Feeding Biology of *Ocenebra lurida*

(Prosobranchia: Muricacea): Diet, Predator-Prey

Size Relations, and Attack Behavior

by

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Abstract. Field observations on individuals from an unusually dense intertidal population of *Ocenebra lurida* (Middendorff, 1849) revealed several interesting features about the feeding biology of this rather enigmatic predatory neogastropod. (1) Unlike the more common drilling gastropods in the northeastern Pacific, *O. lurida* preyed most heavily upon limpets: of 231 feeding observations, 55.0% were limpets (*Lottia pelta* [*=Collisella pelta*], *L. strigatella* [*=C. strigatella*], and *Tectura scutum* [*=Notoacmea scutum*]), 42.0% were barnacles (*Balanus glandula, B. crenatus, Semibalanus cariosus*, and *Chthamalus dalli*), 2.2% were mussels (*Mytilus edulis*), and 0.8% were other prey (*Calliostoma ligatum* and *Spirorbis* sp.). (2) The mean size of both limpets and barnacles consumed increased with increasing predator size, although this increase was not significant statistically for barnacles. (3) Over a broad range of predator size, both the mean and the maximum shell length of eaten *T. scutum* exceeded that of *L. pelta* (by 7 and 5 mm respectively). This observed difference in maximum shell length corresponded rather closely to that expected if the limit to vulnerability were determined by shell thickness, but it could also have resulted from differences in food value between the two species. (4) As observed for the Australian *Dicathais aegrota*, the distribution of drill sites on limpet shells was distinctly nonrandom: 85% of 124 drill holes were located in the posterior half of the limpet's shell and 95% were medial to the pedal retractor muscle scar. (5) When eating limpets, *O. lurida* tended to consume the gonad first, followed by the digestive gland and then the foot, but the foot was eaten only when the shell length of the limpets was less than that of *O. lurida*. (6) When feeding on the barnacle *Semibalanus cariosus*, *O. lurida* attacked lateral wall plates almost exclusively (37 of 38) and nearly half of the attacks (46%) occurred at the sutures between adjacent plates. Because sutures form only about 15% of the periphery, these results suggest a preference for sutural attack. (7) Patterns in the degree of completion of unfinished drill holes suggest that larger *O. lurida* attack limpets sooner after tidal immersion than smaller ones.

INTRODUCTION

Depending on the taxonomic authority, from four to six species of the cosmopolitan neogastropod genus *Ocenebra* occur along the shores of the northeastern Pacific (KOZLOFF, 1987): *O. interfossa* Carpenter, 1864, *O. lurida* (Middendorff, 1849), *O. orpheus* (Gould, 1829), *O. painei* (Dall, 1903), *O. sclera* (Dall, 1919), and the introduced *O. japonica* (Dunker, 1869). According to RADWIN & D'ATTILIO (1976), however, *O. sclera* is a synonym of *O. lurida* and *O. japonica* is actually *Ceratostoma inornatum* (Récluz, 1851). Because some species are pests, much of the knowledge of the feeding biology of *Ocenebra* derives from studies of species in commercial oyster beds (BARRY, 1981; CHAP-

MAN & BANNER, 1949; CHEW & EISLER, 1958; HANCOCK, 1960). Two species of *Ocenebra* have also been studied under more natural conditions: *O. poulsoni* from California (FOTHERINGHAM, 1971) and *O. lumaria* from Japan (LUCKENS, 1970a, b). Information on the biology of species from the northeastern Pacific, however, is scarce and consists either of anecdotal observations (geographic range, shell color variation, and an unusual mode of feeding in *O. lurida*; TALMADGE, 1975) or circumscribed data collected as part of a larger study (feeding and growth in the laboratory, and notes on natural densities of *O. interfossa* and *O. lurida*; SPIGHT *et al.*, 1974). In addition, although prey items have been reported for various *Ocenebra* species worldwide, most of these reports consist of laboratory or

anecdotal observations; hence, remarkably little is known about the normal feeding biology of species in this cosmopolitan genus.

MATERIALS AND METHODS

Most of the field observations were obtained from an unusually dense intertidal population of *Ocenebra lurida* (approx. 1-3/m^2) on the east side of Turn Island, San Juan Islands, Washington (U.S.A.; 48°32'10"N, 122°58'10"W). These observations were made during low tides on five different dates from 1 April to 12 May 1978 (1 IV, 2 IV, 7 V, 10 V, 12 V). A few additional feeding observations were also recorded from Tatoosh Island, Washington (48°19'N, 124°40'W) on 29-30 July 1978. The habitat at Turn Island consisted of a heterogeneous assemblage of rocks and boulders interspersed with bedrock promontories. Most feeding observations were obtained from the lower shore (−0.5 to +0.5 m, U.S. datum). Within this tidal range the rock surfaces were rather barren. Macroalgae were virtually absent, and barnacles were sparse and nearly all roughly one year old or less based on size (<10 mm basal diameter) and lack of weathering on the skeletal plates. Limpets were the most conspicuous invertebrates.

The shell lengths (apex to tip of siphonal canal to 0.1 mm) of both feeding and nonfeeding snails were recorded as well as the number of mating pairs observed on most dates. If a snail was feeding, the size and identity of its prey were also noted. Prey size was measured with Vernier calipers to 0.1 mm as follows: limpets—shell length and shell width; barnacles—anteroposterior opercular diameter inside the parietal plates; mussels—maximum shell length.

Many but not all prey items observed being attacked were collected and taken to the laboratory to determine more precisely the location of attack, the extent of tissue eaten, and, for limpets, the degree of completion and size of the drill hole. The percentage completion of unfinished drill attacks was estimated by eye as a percentage of the shell which had been penetrated at the site of attack. Both maximum and minimum outer drill hole diameters in the limpet shells were measured under a dissecting microscope using a calibrated ocular micrometer. For both of the commonly consumed species of limpets, average diameter (mean of maximum and minimum diameters) of completed drill holes correlated highly with *Ocenebra lurida* shell length (Figure 1; $r^2 = 0.88$; $n = 52$). Using this regression, predator size was estimated for a sample of drilled, dead shells collected at the time of the feeding observations. The only other predatory gastropods observed in the immediate vicinity were the buccinid *Searlesia dira* and the thaidid *Thais emarginata* (=*Nucella emarginata*). Because buccinids are not known to drill (TAYLOR *et al.*, 1980), and *T. emarginata* eats limpets only extremely rarely (see discussion), *O. lurida* was most likely responsible for the drill holes in these dead limpet shells. Furthermore, because of their circular to subcircular outline and nearly parallel sides in the upper half, these holes would not have been made by octopus.
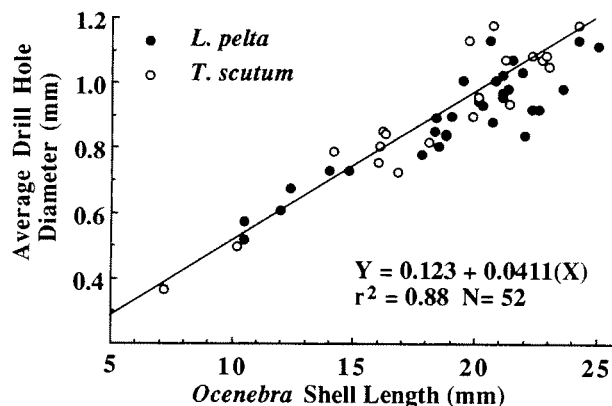

Figure 1

Average outer diameter of drill hole ([max. diam. + min. diam.]/2) as a function of *Ocenebra lurida* shell length for two species of limpets, *Lottia pelta* and *Tectura scutum*.

