#### FEEDING BEHAVIOR OF POLINICES DUPLICATUS

AND RESULTING COLOR CHANGES OF THE

SHELL'S CALLUS

A Thesis Presented

to

the Faculty of the Department of Biology

University of Houston

In Partial Fulfillment of the Requirements for the Degree Master of Science

by ·

William M. Davies

May, 1977.

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The purpose of this study was to investigate the relationship between the feeding behavior of Polinices duplicatus and resulting color changes of the shell's callus. A mean feeding rate of 0.81 clams per day with a maximum feeding rate of 1.21 clams per day was determined. Feeding rates expressed as percent of the snail dry weight were 8.9% per day at maximum and 4.8% per day on average. Weathering of dead Polinices shells resulted in brown calluses, while brown was never found in the calluses of living snails. This weathering process was much slower than changes in the callus due to diet, never occurring more rapidly than 60 days. A change from purple to white while feeding (11.1 days) was found to be approximately three days longer than the reverse change during starvation. Diameter of the borehole was significantly correlated with the size of the snail, and variability of the borehole diameter increased with increasing snail size. Polinices drilled the left value of bivalue prey 60% of the time.

Snails with aperture widths of 1.5 to 1.9 cm were cannibalized most frequently, and the proportion of purple calluses was not a strong indicator of the amount of cannibalism.

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#### Introduction

Unlike plants, many pigmented animals cannot synthesize "de nova" their own pigments. Instead they must assimilate pigments from their diets (Fox, 1953). Copepods and brine shrimp (<u>Artemia salina</u>) take up  $\beta$ -carotene, a carotenoid pigment, from algae (Thommen, 1971). This pigment in turn becomes the flamingo's feather pigment when the crustaceans are consumed by the bird (Conway, 1959; Roulsen, 1960; Fox, 1962). Thus, if carotenoids are missing from the diet of certain birds, e.g. flamingoes, cock-of-the-rock and scarlet ibis, a definite fading of the plumage occurs, whereas a dietary supplement of carotenoids gives rise to deeper plumage color and to significantly higher concentration of pigment isolated from the feathers (Thommen, 1971).

Invertebrates fare no better than vertebrates in their ability to synthesize pigments. In the Mollusca, the mussel <u>Mytilus californianus</u>, a specialized filtering consumer of fine detritus and small plankton, selectively assimilates certain dietary carotenoids which it modifies into "unusual" derivatives (Fox, 1953). Gastropods also procure pigments from their diets. Moore (1936) showed that the dog whelk <u>Thais lapillus</u> may be banded or non-banded, depending on its diet. Ino (1940) found that the type of algal food consumed by topshells (<u>Turbo</u> spp.) influenced shell color. Likewise, the shell coloration of the red abalone has been shown to be directly affected by the type of algae consumed (Leighton, 1961). Other studies have shown that pigments in the soft parts are also derived from the diet (Kropp, 1931; Fox, 1953; Winkler, 1959; Hyman, 1967).

Turner (1958) found a population of the moon snail <u>Polinices duplicatus</u> which differed from previous descriptions (Say, 1822; Minor, 1950; Abbott, 1955) in that the callus was white instead of brown (see Figure 1). He experimentally determined that the discrepancy was due to lack of a suitable food and that the callus turned from white to brown as a result of starvation. This suggests that if diet is a strong determinant of color, then color (in these cases) must be an equally strong indicator of diet.

The purpose of this study was to investigate the relationship between the feeding behavior of <u>P</u>. <u>duplicatus</u> and resulting color changes of the callus. A maximum feeding rate was determined, since previous studies concerning feeding rates of <u>Polinices</u> spp. (Belding, 1930; Bernard, 1967; Giglioli, 1949; Giglioli, 1952; Turner, 1949; Wheatly, 1947) have been ambiguous. Boring behavior was studied with respect to size and location of the borehole. Distribution of borehole diameters in a sample of prey shells may yield an estimate of the predator size distribution, if the diameter of the borehole is a consistent predictor of predator size.

