



Title	Prey utilization by <i>Neptunea arthritica</i> (Caenogastropoda: Buccinidae) : predation on gastropods and size-related variation
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1 Prey utilization by *Neptunea arthritica* (Caenogastropoda: Buccinidae): predation on gastropods
2 and size-related variation

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11 Running head: Predation in *Neptunea*

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14

Abstract

15 The whelk *Neptunea arthritica* (Buccinidae) is a common fishery species in Hokkaido, northern

16 Japan. Although ecological information is needed for fisheries management, there is only one

17 paper examining the foraging ecology of this species and this reported that *N. arthritica* preyed

18 mainly on the invasive mussel *Mytilus galloprovincialis*. To date, no studies have examined

19 utilization of native prey species by this whelk. Here, we report the findings of a study on the

20 native prey utilization by *N. arthritica* in an area where *M. galloprovincialis* is not present. We

21 conducted line transect sampling every month from May 2018 to May 2019 on the western

22 coast of Hakodate Bay, southwestern Hokkaido, Japan. Prey items were composed mostly of

23 gastropods (72%), followed by bivalves (24%), and only a small amount of carrion (< 4%).

24 Overlapping spatial distributions were observed among size classes of *N. arthritica*, while the

25 prey utilization varied with body size. Small individuals (<30 mm in shell height) preyed mainly

26 on the small colloniid gastropod *Homalopoma sangarense*, while larger individuals (>40 mm)
27 preyed mainly on two tegulid gastropods (*Chlorostoma lischkei* and *Omphalius rusticus*) and
28 two venerid bivalves (*Protothaca euglypta* and *Ruditapes philippinarum*). There were positive
29 size relationships between whelk body size and prey size for prey categories (Vetigastropoda,
30 Caenogastropoda and Bivalvia) and even for the same prey species (*H. sangarense*, *O. rusticus*
31 and *P. euglypta*). These results suggest that *N. arthritica* is a predator of mobile gastropods,
32 especially during its early life stage, in areas without the invasive Mediterranean mussel. It is
33 possible that the foraging strategy of *N. arthritica* may differ quite markedly between areas with
34 and without the invasive mussel.
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Introduction

38 *Neptunea arthritica* (Caenogastropoda: Buccinidae) is a carnivorous whelk, dwelling in rocky
39 intertidal and subtidal zones in coastal waters from northern Japan to Sakhalin, Russia (Higo,
40 Callomon & Goto, 1999; Okutani, 2017). This species is commercially important in inshore
41 fisheries in Hokkaido, the northernmost of Japan's main islands (Ueda *et al.*, 2003), and
42 ecological information about this species is needed for the management of the fisheries. Several
43 studies have documented the reproductive ecology (Takamaru & Fuji, 1981; Fujinaga, 1985;
44 Kawai *et al.*, 1994; Miranda *et al.*, 2009) and the growth pattern (Fujinaga, 1987; Suzuki *et al.*,
45 1996; Miranda, Fujinaga & Nakao, 2008) of this species. However, as far as we know, there is
46 only one paper examining the foraging ecology of this *N. arthritica* (Fujinaga & Nakao, 1999).

47 According to Fujinaga & Nakao's (1999) study in Usu Bay, south-central Hokkaido,
48 most (76%) of the 528 individuals of *N. arthritica* observed preyed on the Mediterranean
49 mussel *Mytilus galloprovincialis* (the authors used the name *M. edulis*), with some individuals
50 (20%) scavenging on carrion. *Neptunea arthritica* may prefer to prey on *M. galloprovincialis*
51 because it is an abundant and sessile species. However, *M. galloprovincialis* is an invasive
52 species with a scattered distribution in Hokkaido (Iwasaki *et al.*, 2004; Brannock, Wethey &
53 Hilbish, 2009) and so there are many local populations of *N. arthritica* that do not coexist with
54 this mussel.

55 Local populations of predatory gastropods often exhibit dietary specialization, to
56 utilizing locally abundant prey species (Rovero, Hughes & Chelazzi, 1999; Sanford *et al.*, 2003;
57 Sanford & Worth, 2009). Since *N. arthritica* is characterized by direct development without a
58 planktonic stage (Fujinaga & Nakao, 1995), restricted gene flow among populations could result
59 in increased genetic differentiation with increasing geographic separation (Azuma *et al.*, 2011).

