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Source: *Ecology*, Vol. 67, No. 6 (Dec., 1986), pp. 1493-1501
Published by: Wiley on behalf of the Ecological Society of America
Stable URL: http://www.jstor.org/stable/1939080
Accessed: 07-04-2017 17:06 UTC

Ecology, 67(6), 1986, pp. 1493–1501

FORAGING BEHAVIOR AND PREY SELECTION BY THE AMBUSH ENTANGLING PREDATOR *PLEUROBRACHIA BACHEI*[1]

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Abstract. Ctenophores and other gelatinous predators in the ocean are ephemeral in their spatial and temporal distributions, but often have a dramatic impact on the dynamics of their prey populations. Considerable information is currently available on the functional and numerical responses of several nearshore ctenophore species; however, an understanding of their potential for shaping the structure of natural zooplankton assemblages requires further information on the selective nature of their predation.

Prey selection by the tentaculate ctenophore *Pleurobrachia bachei* was examined in the laboratory with predation experiments and videotaped observations of predator and prey behavior. Prey types offered to the ctenophore included each of the developmental stages of *Calanus pacificus*, adult *Acartia clausii*, and adult *Pseudocalanus* sp. *Pleurobrachia* exhibited an unusual, bimodal pattern of prey selection on the different developmental stages of *Calanus*. *Calanus*' vulnerability increased through the naupliar stages, dropped at the first copepodid stage, and then rose again throughout the subsequent copepodid stages prior to another decline at the adult stage. Adult *Acartia* and *Pseudocalanus* were found to be among the most vulnerable of the prey types offered to *Pleurobrachia*. We conclude that *Pleurobrachia*'s diet is determined by the relative availability and vulnerability of prey, and that vulnerability to the ctenophore can be predicted from prey swimming speeds and the susceptibility of prey after encounter.

Key words: *ambush predator; copepods; ctenophores; entangling predator; selective predation; zooplankton.*

INTRODUCTION

Knowledge of the ocean's gelatinous fauna has improved dramatically over the last decade with the advances in new sampling methods and in situ observational techniques (see review in Harbison 1983). Nevertheless, the role of gelatinous zooplankton in marine food webs is still widely debated. An understanding of the trophic importance of these organisms is elusive, due in part to the ephemeral nature of their spatial and temporal distributions, but also because much of their basic feeding biology still needs to be explored. This latter point is especially apparent in the trophic ecology of gelatinous predators, a group that is conspicuously underrepresented in freshwater (Greene 1985). Included in this category are members of the phylum Ctenophora. The ability of ctenophores to affect the dynamics of copepod populations substantially has been well documented (Anderson 1974, Kremer 1979, Deason 1982, Deason and Smayda 1982, Harris et al. 1982, Sullivan and Reeve 1982). Feeding and growth rate experiments with ctenophores (Bishop 1968, Hirota 1974, Reeve et al. 1978, Reeve 1980, Sullivan and Reeve 1982) have revealed a tremendous capacity in these predators for regulating the abundance of their prey. This regulatory capacity is the result of functional responses allowing individuals to ingest up to 10 times their body carbon per day and growth responses enabling populations to nearly double their biomasses each day. Despite considerable experimental data on these rate processes, a more complete understanding of the role of ctenophores in structuring marine food webs requires further information on the selective nature of their predation. The present investigation explores the foraging behavior and patterns of prey selection in the tentaculate ctenophore *Pleurobrachia bachei.*

Pleurobrachia's foraging behavior is stereotyped and thus is amenable to the type of experimental component analysis pioneered by Holling (1966). The ctenophore's predatory repertoire consists of two basic behaviors: searching for prey and handling prey. When searching for prey, *Pleurobrachia* initially sets its tentacles by swimming oral pole forward, often in a curved or helical pathway, and allowing the two main tentacles and numerous lateral tentilla to relax and expand behind it. Once the tentacles are set, the ctenophore typically drifts passively with tentacles extended. Occasionally, *Pleurobrachia* retracts its tentacles to varying degrees and swims to another location before resetting them. This behavior as well as the degree of tentacular extension appear to be regulated by hunger level (Reeve and Walter 1978). In several respects, the behavior of *Pleurobrachia* and other tentaculate predators can be viewed as analogous to that of orb-weaving spiders (Biggs 1977). In the searching mode, both groups of predators primarily "sit and wait" for prey to encounter their capture surfaces. Although orb-weaving spiders (Olive 1982) and tentaculate ctenophores may move to new foraging locations in response to prey

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[1] Manuscript received 1 July 1985; revised 13 March 1986; accepted 17 March 1986.