Statistical analyses were conducted using the microcomputer routines in Statview 512+® (Version 1.0, Abacas Concepts, Berkeley, CA, U.S.A.) except for the analysis of covariance (ANCOVA) and multi-way contingency table analyses which were conducted with BMDP Statistical Software (programs 1V and 4F respectively; DIXON, 1983).

RESULTS

Activity and Diet

At Turn Island, from 59 to 103 *Ocenebra lurida* were observed per day when the feeding observations were made. With one exception, on each date the majority of snails found were in the process of feeding (mean percent feeding = 61% ± 12.4 SD, $n = 5$ dates, range = 44–75%), and no significant difference in shell length existed either among dates ($P = 0.54$), or between those feeding and those not feeding on a particular date ($P = 0.34$ between activities; two-way ANOVA).

A total of 241 prey items from 11 species of prey were observed in the diet (Table 1). At Turn Island, *Ocenebra lurida* preyed predominantly upon limpets (55.0%), almost exclusively *Tectura scutum* (Rathke, 1833) (=*Notoacmea scutum*) and *Lottia pelta* (Rathke, 1833) (=*Collisella pelta*) (following the nomenclature of LINDBERG [1986]). Barnacles of four species formed the second most common component of the diet (42.0%; primarily *Semibalanus cariosus* (Pallas, 1788) and *Balanus glandula* Darwin, 1854, but also *B. crenatus* Brugière, 1789, and *Chthamalus dalli* Pilsbry, 1916). Mussels (*Mytilus edulis* L.), *Calliostoma ligatum* (Gould, 1849), and *Spirorbis* sp. were eaten only occasionally. Although no quantitative observations were made of actual prey availability at this site, the proportions of prey eaten appeared to be representative of the proportions available on the lower shore. Barnacles made up a large fraction of the observations from Tatoosh Island (80%; Table 1); because of the very small sample size,

Table 1

Species composition of the diet of *Ocenebra lurida* and mean size of predator consuming each prey species from two sites. Observations for Turn Island were pooled over five days.

	Turn Island		Tatoosh Island	
Prey species	n (%)	Mean predator shell length (mm; ± SE)	n (%)	Mean predator shell length (mm; ± SE)
Limpets				
Tectura scutum	48 (20.8)	19.4 ± 0.55	—	
Lottia pelta	78 (33.8)	19.4 ± 0.38	2 (20)	19.3 ± 2.30
L. strigatella	1 (0.4)	21.1	—	
Total limpets	127 (55.0)		2 (20)	
Barnacles				
Semibalanus cariosus	71 (30.7)	19.3 ± 0.32	3 (30)	18.2 ± 1.86
Balanus glandula	17 (7.4)	19.1 ± 0.69	3 (30)	18.6 ± 1.89
B. nubilus	—	—	1 (10)	15.4
B. crenatus	3 (1.3)	19.5 ± 2.30	—	
Chthamalus dalli	6 (2.6)	17.9 ± 1.86	1 (10)	9.1
Total barnacles	97 (42.0)		8 (80)	
Other species				
Mytilus edulis	5 (2.2)	19.4 ± 0.42	—	
Calliostoma ligatum	1 (0.4)	18.9	—	
Spirorbis sp.	1 (0.4)	2.8	—	
Total other	7 (3.0)		—	
Total observations	231		10	

however, this value may not be representative for the population as a whole.

Predator-Prey Size Relations

For the two most commonly consumed species of limpets, *Tectura scutum* and *Lottia pelta*, both the mean size (log-transformed to homogenize the variance) and the size range of prey eaten increased with increasing predator size (Figures 2a, b). A similar trend was observed for the two most commonly consumed barnacle species, *Semibalanus cariosus* and *Balanus glandula*, but in both cases the increase in mean, log-transformed prey size was not significant ($P = 0.096$ and $P = 0.24$ respectively; Figure 2c). Somewhat surprisingly, a given sized *Ocenebra lurida* ate significantly larger *T. scutum* than *L. pelta* on average ($P < 0.001$, ANCOVA on log-transformed predator and prey shell lengths—a small, but statistically significant difference existed between the slopes [$P = 0.033$], but this would diminish rather than amplify the difference between adjusted means). For a mid-sized *O. lurida* (19.0 mm), the adjusted mean prey sizes were 18.6 mm (95% confidence interval = 16.0–21.5) and 9.7 mm (95% confidence interval = 8.7–10.9) respectively. In addition, over a broad range of predator size, the maximum size of *T. scutum* eaten exceeded that of *L. pelta* (Figures 2a, b).

Although the mean and range of sizes of prey eaten increased with increasing predator size, the average size of *Ocenebra lurida* eating a particular species of prey did not vary among prey species (Table 1; $F = 0.272$, $P =$

0.93; one-way ANOVA on predator shell length for all prey species for which more than five observations were recorded). One possible suggestion of a size-related dietary difference was the single observation of a 1.5-mm-diameter *Spirorbis* sp. being consumed by a 2.8-mm *O. lurida*; *Spirorbis* may serve as an alternative prey for very young snails.

Patterns of Drilling and Tissue Consumption in Limpets

When *Ocenebra lurida* attacked limpets, drill holes were clustered in the posterior half of the shell (82.8% and 86.4%), and nearly all (98.3% and 92.4% for *Tectura scutum* and *Lottia pelta* respectively) were within the perimeter of the pedal retractor muscle (Figure 3). All of these frequencies differ significantly from those expected if *O. lurida* drilled these regions in proportion to the area of the shell they represent (50% anterior vs. posterior, and 58.5% and 56.3% for the area internal to the muscle scar in *T. scutum* and *L. pelta* respectively; $P < 0.001$; with Yates' correction for continuity, χ^2 values all exceeded 23 for 1 df). A multiple-regression analysis revealed that larger *O. lurida* tended to drill closer to the apex than smaller ones, but this relationship was not strong (Figure 4) and was significant statistically only for *T. scutum* (Table 2). A similar analysis of drill-site location along the anteroposterior axis of limpets revealed no significant associations with predator or prey size. Hence, the site of attack did not depend strongly upon either predator or prey size.

