Predation by the Nudibranch *Dirona albolineata* on Three Species of Prosobranchs[1]

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NUDIBRANCHS as a group prey on a diverse assemblage of animals including sponges, coelenterates, tunicates, barnacles, crustaceans, ectoprocts, polychaetes, egg masses, and carrion (see review papers of Miller, 1961; Swennen, 1961; Thompson, 1964). Only a few nudibranchs are known to prey on other molluscs, usually opisthobranchs. These include: *Gymnodoris alba* (Bergh, 1877) which eats *Favorinus* sp. and *Aeolidella* sp.; *Gymnodoris bicolor* (Alder and Hancock, 1866) which eats *G. okinawae* Baba, 1936 and *G. plebeia* (Bergh, 1877) (see Kay and Young, 1969); *Phidiana pugnax* Lance, 1962 which eats other eolids (Lance, 1962); and *Roboastra* sp. which eats *Nembrotha eliora* Marcus, 1967 (Farmer, personal communication). *Hermissenda crassicornis* (Eschscholtz, 1831), in the laboratory, will eat other nudibranchs including its own species, but this behavior is likely to be caused by starvation and is of little importance in the field (Swennen, 1961).

In this paper, I report some observations on predation by a nudibranch, *Dirona albolineata* MacFarland, 1912, on three species of prosobranchs in nature and in the laboratory.

NATURAL HISTORY AND PRELIMINARY OBSERVATIONS

Throughout the year, *D. albolineata* may be found in densities of 0.01 to 5/m^2 on mud, gravel, and rock substrata from the intertidal to depths of at least 60 m in the San Juan Islands, Washington. In these habitats, it is apparently an unselective predator scraping up ectoprocts, hydroids, small crustaceans, sponges, barnacles, and tunicates, plus other organisms such as diatoms, coralline algae, and detritus (Harris, 1965; author's unpublished observations). Occasionally, I have observed *D. albolineata* specializing on one type of prey if that prey is very abundant. For example, a population from Eagle Point, San Juan Island preys on arborescent or crustose ectoprocts that may comprise about 50 percent of the benthic fauna for much of the year.

During March, 1969, while diving on a reef off Brown Island, Friday Harbor, Washington (long. 123°0′40″ W, lat. 48°32′30″ N), I collected 40 specimens of *D. albolineata.* This rocky reef, 5 to 15 m deep, is partially covered with sandy mud and supports a sparse flora of *Zostera marina* L., *Laminaria* spp., and *Constantinea simplex* Setchell. There were a few holothurians, *Parastichopus californicus* (Stimpson, 1857); bivalves, *Pododesmus macroschisma* (Deshayes, 1839); and barnacles, *Balanus* spp. Crawling over the algae, mud, and rock were numerous prosobranchs, *Margarites pupillus* Gould, 1849, and *Lacuna carinata* Gould, 1849, with somewhat fewer *Margarites helicinus* (Phipps, 1774). Unfortunately, no quantitative measures of the snails' densities were made. There were very few of the epibenthic organisms upon which *Dirona albolineata* normally feeds.

To determine what *D. albolineata* was eating on this relatively barren reef, I placed 31 of them in clean aquaria with running seawater and examined the fecal strings. All animals defecated opercula and pieces of shell of *Lacuna.* Four animals also defecated *Margarites pupillus* opercula and shell fragments, while five others defecated parts of *M. helicinus* shells. Other hard parts found in the fecal strings were: *Balanus* sp. (one *Dirona*); byssus from *Chlamys* sp. (one *Dirona*); amphipods (1); hydroid, *Aglaophenia struthionoides* (1); tiny bivalves (1); and fragments of the ectoproct, *Bugula* sp. (4). Varying amounts of sand were found in all the fecal strings. The only organic matter in the fecal string, aside from mucus, consisted of a few prosobranch digestive glands and odontophores.

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The high proportion of prosobranchs in the diet was somewhat surprising and prompted a series of experiments to answer four questions: (1) Does *Dirona albolineata* have a real prey preference with regard to the prosobranchs? (2) What is the predation rate on each species? (3) What proportion of its own dry weight does *D. albolineata* ingest per day? (4) Where in the digestive tract are the shells crushed?

METHODS

Specimens of *D. albolineata* were kept at the Friday Harbor Laboratories in seawater tables supplied with running seawater and were given *Margarites* spp. and *Lacuna* to eat.

The test animals, measured from the tip of the tail to the anterior edge of the oral veil while actively crawling, were 6 to 9 cm long. By using animals of about the same size and by minimizing the effects of starvation, variation in the feeding rates and size of prey taken was reduced, thus making feeding rates and behavior more comparable.