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patchiness, in general, prey motility is more important than predator motility in initiating predator–prey encounters. Thus both groups can be classified as ambush entangling predators (Greene 1985). Once a prey item is encountered and successfully entangled by *Pleurobrachia,* the ctenophore responds with a characteristic handling response. Initially, both tentacles contract, "and as the prey approaches the mouth, *Pleurobrachia* begins to rotate in a plane which draws the tentacle (bearing the prey) across the mouth region. The portion of the tentacle bearing the prey . . . is draped over the mouth" and the prey item is wiped in (Reeve and Walter 1978:259). The animal usually completes several rotations during the handling process, and often relaxes the free tentacle (i.e., the tentacle not bearing the prey item) before the handling phase is complete. The free tentacle can then begin "fishing" again. However, usually both tentacles must be unencumbered with prey before *Pleurobrachia* resets them fully in the manner previously described.

Experimental component analysis of this behavior requires quantification of the variables that determine *Pleurobrachia*'s encounter rates with prey and the prey's subsequent susceptibilities to the predator (i.e., the proportions of encountered prey that are successfully ingested by the predator, Greene 1983). Since these variables are typically functions of prey type (i.e., species and developmental stage) and predator size (Thompson 1975), we have conducted predation experiments and behavioral observations with each prey type separately and with a single size class of *Pleurobrachia* (8 mm diameter, reproductively mature). Our predation experiments were designed to characterize the ctenophore's functional responses to various prey and to compare the relative vulnerabilities of the different prey types to *Pleurobrachia.* Our behavioral observations were designed to estimate prey swimming speeds, prey susceptibilities to the predator, and predator handling times. Together, these two complementary approaches can be used to elucidate the characteristic features of *Pleurobrachia*'s foraging behavior and prey selection patterns.

METHODS

Collection and maintenance of experimental animals

The Strait of Georgia–San Juan Archipelago–Puget Sound region of the northeastern Pacific is particularly rich in gelatinous zooplankton (Mills 1981). *Pleurobrachia bachei* can be found in the region commonly, if somewhat sporadically, throughout the spring and summer (Mills 1981). For this investigation, ctenophores were hand-collected individually in plastic beakers from the surface waters surrounding the floating docks at the Friday Harbor Laboratories on San Juan Island, Washington. Captured specimens that appeared undamaged were brought back to the laboratory and placed in two 20-L plastic containers. These stock containers were placed in a seawater table continuously supplied with running seawater at ambient surface temperatures (10°–14°C). Ctenophores were fed daily with zooplankton (predominantly late copepodites of *Acartia clausii*) collected from Jakle's Lagoon and Conover's Last Chance Lagoon; both are small lagoons situated on San Juan Island. With periodic exchanges of fresh seawater (approximately every other day) and regular feeding, *Pleurobrachia* could be maintained in healthy, experimental condition for several weeks.

Three species of calanoid copepods were used as experimental prey: *Acartia clausii, Calanus pacificus,* and *Pseudocalanus* sp. *Acartia* were collected from Jakle's Lagoon with near-surface ($\approx$2–4 m), oblique plankton tows using a 251-μm mesh, 0.25-m net. *Calanus* were collected from San Juan Channel with deep ($>$150 m), vertical plankton tows using a 571-μm mesh, 1-m net. *Pseudocalanus* were collected from San Juan Channel with moderately shallow (50–75 m), vertical plankton tows using a 251-μm mesh, 0.5-m net. The zooplankton from all tows were brought back to the laboratory, where adult females of all three experimental prey species were hand-sorted from the samples using a Wild dissecting microscope and large-bore pipette. Prior to experiments, holding stocks of *Acartia* and *Pseudocalanus* females were maintained in a 12° cold room on a diet of *Thalassiosira weissflogii. Calanus* females were maintained under the same stock conditions as the other species; however, they were only kept as a source of eggs for initiating copepod cultures. The procedures employed for culturing *Calanus* are described by Landry (1983). These copepod cultures, also raised at 12° on a diet of *T. weissflogii,* provided all 12 developmental stages of *Calanus* for the predation experiments with *Pleurobrachia.*

Predation experiments

Three sets of predation experiments were conducted: functional response experiments, single-prey experiments, and mixed-prey experiments.

Functional response experiments were conducted to determine the effects of prey density on predator ingestion rates (Table 1A). These experiments were run in two series, one with adult female *Acartia* and the other with adult female *Pseudocalanus.* In each series, *Pleurobrachia* were offered varying initial densities of prey. Data from these experiments were analyzed with the Holling disc equation (Holling 1959*b*).

Single-prey experiments were conducted to determine the relative vulnerability of each prey type to the predator (Table 1B). These experiments were run with fixed initial densities of each prey type, adult female *Acartia* and *Pseudocalanus,* as well as nine different prey types of *Calanus*: (1) NI,II: naupliar stages 1 and 2, (2) NIII,IV: naupliar stages 3 and 4, (3) NV,VI: naupliar stages 5 and 6, (4) CI: copepodite 1, (5) CII: copepodite 2, (6) CIII: copepodite 3, (7) CIV: copepodite 4, (8) CV: copepodite 5, (9) CVI: copepodite 6 (adult female).