60 In local populations of *N. arthritica* that co-occur *M. galloprovincialis*, rapid microevolution
61 may occur for preying on the invasive mussel. However, there are many studies reporting mass
62 mortality events of *Mytilus* spp. (Tsuchiya, 1983; Myrand & Gaudreault, 1995; Kubota, 1997;
63 Harley, 2008; Peperzak & Poelman, 2008). Rapid microevolution to prey on a nonnative species
64 may become maladaptive if that nonnative species is no longer present (e.g. Singer & Parmesan,
65 2018). Singer & Parmesan (2018) reported the extinction of a butterfly population that preferred
66 exotic plant species to native host plants as being due to the loss of non-native host even though
67 the native host species was present. This is because the butterfly population became highly
68 dependent on non-native plant species and lost the adaptations required to feed on the native
69 host plants. Understanding the prey utilization of *N. arthritica* in areas where *M.*
70 *galloprovincialis* is absent is therefore important not only for careful management of whelk
71 populations, but also to conserve *N. arthritica* in areas where *M. galloprovincialis* forms a major
72 part of its diet and mass mortality of the mussel could lead to the whelk's extinction.

73 Prey utilization can be highly variable with predator size and this phenomenon has
74 been widely described in predatory gastropods (Paine, 1966; Nybakken & Perron, 1988; Abe,
75 1989; Hughes, Burrows & Rogers, 1992; Tan & Oh, 2003; Averbuj *et al.*, 2012; Clements &
76 Rawlings, 2014; Chang & Duda, 2016; Robinson & Peters, 2018). For example, *Nucella*
77 *lapillus*, a predator of barnacles and mussels, shows ontogenetic variations in prey utilization
78 with mussels gradually dominating in the diet as the predator species attains larger sizes
79 (Hughes, Burrows & Rogers, 1992). On the other hand, with growth *Buccinanops cochlidium*
80 changes foraging tactics, changing from an obligate scavenger to a facultative scavenger that
81 usually consumes bivalves (Averbuj *et al.*, 2012). To date, however, no studies have examined
82 prey utilization in *N. arthritica* with respect to the body size of this species.

83 Here, we investigate prey utilization by *N. arthritica* in an area where the invasive
84 mussel *M. galloprovincialis* is not present, focusing on prey utilization in relation to the body
85 size of the whelk.

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Material and Methods

88 *Study site*

89 The study site was a rocky shore at Kattoshi (41°44'N, 140°36'E) on the western coast of
90 Hakodate Bay, southwestern Hokkaido, Japan (Fig. 1). During low tide, the shore platform is
91 partly exposed from the seawall to about 200 m offshore. *Neptunea arthritica* is abundant at the
92 study site, where this species is currently protected from fishing. *Mytilus galloprovincialis* does
93 not occur at the study site. Although there are small beds of the native mussel *Septifer virgatus*
94 outside the study area, neither in the field nor the lab have we observed predation of this mussel
95 by *N. arthritica* (Yamakami, unpubl.).

96

97 *Field investigation*

98 To quantify prey utilization by *N. arthritica*, we conducted line transect sampling every month
99 from May 2018 to May 2019 during low tide. We ran a set of four 150-m-long line transects
100 extending offshore from the seawall. Each transect was setup using a tape measure and the
101 transects were spaced at 30-m intervals. All individuals of *N. arthritica* along the line and
102 within 1-m width on both sides of the line were sampled and care was taken not to overlook
103 partially hidden whelks, such as those burrowing in the sediment or beneath stones. Seasonal
104 storms meant that we had to shorten the total length of the four line transect by 25 m in May
105 2018, 20 m in June 2018 and 10 m in September 2018 and March 2019.

106 Each time we found a whelk, we measured its shell height (as a proxy for body size) to
107 the nearest 0.1 mm using a calipers. The distance from the seawall (0 to 150 m) to the sampling
108 point was also recorded to the nearest 0.1 m. We regarded a whelk as a ‘foraging individual’
109 when its foot or proboscis was seen to be in direct contact with a prey animal , and recorded the
110 identity of the prey to the lowest possible taxonomic level. We also recorded the size of
111 molluscan prey (i.e. length of the longest axis) with calipers to 0.1 mm-accuracy. Size was
112 equivalent to the following measures for the four molluscan groups studied: shell length for
113 Patellogastropoda and Bivalvia taxa,, shell width for Vetigastropoda and shell height for (3)
114 Caenogastropoda (Fig. 2). Whelks were seen scavenging on carrion (i.e. dead crabs and
115 echinoids); we did not measure the body size of these prey items, although we measured the
116 shell height of the whelk observed scavenging. Less than 3 min were taken for measuring and
117 recording each predator-prey encounter; after that, all whelks and prey taxa were released back
118 to their respective sampling points. The raw data are available in the Supplementary Material.

