**Foraging Activity and Prey-size Selection in *Nucella freycineti* (Deshayes)
(Neogastropoda: Muricidae)**

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Abstract: The seasonal preferences for prey species and prey size by the dogwhelk *Nucella freycineti* (Deshayes) were investigated on an intertidal rocky shore in Hokkaido, northern Japan. Adult dogwhelks (> 25 mm shell length) mainly preyed upon the mussels *Septifer virgatus* and *Mytilus* sp. in the field throughout the year. In the laboratory, they preferred *Mytilus* sp. over *S. virgatus* in June, and this preference increased in August. The prey values of the two mussels were compared using the formula (energy amount of one prey) / (drilling time). I assumed that the dry tissue weight of the prey reflected the energy content and that the valve thickness of the prey reflected the drilling time. Although the dry weights of *Septifer* and *Mytilus* were not significantly different in June, *Mytilus* sp. became heavier than the same size *S. virgatus* for all sizes in August. Indices of valve thickness (valve thickness – shell length ratio) at the point in mussel shells where dogwhelks preferred to make a hole before feeding were not significantly different between the two mussel species, indicating that the drilling times of both prey types may be almost the same. These results suggest that *Mytilus* sp. and *S. virgatus* have almost the same prey value in June, but *Mytilus* sp. is a more valuable prey in August. Although the energy content of one prey and drilling effort required were used to estimate the prey value, this study suggests that other factors (e.g., morphological differences of prey, nutritional quality of prey) might be also important for seasonal prey selection. Dogwhelks selected significantly larger mussels in summer than in winter both in the laboratory and field. Hence, dogwhelks consume optimal species (more valuable species) and prey size (bigger sizes) in warm periods, but the foraging behavior is restricted by environmental conditions in cold periods.

Key words: foraging activity, *Mytilus*, *Nucella freycineti*, prey-size selection, *Septifer*

INTRODUCTION

The dogwhelk *Nucella* is a predator on northern intertidal rocky shores of the Pacific and Atlantic. Its prey are sessile animals such as mussels and barnacles, and prey preference develops as a result of dietary condi-

tioning (Hughes & Dunkin 1984b). Dogwhelks prefer larger prey in the laboratory, and their foraging behavior has been explained by energy maximization per unit foraging time (Dunkin & Hughes 1984; Hughes & Dunkin 1984b). In the field, however, environmental conditions such as wave action, desiccation, and risk of predation may modify such responses (Menge 1978; Etter 1989). Field studies have detected size-selective predation, but size selection is restricted by many environmental conditions (e.g., Burrows & Hughes 1989; Hughes & Burrows 1991). Foraging behavior of dogwhelks in the field is therefore a natural example of constrained optimization in foraging behavior (Hughes & Burrows 1991).

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Nucella freycineti (Deshayes) is a predatory marine gastropod common on rocky intertidal shores of the Northwest Pacific (Okutani 2000). It shows clear seasonal changes in metabolism, growth, and reproduction (Kawai 1993). The physical environment in this region also shows clear seasonal patterns (Fuji 1988; Kawai & Nakao 1993). The energy demands of the dogwhelk and habitat conditions vary with season, suggesting that the dogwhelk *N. freycineti* might show different foraging behavior in each season.

This study aims to (a) describe the seasonal preference of *N. freycineti* for prey species in the field, (b) determine its seasonal change of the preference for different sizes and species of prey and their prey value, and (c) discuss its seasonal foraging strategy.

MATERIALS AND METHODS

Field observations

The study area was a wave-exposed shore at Usujiri, Hokkaido, Japan (42° 21' N; 140° 57' E), which is dominated by the barnacle *Chthamalus challengerii*, the periwinkle *Littorina brevicula*, and the mussel *Mytilus* sp. and *Septifer virgatus* (see Fuji & Nomura 1990; Kawai 1993). The maximum and minimum water temperatures in this study area were 20°C in September and 3°C in February (Kawai 1993). I made field observations from April 1990 to June 1991 and used 64 fixed quadrats (1 × 1 m) in the intertidal zone and 6 fixed quadrats in the subtidal zone (Kawai & Nakao 1993). By walking along the shore at low tide in the intertidal area and by skin diving at high tide in the subtidal area, I counted the number of foraging dogwhelks and recorded the species names of prey to study the seasonal preference for prey species in each quadrat once a month at the first spring tide. A dogwhelk was considered to be feeding if its proboscis was inserted into a bivalve or its foot covered an empty barnacle with cleaned-out wall plates. The shell lengths of both preys and dogwhelk were measured to the nearest 0.1 mm using a caliper.