Ocenebra lurida also appeared to consume limpet tissue

in a repeatable order (Table 3). Following completion of the drill hole, the gonad appeared to be eaten first, followed by the digestive gland, and both were completed before the foot was attacked. In only a small portion of the cases (8 of 58) was the foot actually being consumed. These were restricted to cases where the limpets were small relative to the size of the predator (Figure 5), although this pattern was not quite significant statistically ($P = 0.056$; contingency table analysis of counts of the ratio prey length:predator length that were pooled into four categories [<0.5, $0.5-0.99$, $1.0-1.49$, ≥1.5] to reduce the impact of small frequencies per cell).

Biases Associated with Feeding Observations During Low Tide

To assess whether feeding observations obtained at low tide were biased by differences in handling times (FAIRWEATHER & UNDERWOOD, 1983), at least with respect to the sizes of limpets being eaten by different sized *Ocenebra lurida*, attacks on limpets were divided into two groups based on whether drilling was still in progress or whether drilling was completed and flesh was being consumed. The proportion of completed drill holes declined with increasing limpet size for both species of limpets (Table 4a) but this decline was not significant statistically for either species or when both limpet species were analyzed simultaneously via a multi-way contingency table (Partial $P = 0.076$, Marginal $P = 0.075$ for dependence of hole status on limpet size; full analysis not presented—$P > 0.5$ for all remaining second and third order effects). In addition, although a higher overall proportion of drill holes had been completed on *Lottia pelta* than *Tectura scutum* (Table 4), this difference was also not significant ($\chi^2 = 0.36$, $P > 0.5$; 2×2 contingency table analysis). Curiously, when considering only those cases where drilling was still in progress, the degree of completion of the drill hole actually increased with increasing limpet size, although this relationship was significant statistically only for *L. pelta* ($P = 0.022$; Figure 6a).

The proportion of *Ocenebra lurida* that had completed drilling and were eating flesh did not vary dramatically with predator size either (Table 4b). The largest *O. lurida* were least likely to have completed drilling on both species of limpet; however, the overall trend with predator size was not consistent between species and the differences with predator size were only weakly significant for *Lottia pelta*. For the cases where drilling was still in progress, however, the degree of completion of the drill hole declined significantly with increasing predator size for *L. pelta* ($P = 0.007$; Figure 6b) but no such relationship was observed for *Tectura scutum* ($P = 0.9$; Figure 6b).

As a whole, when considering the larger of the two limpet species (*Tectura scutum*), the status of the drill hole in these observations made at low tide was unbiased with respect to either limpet or predator size. The only consistent bias these data revealed was a dependence of the
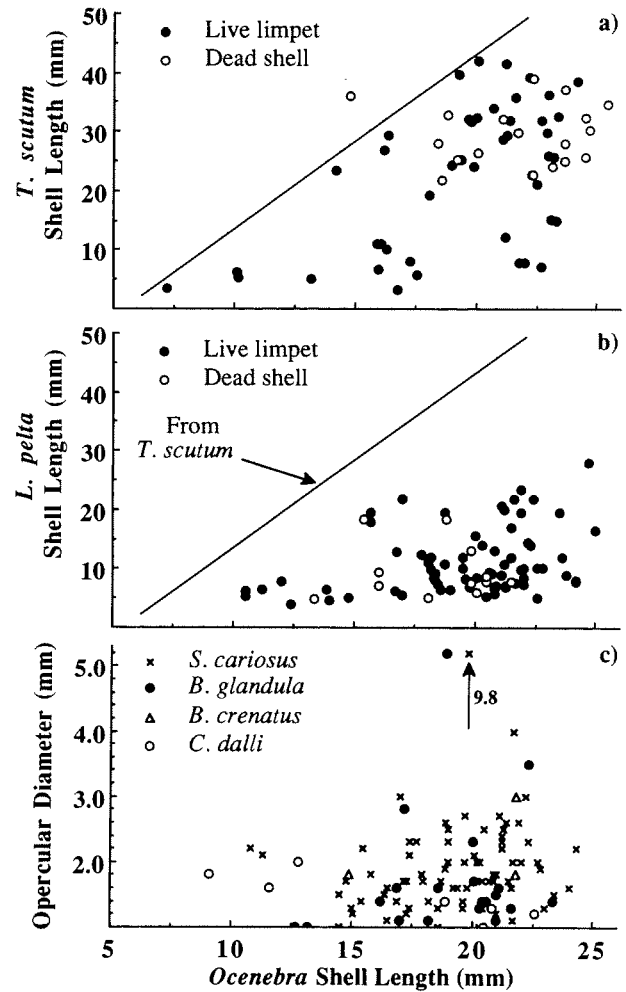

Figure 2

Prey size as a function of *Ocenebra lurida* shell length for six species of prey. (a) *Tectura scutum* (the line, fitted by eye, represents the upper limit to the size of limpet eaten where the predator size was known with certainty), (b) *Lottia pelta* (the line is identical to that in [a] for comparison), and (c) four species of barnacles. The regression equations of prey size (Y) on predator size (X) for the four most common prey species are (slope ± SE): *T. scutum*, $\log(Y) = 0.415 + 0.045 \pm 0.0080 \log(X)$ ($r^2 = 0.34$, $P < 0.001$, $n = 66$); *L. pelta*, $\log(Y) = 0.554 + 0.023 \pm 0.0064 \log(X)$ ($r^2 = 0.14$, $P < 0.001$, $n = 82$); *S. cariosus*, $\log(Y) = 0.059 + 0.011 \pm 0.0063 \log(X)$ ($r^2 = 0.04$, $P = 0.096$, $n = 74$); *B. glandula*, $\log(Y) = -0.147 + 0.018 \pm 0.0149 \log(X)$ ($r^2 = 0.077$, $P = 0.24$, $n = 20$).

proportion of drill hole completed on both limpet and predator size for the smaller sized limpet (*Lottia pelta*).