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Results

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A total of 197 foraging and 2,691 non-foraging individuals of *Neptunea arthritica* were found during the study from May 2018 to May 2019. Overlapping spatial distributions were observed on the platform among individuals of different size classes, showing that *N. arthritica* was most abundant at a distance of more than 50 m offshore (i.e. from the from the seawall), regardless of their size throughout the year (Fig. 3). Foraging individuals were found in all months (Table 1) with no clear seasonal pattern in foraging frequency (χ^2 test: $\chi^2 = 15.192$, $P = 0.231$).

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In the study area, *N. arthritica* consumed 17 identifiable prey items (Table 2). There were 142 foraging events of preying on gastropods (72.08%), 48 events of preying on bivalves (24.37%) and 7 events of feeding on carrion (3.55%). During predation, *N. arthritica* captured

130 single prey items using its foot (Fig. 4). Gastropods were attacked through the shell aperture o
131 gastropods, whereas bivalves were attacked at the shell margin (Fig. 4). Predation scars were
132 observed on the shells of mollusc prey, such as on the outer rim of the operculum in gastropods
133 and the ventral shell margin in bivalves (Fig. 5).

134 Diet composition differed for whelk size classes above and below 30–40 mm (Fig. 6).
135 *Homalopoma sangarens*, small colloniid gastropod, was dominant in the diet of small
136 individuals of *N. arthritica* (<30 mm). In contrast, *H. sangarens* was not preyed on by large
137 individuals (>40 mm), which instead fed on two tegulid gastropods, *Chlorostoma lischkei* and
138 *Omphalius rusticus*, and two venerid bivalves, *Protothaca euglypta* and *Ruditapes*
139 *philippinarum*. Intermediate-sized (30–40 mm) individuals of *N. arthritica* showed a diet of
140 intermediate composition, but they also preyed on the small nassaliid *Reticunassa fratercula* at
141 a higher rate compared to the other two size classes. No individuals of *N. arthritica* in the 0–10
142 mm size class were seen foraging; individuals of this size were observed in August and
143 September 2018, just after the hatching season.

144 Linear regression analysis showed significant positive slopes for the relationships
145 between whelk and prey size for three of the four prey categories (Table 3, Fig. 7), with larger
146 *N. arthritica* tending to prey on larger prey. For the fourth prey category, Patellogastropoda, this
147 was not the case and that is probably due to the small sample size. In the case of the six main
148 prey species, linear regression analysis revealed a significant size relationship for *H.*
149 *sangarens*, *O. rusticus* and *P. euglypta*, but not for *C. lischkei*, *R. fratercula* and *R.*
150 *philippinarum*, again probably due to the small sample size (Table 4).

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Discussion

153 This is the first study to investigate the diet of *Neptunea arthritica* in an area where the invasive
154 mussel *Mytilus galloprovincialis* is not present. At our study site, *N. arthritica* consumed a
155 variety of mobile prey, including gastropods and bivalves, with gastropods (72%) as the most
156 important component. We also observed *N. arthritica* feeding on carrion, mainly crabs and
157 echinoids. In contrast to the study of *N. arthritica* in Usu Bay, which found that most of the prey
158 were sessile taxa (i.e. 76% of the diet was *M. galloprovincialis*; Fujinaga & Nakao, 1999),
159 predation of native sessile bivalves (e.g. *Porterius dalli*, *Septifer keenae*, *Septifer virgatus* and
160 *Irus mitis*) was not observed at our study site. Our results show that the diet of *N. arthritica*
161 varies geographically, ranging from mobile gastropods to sessile bivalves, and that prey
162 availability in the local environment could lead to significant interpopulation differences in the
163 diet of *N. arthritica*.