Hypotheses that the rate of color loss (purple to white) of the callus during feeding equals the rate of color loss due to bleaching by the sun and that the rate of color change (purple to white) during feeding equals its rate of appearance (white to purple) during starvation were tested. A purple callus indicates a lack of suitable prey (Turner, 1958), at

# Figure 1. Diagram of <u>Polinices</u> <u>duplicatus</u> indicating the button like callus covering the umbilicus.



which time <u>Polinices duplicatus</u> may become cannibalistic. Hypotheses that the degree of cannibalism is correlated with the proportion of shells with purple calluses and that cannibalism affects all size classes evenly were tested.

#### Methods and Materials

Samples of organisms and shells were collected by hand during low tides. Most <u>Polinices duplicatus</u> individuals were captured at San Luis Pass, Galveston County, Texas. Mollusk shells and live <u>Donax</u> were gathered at various sites along the beach between Galveston and Freeport, Texas.

Live organisms were maintained in 38 liter covered aquaria equipped with filters. Most experiments were conducted in five aquaria bisected by perforated plexiglass sheets. Holes in the dividers were sufficiently large to allow circulation of water between the two compartments of each tank, but too small to permit exchange of animals. Temperature was held between 23° to 27°C, and salinity was kept between 26°/...

Size-specific feeding rates of <u>Polinices</u> <u>duplicatus</u> were determined by placing one snail of known wet weight and aperture width in each 19 liter compartment and adding 25 <u>Donax</u> <u>variabilis</u> for one week. Preliminary results indicated that this was an abundant food supply. Each snail's aperture width and weight were measured and the numbers of live, undrilled dead and drilled dead <u>Donax</u> were recorded weekly. Dead <u>Donax</u> were replaced. The length of each drilled <u>Donax</u> individual was converted to dry weight by a regression equation. Statistical tests used in this study were described by Sokal and Rohlf (1969).

Drilled <u>Donax</u> shells from the feeding experiment were used to discern if the size of the predator could be predicted from the diameter of the borehole. The inside diameter of each borehole was measured to the nearest 0.001 mm with an ocular micrometer and the shells were scored as to which valve was drilled.

To test for a preference for freshly collected <u>Donax</u> individuals over laboratory held individuals, nine <u>Polinices</u> individuals that had been starved for two weeks were offered 10 clams of each type. The clam types were distinguished by dots of green and red paint, respectively. The "fresh" <u>Donax</u> were captured one day prior to each run of the experiment and the "starved" <u>Donax</u> were held in the laboratory without food for 1, 2, 3 or 4 weeks before the experiment, yielding four experiments differing in the intensity of the difference between the clam types. The number of each clam type consumed was recorded after four days, and all <u>Donax</u> individuals were replaced for another run. A test period of four days was used in order to reduce the effect of changing proportions of available prey. Each snail was used for four 4-day experiments.

In order to determine the rate of bleaching of color from the calluses of dead <u>Polinices</u> shells, 20 shells were exposed to direct sunlight for two years on the roof of the University of Houston Science Building. Initially, there were four white, four brown and 12 purple calluses. These shells were checked every two weeks for the first two months and then again at the end of the experiment. Another five dark purple <u>Polinices</u> shells were placed on a south-facing window sill and checked daily for changes in the color of the callus for one year. Description of the color of the callus is obviously subjective. In an effort to impart a measure of objectivity into these descriptions the Pantone Universal Color Matching System was used (Pantone, Inc., Moonachie, New Jersey). The Pantone System consists of a large color chart with each hue having an identifying number. In this study Pantone 256, 257, 516 and 517 represented light purple, and Pantone 260, 261, 262, 511 and 512 represented dark purple. Pantone 483, 490, 491, 497, 498, 499, 509 and 510 are good examples of callus colors which were designated as brown, and white was considered an absence of pigment.