Patterns of Drilling and Tissue Consumption in Barnacles

When attacking the barnacle *Semibalanus cariosus*, *Ocenebra lurida* drilled lateral plates almost exclusively and nearly half of these attacks occurred at the margins between
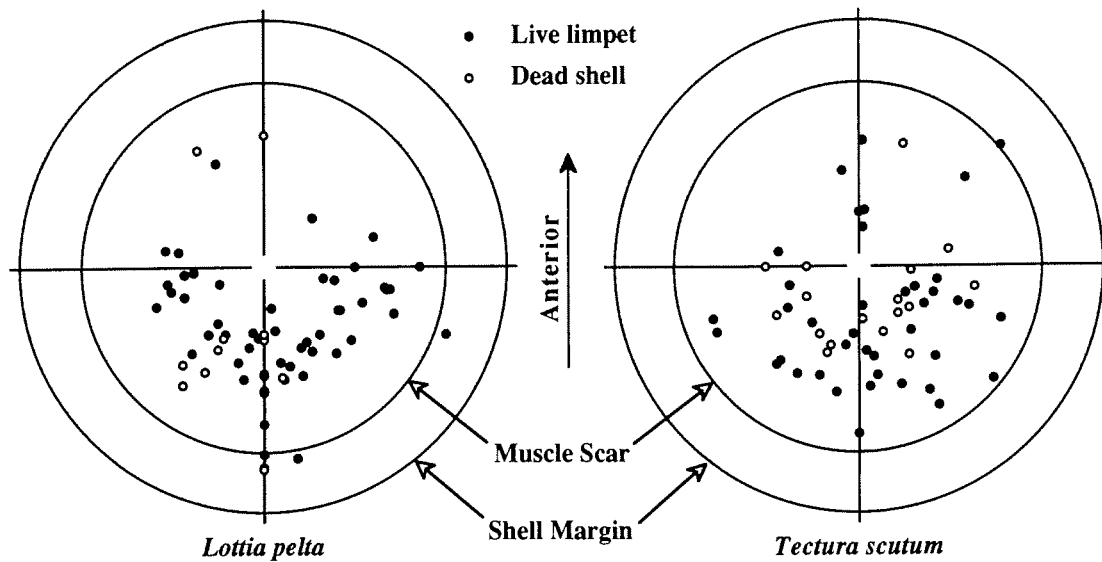
Figure 3

Polar coordinate plots of sites of attack by *Ocenebra lurida* on two species of limpets, *Lottia pelta* and *Tectura scutum*; distance from origin = (distance from apex to center of drill hole)/(distance from apex to shell margin in the same direction as the drill hole). Note that the origin of these figures corresponds to the apex of the shell even though the apices of these limpets are not precisely in the center of the shell.

plates (Table 5). Too few attack sites were noted for the remaining species to discern any patterns although, in contrast to *S. cariosus*, 3 of 5 attacks on *Balanus glandula* occurred at the opercular plates. For all barnacle species pooled, the frequency of attacks at the sutures between skeletal plates nearly equalled that through the plates.

Curiously, in the eight instances where the proboscis was observed unambiguously (six cases for *Semibalanus cariosus*, and one each for *Balanus glandula* and *Chthamalus*) it was always observed to be inserted between the

opercular plates even though the site of drilling was located elsewhere. Similarly, in the 12 cases in which it was possible to verify that *S. cariosus* tissue had been consumed, the drill hole was found to be too small to permit passage of the proboscis: the diameter of final penetration was well less than half the outer diameter.

Maturity and Reproduction

On three dates, notes on the degree of closure of the siphonal canal and the sizes of copulating pairs were re-
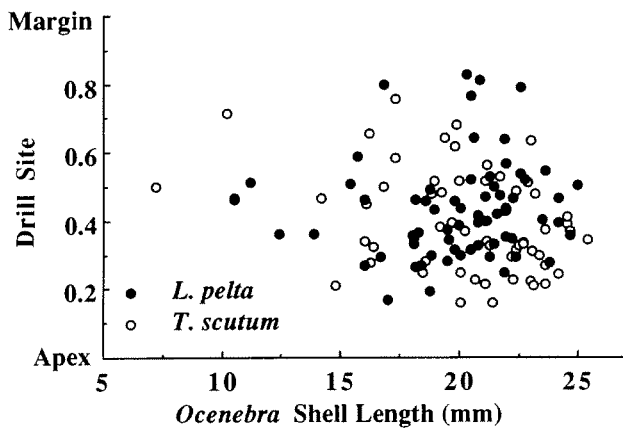

Figure 4

Location of drill site (expressed as proportion of distance from apex to margin of shell) as a function of *Ocenebra lurida* shell length for two species of limpets, *Lottia pelta* and *Tectura scutum* (see Table 2 for statistical analysis).
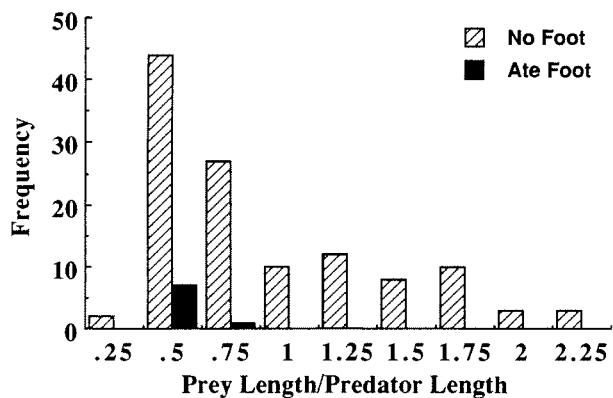

Figure 5

Frequency with which *Ocenebra lurida* was observed to be consuming the foot of limpets as a function of the ratio of the shell lengths of prey and predator. Data for *Tectura scutum* and *Lottia pelta* combined. No foot—other tissues had been consumed, but the foot was still intact. Ate foot—at least some portion of the foot had been consumed.

Table 2

Results from a multiple-regression analysis of drill hole position (dependent variable = proportion of distance from apex to shell margin) as a function of *Ocenebra lurida* and prey size (data in Figure 4).

	Lottia pelta	*Tectura scutum*
Coefficient		
Intercept	0.637	0.683
Ocenebra shell length (mm; ± SE)	−0.0081 ± 0.00547	−0.0150 ± 0.00604
Significance of coefficient (P)	0.15	0.016*
Limpet shell length (mm; ± SE)	−0.0042 ± 0.00355	0.0007 ± 0.00206
Significance of coefficient (P)	0.24	0.74
r^2	0.080	0.112
P (from ANOVA)	0.069	0.038*

* $P < 0.05$.

corded for *Ocenebra lurida* (Figure 7). Three categories of canal closure were recognized: fully open, transitional (beginning to close), and completely closed. Several lines of evidence suggest that the degree of closure of the siphonal canal reflects the state of maturity: (a) all individuals above 22 mm shell length had fully closed siphonal canals, (b) all individuals less than 16 mm had fully open siphonal canals, (c) snails noted actively copulating all had fully closed siphonal canals, and (d) the size distribution of copulating snails was indistinguishable statistically from that of solitary snails with closed canals ($\chi^2 = 2.06$, $P = 0.56$, for the four size categories: <18.9, 19.0–20.9, 21.0–22.9, ≥23). The siphonal canal thus does not appear to close intermittently over the life of an individual snail, a pattern which parallels rather closely that reported for *O. lumaria* (LUCKENS, 1970b). Using this criterion, maturity occurred around 16 to 19 mm shell length (Figure 7).

