Feeding Morphologies and Distribution Patterns of Marine Cladocera in the Lower Chesapeake Bay

Sandra Layne Gilchrist
Old Dominion University

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FEEDING MORPHOLOGIES AND DISTRIBUTION PATTERNS
OF MARINE CLADOCERA IN THE
LOWER CHESAPEAKE BAY

by

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A.A. March 1975, Florida State University
B.S. December 1976, Florida State University

A Thesis Submitted to the Faculty of
Old Dominion University in Partial Fulfillment of
Requirements for the Degree of

MASTER OF SCIENCE
OCEANOGRAPHY

OLD DOMINION UNIVERSITY
August 1979

Approved by:

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ABSTRACT

Feeding Morphologies and Distribution Patterns of Marine Cladocera in the Lower Chesapeake Bay

Sandra Layne Gilchrist
Old Dominion University, 1979
Director: Dr. A. J. Provenzano, Jr.

Temporal and spatial distributions of marine cladocera in the lower Chesapeake Bay estuary were observed over a year-long sampling period. The distributions of cladoceran species throughout the Bay were studied in relation to temperature and salinity. A survey of the species over the entire Bay is included to establish distribution patterns of the various species during a short time period.

Theoretical mathematical principles were used to predict feeding abilities of the Bay species. Mouthparts are described qualitatively and quantitatively to infer function. A mandibular index developed by Itoh (1970) was revised and employed in evaluating feeding methods interspecifically and intraspecifically.

Illustrations of primary and secondary feeding structures were made and used for taxonomic verification of the species. Discrepancies in keys prepared for geographically isolated populations by workers in various parts of the United States, Russia, and South America necessitated a re-evaluation of fundamental taxonomic characteristics to include modifications for Bay species noted during the course of the present study.
ACKNOWLEDGEMENTS

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INTRODUCTION

Five of the seven cosmopolitan marine cladoceran species are found commonly in Chesapeake Bay plankton; Podon polyphemoides, P. leuckarti, P. intermedius, Evadne tergestina, and E. nordmanni (Bosch and Taylor, 1973; Bryan and Grant, 1974). Other species are less common in the Bay; Penilia avirostris (Bosch and Taylor, 1968), Evadne spinifera (Bryan, 1977), and a freshwater species, Leptodora kindtii (Goodwyn, 1968). These cladoceran species are often predominant in the plankton and appear to be important in food webs of the estuary (Duke and Simyukova, 1965) and major oceanic fisheries (Selvakumar, 1970).

Temperature and salinity are thought to govern distributions worldwide, although discrepancies exist in tolerance limits reported for each of the species. Bay cladocerans overlap both temporally and spatially during peak densities, suggesting that another factor may be influencing the distributions in the estuary. Bryan (1977) suggested that cladoceran feeding habits may play a role in the distributions, but offered no evidence to support this conclusion.

Deductions from populational studies support the claim that community structure is governed by feeding in that fertility of sexual and parthenogenetic females fluctuates with quality and quantity of available food (Onbe, 1978). Onbe inferred the types of food selected by marine species, although no direct evidence was given.

Other conclusions about cladoceran feeding habits come from records of animals collected in conjunction with cladocerans in plankton tows and from gut content analyses (Lochhead, 1936; DellaCroce and Beltanin, 1968). Problems inherent in both techniques preclude accurate assessment of cladoceran feeding modes.
The paucity of information on cladoceran feeding habits is due largely to the failure of past and present workers to maintain laboratory cultures of any marine species (Onbe, 1978). Although extended culture has not been successful, 24-hour experiments have yielded some cognizance of particle size ranges selected by cladocerans (Pavlova, 1959).

The imprecision in determining food selection through gut analyses or associations in plankton tows and the inability to maintain laboratory cultures for extended periods necessitates another approach for determining cladoceran feeding habits. In the present study, feeding appendages are examined qualitatively and described mathematically in order to infer function from form. Distribution patterns observed throughout the year in the lower Bay are discussed in terms of predicted feeding habits.

Knowledge gained from the present study should prove useful in understanding population dynamics of cladoceran species which are important in the food webs of commercial fishes, and in future attempts to culture marine cladocerans.

**Experimental Objectives**

Crustacean mouthparts have been described by many authors. Parsons and Takahashi (1973) concluded from their review that carnivores, omnivores, and herbivores generally have distinctively different feeding morphologies.