164 Differentiation of foraging traits among local populations has been described for some
165 predatory gastropods (Rovero, Hughes & Chelazzi, 1999; Sanford *et al.*, 2003; Sanford &
166 Worth, 2009). For example, on the western coast of North America, southern populations of
167 *Nucella canaliculata* consume the native mussel *Mytilus californianus*, whereas northern
168 populations do not, *M. californianus* being absent from this part of the range of *N. canaliculata*
169 (Sanford *et al.*, 2003; Sanford & Worth, 2009). While *Nucella lapillus* on a mussel-dominated
170 shore can employ the gape-insertion method to consume the mussel *M. edulis*, *N. lapillus* on a
171 shore where mussels are absent does not use this method of attack (Rovero, Hughes & Chelazzi,
172 1999). Thus, although *Nucella* species may have the potential to utilize various prey species,
173 this does not mean that they can easily switch major prey species. No studies have demonstrated
174 that *N. arthritica* populations dependent on *M. galloprovincialis* can switch to mobile
175 gastropods in the event of mass mortality of the mussel (Tsuchiya, 1983; Myrand & Gaudreault,
176 1995; Kubota, 1997; Harley, 2008; Peperzak & Poelman, 2008). Further studies are needed to

177 clarify whether individuals from populations dependent on *M. galloprovincialis* have the
178 ability to consume native prey, especially mobile species.

179 The present study provides the first observations of size-related variation in prey
180 utilization in the genus *Neptunea*. As *N. arthritica* reaches larger sizes, two dietary changes are
181 evident: (1) a shift in prey species or prey category and (2) an increase in both intra- and
182 interspecific prey size. These changes have been reported for other predatory gastropods (Abe,
183 1989; Hughes *et al.*, 1992; Tan & Oh, 2003; Clements & Rawlings, 2014; Robinson & Peters,
184 2018). Since *N. arthritica* in our study site shows considerable distributional overlap in size,
185 prey variation in relation to whelk size could be interpreted as size-linked intraspecific resource
186 partitioning (Polis, 1984); this may reduce niche overlap among the different size classes of this
187 species.

188 Our results also suggest that predation in *N. arthritica* has two possible size-related
189 constraints. The first constraint is foot size, which limits the size of prey that can be taken. The
190 size of the prey-capture apparatus often limits the consumption of prey above and/or below a
191 certain size threshold in many predators, including gastropods (Paine, 1976; Ap Rheinallt, 1986;
192 Nilsson & Brönmark, 2000; Chiba & Sato 2012). Our field observations suggest that the foot of
193 *N. arthritica* plays an important role in the capture and handling of prey, and similar findings
194 have been reported for other predatory gastropods (Morton 1985, 1986; Scolding, Richardson &
195 Luckenbach, 2007; Bigatti *et al.*, 2009, 2010; Chiba & Sato, 2012). Therefore, foot size, which
196 increases as a function of body size, may be the limiting factor of for prey capture in *N.*
197 *arthritica*. This is consistent with the significant positive correlation that we observed between
198 whelk size and prey size for three prey species. The second constraint is the availability of
199 specific prey items with respect to microhabitat use. Marine invertebrates, including gastropods,
200 generally use more protective microhabitats in their early life stages because of greater

201 vulnerability to predation and other environmental stresses (Gosselin, 1997 and references
202 therein; Schoepf, Herler & Zuschin, 2010; Takami & Kawamura, 2018). In our study site, most
203 small *N. arthritica* prey on rocky-bottom prey species (e.g. *H. sangarensis*), whereas
204 intermediate-sized and large individuals prey on both rocky-bottom prey species (e.g. Tegulids)
205 and sandy-bottom prey species (*R. fratercula* and various venerids). This suggests that in *N.*
206 *arthritica* microhabitat use may be size-dependent and this in turn may affect what prey can be
207 taken at different growth stages. In fact, at our study site, we found *N. arthritica* on both rocky
208 and sandy bottoms, but small individuals seemed to have a stronger association with rocky
209 bottom habitats (Yamakami, personal observation).