Although no egg capsules were noted, from 3 to 5 copulating pairs were observed (mean = 11% ± 3.2 SD, $n = 4$, range = 7.1–14.3% of all snails observed on each date) on all but the last date of observation at Turn Island (12 May). In addition, one copulating pair was observed out of 12 snails on Tatoosh Island on 5 July. Hence, although the reproductive season is by no means delimited by these data, they do indicate that active copulation was occurring in late spring and early summer and are consistent with the times of reproductive activity noted by SPIGHT *et al.* (1974).

Table 3

Frequencies with which *Ocenebra lurida* were observed to have consumed various portions of limpet flesh. Data from all limpet species pooled, but only for cases where the drill hole had been completed.

Tissues eaten	n (%)
None	8 (13.8)
Gonad only	30 (51.7)
Gonad + digestive gland only	12 (12.7)
Gonad + digestive gland + <50% of foot	3 (5.2)
Gonad + digestive gland + >50% of foot	5 (8.6)

DISCUSSION

Limpet-Feeding Habit

Ocenebra lurida appears to be an unusual member of the drilling gastropod fauna of the northeastern Pacific
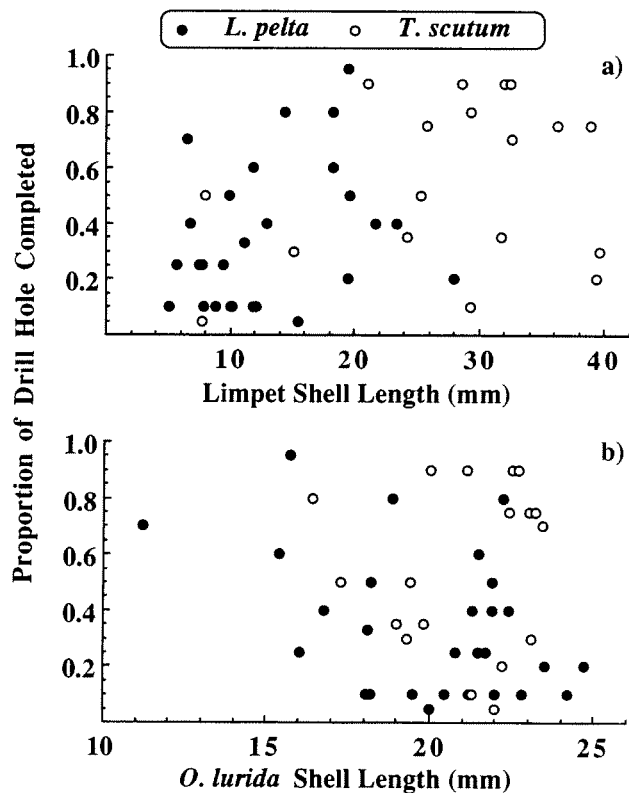

Figure 6

Proportion of drill hole completed through the shell as a function of limpet size (a) and size of *Ocenebra lurida* (b) for two species of limpets. Multiple regression equations for each limpet species are (coefficient ± SE): *Lottia pelta* ($n = 27$)—proportion completed = 0.018 ± 0.007(prey length, $P = 0.022$) − 0.042 ± 0.014(predator length, $P = 0.007$) + 0.959; *Tectura scutum* ($n = 19$)—proportion completed = 0.010 ± 0.007(prey length, $P = 0.17$) + 0.004 ± 0.035(predator length, $P = 0.91$) + 0.171.

Table 4

Frequencies at which *Ocenebra lurida* were found in the process of drilling vs. feeding on live limpets as a function of prey and predator size. Class limits are shell lengths (mm) and were chosen to obtain frequencies as nearly equal as possible. *P* values from two-way contingency table analyses.

a) Sizes of limpets in the process of being drilled or eaten

	Lottia pelta			*Tectura scutum*		
Prey percentile	Prey class limit	Drilled *n*	Eaten *n* (%)	Prey class limit	Drilled *n*	Eaten *n* (%)
Smallest ⅓	<7.8	5	16 (76.2)	<21.5	5	8 (61.5)
Middle ⅓		9	12 (57.1)		6	7 (53.8)
Largest ⅓	≥11.3	13	10 (43.5)	≥31.0	8	6 (42.9)
		P = 0.088			*P* = 0.62	

b) Sizes of *O. lurida* in the process of drilling or eating

	Lottia pelta			*Tectura scutum*		
Predator percentile	Predator class limit	Drilled *n*	Eaten *n* (%)	Predator class limit	Drilled *n*	Eaten *n* (%)
Smallest ⅓	<18.8	9	12 (57.1)	<19.4	4	9 (69.2)
Middle ⅓		5	17 (77.3)		6	7 (53.8)
Largest ⅓	≥21.3	13	9 (40.9)	≥22.0	9	5 (35.7)
		P = 0.049			*P* = 0.22	

because of the high frequency with which it consumes limpets (53.5%; Table 1). Limpets are at best rare in the diets of species of *Thais* (or *Nucella*) including *T. canaliculata* (1 out of 2001 observations), *T. emarginata* (4 of 2082 observations), *T. lamellosa* (0 of 889 observations), and *T. lima* (14 of 518 observations; all from PALMER, 1980). STIMSON (1970) also reported only a single instance of *T. emarginata* drilling a *Collisella scabra* and reported no attacks on *Lottia gigantea*. WEST (1986), on the other hand, reported that limpets (mainly *C. scabra*, but occasionally *Lottia limatula* [=*Collisella limatula*]) made up a somewhat
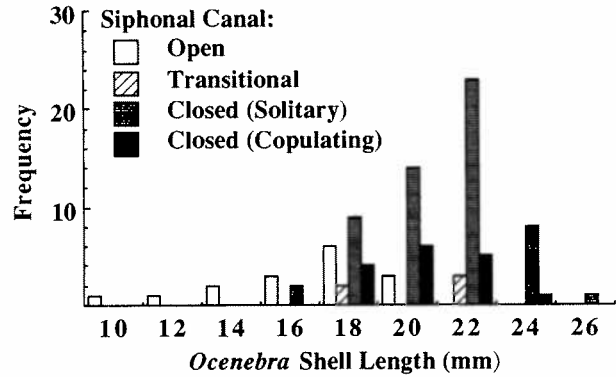

Figure 7

Frequency of *Ocenebra lurida* observed at different degrees of closure of the siphonal canal in the latter part of the study. Open—siphonal canal fully open, shell still exhibiting active recent growth; Transitional—siphonal canal beginning to close over, apertural lip beginning to thicken; Closed—fully closed siphonal canal, usually with a thickened lip, little or no evidence of recent shell growth (solitary—individual snails in the field; copulating—snails observed actively copulating in the field).

larger fraction of the diet overall for *T. emarginata* from central California (30 of 632 observations). Limpets are also uncommon in the diets of other thaidid gastropods from this geographic region. STIMSON (1970) noted that, when given a choice of *Mytilus edulis* and lottiid limpets in the lab, *Acanthina spirata* consumed mussels exclusively, and LUBCHENCO MENGE (1974) reported that *Acanthina punctulata* rarely consumed limpets (4 of 132 observations) even though limpets were available. Hence, at most, limpets make up less than 5% of the diet of thaidid gastropods from the northeastern Pacific.