The relationship of feeding modes to distributions of marine cladocerans in the lower Chesapeake Bay is approached first by establishing distributions in terms of physical factors, and secondly by relating feeding morphologies to distribution patterns. The distributions were examined in terms of temperature and salinity to evaluate previous
suppositions that these factors which appear to influence open ocean distributions also explain patterns observed within the Chesapeake Bay estuary.

The premise that form follows function is used to examine interspecific and intraspecific morphological variations in feeding habits in relation to Bay distribution patterns. Qualitative evaluations, determined by contrasting structural features of the mouthparts, and quantitative comparisons, made for each species by using a modified mandibular index to separate species into feeding categories, form the bases for studying popational patterns.

By combining the qualitative evaluations and the quantitative comparisons, speculations about population interactions are possible.
EXPERIMENTAL METHODS

Sample Collection

Monthly samples were taken from May, 1978 through May, 1979 at stations chosen to provide a wide range of temperature and salinity combinations (figure 1). At each station, two ten minute tows were made during various states of the tidal cycle using half-meter diameter, 153μ mesh zooplankton nets at depths of 3 m and 5 m (± 0.5 m). All tows were made on straight-line courses. The wire angles for the top net were checked at the beginning, middle, and end of each tow to adjust for proper sampling depth. Angles for the bottom net were estimated from angles of the upper wire, and proper adjustments for depth were made. Temperature and salinity were measured for each station from the surface to 5 m at 1 m intervals using an RS-5 inductive salinometer (Cahl Scientific Corporation, El Cajon, California).

An extended sampling trip was completed in May, 1978 along the axis of Chesapeake Bay (figure 2) at stations selected to sample widely varied temperature and salinity gradients during a short period of time. Most stations selected corresponded to sites chosen for a previous study (Bryan, 1977) and thus distribution records could be compared. Samples collected from the May cruise were examined for cladoceran diversity.

Nets were rinsed thoroughly and contents of the cod end jars were placed into three liter containers. Samples which contained ctenophores and scyphozoan medusae were screened through cheesecloth prior to making dilutions. Volumes were brought to 2.5 liters with seawater; 0.25 liter subsamples were taken, and were preserved in a 5% buffered formalin solution. Additional buffered formalin was added to the subsamples later to bring the concentrations to 10%. 
Figure 1. Sampling stations in the lower Chesapeake Bay. Tows were taken within a half-mile radius of station center. Station sequence was for purposes of data recording only and does not necessarily reflect order taken for the cruises.
Nautical Miles

2.

LIGHT TOWER

R/V HOLTON

Nautical Miles

0 5 10

76°30'

76°
Figure 2. Cruise track for axial Bay survey conducted May 9 through May 19, 1978. Stations are numbered in increasing value towards the uppermost stations. All stations were sampled twice during the course of the cruise.
Laboratory Procedure

One of two samples taken from each depth was examined for each station for each sampling period. Cladoceran species were noted by searching the entire samples in 10 ml aliquots. If no cladocerans were observed in the first sample examined from a particular depth, the second sample from that depth was scanned. Animals were separated first by genera, and were identified later to the species level.

Because descriptions from the literature for the various species were conflicting and key characteristics were not defined clearly, a working taxonomic key was compiled (Appendix A). Representative animals were illustrated using a Wild M20 binocular microscope equipped with a camera lucida (Appendix B).

The samples were then numbered consecutively and random number tables were used to select samples for examination. If all species were not represented in the selected sample, another sample was chosen in the same manner until at least 50 individuals of each species were available for dissection.

Identified animals were cleared with hot 5% KOH, stained with acid fuschin, and mounted temporarily in lactic acid. Gross and morphological lengths (figures 3 and 4) were measured using a Wild M8 dissecting microscope. After dissection, length parameters used to calculate the modified mandibular index (figure 5) were measured with an ocular micrometer mounted within a Wild M20 binocular microscope.

Samples taken from the ten day May cruise were treated the same as monthly samples. Samples were examined for the presence of various species. No animals were taken from the extended cruise for calculating the mandibular index.
Figure 3. Gross and morphological lengths of Podon. The line segment a to a' denotes gross length and the line segment b to b' denotes morphological length.
Figure 4. Gross and morphological lengths of Evadne. The line segment between a and a' denotes the morphological length and the line segment between b and b' denotes the gross length.
Figure 5. Modified mandibular index, where $w_i$ is the width between each tooth, $h_i$ is the height of each tooth, $W$ is the overall width of the mandible, and $H$ is the overall height of the mandible.
Statistical Methods