210 Polychaetes have been found frequently in the gut contents of several species of
211 *Neptunea*, including *N. antiqua* (Blegvad, 1914; Taylor, 1978), *N. communis* (North et al.,
212 2019), *N. heros* (Shimek, 1984; North et al., 2019), *N. ventricosa*, *N. pribiloffensis* and *N. lyrata*
213 (Shimek, 1984). Thus, our initially expectation was that *N. arthritica* would prey on polychaetes
214 in areas where *M. galloprovincialis* was absent. Whelks consume polychaetes by extending the
215 proboscis (Pearce & Thorson, 1967), and have been observed in the field inserting the proboscis
216 into the substrate (Rosenthal, 1971; Shimek, 1984; Fujinaga & Nakao, 1999). However, this
217 behaviour was not exhibited by any of the foraging individuals we observed at our study site,
218 although all individuals, including those hidden in the sand, were captured and carefully
219 examined. If *N. arthritica* also preys on polychaetes at our study site, the shorter period of
220 manipulating the polychaete prey prior to ingestion as compared to molluscan prey, may have
221 caused us to overlook polychaete predation (Fairweather & Underwood, 1983). Therefore,
222 further verification (e.g. through gut content analysis and laboratory feeding experiments) is
223 needed to determine whether *N. arthritica* also preys on polychaetes at our study site.

224 Our findings provide important insights into the attack methods of *N. arthritica*.
225 Members of the genus *Neptunea* are characterized by large salivary glands that secrete the
226 neurotoxin tetramine (Fänge, 1957; Asano & Ito, 1959; Shiomi *et al.*, 1994; Watson-Wright *et*
227 *al.*, 1992; Kawashima, Nagashima & Shiomi, 2002), and published data have shown that there
228 is a relationship in the seasonal fluctuation of tetramine concentration and foraging activity
229 (Power, Keegan & Nolan, 2002). Power, Keegan & Nolan (2002) indicated that tetramine may
230 have a function in predation: *N. antiqua* could consume mussels without leaving any sign of
231 attack as this species is able to use a shell-wedge strategy to open the valve. In this study, we
232 found that *N. arthritica* left predation/attack marks on the prey's shell, most strikingly a small
233 'gap' on the outer rim of the opercula or between the valves. Such 'gaps' are made by some
234 predatory gastropods; although these holes are too small for the predator to insert their
235 proboscis into to ingest the prey's tissues, they are thought to allow the introduction of toxins
236 used in paralyze the prey (Urrutia & Navarro, 2001; Herbert, 2004; Herbert, Whitenack &
237 McKnight, 2016). Similarly, the attack signature of *N. arthritica* suggests the possibility that it
238 also uses tetramine for predation; if so, this may explain why *Neptunea* and othera predatory
239 molluscs that do not bore the shells of their molluscan prey can consume prey that are well
240 protected by either an operculum or a set of valves.

241 In conclusion, our study of *N. arthritica* shows that in the study area this species is a
242 predator of mobile gastropods and that the whelk's prey utilization (prey species and/or size)
243 varies with respect to its body size. However, prey utilization by *N. arthritica* at other localities
244 where *M. galloprovincialis* is absent remains unknown. Further studies of inter-population
245 variation in the diet, prey selectivity and attack methods of this species could provide insights
246 into its adaptation, fisheries management and conservation.

247

248

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480 **Table 1.** The number of foraging individuals of *Neptunea arthritica* and the foraging proportion
 481 at Kattoshi, as observed each month, from May 2018 to May 2019.

482

Month	2018									2019			
	M	J	J	A	S	O	N	D	J	F	M	A	M
Total	123	218	183	208	220	254	284	326	299	139	240	329	262
Foraging	7	12	9	15	19	22	18	9	22	7	18	25	14
Foraging proportion	0.06	0.06	0.05	0.07	0.09	0.09	0.06	0.03	0.07	0.05	0.08	0.08	0.05

483 **Table 2.** List of prey consumed by *Neptunea arthritica* at Kattoshi from May 2018 to May 2019.

Prey items	<i>n</i>	Mean prey size (mm)	Mean whelk size (mm)
Gastropoda			
Patellogastropoda			
<i>Lottia tenuisculpta</i>	6	6.2 ± 0.4	24.5 ± 2.0
<i>Lottia emydia</i>	1	7.2	33.2
Vetigastropoda			
<i>Homalopoma sangarens</i>	80	6.0 ± 1.0	21.8 ± 5.2
<i>Lirularia iridescens</i>	2	4.2 ± 0.5	25.5 ± 2.9
<i>Cantharidus japonicus</i>	4	5.8 ± 0.3	32.2 ± 3.4
<i>Omphalius rusticus</i>	11	14.5 ± 6.1	47.1 ± 10.0
<i>Chlorostoma lischkei</i>	17	16.5 ± 6.5	50.4 ± 10.1
Caenogastropoda			
<i>Alvania concinna</i>	2	2.9 ± 0.2	11.5 ± 1.9
<i>Barleeia angustata</i>	2	2.2 ± 0.4	11.8 ± 1.0
<i>Reticunassa fratercula</i>	14	8.5 ± 1.9	29.2 ± 7.4
<i>Lirabuccinum fuscolabiatum</i>	1	19.2	49.3
<i>Ocenebrellus inornatus</i>	2	26.6 ± 6.7	55.8 ± 2.2
Bivalvia			
Veneroidea			
<i>Protothaca euglypta</i>	39	19.0 ± 7.8	46.0 ± 12.3
<i>Ruditapes philippinarum</i>	8	15.0 ± 5.1	51.5 ± 13.9
<i>Heteromacoma irus</i>	1	20.8	54.4
Carrion			
Malacostraca	4	---	40.1 ± 14.6
Echinoidea	3	---	57.5 ± 10.6
Total	197	---	---