Among non-drilling gastropods, *Searlesia dira* also consumes limpets regularly (from 10 to 31% of diet; LOUDA, 1979). However, because *Searlesia* appears to feed primarily via scavenging (LOUDA, 1979), the prevalence of limpets in the diet more likely reflects their availability as dislodged or moribund prey than a dietary preference.

Table 5

Frequencies of attack by *Ocenebra lurida* at various locations on the skeletal plates of barnacles; data from Turn Island and Tatoosh Island pooled.

	Opercular plates			Parietal plates			Unable to determine drill site
Prey species	At suture	Through	Total	At suture	Through	Total	
Semibalanus cariosus	—	1	1	17	20	37	13
Balanus glandula	3	—	3	1	1	2	5
B. crenatus	—	—	—	—	—	—	2
B. nubilus	—	—	—	1	—	1	—
Chthamalus dalli	—	—	—	1	—	1	2
Total (%)	3 (75.0)	1 (25.0)	4 (6.0)	20 (48.8)	21 (51.2)	41 (61.2)	22 (32.8)

The relative rarity of limpets in the diet of drilling gastropods from the northeastern Pacific is rather enigmatic for two reasons: (1) limpets are a common and conspicuous component of this rocky shore community and are consumed frequently by other predators which clearly recognize them as potential prey (MERCURIO et al., 1985, and references therein), and (2) gastropods which prey frequently upon limpets are common on many other limpet-inhabited shores (BLACK, 1978; FAIRWEATHER et al., 1984; McQUAID, 1985; MENGE, 1973; MOORE, 1938; WEST, in press; reviewed in BRANCH, 1981), although not all of them attack limpets by drilling (e.g., MENGE, 1973; MORAN, 1985). The rarity of limpets in the diet of thaidid gastropods from the northeastern Pacific is particularly curious for these reasons. Unfortunately the present data shed no light on this problem.

Perhaps limpets are a lower quality prey than the barnacles and mussels which make up the bulk of the diet of most thaidid gastropods (TAYLOR et al., 1980). These alternative prey on which they grow rapidly (PALMER, 1983) may be sufficiently common and their availability may be sufficiently predictable that, when given a choice, thaidid gastropods simply reject limpets as undesirable on most occasions. Ironically, for the starfish Leptasterias hexactis, three of the four most energy rich prey in terms of calories per unit handling time were limpets, and limpets ranked highly both in terms of electivity in the field and in terms of laboratory choice experiments (MENGE, 1972). The low frequency of limpets in the diet of thaidid gastropods from the northeastern Pacific remains a puzzle.

Predator-Prey Size Relations

As in other predator-prey systems where the sizes of prey are comparable to that of the predator (BERRY, 1982; BROOM, 1982; HUGHES, 1980; LUBCHENCO MENGE, 1974; MENGE, 1972; PAINE, 1976; VERMEIJ, 1978), the average size of prey items eaten by Ocenebra lurida, as well as the size range, increased with increasing predator size. This pattern was most striking for the two most commonly consumed species of limpet (Figures 2a, b). A similar trend was observed for barnacles but it was not significant statistically, presumably because of the small size range of barnacles available at the site studied. The lack of feeding by small O. lurida on large limpets could reflect a physical constraint imposed by the maximum thickness of shell through which they can drill, as observed by KITCHELL et al. (1981) for Polinices. Alternatively, it could reflect a lower food value of large limpets to small O. lurida. In Thais emarginata such a decline occurs when small snails attack large mussels because, even though more tissue is available in larger prey, a small snail is unable to consume it rapidly enough before it begins to decompose (PALMER, 1980).

The observation that Ocenebra lurida ate larger Tectura scutum than Lottia pelta was unexpected. Unfortunately, because no measurements were taken on limpets accessible
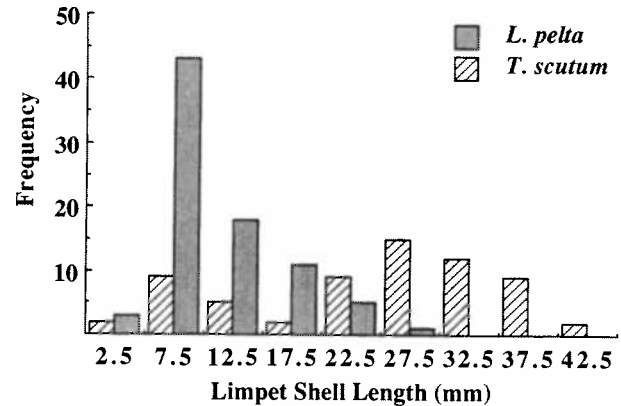

Figure 8

Size-frequency distribution of limpets (Lottia pelta and Tectura scutum) actually eaten by Ocenebra lurida at Turn Island over the duration of the study.

to but not eaten by O. lurida, some of this difference could have been due to differences in the average size of limpets occurring on the eastern shore of Turn Island. For example, although the average size of T. scutum eaten was greater than that of L. pelta (Figure 8), such differences could have resulted either from differences in the sizes available or differences in the sizes selected. Tectura scutum does reach a larger maximum adult size than L. pelta (MORRIS et al., 1980), but average size of both species varies considerably among habitats. On nearby Turn Rock, the densities of these two species are quite similar (table 5 of DAYTON, 1971), but data on sizes were not presented. The lack of data on availability notwithstanding, however, larger limpets of both species were eaten by larger O. lurida (Figures 2a, b); hence, larger limpets were most likely also available to smaller O. lurida because they were intermingled on the shore.