A systematic error estimation was made for Itoh's index using the following series of calculations adapted from Beers (1962):

\[
\frac{w_i}{W} \rightarrow \frac{w_i}{W} + \frac{\Delta w}{W} \tag{1}
\]

\[
\Delta w = (w_i)^2 + (w)^2 \tag{2}
\]

\[
\frac{h_i}{H} \rightarrow \frac{h_i}{H} + \frac{\Delta h}{H} \tag{3}
\]

\[
\Delta h = (h_i)^2 + (w)^2 \tag{4}
\]

\[
\frac{w_i h_i}{WH} \rightarrow \frac{w_i h_i}{WH} + \frac{\Delta e}{WH} \tag{5}
\]

\[
e = (\Delta h)^2 + (\Delta w)^2 \tag{6}
\]

where \(w_i\) is the width between each tooth, \(h_i\) is the average height for each tooth, \(W\) is the width of the mandible at the widest part, \(H\) is the height of the mandible measured from the widest point, \(w\) is the systematic error for the width calculations, \(h\) is the systematic error for the height calculations, and \(e\) is the combined error for all measurement calculations.

Estimating a error of 0.0005 mm for each measurement, \(e\) is approximately 0.001. This amount, \(e\), was added to the calculation of Itoh's index so that the final modified formula (MFI) is as follows:

\[
MFI = \frac{10^4}{N} \times \sum_{i=1}^{N-1} \frac{w_i h_i}{WH} + 10^4 \times \frac{N-1}{N} \times e \tag{7}
\]

where \(N\) is the number of teeth. Calculations for error in line placements were made for each measurement and appear in Appendix 3.

Size classes for the animals were estimated by means of polymodal frequency analyses—graphical probability method (Cassie, 1950), because
no other method has been developed for accurately determining the age (size) classes for preserved cladocera (Baker, 1938).

Descriptive statistics for morphological measurements were calculated for all size classes of each species. Mean values for the species were compared interspecifically and intraspecifically using the following statistic:

$$z = \frac{(x_1 - x_2) - \bar{\delta}}{\sigma_{x_1 - x_2}}$$  \hspace{1cm} (3)

where the null hypothesis was that $u_1 - u_2 = 0$. $\bar{\delta}$ was assumed to be zero for the calculations (Miller and Freund, 1977).

**Tests for variations of Itoh's Index**

Measurements for calculations of the modified index are subjective in that the observer must decide what constitutes the widest part of the three dimensional mandible proper, where measurements for the teeth originate, and how the widths of the the teeth will be measured. To test variations that might arise from these decisions, a series of mandibular measurements were taken on individuals of all marine species collected (except E. spinifera, which were rare in the collections). Parameters were measured as indicated in figures 6, 7, and 8.
Figure 6. Alternative measurements for Modified Index using center of teeth to measure tooth height.
Figure 7. Alternative measurements for Modified Index using various widths for mandible.
Figure 8. Alternative measurements for Modified Index using skewed axes to measure height and width of mandible.
LITERATURE REVIEW

Investigators recording physical parameters relating to cladoceran distributions do not report consistent results. Rammner (1930) reported that *P. polyphemoides* has a tolerance range of 2.46°C to 17.92°C and a salinity tolerance range of 1.05 ppt to 35.0 ppt. In this and all other reports, tolerance range or limit will be functionally defined as the LD 50 level of the species, and thus, measurements will be rounded to tenths for all studies. In other reports, the range below 13 ppt salinity was omitted (Bryan, 1977; Onbe, 1978). Peak densities occur in May and January in Chesapeake Bay (Bryan, 1977), but small numbers of *P. polyphemoides* are reported in the Bay year-round. Abundance peaks coincide temporally with rapidly changing temperature patterns.

Salinity and temperature tolerances recorded for *P. intermedius* from various geographical areas are not consistent. Gieskes (1971a) suggested that the lower tolerance limit of this species in the Bay is 13°C and the upper salinity tolerance limit is 34.8 ppt. Bryan and Grant (1974) amended the above ranges to include temperatures of 18.3°C up to 26.4°C and salinities from 15.8 ppt to 27.6 ppt. Peak population densities vary in different areas, but are generally only recorded in the period July through August in the Bay, and then only in the Bay mouth area.

Tolerance ranges for *P. leuckarti* have not been well documented. This species apparently maintains populations within the temperature range of 6.5°C to 13.0°C. The upper salinity limit has been reported as 34.8 ppt. A peak population size has been recorded in March and April only near the Bay mouth.