Experiments for prey preference

To find out the preferred prey species and size, I conducted an experiment from 26 May to 30 June 1994 (Experiment 1) in a large aquarium (2.0 × 1.2 × 0.7 m) supplied with a continuous flow of seawater from the sea at Usujiri. The water temperature in the aquarium is similar to water temperature in the field. Because dogwhelks mainly foraged on *Septifer virgatus* and

Mytilus sp. in the field (see Results), I used these mussel species as standard prey. I used dogwhelks of shell lengths ranging between 25 to 30 mm that were mature (Kawai & Nakao 1993) to avoid any possible size-dependent prey preference. Before the experiment, I kept 3 dogwhelks in the aquarium without food for 10 days, after which each was placed individually into a cage of 20 × 13 × 8 cm together with 10 *Mytilus* sp. (2 mussels of < 10 mm shell length (SL), 2 mussels of 10–20 mm SL, 3 mussels of 20–30 mm SL, 3 mussels of > 30 mm SL) and 10 *S. virgatus* (2 mussels of < 10 mm SL, 2 mussels of 10–20 mm SL, 3 mussels of 20–30 mm SL, 3 mussels of > 30 mm SL) collected from the same area where the dogwhelks were found. The size frequency distributions of the two species of mussels in each cage were similar to those in the field. I measured the shell lengths of the eaten prey each week and replaced the empty shells with prey of similar size.

I investigated the preference for *Mytilus* sp. and *S. virgatus* by the dogwhelks from 13 July to 11 August 1994 (Experiment 2). Before the experiment, I kept dogwhelks measuring between 25 to 35 mm in size in the aquarium for 10 days without food. I used mussels of 25 to 35 mm in shell length to minimize the influence of prey size on prey species selection, because dogwhelks preferred mussels of 30 mm (see Results of Ex. 1). I used 8 cages (20 × 13 × 8 cm) and put one dogwhelk with 10 *Mytilus* sp. (2 mussels of < 10 mm SL, 2 mussels of 10–20 mm SL, 3 mussels of 20–30 mm SL, 3 mussels of > 30 mm SL) and 10 *S. virgatus* (2 mussels of < 10 mm SL, 2 mussels of 10–20 mm SL, 3 mussels of 20–30 mm SL, 3 mussels of > 30 mm SL) into each cage. I used the same procedure as in Experiment 1.

To study seasonal differences in prey size preference, I conducted a one-year experiment from February 1991 to February 1992 (Experiment 3). Before the experiment I kept dogwhelks of 20–40 mm in the aquarium for 10 days without food. I put 20 small cages (20 × 13 × 8 cm) in the aquarium and placed one dogwhelk into each cage together with 20 *S. virgatus* (4 mussels of < 10 mm SL, 4 mussels of 10–20 mm SL, 6 mussels of 20–30 mm SL, 6 mussels of > 30 mm SL) with a size frequency distribution similar to that in the field and put in a new dogwhelk each month. I reared them for at least 3 weeks each month. I measured the shell length of drilled prey, removed empty shells weekly from cages, and replaced them with shells of the same size.

Prey value

To compare prey preference between *Mytilus* sp. and *S.*

virgatus consumed in Experiments 1 and 2, I calculated a prey value to evaluate the quality of prey using the following formula:

$$W_i = G_i / T,$$

where W is the prey value (W_m is the prey value of *Mytilus* sp., W_s is the prey value of *S. virgatus*), G is the prey energy value expressed as the dry tissue weight, i is the prey type (m means *Mytilus* sp., s means *S. virgatus*), and T is the mean drilling time by a snail attack.

Although the searching time is important for prey selection, I assumed that the mean search times were the same in these experiments to compare the prey value between *Mytilus* sp. and *S. virgatus*, because the same numbers of *Mytilus* sp. and *S. virgatus* were placed into each cage. I also assumed that the dry tissue weight of the prey reflected the energy content (Hughes & Dunkin 1984a) and that the valve thickness of the prey reflected the drilling time.