484

485 The mean size and SD of both whelk and prey consumed are given for each species.

486 Species are listed in ascending order of mean whelk size for each prey type.

487 **Table 3.** Summary of linear regression analysis for the effect of whelk size on the prey size of
 488 each of four major prey taxa, showing estimates of the parameters, standard errors, *t*-statistics and
 489 *P*-values.

	Estimate	SE	<i>t</i>	<i>P</i>
Patellogastropoda (<i>n</i> = 7)				
Intercept	3.537	1.113	3.177	0.025
Whelk size	0.107	0.043	2.505	0.054
Vetigastropoda (<i>n</i> = 114)				
Intercept	-1.009	0.685	-1.473	0.143
Whelk size	0.323	0.021	15.064	<0.001
Caenogastropoda (<i>n</i> = 21)				
Intercept	-3.568	1.773	-2.013	0.059
Whelk size	0.449	0.055	8.17	<0.001
Bivalvia (<i>n</i> = 48)				
Intercept	-0.307	3.197	-0.096	0.924
Whelk size	0.396	0.066	6.033	<0.001

490

491 Bold font indicates statistical significance ($P < 0.05$).

492 **Table 4.** Summary of the linear regression analysis for the effect of whelk size on the prey size of
 493 six major prey species, showing estimates of the parameters, standard errors, *t*-statistics and *P*-
 494 values.

	Estimate	SE	<i>t</i>	<i>P</i>
<i>Homalopoma sangarens</i> (<i>n</i> = 80)				
Intercept	4.912	0.444	11.07	<0.001
Whelk size	0.05	0.02	2.52	0.014
<i>Omphalius rusticus</i> (<i>n</i> = 11)				
Intercept	-9.829	5.276	-1.863	0.0954
Whelk size	0.518	0.11	4.712	0.001
<i>Chlorostoma lischkei</i> (<i>n</i> = 17)				
Intercept	3.163	7.829	0.404	0.692
Whelk size	0.265	0.153	1.736	0.103
<i>Reticunassa fratercula</i> (<i>n</i> = 14)				
Intercept	5.028	1.97	2.553	0.025
Whelk size	0.12	0.066	1.829	0.092
<i>Protothaca eiglypta</i> (<i>n</i> = 39)				
Intercept	-2.588	3.35	-0.773	0.445
Whelk size	0.468	0.07	6.655	<0.001
<i>Ruditapes philippinarum</i> (<i>n</i> = 8)				
Intercept	2.038	5.806	0.351	0.738
Whelk size	0.252	0.109	2.304	0.061

495
 496 Bold font indicates statistical significance (*P* < 0.05).

497

498

Figure captions

499 **Figure 1.** Map of study sites. **A.** Hokkaido with Hakodate Bay (boxed inset). **B.** The location of
500 Kattoshi (solid circle) in Hakodate Bay.

501

502 **Figure 2.** Shell measurements taken each category of molluscan prey (measurements taken
503 along maximum dimension). **A.** Patellogastropoda. **B.** Vetigastropoda. **C.** Caenogastropoda. **D.**
504 Bivalvia. Abbreviations: SL, shell length; SW, shell width; SH, shell height.

505

506 **Figure 3.** The horizontal distribution of three size classes of *Neptunea arthritica* on the
507 intertidal platform at Kattoshi, as sampled (May 2018 to May 2019) from the seawall to a
508 distance of 150 m offshore.