Limits for *E. nordmanni* have not been scrutinized since the early
1900's. Temperature limits have been reported as 6°C up to 18°C and salinity limits have been recorded as 1.5 ppt to 34.5 ppt (Rammner, 1930).

E. tergestina has been recorded in areas with temperatures ranging from 15.7°C to 27.8°C (Baker, 1938). Cleve (1901) suggested that the salinity range for this species is stenohaline with distributions limited to areas with 32.0 ppt to 38.5 ppt salinities. Locally, this species has been recorded only in the Bay mouth area.

A shelf-water species, E. spinifera, has been recorded only rarely in the lower Bay (Bryan, 1977). Temperature and salinity ranges have not been established clearly for this animal. The northernmost record of the species was off the coast of New England while the southernmost extent recorded was off the western coast of Australia (Baker, 1938).

The final species examined in this study is the only marine representative of Ctenopodidae. Penilia avirostris has been found surviving in areas with temperatures ranging from 12°C to 20°C. However, some adults have been found in areas where temperatures were 3.7°C. Salinity tolerance levels have not been well defined for the species. Maximum densities appear near the Bay mouth in November with smaller peaks occurring year-round (Bryan, 1977).

Although distributional patterns of marine cladocerans have been attributed to salinity and temperature, few studies demonstrate this premise. Cieskes (1971b) suggested that temperature and salinity are predominant controlling factors in population dynamics of marine cladocerans found in the North Sea. He implied that food may play a minor role in abundance patterns but discounted feeding as a major influence upon population structures. Cieskes (1971c) examined the anatomical differences
between *P. leuckarti* and *P. intermedius* and concluded that the major variation in the species is size, with the mouthparts appearing to be very similar. He further remarked that the mouthparts were clearly those of predatory species. He proposed that the smaller species occurred in the North Sea in spring and early summer, feeding upon small particles, while the larger species, *P. intermedius*, appeared in late summer and fed upon larger particles. Salinity and temperature preferences of the species were thus causally related to the succession in food availability. Populations do not appear to overlap in the open ocean, and thus no species interactions have been observed.

Bryan (1977) deduced conclusions similar to Gieskes for populations studied in the Chesapeake Bay. Although Bryan acknowledges the influence of feeding upon the populations, he claims that predation and physical parameters (temperature and salinity) are more likely shaping factors in distributional patterns observed in the Chesapeake Bay.

Neither of these studies addressed the question of coincidental occurrences of peak densities of cladoceran species in areas overlapping in temperature and salinity ranges.
Feeding

Evidence of carnivorous feeding habits of Polyphemidae is circumstantial. Bainbridge (1958) asserted that the large complex eye of *E. nordmanni* enables the species to actively seek prey from a distance during the daytime. He claimed that this ability clearly established the species as carnivorous. There have been no behavioral observations to support his suppositions.

Other workers (Bosch and Taylor, 1970) have conjectured that *P. polyphemoides* is probably carnivorous because eggs and larvae of copepods have been reported in the grasp of preserved specimens. Further support of the carnivorous habits of *P. polyphemoides* was provided by Cieskes (1971b) who recorded the presence of chitinous materials around the mouthparts of preserved cladoceran specimens. He concluded that the material was most likely from copepod larvae. There have been reports of phytoplankton cells found in the guts of this species (Lebour, 1922; Bainbridge, 1958). However, these reports have been discounted as records of items ingested along with the primary food sources of copepods and titinids.

Rammner (1930) suggested that polyphemid cladocerans ingest only organic detritus from which they absorb nutrients. Bainbridge (1958) proposed that *E. nordmanni* 'sucks out' living materials from prey and absorbs nutrients in this manner. These claims are thought to be supported by gut analyses which have revealed only gray materials found in cladoceran digestive tracts.

Ctenopodidae have been studied in the Soviet Union in detail because of their importance to the larvae of commercial fishes. *P. avirostris* was the first marine ctenopodid cladoceran studied for gut content.
Pavlova (1959) examined the water absorption rate for *P. avirostris* from which he concluded that complete assimilation of particles took approximately 15–20 minutes.

*P. avirostris* has the characteristic leaf-like appendages exhibited by all members of its family. Because of the nature of the appendages, Bryan (1977) states that the species is most likely a filter feeder.

Field investigations of temporal feeding patterns of *P. avirostris* have led to the conclusion that feeding proceeds throughout the day with more items being captured during the afternoon and evening hours than the morning and night hours (DellaCroce and Gaino, 1968–69). This report also concluded that *P. avirostris* was a filter feeder.