Mixed-prey experiments were conducted to test the assumption that results from single-prey experiments were meaningful in predicting selection patterns in mixed-prey assemblages (Table 1C). These experiments were run with varying proportions of adult female *Acartia* and *Pseudocalanus.*

The data from single- and mixed-prey experiments were used to calculate instantaneous prey mortality rates and predator clearance rates according to the following equations:

$$N_t = N_0 \exp(-mt) \qquad (1)$$

$$F = V \cdot m/P, \qquad (2)$$

where N_t is the final number of prey per jar, N_0 is the initial number of prey per jar, m is the instantaneous prey mortality rate, t is the duration of the experiment, F is the predator's clearance rate, V is the volume of the experimental jar, and P is the number of predators per jar. These equations assume a constant clearance rate by the predator, an exponential decline in prey numbers throughout the experiment, and no cumulative loss in predator search time while handling prey. Although this last assumption is not strictly true (see Results and Discussion: Functional Response Experiments), it is closely approximated at the low prey densities in our experiments since individual handling times are relatively short (see Table 2. Errors introduced by this approximation were always <4%, except for *Calanus* CV and adult stages where potential errors may have been much higher. See Results and Discussion: Behavioral Observations).

In all three sets of predation experiments, treatment and control jars were replicated. Prey mortality in control jars was always negligible (i.e., never significantly different from zero), and thus all prey not recovered from treatment jars were assumed to have been ingested by the predator.

Behavioral observations

The mechanisms underlying *Pleurobrachia*'s prey selection patterns were investigated in the laboratory using a Panasonic videotape system. Estimates of prey swimming speeds, prey susceptibilities, and predator handling times were made for adult female *Acartia,* adult female *Pseudocalanus,* and all copepodid stages of *Calanus.* Prey swimming speeds were also determined for the second, third, fifth, and sixth naupliar stages of *Calanus.*

Observations of predator-prey encounters were conducted in a temperature-controlled (10°–12°), 54-L aquarium. A white fluorescent lamp provided the necessary illumination for videotaping. Although the copepods responded to this light source, we only used these tapes to estimate prey susceptibilities and predator handling times, two variables we assumed to be unaffected by the presence of light. An encounter was scored whenever a copepod made physical contact with *Pleurobrachia*'s tentacles. This usually elicited the ctenophore's handling response, but not in all cases. A successful encounter for the ctenophore was scored whenever the copepod was ingested. Handling times were measured from the initiation of successful encounters until the ctenophores reset their tentacles.

TABLE 1. Experimental conditions of predation experiments conducted with *Pleurobrachia bachei.*

A) Functional response experiments
  Predator: *P. bachei* (8 mm), $P = 1$ predator/jar
  Prey types*: *A. clausii* (CVI♀), *Pseudocalanus* sp. (CVI♀)
  Initial prey densities: N_0 varied from 25–200 prey/jar
  Experimental jars = 10, control jars = 2
  Experiment duration: t = 12–24 h (dark)
  Jar volume: V = 3.785 L
  Rotating wheel: 1 rpm
  Temperature: 12°C

B) Single-prey experiments
  Predator: *P. bachei* (8 mm), $P = 1$ predator/jar
  Prey types*: *A. clausii* (CVI♀), *C. pacificus* (NI–CVI♀), *Pseudocalanus* sp. (CVI♀)
  Initial prey densities: N_0 = 50 prey/jar for nauplii
  N_0 = 25 prey/jar for copepodites
  Experimental replicate jars = 4–8, control jars = 2
  Experiment duration: t = 12 h (dark)
  Jar volume: V = 3.785 L
  Rotating wheel: 1 rpm
  Temperature: 12°C

C) Mixed-prey experiments
  Predator: *P. bachei* (8 mm), $P = 1$ predator/jar
  Prey types: *A. clausii* (CVI♀), *Pseudocalanus* sp. (CVI♀)
  Initial prey densities: N_0 = 30 prey/jar of the following prey mixtures: *A. clausii* (CVI♀) : *Pseudocalanus* sp. (CVI♀)
    10:20
    15:15
    20:10
  Experimental replicate jars = 5, control jars = 2
  Experiment duration: t = 12 h (dark)
  Jar volume: V = 3.785 L
  Rotating wheel: 1 rpm
  Temperature: 12°C

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* CVI = copepodite 6 (adult). NI = naupliar stage 1. Copepod development involves six naupliar stages and six copepodid stages.

Prey swimming speeds were estimated from another series of videotaped observations (see Greene and Landry 1985). These observations of cruising speeds were conducted with nauplii swimming in a small (0.075-L), temperature-controlled chamber and copepodites swimming in a 5.4-L chamber submerged in the aquarium described above. The temperature was maintained between 8°–10° in both containers, and a Vicon low light level illuminator provided infrared illumination for videotaping. Infrared light falls outside the typical spectral sensitivity range of microcrustacean zooplankton (Forward 1976), and the copepods did not appear to respond to this particular light source. The procedures for analyzing videotapes to estimate prey swimming speeds are described by Greene and Landry (1985).