Three hypotheses could account for the consumption of Tectura scutum to a larger size than Lottia pelta: (1) the two species may differ in the success of some escape behavior, (2) for limpets of the same shell length, the two species may differ in their food value, or (3) the two species may differ in their relative vulnerability to attack once captured. I am not aware of any data to address the first hypothesis for these prey species. Lottia pelta, however, do have a larger body mass for a given shell length than T. scutum (23% larger dry mass for a 20-mm limpet; 8.5 vs. 6.9 mg computed from MENGE [1972]). On this basis L. pelta should be more desirable as prey and hence eaten to a larger size assuming (1) that the handling times for limpets of the same shell length were comparable for both species, and (2) that energy per unit handling time decreases with increasing prey size, as it does above the "optimum" prey size (HUGHES, 1980).

Differences in shell thickness, however, seem more likely to account for the observed pattern of consumption. Over the size range of limpets where differences in maximum
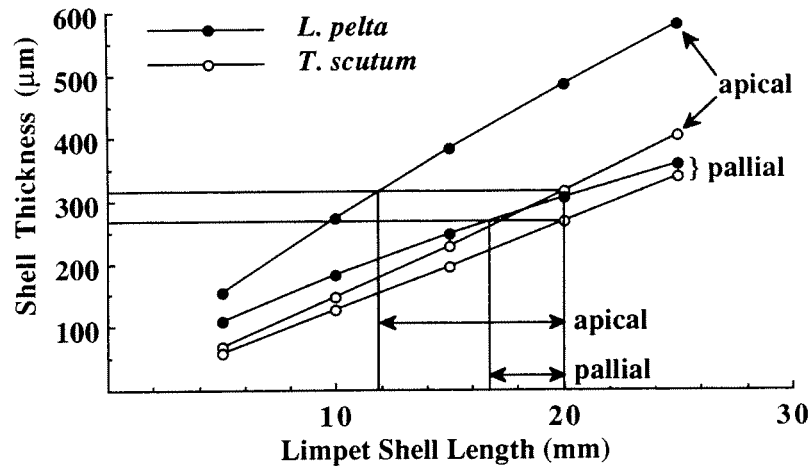
Figure 9

Comparison of shell thicknesses medial to the pedal retractor muscle for two species of limpets (computed from regressions of R. B. Lowell [unpublished data]). Apical—shell thickness at apex of shell; pallial—shell thickness just medial to the pedal retractor muscle. Horizontal and vertical lines illustrate how the expected difference in maximum size of vulnerability of *Lottia pelta* was estimated compared to a 20-mm *Tectura scutum*: if 20 mm was the maximum size of vulnerability of *T. scutum* to a given sized *Ocenebra lurida* (approximately 12.5 mm in this case; see Figure 2a) and if this maximum size of vulnerability was determined by the thickness of the limpet's shell, these lines indicate the shell length of *L. pelta* having the same medial shell thickness (12 mm based on apex thickness, 17 mm based on "pallial" thickness).

size eaten were detected (10–20 mm), *Lottia pelta* has a consistently thicker shell medial to the pedal retractor muscle than *Tectura scutum* (Figure 9). A thicker shell would lead to an increased handling time and hence it could result in a decreased food value for *L. pelta* if the longer handling time overwhelmed the benefits of the tissue mass differences noted above.

A thicker shell, on the other hand, may also reduce vulnerability by exceeding the depth to which a given sized *Ocenebra lurida* may drill. Assuming that the maximum size to which a limpet is vulnerable to a given sized *O. lurida* is determined by the depth to which it can drill (as observed for *Polinices* when drilling bivalves; KITCHELL *et al.*, 1981), then the expected *difference* in maximum size of vulnerability based on shell thickness may be calculated. This difference is on the order of 5 mm in shell length (the predicted value ranges from 3 mm based on shell thickness near the pedal retractor muscle, to 8 mm based on thickness at the apex comparing *Lottia pelta* to a *Tectura scutum* of 20 mm shell length; Figure 9). Rather remarkably, the *observed* difference in the maximum size of limpets eaten in this size range is approximately 7 mm shell length (Figure 2b). Furthermore, if this interpretation is correct, the maximum depth to which *O. lurida* can drill would be roughly 300 μm (Figure 9) for a 12.5-mm *O. lurida* (that size for which the maximum size of *T. scutum* eaten was approximately 20 mm; Figure 2a). In the absence of direct evidence for unsuccessful attacks, however, this estimate remains tentative.

Both *Lottia pelta* and *Tectura scutum* have similar shell microstructures (shell-structure group 1 of MAC-CLINTOCK, 1967); hence, microstructural differences would

not account for differences in vulnerability between these species.

Two additional pieces of information suggest that the consumption of *Tectura scutum* to a larger size than *Lottia pelta* may have an energetic rather than a mechanical basis. First, FRANK (1982) reports that black oystercatchers (*Haematopus bachmani*) consume *L. pelta* to a smaller size than *T. scutum* (approximately 10 vs. 14 mm shell length). Second, data of G. M. Branch (unpublished observations), also on feeding by *H. bachmani*, yield selectivity curves whose peaks and whose upper and lower limits are consistently on the order of 5 to 10 mm shell length larger for *T. scutum* than *L. pelta*. These data, taken from five separate areas of shore, indicate that *H. bachmani* also prefers larger *T. scutum* than *L. pelta*. The remarkably similar patterns of size preference exhibited by both *H. bachmani* and *Ocenebra lurida* seem unlikely to be due to mechanical properties of the shell or foot given the radically different modes of attack of these two predators. Rather, these size preferences would seem most simply accounted for by differences in the flesh weight-shell length ratios between these two species of limpet.

Attack Behavior

Compared to other limpet and barnacle predators, *Ocenebra lurida* used very similar modes of attack. In particular, when attacking limpets, its behavior is strikingly similar to that of *Dicathais aegrota* of Western Australian shores (BLACK, 1978). Both species attack preferentially the posterior region of the limpet shell within the perimeter of the pedal retractor muscle (Figure 3). As suggested by

Black, the presumed adaptive value of such a behavior lies in the more immediate access to the energy-rich gonad and digestive gland. Because snails which drill limpets run the risk of being dislodged when the limpet releases hold of the substratum, and also because they may be unable to consume all the tissue before losing hold of their once-moribund prey, they would benefit from consuming these energy-rich tissues first.

That the gonad and digestive gland were consumed prior to the foot (Table 3) is due in part to their anatomical relation to the site of attack, but the actual order of tissue consumption was not quite so simplistic. If tissue were consumed purely as a function of proximity to the drill hole, portions of the foot would be consumed before the gonad and digestive gland had been completed because the distance from the shell to the foot is less than from the posterior to the anterior end of the viscera. Yet I commonly observed viscera being consumed to a greater distance anterior to the drill hole than the distance from the drill hole to the foot.

The observation that limpet feet were consumed exclusively in cases where the limpet was smaller than the predator (Figure 5) suggests that *Ocenebra lurida* may, in fact, not be able to retain its hold upon larger limpets to permit all the flesh to be consumed. This would provide another advantage to the preferential consumption of viscera. These observations do not appear to be biased by differences in handling times because drill holes were not significantly more likely to have been completed on small limpets compared to larger ones (Table 4; for an extensive discussion of such biases see FAIRWEATHER & UNDERWOOD, 1983).