Few workers have examined feeding of cladocerans directly. The most successful endeavor to date has been a study in which gut contents have been correlated with feeding structures (Lochhead, 1936). It is concluded from this report that *P. avirostris* could be a filter feeder or herbivore.

The feeding structures of *Evadne* and *Podon* species found off the west coast of the United States have been studied in detail by Baker (1938). Descriptions and illustrations in her monograph appear to be somewhat incomplete and do not seem accurate for the species found in Chesapeake Bay.
RESULTS

**Distributions and Physical Data**

The lowest salinities were recorded on the western side of the Bay and into the upper Bay (Table 1). At all stations above Annapolis, Maryland from which freshwater and marine species were taken during the May cruise had salinities below the detection limits of the inductive salinometer and were assumed to be zero for the purposes of this study. Heavy rainfall and runoff were recorded in the upper Bay area during this period (May 9 through May 19, 1978).

In areas where salinities were below 1 ppt and recorded average temperatures were relatively constant (± 0.9°C) during the ten day period, several species of freshwater cladocera were recorded in the upper Bay region. The two primary representatives of freshwater species found in the samples were *Leptodora* and *Daphnia*. Of the two genera, specimens of *Leptodora* were more common in most areas (2.2:1). *Leptodora* was the only freshwater genus found in areas where brackish salinities were recorded (salinities ranging from 0 ppt up to 6.4 ppt; Table 1).

Cladocerans were represented at each station sampled, although the upper Bay stations (834 through 930; figure 2) consisted primarily of freshwater species. During the sampling period in early May, when peak reproductive periods are reported for all of the marine species found in the Bay with the exceptions of *E. tergestina* and *P. intermedius* (Bryan, 1977); *E. nordmanni* appeared to be the most ubiquitous of all species examined.

The salinity range recorded for *E. nordmanni* during the May upper Bay cruise was between 9.2 ppt and 25.1 ppt. This species was the most abundant cladoceran in the upper Bay samples where salinities were around
Table 1. Occurrences of cladocera in Chesapeake Bay from cruise May 9 through May 19, 1978.

<table>
<thead>
<tr>
<th>Station Number</th>
<th>Fenilia avirostris</th>
<th>Evadne tergestina</th>
<th>Evadne nordmanni</th>
<th>Evadne spinifera</th>
<th>Podon polyphemoides</th>
<th>Podon leuckarti</th>
<th>Podon intermedius</th>
<th>Leptodora kindtii</th>
<th>Temperature (°C)</th>
<th>Salinity (ppt)</th>
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<tr>
<td>609</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td>15.8-14.8</td>
<td>21.2-25.1</td>
</tr>
<tr>
<td>707</td>
<td>X</td>
<td>X</td>
<td></td>
<td>X</td>
<td>X</td>
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<td></td>
<td>18.7-17.3</td>
<td>16.0-18.4</td>
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<tr>
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<td>18.0-14.7</td>
<td>12.5-15.1</td>
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<td>18.7-16.8</td>
<td>4.6-11.7</td>
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<td>744</td>
<td>X</td>
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<td>17.0-15.5</td>
<td>6.5-11.0</td>
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15 ppt (ratio of this species to the next most abundant marine species was 3.2:1; Table 1). The above range falls within the wide salinity range proposed by Rammner (1930). Although the animals should have been able to tolerate physical conditions up to station 914 (figure 2), marine species were not found in the samples taken in May.

The lowest temperature recorded at any time on the May cruise was 14.4°C at station 814. This lies slightly above the mean temperature tolerance for *E. nordmanni* suggested by Rammner (1930) and slightly below the lower tolerance limit for the species recorded by Bryan (1977), pointing out problems of interpreting distributions of cladocerans in the Bay as related to previously recorded ranges.

The second most widely distributed species in the samples from the ten day cruise was *P. polyphemoides*. This species was encountered at all stations (except 761, 762, and 818) where *E. nordmanni* was reported, although numbers were comparatively low. The temperature range for the species during May was from 14.7°C to 18.7°C while the salinity range where animals were taken was from 4.3 ppt to 25.1 ppt.

The three remaining species found during May appeared to be confined to the lower Bay. Abundance patterns of the species, *P. avirostris*, *P. leuckarti*, and *E. spinifera* could not be determined from the data collected during the May study.