Rate of color change of the callus of living <u>Polinices</u> was measured by feeding <u>Donax</u> to 11 snails, which initially had dark purple calluses, until a color change to white was noted. These snails were checked every fifth and seventh day to avoid, as much as possible, interrupting their feeding. Secondly, 11 <u>Polinices</u> individuals which initially had white calluses were starved until the callus turned light purple. These snails were examined every other day.

Samples of <u>Polinices</u> shells were collected from two sites (Eight Mile Road and San Luis Pass) in an attempt to relate the amount of cannibalism to the availability of prey. The size, condition (bored or not bored) and the callus color of each shell were recorded.

Samples of shells of several bivalve species were examined for boreholes to determine the breadth of the diet of <u>Polinices</u> <u>duplicatus</u> in the field. The presence and location of naticid

boreholes were recorded for each shell. Each molluscan species was identified using Abbott(1974).

#### Results

Results of feeding rate experiments in which 11 Polinices duplicatus were each offered 25 Donax variabilis are compiled in Appendix I. The mean number of clams eaten per day (0.81) $\pm$  0.20) compares favorably with previous studies of P. duplicatus feeding rates (Table I). However, the number of Donax eaten per week was not significantly correlated to the mean snail wet weight (r = 0.080, p > 0.05, df = 10), indicating that feeding rate was independent of snail weight, at least in the range of 3.6 to 17.5 g. Prey consumption was converted to dry weight eaten weekly by the regression equation CDW = -33.83 + 4.04 SL (CDW = clam dry weight in mg; SL = clam shell length in cm). This equation was derived by regressing the lengths of 60 Donax individuals on the weights of their tissues, which had been dried at a mean temperature of 105°C for 48 hours. Dry tissues were weighed to the nearest 0.1 mg on a Metler analytical balance. This regression explained a significant portion of the variability in Donax dry weights (F = 416.6, p < 0.001, df = 1,58). These converted data also failed to show a significant correlation with the mean snail wet weight (r = 0.424, p > 0.05, df = 10).

However, the percent increase in wet weight was significantly correlated to the initial wet weight of the snail (r = -0.774, p < 0.001, df = 10). Thus, smaller snails grow proportionately faster than large snails. In order to make these data comparable to studies using different prey species and/ or different snail species, the weekly dry weight of <u>Donax</u>

## Table I. Feeding Rates of <u>Polinices</u> <u>duplicatus</u>

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Investigator	Prey Species	Temperature	Bivalves eaten/day
Mead & Barnes (1903)	"soft clams"	-	Q.67
Belding (1903)	"soft clams"	-	0.87
Turner (1949)	"soft clams"	-	0.33
Sawyer (1950)	"soft clams"	21°C	0.67
		10°C	0.13
Carriker (1951)	V. mercenaria	-	0.15
Current study	<u>D. variabilis</u>	25°C	0.81

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consumed was converted to a percentage of the snails dry tissue weight (Appendix I). Snail dry weights were estimated by regressing the dry weights of 11 snails without shell or operculum on their shell aperture widths. This regression equation, SDW = -356.6 + 469.6 AW (SDW = snail dry weight in mg; AW = aperture width in cm), explained a significant portion of the variability of the snail weights (F = 126.7, p < 0.001, df = 1,9).

The mean inside diameter of the boreholes was significantly correlated to mean shell aperture width (r = 0.769,p < 0.01, df = 11). However, the diameter of the boreholes varied widely among snails of a given shell aperture width (Fig. 2). The maximum increase and decrease in the diameter of the borehole during any one week were recorded for each snail, as were the diameters of the initial and final boreholes (Table II). These results suggest that successive boreholes of the same individual vary greatly. Carriker and Van Zandt (1972) attributed a similar variation in Urosalphinx boreholes to the wide range in size of the accessory boring organ (ABO) in snails of the same size group. They also suggested that variation in the diameter of successive boreholes of an individual snail is directly related to the size of the ABO, which may be affected by the health of the snail, e.g. blood pressure. A sign test on the weekly mean borehole diameters over the entire feeding period showed that the diameter of the borehole increased with increasing size of the snail (S = 39, p < 0.01).