When attacking barnacles, *Ocenebra lurida* exhibited a number of behaviors in common with thaidid gastropods (HART & PALMER, 1987; PALMER, 1982). First, drilling occurred preferentially at the margins of plates rather than through them (Table 5): nearly half of all attacks at lateral plates (20 of 41) occurred at regions of plate overlap even though such regions make up only about 15% of the periphery of the barnacle's skeletal wall (PALMER, 1982). Second, even where tissue had been consumed, most of the drill holes were not enlarged enough to permit passage of the proboscis. Coupled with the few observations where *O. lurida* consumed barnacles from between the gaping opercular plates even though they had been drilled elsewhere, these observations suggest rather strongly that *O. lurida* produces a narcotizing toxin which relaxes barnacles. In this manner, the flesh may be consumed without the additional time and effort required to enlarge the drill hole.

Biases in Feeding Observations Obtained at Low Tide

Although differences in handling times for different prey types may create biases in the "apparent" diet of intertidal predators observed feeding at low tide (FAIRWEATHER & UNDERWOOD, 1983), the data obtained for *Ocenebra lurida*

attacking limpets suggest that such biases had little if any effect on the observed diet. Although drill holes were more likely to have been completed on smaller limpets, this trend was not significant statistically for either limpet species (Table 4). In addition, unfinished drill holes were closer to completion in larger compared to smaller limpets (Figure 6a), a pattern not consistent with the bias expected based on shorter handling times for small limpets.

Rather than revealing a size bias in handling times, the proportion of drill hole completed (Figure 6) seems more likely to reflect the time since an attack was initiated. Because feeding *Ocenebra lurida* were interrupted at random with respect to both predator and prey size, the observations for *Lottia pelta* suggest that *O. lurida* had been drilling larger limpets for a longer time prior to tidal emersion than smaller ones (Figure 6a) and that, following tidal immersion, larger *O. lurida* initiated attacks on limpets earlier than smaller ones (Figure 6b). Multiple-regression analysis revealed that both of these relationships were significant (Figure 6 legend).

Comparison of Diets with Other Species of *Ocenebra*

The paucity of published data precludes very strong conclusions, but the extensive consumption of limpets by *Ocenebra lurida* does appear to differ from the diets of other species of *Ocenebra*. Because of their status as pests, two species are known to prey on commercially grown oysters: the European *O. erinacea* (BARRY, 1981; HANCOCK, 1960; ORTON, 1929), and the western Pacific (but now widely distributed in the NE Pacific via incidental introductions; CARLTON, 1979) *O. japonica* (CHEW & EISLER, 1958; CHAPMAN & BANNER, 1949; considered to be *Ceratostoma inornatum* by RADWIN & D'ATTILIO [1976]). *Ocenebra erinacea* also consumes other prey including both burrowing (*Tapes, Cardium, Mercenaria, Paphia*; HANCOCK, 1960; PIÉRON, 1933) and epifaunal (*Pecten*; PIÉRON, 1933) bivalves, "barnacles, small tubicolous worms, mussels and anomiid bivalves" and possibly *Crepidula* (FRETTER & GRAHAM, 1962:516). For *O. japonica* (=*Ceratostoma inornatum*) oysters appear to be a less desirable prey because, when given a choice, both *Mytilus edulis* and *Tapes japonica* (=*Venerupis japonica*) were eaten more frequently (42.6% and 36.5% respectively) than oysters (20.9%) when all were of comparable size (CHEW & EISLER, 1958). This contrasts with the conclusions of CHAPMAN & BANNER (1949) who reported that oysters were eaten in preference to barnacles and mussels in the laboratory, but their experiments were much less well designed to detect preferences. In Netarts Bay, Oregon, the bivalves *Macoma balthica* and *Clinocardium nuttalli* form the bulk of the diet of *O. japonica* (SQUIRE, 1972 [cited in CARLTON, 1979:384]).

Individuals of the Japanese *Ocenebra lumaria* (also considered to be *Ceratostoma inornatum* by RADWIN & D'ATTILIO [1976]) are reported to eat several species of barnacles (*Chthamalus challengeri, Balanus trigonus, B. albicostatus*, and *B. tintinabulum*) and mussels (*Mytilus edulis*

and *Septifer virgatus*) when these are made available in the laboratory, and when given a choice they prefer *Chthamalus* over *Mytilus* (LUCKENS, 1970a). Except for noting that hatchlings were observed to consume newly settled *Chthamalus*, however, no field observations of diet were reported. Similarly, although providing extensive data on growth and survival, FOTHERINGHAM (1971) mentions only incidentally the diet of the eastern Pacific *O. poulsoni*; they appear to consume boring bivalves primarily (*Penitella penita* and *Lithophaga plumula*; p. 743) at least as adults, while young snails "occasionally feed on barnacles" (p. 750). Similarly, although providing data on growth rates and natural densities for both *O. interfossa* and *O. lurida*, only laboratory observations of feeding by *O. lurida* on *Balanus glandula* and *M. edulis* were reported by SPIGHT *et al.* (1974) who noted that barnacles were eaten in preference to mussels. Finally, TALMADGE (1975) merely reports some anecdotal observations of *O. lurida* rasping pits in the girdle of *Cryptochiton stelleri*, but makes no mention of any other feeding observations, and KILBURN & RIPPEY (1982) report anecdotal observations for the South African *O. purpuroides* which appears to feed on "small tube worms."

As in any local field study, I cannot be sure how representative the diet I have reported is for *Ocenebra lurida* as a whole. I initiated this study specifically because of the rather high densities of *O. lurida* at this intertidal site (approx. 1–3/m^2) and barnacles and mussels happened to be relatively uncommon here. Although I have since observed comparable densities in a relatively wave-exposed cobble and boulder habitat on Cape Beale (Vancouver Island), I have normally encountered *O. lurida* only as scattered individuals at a density well less than 1/m^2 on intertidal shores. Subtidally, however, they may achieve higher densities: SPIGHT *et al.* (1974) report a density of 4.25/m^2 on a subtidal rock wall.

These unfortunately meagre data, diminished further if indeed both *Ocenebra japonica* and *O. lumaria* are correctly *Ceratostoma inornatum* (RADWIN & D'ATTILIO, 1976), permit little to be said here except that, like many muricacean genera (TAYLOR *et al.*, 1980) diets appear to vary considerably among the different species of *Ocenebra*. Whether the diet of *O. lurida* is really unusual for the genus awaits further field studies.

ACKNOWLEDGMENTS

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