Prey property

Almost all dogwhelks drilled a hole on the valve of the prey to insert their proboscis to consume the tissue (see Results). I measured the shell length, height and width, and the distance from the umbo to the hole made in each foraged prey by the dogwhelks in all experiments. I calculated the morphological ratios of shell height–shell length, shell width–shell length, and distance from the umbo to the hole–shell length. Thirty mussels of each species between 25–40 mm shell length were collected at Usujiri. I measured the shell length and thickness of the valve at the midpoint (the preferred place for drilling a hole by dogwhelks in the laboratory, see Results) in each mussel and calculated indices of valve thickness (valve thickness–shell length ratio).

I derived a formula of the relationship between the dry weight and the shell length of each mussel species of the 3 June and 31 August 1994 samples. I collected 30 mussels of each prey species of different sizes at Usujiri and measured their shell lengths. I dried somatic tissues in an oven at 60°C to constant weight and measured them to the nearest 1 mg using an electric balance.

RESULTS

Field observations

Nucella freycineti preyed upon five species in the field during the 15 months of the study (Fig. 1-A). *Septifer*

Fig. 1. Relative proportion (%) of consumed prey observed in the field from April 1990 to June 1991. (A) All dogwhelks, (B) > 25 mm dogwhelks. The figure above each bar indicates the total number of observed feeding dogwhelks.

virgatus and *Mytilus* sp. were the main prey species, composing 80.3% of the total number of prey individuals consumed. Dogwhelks seldom preyed on the barnacles *Chthamalus challengerii* and *Balanus cariosus*, which were common in this area, and only juvenile dogwhelks fed on the bivalve *Lasaea undulata*. Almost all dogwhelks (98.3%) drilled a hole on the valve of the bivalve to insert their proboscis. Figure 1-B shows the monthly preferences of prey foraged by adult dogwhelks with shell lengths larger than 25 mm. Dogwhelks preyed on higher number of *Mytilus* sp. in August, October and November 1990, but the frequency of *Mytilus* sp. in April 1990 and May 1991 was also high, which might have been caused by a lack of observed sample numbers in the field. Table 1 shows the mean prey sizes of *S. virgatus* consumed by adult dogwhelks, the more preferred mussel for adult dogwhelks in the field. Field observations suggested that prey size selected showed largest in summer and smallest in winter. Dogwhelks consumed significantly larger *S. virgatus* in summer (June–August) than in winter (December–February)

Table 1. Seasonal changes in prey size (Mean $\pm$ SD mm) of *Septifer virgatus* consumed by the adult dogwhelks.

Season	Laboratory	Field	Level of significance
Spring	25.3 $\pm$ 7.8	21.3 $\pm$ 6.4	ns
Summer	27.7 $\pm$ 8.3	27.0 $\pm$ 7.1	ns
Autumn	25.4 $\pm$ 7.8	25.3 $\pm$ 10.0	ns
Winter	20.0 $\pm$ 6.2	9.1 $\pm$ 3.7	$P < 0.05$

in the laboratory: Spring, March–May 1991; Summer, June–August 1991; Autumn, September–November 1991; Winter, February, December 1991, January 1992.

in the field: Spring, April, May 1990, March–May 1991; Summer, June–August 1990, June 1991; Autumn, September–November 1990; Winter, December 1990, January–February 1991.

ns: not significant

Table 2. Prey preference for the dogwhelks of Experiments 1 and 2. (Mean $\pm$ SD)

		Food		
		Total	<i>Septifer</i>	<i>Mytilus</i>
Ex.1	Number of cages	3		
	Mean number of prey eaten	5.0 $\pm$ 2.0	1.3 $\pm$ 1.2	3.7 $\pm$ 2.3
	Mean shell length of prey (mm)	29.8 $\pm$ 3.7	30.3 $\pm$ 3.7	29.6 $\pm$ 3.7
Ex.2	Number of cages	8		
	Mean number of prey eaten	4.1 $\pm$ 1.0	0*	4.1 $\pm$ 1.0
	Mean shell length of prey (mm)	31.2 $\pm$ 2.9	–	31.2 $\pm$ 2.9

*One dogwhelk consumed a *S. virgatus*, but this result was omitted from the analysis, because this dogwhelk died before the end of the experiment.

Fig. 2. Monthly prey size (Mean $\pm$ SD mm) of *Septifer virgatus* consumed by dogwhelks from February 1991 to June 1992 in the laboratory aquarium.