Figure 2. Regression of borehole diameters on snail aperture width. Borehole diameters expressed in mm and aperture widths in cm.

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·	Snail Apertur	e Width (cm)	Maximum Increase of	Maximum Decrease of	Duration	Diameter of H	sorehole (mm)
Snail	Beginning of Experiment	End of Experiment	Borehole <sup>1</sup> (mm)	Borehole (mm)	Experiment (weeks)	Beginning of Experiment	End of Experiment
I	1.9	2.8	0.78	0.55	15	1.13	1.60
II	1.2	2.2	0.46	0.75	15	1.00	1.00
III	1.2	2.2	0.45	0.50	15	0.75	0.98
IV	1.3	2.4	0.43	0.43	9	0.62	0.75
V	2.0	2.2	0.60	0,50	6	0.88	1.16
V.I.	1.5	2.6	0.65	0.33	19	0.75	1.20
VII	1.1	2.4	0.42	0.62	15	0,75	1.00
VIII	• 0.8	1.5	0.13.	0.10	15	0.63	0.75
IX	1.2	2.0	0.30	0.30	8	0.63	0.95
X	1.7	2.6	0.65	0.60	6	0.75	1.00
XI	2.8	2.8	Q.70	Q,56	14	Q,98	1.45
XIII	1.0	1.3	0.45	0.30	-	0.65	0.88
XIV	1.8	2.3	0.57	Q.45	-	1.08	0.95
XV	1.0	2.8	0.53	0.75	-	1.20	1.08
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1<sub>Explained</sub> in Results

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A total of 550 <u>Donax</u> individuals were drilled in the laboratory experiments, 61% of which were drilled in the left valve (p < 0.001). In a field sample of 69 drilled <u>Donax</u> <u>variabilis</u> shells with both valves intact, 58% were drilled in the left valve. Negus (1975) found that <u>Natica catina</u> drilled the left valve of <u>Donax vittatus</u> 58% of the time. Furthermore, 60% of 716 drilled <u>Dosinia discus</u> shells with both valves intact collected in the field were bored in the left valve (p < 0.001). Bernard (1967) found <u>Polinices lewisi</u> drilled the left valve of a variety of prey 61% of the time. Thus, several closely related naticid species drill the left valve of their prey about 60% of the time.

Results of the preference feeding experiments designed to determine if <u>Donax</u> held in the laboratory were less acceptable to <u>Polinices</u> than fresh clams are presented in Table III. A Rows x Columns test for independence indicated the numbers of each clam type consumed was independent of the number of weeks the aged <u>Donax</u> were held in the laboratory (G = 1.396, 0.80 > p > 0.70, df = 3). These results show that holding clams in the laboratory should not affect the feeding rates determined in this study.

Calluses of two of five <u>Polinices duplicatus</u> shells with dark purple calluses placed on a window sill and exposed for 6 to 8 hours per day turned brown after 83 days. After an additional 300 days a third callus had turned brown, but none had turned white. No changes in the callus colors of 20 shells exposed on the roof for two years, of which 12 had purple calluses, 4 had brown calluses and 4 had white calluses, could



## Table III. Feeding Preference of Polinices duplicatus

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·	Numbe	r Drilled		Each Week			
Time <u>Donax</u> Held In Laboratory	Fresh (Green)	Laboratory Held (Red)	Total Available	Fresh (Green)	Laboratory Held (Red)		
1 week	14	15	180	0.Q8	0.08		
2 weeks	25	21	180	0.14	0.12		
3 weeks	19	11	180	0.11	0.06		
4 weeks	13	11	180	0.07	0.06		

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be detected after two months. However, 5 of the 12 purple calluses had turned brown after two years. Thus, bleaching of the callus is a relatively slow process.