Margarites pupillus, M. helicinus, and *Lacuna* were collected from the same area as *Dirona albolineata* in about the same ratio and size-frequency as they occurred in the field. This was done by picking up every snail encountered until enough were obtained for the experiments. Their length was measured from the apex to the umbilicus.

For the experiments, *D. albolineata* and the prosobranchs were put in individual plastic aquaria with screen sides. The aquaria were capped and submerged in circulating seawater. At varying intervals, the number of prosobranchs remaining was counted. A subjective estimate of the size of the smallest of those remaining was made at the same time.

Individual feeding rates were calculated from the number of prey eaten per hour within each time interval. The average feeding rate on each prey species was calculated from:

$$\frac{\text{total no. of prey eaten}}{\text{total no. of predators} \times \text{no. of hours in each interval}}$$

The dry weight of six individuals of *D. albolineata* was obtained after they were blotted dry, weighed, dried for 96 hours at 80° C, and reweighed. The dry weight of a sample of 20 *Lacuna* and 10 *Margarites helicinus,* similar in size-frequency to those used in the feeding experiments and with shells removed, was determined in the same way.

To determine where the shells were crushed, four specimens of *Dirona albolineata* were starved for 48 hours. These were then fed for 12 hours on *Lacuna* and *Margarites* after which they were relaxed with succinylcholine chloride (Beeman, 1968) and fixed immediately in 10 percent formalin. A middorsal longitudinal slit in the body wall allowed examination of the digestive tract from the buccal mass to the intestine.

RESULTS

Initial examination of the fecal strings revealed that *Lacuna* was the main component of the diet of *Dirona albolineata* with fewer of the two *Margarites* spp. being consumed. A similar result was obtained in the prey preference experiments (Table 1) when the test animals were given the three species of prosobranchs in the proportion occurring in nature. The percentages of snails eaten in the first time period (44 and 45 hr, Table 1) are as follows: *Lacuna* (feeding rate 0.16 to 0.26/hr), 79 percent; *Margarites helicinus* (feeding rate 0.02 to 0.05/hr), 14 percent; *M. pupillus* (feeding rate 0.02/hr), only about 8 percent. When *Dirona albolineata* was given only one prey species at a time (Table 2), it showed a slightly lower feeding rate on *Lacuna* ($0.83 + 0.39 = 0.61$/hr) compared to *Margarites helicinus* (0.70/hr), whereas none of the *M. pupillus* were eaten. (For comparative purposes, the feeding rates are based on the number of snails eaten in the first time period of each experiment.)

In the feeding experiments constituting Table 1, the smallest animals of *M. pupillus* ($<$ 6 mm long) were always eaten. Small specimens of *M. pupillus* ($<$ 6 mm long) were then offered as prey in various combinations with *Lacuna* and *Margarites helicinus* (Table 3). In the one case where all three prey species were offered (animal no. 15, Table 3), there was no significant difference ($X^2 = 0.4$) in the feeding rates on *M. pupillus* (0.64, 0.23 in two con-

TABLE 1

FEEDING RATES OF *Dirona albolineata* ON *Margarites pupillus, M. helicinus,* AND *Lacuna carinata* IN THE LABORATORY

	NO. PREY EATEN IN 44 HR				NO. PREY EATEN FROM 44 TO 70 HR				AVERAGE FEEDING RATE (no. eaten/ *Dirona*/hr) FROM 0 TO 44 HR
Dirona Specimen No.	1	2	3	4	1	2	3	4	
Prey Species									
Margarites pupillus	1/10 (0.02)	0/10 —	1/10 (0.02)	2/10 (0.05)	0/9 —	0/10 —	0/9 —	0/8 —	0.02
Margarites helicinus	0/5 —	2/5 (0.05)	2/5 (0.05)	5/5 (0.11)	2/5 (0.08)	3/3 (0.11)	1/3 (0.04)	— —	0.05
Lacuna carinata	10/15 (0.23)	11/15 (0.25)	9/15 (0.20)	15/15 (0.34)	4/5 (0.15)	3/4 (0.11)	4/6 (0.15)	— —	0.26

	NO. PREY EATEN IN 45 HR		NO. PREY EATEN FROM 45 TO 93 HR		AVERAGE FEEDING RATE (no. eaten/ *Dirona*/hr) FROM 0 TO 45 HR
Dirona Specimen No.	5	6	5	6	
Prey Species					
Margarites pupillus	0/5 —	2/7 (0.04)	0/5 —	0/5 —	0.02
Margarites helicinus	0/5 —	2/5 (0.04)	3/5 (0.07)	0/3	0.02
Lacuna carinata	11/20 (0.24)	3/15 (0.07)	6/9 (0.13)	1/12 (0.02)	0.16

NOTE: The specimens of *Dirona albolineata* were 6 to 8 cm long. The prey were presented simultaneously in about the same ratio and size-frequency as they occur in the field. Numbers in the body of the table are: number of snails eaten during the interval / number of snails present at the beginning of the interval. Numbers in parentheses are feeding rates (numbers of prey eaten per hour in the intervals indicated).