(U -test, $P < 0.001$). The sizes of *S. virgatus* eaten by the dogwhelks in spring (March–May) and autumn (September–November) were not significantly different in the field (U -test, $P > 0.05$).

Prey preference

The mean number of prey eaten in each cage over five weeks in Experiment 1 was about 5 individuals (Table 2). Dogwhelks foraged both prey species, but preferred *Mytilus* sp. over *S. virgatus* (binomial test, $P < 0.05$). The mean shell lengths of the two mussel species preyed upon by *N. freycineti* were not significantly different (U -test, $P > 0.05$).

Only *Mytilus* sp. was selected by dogwhelks in Experiment 2 (Table 2). Although one dogwhelk consumed a single *S. virgatus* during the experiment, I omitted this result from the analysis because this dogwhelk died before the end of the experiment.

Seasonal prey size selection

Mean shell lengths of *S. virgatus* foraged by adult dogwhelks in laboratory Experiment 3 ranged from 18.4 ($\pm$ 6.3 SD) mm in February to 29.9 ($\pm$ 7.4) in August; the values showed a clear seasonal curve (Fig. 2). To compare the prey sizes among seasons and between the field and laboratory, seasonal prey sizes in the laboratory (Table 1) were calculated using the data in Fig. 2. Dogwhelks preferred significantly larger prey in summer (June–August) than in winter (December–February) (U -test, $P < 0.001$) (Table 1). Mean prey sizes in spring (March–May) and autumn (September–November) were similar. On the other hand, prey size differed significantly between the field and in the laboratory in winter (U -test, $P < 0.05$), but not in spring, summer and autumn (U -test, $P > 0.05$) (Table 1).

Prey property

The formulas of the shell length–dry weight relationship were not significantly different between *Mytilus* sp. and *S. virgatus* in June (ANCOVA, $F = 0.32$, $P > 0.05$) (Fig. 3), but were significantly different in August (ANCOVA, $F = 19.98$, $P < 0.001$), indicating that *Mytilus* sp. was heavier than *S. virgatus* in August.

Table 3 shows the significant morphological differences (U -test, $P < 0.001$) in shell width–shell length and shell height–shell length ratios between *Mytilus* sp. and *S. virgatus*. Both ratios were larger for *Mytilus* sp. than for *S. virgatus*, indicating *Mytilus* sp. shells were

rounder than *S. virgatus* shells. The positions of the holes were near the center of the valve of both mussel species (mean ratio 0.57) and did not differ between the 2 species (*U*-test, $P > 0.05$). The valve thickness – shell length ratio did not significantly differ between *Mytilus* sp. and *S. virgatus* (*U*-test, $P > 0.05$) (Table 3).

Prey value

The mean thickness of the center of the valve did not differ significantly between *Mytilus* sp. and *S. virgatus* (Table 3), suggesting that the mean drilling times by dogwhelks in both mussel species may be similar. Because the dry tissue weight of *Mytilus* sp. was greater than for *S. virgatus* in August (Fig. 3), the prey energy value of *Mytilus* sp. was higher than for *S. virgatus*. These results showed that *Mytilus* sp. had a higher prey value than *S. virgatus*. The dogwhelks consumed only *Mytilus* sp. in August (Table 2). Accordingly the dogwhelks foraged optimal prey. On the other hand, both mussels had similar prey energy value in June (Fig. 3). Because in June both indices *G* and *T* did not differ significantly between mussel species, both mussel species had equal prey values, but dogwhelks had a low preference for *Mytilus* sp. in the laboratory in June (Table 2).

DISCUSSION

Environmental conditions

Dogwhelks selected significantly larger *Septifer virgatus* in summer than in winter in the laboratory and field (Table 1, Fig. 2). The foraging behavior of marine snails in intertidal areas appears to be strongly influenced by environmental conditions, such as temperature (e.g., Stickle et al. 1985), wave action (e.g., Palmer 1983; Burrows & Hughes 1989; Hughes & Burrows 1991), desiccation (e.g., Burrows & Hughes 1989; Hughes & Burrows 1991), and predation (e.g., Yamada et al. 1998).

Two possible predators (the crab *Hemigrapsus sanguineus* and the sea star *Asterias amurensis*) of *N. freycineti* inhabit the study area. The carapace size of adult *H. sanguineus* is 3–4 cm, so the claw size is too small to crush adult dogwhelks. *A. amurensis* forages adult dogwhelks in the field, but the density of *A. amurensis* was very low in this intertidal area (personal observation). Therefore, these species presumably do not cause intense predation pressure on dogwhelks and therefore might not influence seasonal size selection by *N. freycineti*.