509

510 **Figure 4.** Foraging individuals of *Neptunea arthritica* capturing prey with their foot, as
511 observed in the field in Kattoshi. The prey species are indicated by arrows and are as follows;
512 *Protothaca euglypta* (**A**), *Chlorostoma lischkei* (**B**) and *Homalopoma sangarens* (**C**). Scale
513 bars = 1.0 cm. –

514

515 **Figure 5.** Attack signature (indicated by white arrows) of *Neptunea arthritica* on the shell of
516 two mollusc taxa. **A.** *Homalopoma sangarens* (note outer rim of operculum). **B.** *Protothaca*
517 *euglypta* (note valve margin). Scale bars: **A**, 2.0 mm; **B**, 1.0 cm.

518

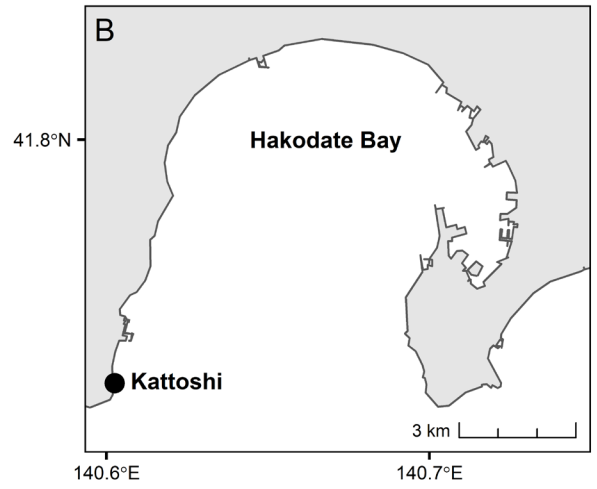
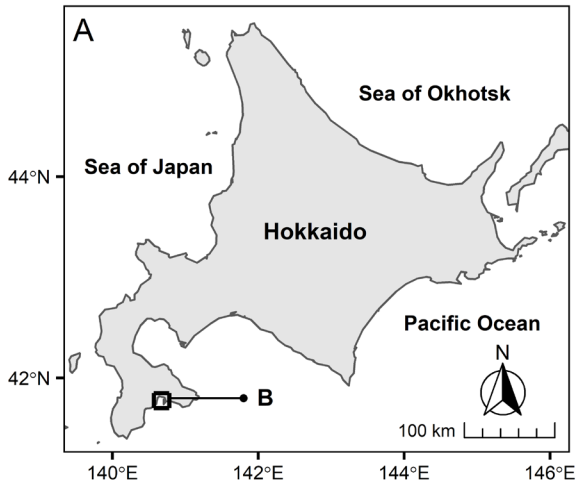
519 **Figure 6.** Species composition (percent volume) of prey consumed by *Neptunea arthritica*
520 among size classes at Kattoshi from May 2018 to May 2019. The total number of foraging

521 individuals is shown above each bar with the number of all individual observed within
522 parentheses. ND indicates No data.

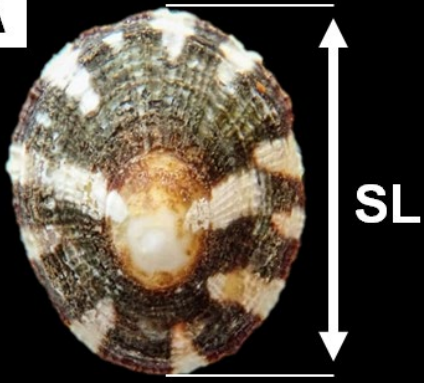
523 **Figure 7.** The size relationships between the whelk *Neptunea arthritica* and the four prey
524 categories studied. **A.** Patellogastropoda ($n = 7$). **B.** Vetigastropoda ($n = 120$). **C.**
525 Caenogastropoda ($n = 21$). **D.** Bivalvia ($n = 48$). Dashed lines represent significant regression
526 lines. Regression equations are presented in Table 3.

527

528



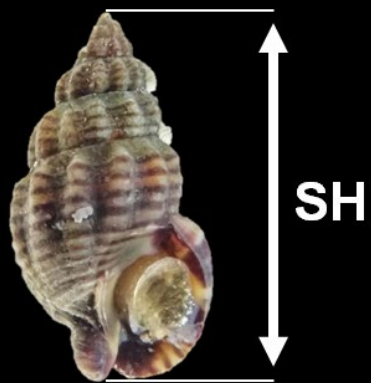
A



B



C



D