TABLE 2

FEEDING RATES OF *Dirona albolineata* ON *Margarites pupillus*, *M. helicinus*, AND *Lacuna carinata* IN THE LABORATORY

	TRIAL 1			TRIAL 2			AVERAGE FEEDING RATE (no. eaten/ *Dirona*/hr) in TRIAL 2
	NO. PREY EATEN IN 46 HR			NO. PREY EATEN IN 44 HR			
Dirona Specimen No.	7	8	9	10	11	12	
Prey Species							
Margarites pupillus	0/45	—	—	—	—	—	
	—	—	—	—	—	—	—
Margarites helicinus	—	32/36	—	—	—	—	
	—	(0.70)	—	—	—	—	—
Lacuna carinata	—	—	38/54	16/45	16/35	20/35	
	—	—	(0.83)	(0.36)	(0.36)	(0.45)	0.39

NOTE: Each prey species is presented individually. The specimens of *Dirona albolineata* were 6 to 8 cm long. The prey were presented in about the same size-frequency as they occur in the field. Numbers in the body of the table are: number of snails eaten during the interval / number of snails present at the beginning of the interval. Numbers in parentheses are feeding rates (numbers of prey eaten per hour in the intervals indicated).

secutive time periods) and *Lacuna* (0.64, 0.37 in the same periods). That this *Dirona albolineata* ate only one *Margarites helicinus* is probably a result of the low initial density of *M. helicinus* relative to the other two snails.

No specimens of *M. pupillus* were eaten (Table 2), probably because the smallest one (7.5 mm) was too large to be crushed by *Dirona albolineata*. When small individuals of *Margarites pupillus* (< 6 mm were presented along with *M. helicinus* and *Lacuna*, the average feeding rates were about the same: 0.18 *Margarites pupillus*/hr, 0.25 *M. helicinus*/hr, and 0.26 *Lacuna*/hr (Table 3). Although not all the test animals were offered all the prey species, other nonquantitative observations suggest that these rates are probably representative.

The mean length of the specimens of *Dirona albolineata* collected and used in the experiments was 7 cm with a standard deviation of 1 cm. On the basis of six animals ranging from 3.5 to 9 cm long, the relationship between dry weight (DW) and length (L) was found to be:

$$DW = 0.0212 + 0.082L$$

where r, the correlation coefficient, was 0.98. The average dry weight of *Lacuna* was 3.6 mg and that of *Margarites helicinus* was 5.3 mg. *M. pupillus* was not considered because those animals that could be eaten had very little organic tissue and they were numerically unimportant in the diet of *Dirona albolineata*.

Using the grand mean of feeding rates of *Dirona albolineata* on *Lacuna* and *Margarites helicinus* from Table 1, it can be calculated that a *Dirona albolineata* of average size (70 mm long, 591 mg dry weight) eats:

5.04 *Lacuna*/day × 3.6 mg/*Lacuna*
= 18.1 mg dry wt/day
0.84 *M. helicinus*/day × 5.3 mg/*M. helicinus*
= 4.4 mg dry wt/day
Total 22.5 mg dry wt/day

or about 3.8 percent of its own dry weight per day in laboratory experiments. This is a slight underestimate because the *M. pupillus* has not been included.

A maximum intake for the laboratory situation may be found using the feeding rates from Table 2. The average *Dirona albolineata* (see above) eats:

16.8 *M. helicinus*/day × 5.3 mg/*M. helicinus*
= 88.8 mg dry wt/day
19.9 *Lacuna*/day × 3.6 mg/*Lacuna*
= 71.6 mg dry wt/day
Total 160.4 mg dry wt/day

or about 27.1 percent of its own weight per day.

TABLE 3

FEEDING RATES OF *Dirona albolineata* ON *Margarites pupillus, M. helicinus,* AND *Lacuna Carinata* IN THE LABORATORY

	NO. PREY EATEN IN 14 HR			NO. PREY EATEN FROM 14 TO 44 HR			AVERAGE FEEDING RATE (no. eaten/ *Dirona*/hr) IN 44 HR
Dirona Specimen No.	13	14	15	13	14	15	
Prey Species							
Margarites pupillus	—	0/5	9/30	—	0/5	7/21	
	—	—	(0.64)	—	—	(0.23)	0.18
Margarites helicinus	10/39	—	1/5	11/29	—	0/4	
	(0.71)	—	(0.07)	(0.38)	—	—	0.25
Lacuna carinata	2/5	5/35	9/31	0/3	7/30	11/22	
	(0.14)	(0.36)	(0.64)	—	(0.23)	(0.37)	0.26

NOTE: The specimens of *Dirona albolineata* were 6 to 8 cm long. The specimens of *Margarites pupillus* were less than 7 mm long, whereas *M. helicinus* and *Lacuna carinata* were about the same size-frequency as in the field. Numbers in the body of the table are: number of snails eaten during the interval / number of snails present at the beginning of the interval. Numbers in parentheses are feeding rates (numbers of prey eaten per hour in the intervals indicated).