The mean time for callus color change from purple to white of feeding Polinices individuals was 11.1 + 3.9 days whereas the mean time of the reverse change in starving Polinices was 7.8 + 3.5 days. These means were significantly different (t = 2.104, p < 0.05, df = 20). Snail size was not significantly correlated with the rate of color change of the callus in either group (r = 0.204, p > 0.05, df = 10 and r = 0.044, p > 0.05, df = 10, respectively). These results suggest that the bleaching of color from the callus is a very slow process compared to changes in the callus due to diet. These data also indicate that as the shell of a dead Polinices undergoes weathering the callus changes from purple to brown. The hypothesis that brown calluses only result from the weathering of shells is further supported by the observation that of 230 living Polinices examined in this study none had a brown callus, whereas a collection of 732 shells of dead Polinices contained 121 shells with a brown callus. These proportions were significantly different (t = 341.5, p < 0.001, df = 959).

Results of the field investigation of cannibalism are shown in Table IV. These data represent an attempt to relate the availability of food as indicated by the color of the callus to the amount of cannibalism. The samples from Eight Mile Road had a higher proportion of bored shells than the samples from San Luis Pass. To determine whether some of this difference could be due to differences in the size class

## Table IV. Samples of Dead Polinices Shells

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Location	Date	Sample Size	% Drilled	% with purple callus
San Luis Pass				
Sample #1	5/9/76	233	1.92	82.69
Sample #2	5/27/76	285	0.93	94.09
Eight Mile Roa	d, Galveston			
Sample #1	5/11/76	206	6,59	84.10
Sample #2	8/16/76	140	17.80	93.75

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distributions, as suggested by Fox (1975), the proportion of shells in each of several size classes was graphed in Figure 3. A series of Kolomogorov-Smirnov tests indicated that the size distribution of Sample 2 from Eight Mile Road was significantly different from the other distributions (D = 22, p < 0.001). This sample contained a higher proportion of small shells, which were more frequently drilled than the larger shells (see Figure 3). No relationship between the callus color and the degree of cannibalism was found in the remaining three samples (r = -0.543, p > 0.05, df = 5).

Results of field samples to determine the breadth of the diet of <u>P</u>. <u>duplicatus</u> are presented in Table V. The number of right and left values of each species collected were recorded, as were the numbers of each value drilled. These results suggest that <u>Polinices duplicatus</u> consumes a variety of prey and that some prey are consumed more frequently than others. <u>Dosinia discus</u> was the most frequently drilled, followed by <u>Noetia ponderosa</u> and <u>Donax variabilis</u>.

Figure 3. Proportion of dead <u>Polinices</u> shells in each of several size classes. The +++ line represents the proportion of the total drilled in each size class. Size classes were based on aperture widths measured in cm.



Table V.	Proportion	of	various	bivalve	shells	drilled	Ъу	Polinices duplicatus	

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		Right			Left	
Species	Number Observed	Number Drilled	Proportion Drilled	Number Observed	Number Drilled	Proportion Drilled
Anadara ovalis	34	1	0.029	35	6	Q.057
Anadara brasiliana	35	6	Q.171	51	11	0.216
Anadara baughmani	39	0	0.000	56	2	0.036
<u>Barbatia</u> cancellaria	7	0.	0.000	11	1	0.091
Barbatia tenera	77	0	0.000	179	6	0.034
<u>Noetia</u> ponderosa	153	26	0.170	189	84	Q.444
<u>Donax</u> variabilis	133	37	0.278	321	64	0.199
Dosinia discus	277	83	0.300	281	127	0.452
<u>Mulinia</u> lateralis	221	26	0.118	227	34	0.150
<u>Rangia</u> . cuneata	248	10	0.040	40	3	0.075

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Table V. (Continued)