Fig. 3. Relationship between shell length (*X*, mm) and dry weight (*Y*, mg) of *Mytilus* sp. and *Septifer virgatus* in June and August. (*Mytilus* sp. in June: $\log(Y) = 2.48 \log(X) - 4.47$; *S. virgatus* in June: $\log(Y) = 2.62 \log(X) - 4.67$; *Mytilus* sp. in August: $\log(Y) = 2.65 \log(X) - 4.73$; *S. virgatus* in August: $\log(Y) = 2.81 \log(X) - 5.06$)

Table 3. Morphological ratios (mean $\pm$ SD) in *Mytilus* sp. and *Septifer virgatus*. SW: shell width, SL: shell length, SH: shell height, H: length from umbo to hole, ST: shell thickness at the center of valve. Level of significance shows results of *U*-test.

	<i>Mytilus</i> sp.	<i>S. virgatus</i>	Level of significance
SW / SL	0.50 $\pm$ 0.03	0.40 $\pm$ 0.04	$P < 0.001$
SH / SL	0.53 $\pm$ 0.05	0.42 $\pm$ 0.03	$P < 0.001$
H / SL	0.60 $\pm$ 0.16	0.54 $\pm$ 0.15	ns
ST / SL	0.02 $\pm$ 0.01	0.02 $\pm$ 0.01	ns

ns: not significant

The maximum and minimum water temperatures in the study were 20°C in September and 3°C in February (Kawai 1993), which paralleled the seasonal change in mean prey size (Kendall's coefficient of rank correlation = 0.41, $P < 0.01$) (Fig. 2). Only the winter mean prey sizes were statistically different between in the field and the laboratory, but the mean prey sizes consumed in other seasons in the field tended to be slightly smaller than in the laboratory (Table 1). The main difference in environmental conditions for foraging by the dogwhelks between field and laboratory conditions were wave action, desiccation and tidal cycle. But the study area has relatively calm conditions in late summer and autumn, and intense wave action in winter (Fuji 1988). If wave action affects prey selection in this area, the consumed prey would be bigger in summer than in winter, because bigger prey are usually more profitable (Dunkin & Hughes 1984; Hughes & Dunkin 1984b). This trend was

similar to the seasonal prey size selection observed in the laboratory experiments and field observations of the present study. Dogwhelks aggregate in lower intertidal areas in winter and move to upper intertidal areas to forage prey in summer (personal observation), suggesting that dogwhelks are exposed to air for long periods in summer. If desiccation is an important cause of seasonal prey selection, dogwhelks should select smaller prey in summer than in winter because desiccation could cause physiological stress for the dogwhelk and constrain the foraging behavior. However this is not the case, because the dogwhelks consumed larger size of mussel in summer. Because we did not make tidal cycle in the laboratory experiments, foraging behavior of the dogwhelks in the laboratory was not influenced by tidal cycle. But because tidal cycle was daily cycle, this did not influence in the seasonal prey size selection very much. Therefore, wave action and temperature were presumably the main environmental factors affecting the seasonal prey selection by *N. freycineti*.

In summer, dogwhelks are active and need much energy for their metabolism, growth and maturation in summer (Kawai 1993). In this season, dogwhelks selected bigger mussels (Table 1, Fig. 2), which are usually a more profitable size (Dunkin & Hughes 1984; Hughes & Dunkin 1984b). On the other hand, in winter dogwhelks are inactive and the amount of energy needed to stay alive is lower than in summer (Kawai 1993). Dogwhelks selected smaller prey during winter (Table 1, Fig. 2), possibly because they could more easily feed upon smaller prey than larger prey and therefore reduce the energetic costs for acquiring food. Therefore, these foraging behaviors of dogwhelks are a natural example of constrained optimization in foraging behavior.