To determine where the shells were crushed, I examined four specimens of *Dirona albolineata.* Three had pieces of crushed shell in the posterior part of the esophagus and one had some pieces of *Lacuna* shell in the buccal mass. The esophagus of the latter *Dirona albolineata* was empty for most of its length, but a large wad of broken shells and bodies of *Lacuna,* with opercula still attached, began 7 mm anterior to the stomach and continued into it. One other *Dirona albolineata* had broken shell mixed with the bodies of *Lacuna,* again with opercula still attached, in the last 5 mm of its esophagus. The animal with no shell in the esophagus apparently had not eaten recently as the stomach was almost empty.

DISCUSSION

Dirona albolineata, as a species, is an unselective predator eating almost any potential prey it encounters. In faunistically diverse areas, *D. albolineata* may eat ectoprocts, hydroids, small crustaceans, sponges, barnacles, and tunicates. However, individuals or restricted populations may become temporarily specialized on a particular prey species or type of prey (i.e., ectoprocts) if that prey becomes very abundant.

In the area studied, three prosobranchs, *Lacuna carinata, Margarites helicinus,* and *M. pupillus,* were very abundant and the only prey species present. The abundance of snails in the gut of *Dirona albolineata* taken from the field was in the order *Lacuna* > *M. helicinus* > *M. pupillus.* It is not clear whether this is the result of an active prey selection by *Dirona albolineata* or not. It may be that the first two species are actively sought out by *D. albolineata* and that occasionally *Margarites pupillus* is ingested accidentally. Or it may be that an attempt is made to eat any prosobranch that is encountered and only those with shells heavy enough that they can not be crushed (for instance, *M. pupillus* over 7 mm long) are rejected. The latter seems more likely in view of the generally polyphagous habit of *Dirona albolineata* and the fact that tiny specimens of *Margarites pupillus,* with their fragile shells, are eaten about as readily as the other two species tested. *M. pupillus* was slightly more common than *M. helicinus* in the area studied (each *Margarites* species being about 20 to 30 percent of the total snail population), but the proportion of *M. pupillus* less than 7 mm long was about 10 percent of this. Thus, the chance of *Dirona albolineata* contacting a small *Margarites pupillus* was low, possibly accounting for their rarity in the diet of *Dirona albolineata.*

That the jaws crush the shells is supported by two lines of evidence. First, there are no grinding plates anywhere in the digestive tract that could crush the shells although *D. albolineata* has a massive and powerfully muscular buccal mass (MacFarland, 1912). Second, the presence of crushed pieces of shell in the jaws and posterior esophagus make it almost certain that breakage occurs in the jaw.

The sequence of events in the predation by *D. albolineata* on these prosobranchs is concluded to be as follows. *D. albolineata* crawls rapidly in a more or less random fashion over the substratum. The oral veil probably acts as a contact chemoreceptor for, when it touches a snail or other potential prey, it lifts up slightly and passes over the prey. The mouth is placed over the snail and the snail is held between the lips and jaws. *D. albolineata* attempts to crush the snail with the jaws and, if successful, swallows the crushed snail. Digestion takes place rapidly. The shell fragments, radulae, and opercula are compacted with mucus in the intestine and voided. If *D. albolineata* is unsuccessful in crushing the prey, it simply drops the prey and continues on.

D. albolineata, ingesting 4 to 27 percent of its own dry weight per day, is not unlike other molluscs in this regard. *Conus* eats 1 to 10 percent of its body weight per day (Kohn, 1959, 1968). Nudibranchs like *Onchidoris bilamellata* (Linnaeus, 1767), *Caloria militaris* (Alden and Hancock, 1864), and some species of *Dendronotus* eat 1 to 25 percent of their dry weight per day (author's unpublished observations).

SUMMARY

Dirona albolineata is an unselective predator that will eat ectoprocts, hydroids, crustaceans, sponges, tunicates, plus much of the bottom detritus. A population from Brown Island, Washington was found to prey on three species of prosobranchs: *Lacuna carinata, Margarites helicinus,* and *M. pupillus.* Although there was no real prey preference, *Dirona albolineata* was unable to crush shells of *Margarites papillus* longer than 7 mm. The prosobranchs were crushed in the jaws of *Dirona albolineata.*

Like other molluscs, *D. albolineata* ingests 4 to 27 percent of its own dry weight per day.

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