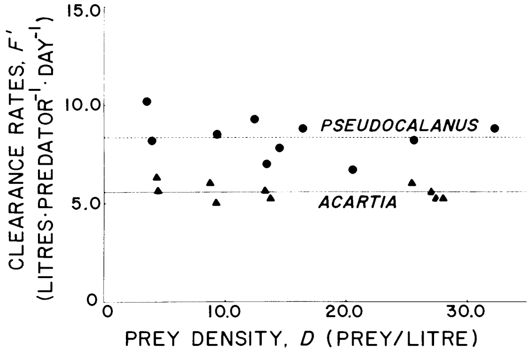

FIG. 1. Adjusted clearance rates as functions of prey density for *Pleurobrachia* feeding on adult *Acartia* and *Pseudocalanus*. —— mean adjusted clearance rate on adult *Acartia* ($F' = 5.56$ L·predator^{-1}·d^{-1}), – – – mean adjusted clearance rate on adult *Pseudocalanus* ($F' = 8.35$ L·predator^{-1}·d^{-1}).

RESULTS AND DISCUSSION

Functional response experiments

Understanding the dynamics of predator–prey systems requires quantification of the predator's functional response to variations in prey density (Solomon 1949, Holling 1959*a*, *b*, 1966, Hassell 1978). Previous investigations have shown that ctenophores are apparently insatiable consumers of copepods (Reeve and Walter 1978, Reeve et al. 1978, Kremer 1979, Reeve 1980). The type 1 functional response of lobate ctenophores increases linearly with prey density even at very high food levels. Reeve et al. (1978) have reported that the functional response of *Pleurobrachia*, although initially linear, eventually levels off at high prey densities due to "mechanical saturation" of the feeding mechanism. This result suggests that the Holling (1959*b*) disc equation may be the proper model to describe the functional response curve of *Pleurobrachia* and other cydippid ctenophores.

The Holling disc equation describes a type 2 functional response curve (Holling 1959*a*). Rewritten in the terminology of zooplankton feeding studies, it takes the following forms:

$$Y = T_S \cdot D \cdot F' \quad (3)$$

$$Y = (T_T - T_H) \cdot D \cdot F' \quad (4)$$

$$Y = [T_T - (bY)] \cdot D \cdot F', \quad (5)$$

where Y is the number of prey ingested by the predator over time T_T, D is the mean prey density, F' is the searching or clearance rate of the predator adjusted for the time spent handling prey, T_S is the time spent searching for prey, T_H is the time spent handling prey, T_T is the total time spent searching for and handling prey, and b is the handling time per prey item ingested. In terms of an ingestion rate I, Eq. 3 is equivalent to the following:

$$I = (1 - bY/T_T) \cdot D \cdot F'. \quad (6)$$

Two parameters, b and F', must be estimated to generate a functional response curve of ingestion rate vs. prey density. In most studies to date, both parameters have been estimated by regression techniques applied to data from functional response experiments. This often yields unrealistic and/or misinterpreted parameter values (see Juliano and Williams 1985, Williams and Juliano, 1985). In analyzing each series of our functional response experiments, we used the mean of our observed handling times for that prey type (Table 2) to estimate b, and then solved for F' in each experimental replicate (Fig. 1). No significant relationship was found between adjusted clearance rate and prey density in either series ($P > .05$). Therefore, a mean adjusted clearance rate was estimated for *Pleurobrachia* feeding on each prey type. Functional response curves were constructed with parameter values of $F' = 5.56$ L·predator^{-1}·d^{-1} and $b = 32$ s for *Acartia* and $F' = 8.35$ L·predator^{-1}·d^{-1} and $b = 66$ s for *Pseudocalanus* (Fig. 2). These curves are extrapolated beyond the prey densities for which we have feeding data to illustrate the potential cumulative effect of predator handling times. The extrapolations assume that adjusted clearance rates and handling times are independent of prey density over the whole range of food levels. These assumptions may be violated at very high den-