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		Right		Left				
Species	Number Observed	Number Drilled	Proportion Drilled	Number Observed	Number Drilled	Proportion Drilled		
<u>Tellina</u> alternata	15	0	0.000	11	4	0.364		
<u>Chione</u> <u>cancellata</u>	4	0	0.000	9	0	0.000		
<u>Tagelus</u> plebeius	7	0	0.000	5	Q	0.000		
Dinocardium robustum	<b>6</b> ·	1	0.167	Q	0	0.000		
Raeta plicatella	. 8 .	4	0.500	1	0	0,000		
Mercenaria campechiensis	2	0	0.000	1	Q	Q.Q00		
Argopecten irradians	2	0	0.000	Q	. 0	<b>Q.</b> QOQ		
Brachidontes exustus	2	0	0.000	2	Q	0.000		
Nuculana spp.	10	1	0.100	Q	Q	<b>0.</b> 000		

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#### Discussion

Several important findings were made concerning the color changes of the callus of Polinices duplicatus. In dead shells undergoing weathering, purple calluses turn brown, a color which is not found in the calluses of living snails. On more than 230 live individuals encountered during the study none displayed a brown callus, while a brown callus resulted from exposure to sunlight of the purple pigment of five shells on the roof and three shells in the laboratory. A field sample of dead Polinices shells contained a significantly higher proportion of shells with a brown callus than did the living snails examined. These results suggest that reference to brown in the callus of a living Polinices can be attributed to differences in the subjective naming of colors. The colors considered brown in this study are identified by the Pantone Universal Color Matching System (see methods).

The rate of color change of the callus due to weathering is much slower than changes in the callus due to diet. These results showed that fading of the callus never occurred more rapidly than 60 days, while the mean time of callus color change in feeding individuals (purple to white) was 11.1 days. After two years, no callus had turned white due to weathering. Thus, in a sample of shells a white callus can be attributed to an abundant food supply. Shells of recently dead individuals will not be bleached white.

The rate of disappearance of purple from the callus during

feeding (11.1 days) is slower than its appearance during starvation (7,8 days). Pigment deposited in the callus is not reabsorbed, but is covered by shell layers lacking the pigment. This was evident in a cross-section of the callus, which shows banding of purple and white. During periods of starvation the rate of shell deposition is reduced (Zischke, et al, 1970); the shell deposited may serve as a "dump" for compounds which the snail cannot metabolize (Comfort, 1951). When food becomes available the snail resumes growth, and layers of shell lacking the pigment are secreted. As Fox (1953) has said, "...one must assume that such animals (certain mollusca) derive their biliochromes from haems in the diet or from the catabolism of their own tetrapyrrolic compounds." However, Comfort (1951) found haems to be absent from the bile of mollusca. Therefore, bilin pigments probably come from the breakdown of the mollusk's own tetrapyrrolic compounds. This information fits well with the observation that P. duplicatus can survive long periods without food and remain relatively active. Furthermore, the pigment involved in the shell color changes of the red abalone (Leighton, 1961) and the Turbo shell (Tixier and Lederer, 1949) was a bilin. The appearance of pigment in the callus of Polinices during periods of starvation appears to represent the metabolization of a storage material.

A cross-section of the callus offers a dietary record of a snail's life, with dark layers representing periods of starvation and white zones periods of abundant food. However, there are several problems with using the color of the callus as an indicator of diet in living <u>Polinices</u> individuals or in using the sectioned callus as a dietary record of a dead individual. The amount of food and time necessary to effect a color change varies among individuals. Altough this study and Zischke <u>et al</u> (1970) showed small snails grow proportionately faster than large snails, no significant correlation was found between rate of color change and snail aperture width. Some snails underwent one complete color change cycle in approximately 20 days, but after two to three months had failed to undergo further changes. Other individuals never changed callus color whether the initial callus color was purple or white.

Some of these difficulties with using callus color as an indicator of diet can be explained by differences in metabolism among individuals. Another relevant factor is the effect of photoperiod and tidal rhythms. This genus of snails remains buried in the sand during the day, but emerges at night to feed (Wheatly, 1947; Giglioli, 1952; Bernard, 1967). In the laboratory more snails were active at night. However, these snails also become active when uncovered by receding tides (Wheatly, 1947). The absence of tides in the laboratory may have affected the activity of the snail and thus the feeding rate.