Prey value

Dogwhelks consumed only *Mytilus* sp. in Experiment 2 (August) (Table 2). In August, *Mytilus* sp. had a higher

prey value (W) than *S. virgatus*, indicating that the dogwhelks foraged the optimal prey. However, prey values were equal in June. Nevertheless, dogwhelks had a low preference for *Mytilus* sp. in Experiment 1 (June) (Table 2), suggesting that the amount of energy of one prey and the mean drilling time investigated in this study were inadequate for evaluating prey value. Rather dogwhelks prefer *Mytilus* sp. because of other factors. Here, I discuss three possible explanations. First, the encounter rate of prey influences prey species selection, as seen in the muricid gastropod *Acanthina spirata* (Murdoch 1969). In the present study, I used the same number of *Mytilus* sp. and *S. virgatus* in the laboratory, so the encounter rates for the two mussel species were similar. Therefore, the encounter rate might not strongly influence prey selection by *N. freycineti*. Second, the nutritional quality of prey (Belovsky 1978) might influence selection by dogwhelks, although I do not have any data on this. Third, morphological properties of mussels might influence prey selection. The shell width–shell length and shell height–shell length ratios of *Mytilus* sp. were higher than for *S. virgatus* (Table 3), indicating that *Mytilus* sp. shells were rounder than *S. virgatus* shells. Although both mussel species generally aggregate to form mats in the field, dogwhelks probably have easier access to the valve surface near the center (i.e., near the optimal position to make a hole) of *Mytilus* sp. as compared to *S. virgatus*, because in the field *S. virgatus* shells occur much closely together than *Mytilus* sp. shells do, which could possibly prevent access to the favored drilling sites in the *S. virgatus* shells. However, morphological differences between mussel species may not strongly influence prey preference, because dogwhelks preferred *Mytilus* sp. in the laboratory when the mussels did not form mats. On the other hand, the thickness of the periostracum layer in the mussels may also influence prey preference (Harper & Skelton 1993).

Table 4. Mean number of *S. virgatus* and *Mytilus* sp. consumed by adult dogwhelks in experimental quadrats in cold (April and May 1990 and December 1990–May 1991) and warm (June 1990–November 1990 and June 1991) temperature periods at Usujiri.

		<i>Mytilus</i> sp.	<i>S. virgatus</i>	References
Cold temperature period	Number (individuals / m ²)	0.03	0.19	this study
	Ratio (<i>S. virgatus</i> : <i>Mytilus</i> sp.)		6.50	
Warm temperature period	Number (individuals / m ²)	0.34	0.44	this study
	Ratio (<i>S. virgatus</i> : <i>Mytilus</i> sp.)		2.58	
Mean density	Number (individuals / m ²)	239	2788	Fuji & Nomura (1990)
	Ratio (<i>S. virgatus</i> : <i>Mytilus</i> sp.)		11.66	

Seasonal prey species selection in the field

To study the seasonal preference of *N. freycineti* between *Mytilus* sp. and *S. virgatus* in the field, I compared the density and number of consumed mussels in the field, even though density might not be a good indicator of actual encounter rate in the field because mussels were not randomly distributed in the field and dogwhelks do not randomly move, and so density does not reflect the actual encounter rate. Adult dogwhelks foraged 14 *Mytilus* sp. and 44 *S. virgatus* in the field (Fig. 1), i.e., a 1 : 3.1 ratio. Fuji & Nomura (1990) reported that the mean densities of *Mytilus* sp. and *S. virgatus* were 239.1 and 2787.9 (ind. / m²) in the study shore, respectively, i.e., a 1 : 11.7 ratio (Table 4). These ratios indicated that *Mytilus* sp. was consumed 3.7 times more often than expected from the density alone. The ratio of consumed mussels (*S. virgatus* : *Mytilus* sp.) was 1 : 2.6 in warm periods and 1 : 6.5 in cold periods. The decrease in the preference for *Mytilus* sp. in cold periods may have been because *Mytilus* sp. was a less valuable prey in winter (Table 2) or the severe environmental conditions in winter may impose also prey selection. Dogwhelks fed more frequently in summer than in winter, and the diet comprised a larger set of prey types in summer than in winter, so dogwhelks tended to select the encountered prey. Although more experiments are needed to clarify the factors that affect seasonal prey selection, seasonal prey-species selection occurred in the field.

CONCLUSION

Seasonal foraging behavior of *N. freycineti* was explained by a complex set of factors. Dogwhelks forage on optimal prey (i.e., bigger sizes and more valuable species) when the environment is suitable for dogwhelks (summer: warm temperature, calm waves). But they might consume mussels of smaller size and show weak preference for species when environmental conditions are severe (winter: low temperature, intense wave action).

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