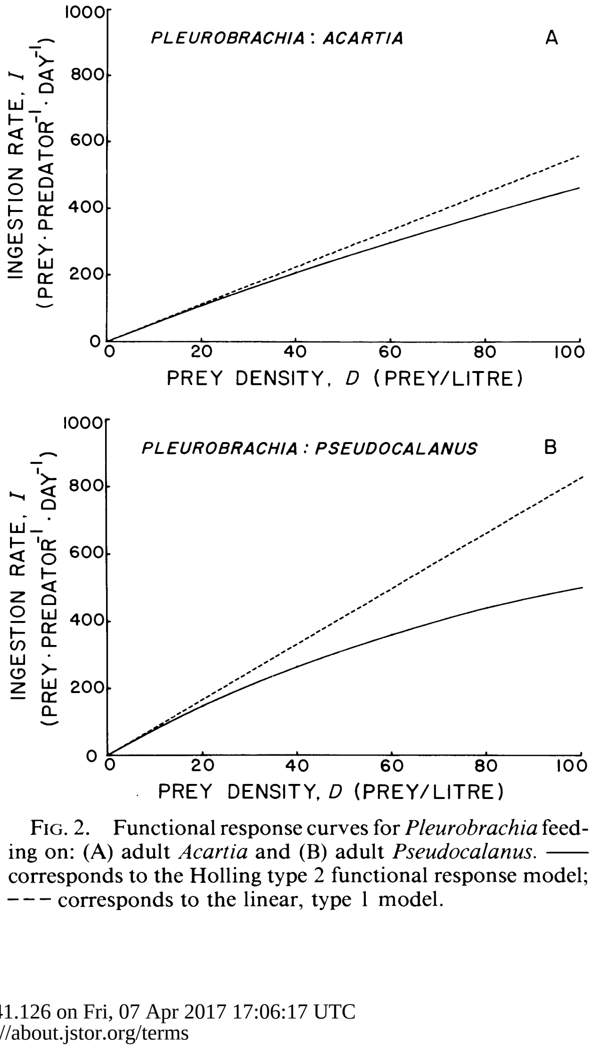

FIG. 2. Functional response curves for *Pleurobrachia* feeding on: (A) adult *Acartia* and (B) adult *Pseudocalanus*. —— corresponds to the Holling type 2 functional response model; – – – corresponds to the linear, type 1 model.

TABLE 2. Prey specifications for laboratory-reared nauplii and copepodites of *Calanus pacificus* and field-collected adult females of *Pseudocalanus* sp. and *Acartia clausii*. Estimates of variability are 95% confidence intervals. N/A = not available.

Prey type	Total length (mm)	Dry mass† (μg)	Mean swimming speed, $\bar{u}_i$ (mm/s)	Susceptibility to *Pleurobrachia*, S_{ij}	Handling time by *Pleurobrachia*, b_{ij} (s, mean and 95% CI)	Relative vulnerability index, V_{ij} (estimated from behavioral observations)	Mean clearance rate by *Pleurobrachia*, F_{ij} (L·predator^{-1}·d^{-1}, mean and 95% CI)	Relative vulnerability index, V_{ij} (estimated from predation experiments)
				Calanus pacificus				
NI	0.22	N/A	N/A	N/A	N/A	N/A	1.01 ± 0.23	0.12
NII	0.27	N/A	0.89	N/A	N/A	N/A		
NIII	0.33	0.6‡	1.08	N/A	N/A	N/A	2.50 ± 0.74	0.30
NIV	0.38	1.2‡	N/A	N/A	N/A	N/A		
NV	0.53	1.7‡	1.14	N/A	N/A	N/A	4.19 ± 1.15	0.50
NVI	0.61	2.2‡	0.93	N/A	N/A	N/A		
CI	0.74	5.5‡	0.32	0.80	25.7 ± 5.01	0.11	2.85 ± 0.68	0.34
CII	1.20*	8.9§	1.21	0.72	63.7 ± 8.45	0.38	4.00 ± 0.76	0.48
CIII	1.50*	24.8§	2.15	0.70	155.8 ± 34.62	0.65	4.57 ± 1.34	0.55
CIV	1.80*	60.8§	3.27	0.55	285.1 ± 58.72	0.78	5.41 ± 0.48	0.65
CV	2.50–2.80*	146.8§	3.85	0.45	1185.5 ± 371.66	0.75	6.23 ± 0.90	0.75
CVI adult	2.60–3.00*	200.0§	6.74	0.05	1315.0 (N/A, n = 1)	0.15	1.99 ± 0.61	0.24
				Pseudocalanus sp.				
CVI adult	1.70–2.00*	12.5	3.32	0.70	65.6 ± 9.16	1.00	8.35 ± 0.75	1.00
				Acartia clausii				
CVI adult	0.80–1.00*	2.0	1.61	0.75	32.0 ± 4.15	0.52	5.56 ± 0.29	0.67

* Total lengths from Gardner and Szabo (1982).

† Dry masses determined from laboratory-reared copepods raised at 12.0°–12.5°C with excess food.

‡ J. R. Holt, *personal communication*.

§ J. Vidal (1978).

sities where multiple prey capture events have been observed. Nevertheless, the results are compatible with the clearance rate data reported at high densities by Reeve et al. (1978). The important point illustrated by these figures is that the linear, type 1 model is a reasonable approximation to *Pleurobrachia*'s functional response at low prey densities. This justifies our subsequent use of unadjusted clearance rates in analyzing the results from single- and mixed-prey experiments.

