field (Yamakami & Wada 2021a, b). On the other hand, preferences for *H. sangarense* and...
**Prey preferences of Neptunea arthritica**

R. fratercula appear to be comparable. This is inconsistent with field observations, which indicate low utilization of R. fratercula despite its high abundance (Yamakami & Wada 2021a, b).

Juvenile whelks also showed very different in handling times for H. sangarense and R. fratercula. In fact, N. arthritica consumed R. fratercula about ten times faster than H. sangarense. Moreover, in this study, N. arthritica consumed more R. fratercula than H. sangarense on average. These results support the "apparent preference" hypothesis (Fairweather & Underwood 1983), which states that attacks on prey species that require longer handling times are more likely to be observed in the field. In addition, we also observed relatively few successful attacks on H. sangarense compared to that of R. fratercula. The predation events on H. sangarense reported in Yamakami & Wada (2021a) may have included such unsuccessful attacks. However, we could not determine whether the consumption rate of R. fratercula by N. arthritica in the field actually exceeds that of H. sangarense because R. fratercula can burrow into the sandy bottoms (Zhang & Goshima 2013). Experimental studies in some sandy-bottom bivalves have shown that the presence of sand provides refuge from predation by seastars and crabs (Doering 1982, Smith et al. 1999, Dudas et al. 2005).

Interestingly, results of our feeding experiments indicate that N. arthritica juveniles actually prefer H. sangarense in spite of the additional time required for handling. The gastropods used as prey in this study can be divided into two types that differ in opercular morphology: species with a horny, flexible operculum (B. angustata, R. fratercula, and C. japonicus), and species with a calcareous, hard operculum (H. sangarense). A calcareous, hard operculum is thought to be an effective defensive trait (Vermeij & Williams 2007), because N. arthritica must access the aperture of a shell to consume gastropod prey (Yamakami & Wada 2021a). In many cases, H. sangarense force N. arthritica to excavate the edge of its tick operculum and to create a "small gap" (Yamakami & Wada 2021a). On the other hand, it is difficult to infer the presence of the excavation procedure by traces in the other three species because of the opercular thinness and brittleness. Many drilling predatory gastropods exhibit shorter handling times when no drilling procedure is required or only a small amount of drilling (i.e., it is thick) is needed (Fairweather & Underwood 1983; López et al. 2010). Therefore, our results (i.e., extremely longer handling times and lower attack success rates with H. sangarense) can be interpreted as due to the protection of the aperture by the calcareous, thick operculum. Opercular morphology and its defensive function could be a factor in producing "apparent" preferences, but did not explain the "actual" preference patterns of juvenile N. arthritica. The "actual" prey preferences did not prioritize morphologically vulnerable species that offer reduced handling time, being inconsistent with studies of other predators (e.g., crabs, Elner & Raffaelli 1980; gastropods, Soto et al. 2004, López et al. 2010; octopus, Song et al. 2019). Future studies of behavioral defensive characteristics among prey species may help us to better understand the preferences of this species, as has been done for the interactions between the carnivorous whelk Thais tuberosa and its prey (Castell & Sweatman 1997).

Homalopoma sangarense may be higher quality prey (e.g., high energy content and rich nutrition) than other prey species. A species of drilling whelk Nucella heyseana (Dunker, 1882) shows an actual preference for Mytilus sp. than Septifer virgatus (Kawai 2002, as "N. freycineti") because the latter has lower energy content than the former although the expected handling times by shell thickness were equal between the two prey species. Alternatively, H. sangarense may be easier to capture than other species. Neptunea arthritica appeared to be an active, tracking predator. Hayakawa et al. (2012) reported that C. japonicus exhibits escape responses such as rapid changes in direction and speeding up of crawling in encounters with the murcid carnivorous whelk Ergalatax contractus (Reeve, 1846). They also found that although E. contractus can consume C. japonicus in several hours, in comparison to the long handling time (1 d) required to consume juvenile Turbo sazae Fukuda, 2017 (the species is referred to as "T. cornutus" in the study), the whelks preferentially consumed T. sazae. However, N. arthritica and C. japonicus were often found adjacent to each other in the aquarium (Yamakami personal observation) and attacks (i.e., contact) on C. japonicus were successfully completed in all cases of this study, although the detailed response of C. japonicus was not able to examined due to long interval of video recording.

Predator's prey preference is also influenced by the prey availability and their history (e.g., Sanford et al. 2003). In our sampling site, B. angustata forms a species assemblage cluster with R. fratercula and both species can be seen abundant in similar habitats of somewhat muddy rocky bottom (but B. angustata has a tendency of phytal animal) (Yamakami & Wada 2021b). Cantharidus japonicus forms a species assemblage cluster with H. sangarense and both can be seen in similar habitats of rocky seaweed zone (Yamakami & Wada 2021b). Neptunea arthritica would encounter each species on the sea floor. Although H. sangarense has currently the lowest density of the four gastropod species (Yamakami & Wada 2021b), it was the most dominant species in 1996 (Yoshino et al. 2001). In addition, densities of B. angustata and C. japonicus were much lower compared to the present (Yoshino et al. 2001). Knowledge of how this species responds to changes in prey availability (i.e., how quickly it can switch prey preferences) will be needed to understand the status of its population.

Another important implication of this study is the size-dependence of prey preference. Analyses of the relationship between attack frequency and whelk size suggest that smaller N. arthritica juveniles prefer B. angustata more
strongly than larger ones do. This is consistent with the size range of individuals that actually consume B. angustata in the field (Yamakami & Wada 2021a). Barleeia angustata may be a major prey item in the early life stage of this species until reaches the size 10 mm (after hatching at 6 mm Fujinaga & Nakao 1995), for which the diet is currently unknown, because it is the most abundant gastropod in the study site (Yamakami & Wada 2021b). On the other hand, larger whelks avoid B. angustata possibly because it is small and inefficient, or difficult to handle (Ap Rheinallt 1986). Therefore, size-related changes in prey utilization in the field (i.e., a shift from H. sangarense to tegulid gastropods and venerid bivalves with growth; Yamakami & Wada 2021a) may also be caused by ontogenetic changes in prey preference.

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264  R. YAMAKAMI & S. WADA
Prey preferences of Neptunea arthritica

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