No correlation could be found between tissue consumed and mean wet weight of the snail. This variability between tissue consumed and growth rate has been commonly observed among the gastropods (Zischke et al, 1970). Furthermore,

the snails' health at the time of capture and during captivity may have varied. The death of three individuals during the feeding experiment could not be explained by environmental factors. Handling and captivity may have differential effects among individuals; for example, more aggressive individuals may be more inclined to move about the tank. Several snails escaped from covered aquaria. The number of clams eaten per day may be limited by the physical ability to drill rather than by gut capacity. Thus, a snail might not be able to locate and drill much more than 1.21 clams per day (the maximum feeding rate found in this study) no matter what size it might attain. This upper limit on feeding rate would preclude a linear correlation between size of snail and tissue consumed. However, a log transformation of the data also failed to yield a significant correlation (r = 0.258, p > 0.05, df = 10).

Most of the variation of the mean feeding rates of <u>Polinices</u> can be attributed to the following factors: temperature, different prey species and behavior of the snail. Temperature has been shown to affect the feeding rate of <u>P</u>. <u>duplicatus</u> (Sawyer, 1950) and <u>Urosalphinx cinera</u> (Hanks, 1957; Manzi, 1970). In my study, temperature was held between 23° and 27°C. In most previous studies the temperature at which the experiments occurred was not reported, making comparisons of mean feeding rates among studies difficult.

Use of different prey species in studies of predatory gastropods has added to the confusion. Different prey species contain different quantities of edible tissue per individual which should affect feeding rates expressed as clams eaten per day. Moreover, feeding rate may be a function of predator size. Turner (1950) found <u>P. duplicatus</u> less than 12 mm across the aperture ate proportionately more than larger snails. In order to avoid these problems, weight of prey tissue consumed should be expressed as a percent of the weight of the predator. In this study a snail consumed on the average 4.8% of its own dry body weight per day, which is similar to 6% per day for <u>P. reculuzains</u> (Edwards, 1970) and 3% for <u>Pleuroploaca gigantea</u> (Paine, 1963). Several individuals in my study were near each of these percentages.

Certain behavioral and physiological characteristics of P. duplicatus complicate the study of feeding rates. Several Polinices individuals survived six to eight months in the laboratory without food, a feat Wilbur (1960) attributes to the metabolism of a high concentration of glycogen stored in the mantle of gastropods. Furthermore, being an ectotherm, Polinices duplicatus has a metabolic rate which decreases with decreasing temperature. Therefore, the snail may be able to remain buried in the substrate during the winter months living entirely off stored materials. I had great difficulty finding snails during the winter months even during the lowest tides. Another factor which affects the snail is quality of prey. Carriker (1951) and Paine (1963) found that P. duplicatus preferred thin shelled or incompletely closing bivalves to thick shelled ones. Thus, using a non-preferred prey may result in a reduced feeding rate. So, Polinices may not only become inactive during the winter, but also cease feeding due to handling, captivity or scarcity of acceptable prey.

The attempt to utilize boreholes in shells of prey as an indicator of the size class distribution of the predator population was only partially successful due to a large variance in the diameter of the boreholes of individual snails. If learning is important to boring behavior, variability in the diameter and quality of the borehole should be higher in the smaller size classes. However, Berg (1976) concluded that the boring behavior did not involve learning. There was a significant correlation between snail size and residuals of the regression of borehole diameter on snail size (r = 0.549, p < 0.001, df = 132, Fig. 3), Thus, it appears that variability in borehole diameter increases with the size of the predator. Wells and Wells (1970) found boreholes to be more variable with increasing age in a gastropod and an octopus. Carriker and Van Zandt (1972) suggested that the size of the accessory boring organ, which may be affected by the health of the snail, accounts for the variability in boreholes of individuals of the same size class and of successive holes of the same individual.