Single- and mixed-prey experiments

The prey selection exhibited by a predator while foraging within a mixed assemblage of prey is determined by the relative vulnerabilities of different prey types to the predator and the active dietary choices made by the predator (Pastorok 1981, Greene 1983, Greene and Landry 1985). Our single-prey experiments were analyzed to determine the relative vulnerabilities of the different prey types offered to *Pleurobrachia*. Clearance rates were used as indicators of relative prey vulnerability (Fig. 3). Clearance rates on the different developmental stages of *Calanus* exhibit an unusual, bimodal pattern. Clearance rates steadily increase through the naupliar stages, drop at the CI stage, and then steadily rise again throughout the copepodid stages prior to another decline at the adult stage. Clearance rates on both *Pseudocalanus* and *Acartia* adult females are high relative to most developmental stages of *Calanus*. Maximum clearance rates (≈8.4 L·predator^{-1}·d^{-1}) were observed for *Pseudocalanus* females.

The feeding behavior of *Pleurobrachia* in mixed-prey assemblages can be predicted from the results of

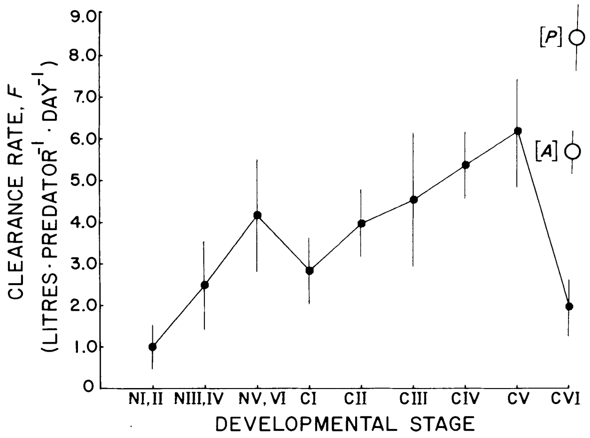

FIG. 3. Clearance rates for *Pleurobrachia* feeding on the different development stages of ● *Calanus*, ○ adult *Acartia* [*A*] and adult *Pseudocalanus* [*P*]. Error bars represent 95% confidence intervals.

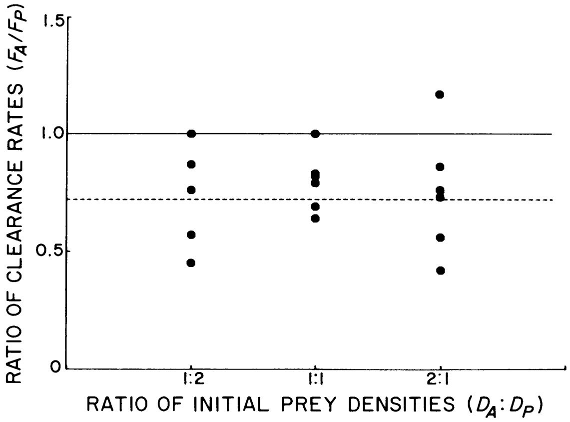

FIG. 4. Results from mixed-prey experiments with *Pleurobrachia* feeding on mixtures of adult *Acartia* and *Pseudocalanus*. Ratios of clearance rates are plotted against ratios of initial prey densities. —— no prey selection (ratio of clearance rates = 1.0). - - - prey selection predicted from single-prey experiments.

single-prey experiments if we assume the ctenophore does not make active dietary choices while foraging. The results of mixed-prey experiments designed to test this assumption are presented in Fig. 4. In all cases, the observed ratios of clearance rates were not statistically distinguishable ($P > .05$) from the ratios predicted from single-prey experiments. We conclude from these findings that the assumption is justified, and that the results from single-prey experiments can be used to predict *Pleurobrachia*'s selection patterns in mixed-prey assemblages.

Behavioral observations

Quantified observations of zooplanktonic predator-prey behavior can provide insight into the mechanisms of selective predation (see reviews by Kerfoot et al. 1980, Greene 1983). Prey swimming speeds, prey susceptibilities to the predator, and predator handling times were observed and quantified for the different prey types offered to *Pleurobrachia*. Table 2 includes estimates for these variables as well as other prey specifications pertinent to our discussion of the mechanisms underlying *Pleurobrachia*'s observed patterns of prey selection.

Prey swimming speeds tend to increase with size and age (Table 2; Greene and Landry 1985: Fig. 4), a relationship commonly observed for zooplankton (see references in Greene 1983:306). Among the developmental stages of *Calanus*, however, we observed a significant decline in swimming speed associated with the NVI to CI metamorphosis. The effect of this reduction in swimming speed on the relative vulnerability of first copepodites to *Pleurobrachia* is addressed in the General Discussion.

Prey susceptibilities to the predator decrease with increases in prey size and age (Table 2), also a relationship commonly observed in zooplanktonic predator–prey interactions (see references in Greene 1983: 306). This relationship arises from the enhanced escape capabilities of prey and reduced handling efficiencies of predators as prey get larger.