This study confirmed a previously reported tendency for <u>Polinices</u> to drill the left value of a variety of prey (Bernard, 1967; Negus, 1975). Verlaine (1936) proposed alimentary conditioning reinforced by the reward of specific kinds of underlying tissues determined the position of the borehole. Negus (1975) suggested that the best grip on the prey shell would be more important than alimentary conditioning in determining the drilling behavior. There might exist in the snails

the kind of genetic "right-handedness" or "left-handedness" reported for other animals (Morgan, 1951). The present study showed individual snails would drill either valve even though there was a preference for the left valve.

The feeding preference experiments indicated <u>P. duplica-</u> <u>tus</u> could not distinguish between <u>Donax</u> held in the laboratory and <u>Donax</u> collected "fresh" from the field. Thus, holding <u>Donax</u> in the laboratory had no effect on feeding rates determined. These results suggest that any differences in metabolites that might exist between "starved" and "fresh" <u>Donax</u> are not detectable by the chemoreception apparatus of <u>P</u>. <u>duplicatus</u>.

The results of the cannibalism study showed that the amount of cannibalism was affected by the size class distribution of the population, as suggested by Fox (1975). The size class most frequently drilled had an aperture width of 1.5 to 1.9 cm. Consequently, the sample which had the highest proportion of shells in this size class also had the highest proportion of cannibalism. However, whether the level of cannibalism is related to the availability of prey or is the result of random encounters of sufficiently different size individuals cannot be determined from my results. Manzi (1971) found <u>Urosalpinx cinerea</u> cannibalism increased with feeding rate, and in all cases of cannibalism a female was the predator.

The data presented in Table V indicate P. <u>duplicatus</u> consumes a variety of prey items with unequal frequencies.

A major problem with using this approach to determine breadth of diet of the snail is the assumption that all causes of mortality are equal. The low proportion of drilled <u>Donax</u> shells may be explained by other mortality factors, i.e. desiccation and disease, being much greater than the predation rate of naticid snails. While some of the shells drilled were thin shelled bivalves (i.e. <u>Dosinia</u>, <u>Donax</u> and <u>Mulinia</u>), thick shelled species, <u>Noetia ponderosa</u> and <u>Anadara brasiliana</u>, were drilled up to 44% and 21% of the time, respectively. Carriker and Van Zandt (1972) found that <u>Urosalpinx</u> could not successfully drill thick shelled prey because the ABO, located in the foot, could be extended only to a limited depth into a borehole. However, in <u>Polinices</u> the ABO is located on the proboscis, therefore certain thick-shelled bivalves may represent a non-preferred, but acceptable prey item.

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# Appendix I. Results of Feeding Rates

i

Snail	Mean Wet Weight (g)	Mean Aperture Width (mm)	Snail Dry Weight (mg)	Total Drilled	Duration of Experiment (wks)	Average <u>Donax</u> Eaten/ Day	Average Dry Weight Eaten/ Day (mg)	Percent Dry Weight Consumed by Snail/Day
I	10.8	24	761.4	65	15	0.62	23.67	3.1
II	5.6	17	432.1	70	15	0.67	23.01	5.3
III	5.7	16	385.8	68	15	0,65	22.26	5.8
IV	5.7	18 .	479.7	61	9	_0.97	31.88	6.7
v	9.3	21	620.6	30	. 6	0.71	26.91	4.3
VI	8.8	19	526.6	123	. 19	0.92	32.24	6.1
VII	6.7	16	385.8	105	15	1.00	34.58	8.9
VIII	3.6	15	338.8	58	15	0.55	18.11	5.4 "
IX	7.8	21	620.6	68	8	1.21	38.16	6.2
x	17.5	28	949.3	42	6	1.00	37.93	4.0
XI	8.5	21	620.6	60	14	0.61	22.70	3.7
XII	17.2	27	902.3	64	12	0.76	26.60	3.0
Mean	8.9	20	585.3			0.81	28.17	4.8
Variance	17.7	1.7 4	0,563.05			0.04	43.48	