Predator handling times increase with prey size and age (Table 2), a relationship expected in zooplanktonic predator–prey interactions and emphasized in the studies by Thompson (1975) and Reynolds and Geddes (1984). Estimates of mean handling times were determined from at least 10 observations for all prey types except *Calanus* stage CV and stage CVI. For these two prey types, successful handling events were so rare (CVI adult females) and/or so variable in duration (CV, CVI adult females), that conclusions from our limited data set must be drawn cautiously. Although the handling time estimates fit the general trend, their accuracy and precision are questionable. In addition, for these two prey types it appears that handling times associated with prey that escape prior to ingestion may be of greater importance in determining the overall time *Pleurobrachia* spends handling prey. Although adult *Calanus* are relatively invulnerable to 8-mm *Pleurobrachia* (Fig. 3), long struggles between the two (>20 min), often culminating in torn tentacles for the ctenophore, can certainly have adverse effects on *Pleurobrachia*'s subsequent feeding success (see Greve 1977).

General discussion

Prey selection can be defined as any differences between the composition of a predator's diet and the availability of prey types in the environment (Ivlev 1961). Most studies of predation fail to distinguish between active behavioral selection, in which a predator actively selects and rejects prey, and fixed behavioral selection resulting from some prey being more vulnerable to the predator than others (Pastorok 1981, Greene 1983). For predators like *Pleurobrachia*, where there is little or no evidence of active dietary choice (Fig. 4), prey vulnerability effectively determines the predator's diet. To understand the prey selection patterns exhibited by such predators, it is important to determine the features of predator-prey interactions that account for differential prey vulnerability.

At a given prey density, the relative vulnerability (V_{ij}) of a particular prey type i to a given predator j can be viewed as the product of the prey's encounter rate (E_{ij}) with the predator and subsequent susceptibility (S_{ij}) to that predator:

$$V_{ij} = E_{ij} \cdot S_{ij}. \qquad (7)$$

For a planktivorous predator, encounter rates with prey vary with the time spent searching for and handling prey, the density and distribution of prey, the perceptive (reactive) volume of the predator, and the swimming patterns of both predator and prey. Models for estimating encounter rates between cruising and ambush raptorial planktivores and their prey have been developed by Gerritsen and Strickler (1977) and Giguere et al. (1982). An equivalent encounter rate model has not been developed for ambush entangling predators like *Pleurobrachia.* For the purpose of comparing relative encounter rates, we propose the following simple relationship: *Pleurobrachia*'s encounter rate with prey type i is directly proportional to the product of the prey's density (D_i) and mean swimming speed ($\bar{u}_i$):

$$E_{ij} = k[D_i \cdot \bar{u}_i], \qquad (8)$$

where k is a proportionality constant with the dimensions of area, L^2. This relationship assumes that other factors, such as ctenophore swimming speed and properties of the ctenophore's tentacles (e.g., tentacular surface area, intertentilla distances) do not account for differential encounter rates with alternate prey types. If these are reasonable assumptions, then Eq. 7 can be rewritten as follows:

$$V_{ij} = k[D_i \cdot \bar{u}_i] \cdot S_{ij}. \qquad (9)$$

To test the above relationship, we have reanalyzed the results from our predation experiments and behavioral observations, and then compared the two. A relative vulnerability index, $\hat{V}_{ij}$ (Greene and Landry 1985), was determined from predation experiments by dividing the mean clearance rate for a given prey type by the mean clearance rate observed for the most vulnerable prey type, *Pseudocalanus* females. Fig. 5 illustrates the behavior of the relative vulnerability index for *Pleurobrachia* feeding on the different prey types used in this study. For comparative purposes, superimposed in Fig. 5 are independent estimates of the relative vulnerability index determined with data from our behavioral observations (Table 2). These were calculated by dividing the product of the mean swimming speed and susceptibility observed for a given prey type by the product of the two variables observed for *Pseudocalanus* females.

The agreement between the two independent estimates of prey vulnerability is quite good (Fig. 5). Adult *Acartia,* adult *Pseudocalanus,* and *Calanus* copepodites CI through CIII are all highly susceptible (70–80%, Table 2) to *Pleurobrachia,* and thus differences in their swimming speeds largely determine the differences in their vulnerability to the ctenophore. Although we do not have the susceptibility data to confirm it, swimming speeds are probably important determinants of relative vulnerability in the naupliar stages of *Calanus,* as well, since their escape capabilities tend to be weak. The strong relationship between prey swimming speed and vulnerability to *Pleurobrachia* appears to account for the decline in vulnerability observed at the CI stage (Fig. 5), a decline corresponding to the significant decrease in swimming speed associated with the NVI to CI metamorphosis. The differences in vulnerability for the late copepodites of *Calanus* (stages CIV-CVI adult female) are strongly influenced by both prey swimming speeds and susceptibilities. Swimming speeds increase during these stages, but, more important, susceptibility drops markedly as *Calanus* increases in body size and postcontact escape capability. The peak in *Calanus*' vulnerability to *Pleurobrachia* occurs at the CV stage; adult *Calanus* are relatively invulnerable because they rarely can be handled successfully by the 8-mm ctenophores used in our experiments.

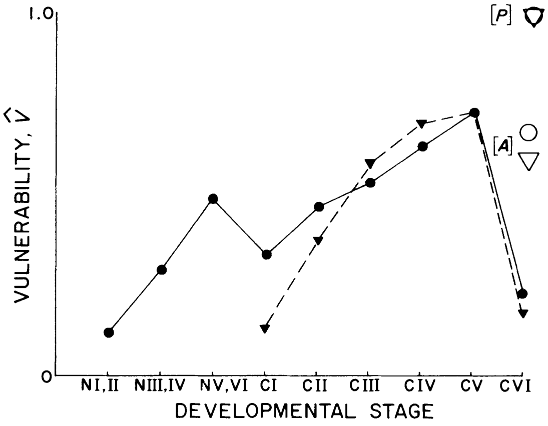

FIG. 5. Relative vulnerability, $\hat{V}$, as a function of prey developmental stage for *Pleurobrachia* feeding on the different development stages of *Calanus,* adult *Acartia,* and adult *Pseudocalanus.* The relative vulnerability indices determined from predation experiments (circles: ● *Calanus,* ○ *Acartia* [*A*], *Pseudocalanus* [*P*]) equal the mean clearance rate for a given prey type divided by that observed for the most vulnerable prey type, *Pseudocalanus* adult females. The indices determined from behavioral observations (triangles: ▼ *Calanus,* ▽ *Acartia* [*A*], *Pseudocalanus* [*P*]) equal the product of mean swimming speed and susceptibility to *Pleurobrachia* attack observed for a given prey type, divided by the corresponding product for *Pseudocalanus* females. Both estimates of the relative vulnerability index for adult *Pseudocalanus* females therefore are equal to 1.0.

The results from our study indicate that *Pleurobrachia* can consume appropriate-sized prey at rates that are roughly proportional to their availability in the plankton, and that this consumption is highly selective. The former result is consistent with the conclusions from most previous studies; the latter is not. In his review of the literature on the ecology of *Pleurobrachia,* Fraser (1970) concluded that, "*Pleurobrachia* is a nonselective carnivore, feeding on what is available in the plankton." Our results enable us to amend this statement to the following: *Pleurobrachia* is a selective carnivore, and its diet is determined by both the relative availability and vulnerability of prey.

This study and a previous study by Bishop (1968) provide consistent evidence that *Pleurobrachia* feeds selectively on its copepod prey. Given the many factors leading to differential prey vulnerability, we predict that selective feeding will be the rule rather than the exception among most ctenophore species. If this proves to be the case, then future research on ctenophore predation should examine the interaction between selective feeding and zooplankton dynamics under different sets of environmental conditions. For example, in the shallow coastal and estuarine waters common to the northwestern Atlantic, irruptions of ctenophores have been shown to decimate local copepod populations (Kremer 1979, Deason 1982, Deason and Smayda 1982). The functional and numerical responses of ctenophores are destabilizing to the dynamics of both predator and prey populations. These responses by the ctenophores, in combination with the prey's lack of a refuge in shallow water, appear to be responsible for the unstable predator-prey dynamics commonly observed in these environments. Under such conditions, selective feeding by ctenophores may strongly influence the dynamics, but not obviously alter the qualitative structure of the zooplankton assemblage.

In the deeper coastal waters and fjords common to the northeastern Atlantic and Pacific, irruptions of ctenophores, particularly *Pleurobrachia* spp., are also commonly observed (Fraser 1970, Hirota 1974, Mills 1981). In these environments, however, copepod populations are often heavily preyed upon, but rarely decimated. Apparently, deeper water columns allow the predator and prey populations to become spatially decoupled at times, thus providing the copepods with a refuge from ctenophore predation. Under such conditions of predator–prey coexistence, selective feeding by ctenophores may have its most obvious effects, altering both the qualitative as well as quantitative structure of the subsequent zooplankton assemblage.

ACKNOWLEDGMENTS

We thank the director and staff of Friday Harbor Laboratories for making our research efforts enjoyable as well as productive. Special thanks are extended to M. Canino, P. Kremer, K. King, C. Ridgeway, and C. Strathmann for assistance in collecting animals for this study. K. Banse, B. Frost, J. Gerritsen, G. R. Harbison, C. D. Harvell, M. Mullin, R. Paine, T. Pennington, M. Reeve, and R. Strathmann provided critical reviews of this manuscript; we appreciate the constructive comments from each of them.

This is contribution number 1423 from the School of Oceanography, University of Washington. Support for this research was provided by grant OCE-8214017 from the National Science Foundation.

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