The temperature range over the area in which *E. spinifera* appeared was as wide as for the more cosmopolitan cladoceran species. Limits recorded in the present study for May were from 14.8°C to 18.7°C. The salinity regime for the species during May extended from 16.0 ppt to 25.1 ppt. This species appeared in the samples in low numbers (less than 1% of the total cladocerans).
P. avirostris also appeared to persist in the Bay mouth area, existing inside the lower Bay in low density population cells. Such cells or patches appeared in low concentrations up to station 724 in May (less than 5% of the total cladocerans). The temperature range over this area extended from 14.7°C to 18.7°C. The salinity range was from 12.5 ppt to 25.1 ppt. These limits correspond to ranges of previously recorded distributions (Steuer, 1933; Bosch and Taylor, 1968).

The presence of P. leuckarti in the lower Bay was recorded up to station 725 during May. This was one of the farthest intrusions into the Bay proper recorded for P. leuckarti. Ranges of temperature and salinity tolerances corresponded to records in previous studies.

The only other cladoceran found in abundance at the stations sampled during the ten day May cruise was the freshwater species, Leptodora kindtii (comprising approximately 15% of the total cladocerans taken from the upper Bay stations). The highest concentrations of this species was at stations 858 through 930 (figure 2). The salinity range over this area was from 0.0 ppt to 6.4 ppt, while the temperature range extended from 14.3°C to 15.2°C (Table 1).

Data from the monthly sampling stations was used to establish both spatial and temporal relationships between marine cladoceran species found in the lower Bay. Overall, the Bay mouth area appeared to support the most diverse complex of cladoceran species throughout the year.

At station 1, two species seemed to have nearly year-round distributions. P. polyphemoides appeared year-round in low numbers (less than 4% of total cladocerans). The other species demonstrating almost year round distributions in the area was P. avirostris. This species was found rarely during October and November, increasing to relatively peak
Table 2. Physical data and species occurrences of marine cladocerans collected at station 1 during the period April, 1978 through March, 1979.

<table>
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<tr>
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<th>28 June</th>
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densities during April (Table 2). Even at peak densities, this species appeared to be a small percentage of the total number of cladocerans taken at this station throughout the sampling period of the present study. The only exception to this observation occurred in November when P. avirostris comprised almost one third of the number of cladocerans taken in the samples.

A second co-occurring temporal group at station 1 contained three species, P. leuckarti, E. spinifera, and E. nordmanni, which were recorded from March through the end of June. Greatest abundances of these species were observed during the beginning of May. E. spinifera usually occurred in small numbers (less than 1% of total cladocerans) while E. nordmanni and P. leuckarti sometimes dominated the total plankton samples. The temperature ranged from a low of 2.9°C up to 24.0°C during the March through June sampling period at station 1, while the salinity varied from 13.2 ppt to 29.7 ppt.

The third temporally co-occurring group of cladocerans at station 1 appeared from June through October. P. intermedius was collected from the end of June through the first part of October, while E. tergestina appeared only from August until the beginning of October. Densities of both species appeared to increase to peaks near the end of August. The temperatures during the June through August sampling period ranged from 20.1°C to 25.5°C and the salinity ranged from 19.6 ppt up to 26.7 ppt.

At station 1, more than one cladoceran species was collected at each sampling time. There was no apparent single dominant species occurring throughout the year.

At station 2 (figure 1; Table 3), P. avirostris became the dominant species during the entire sampling period. Other species exhibited
Table 3. Physical data and species occurrences of marine cladocerans collected at station 2 from April, 1978 through March, 1979.

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scattered distributions during the year. *E. nordmanni* and *P. intermedius* were least common at this station (each less than 3% of the total number of cladocerans taken at the station), suggesting that these species may be restricted to the Bay proper.

*P. polyphemoides* and *E. spinifera* occurred along with *P. avirostris* at station 2 from June through August, although the ratio of the species heavily favored *P. avirostris* (approximately 12:1). *E. spinifera* seemed to follow a low peaking pattern at the station, while *P. polyphemoides* appeared only rarely in the samples (less than 2.5% of total cladocerans).

The final temporally co-occurring group of cladocerans at this station was observed from the middle of July through the beginning of October. This group included *P. leuckarti* and *E. tergestina*. The pattern observed for *E. tergestina* was similar to the distributions noted for the species at station 1. *P. leuckarti*, however, seemed to prefer the offshore waters during the Fall months.

At station 3 (Table 4) *P. avirostris* and *P. polyphemoides* showed similar temporal and spatial distributions. *P. avirostris* seemed to dominate total cladoceran numbers taken at this station throughout the lower Bay sampling period. *P. polyphemoides* was found in low numbers (less than 4% of the total number of cladocerans taken at the station) with slight increases appearing as peaks throughout the year.

*E. tergestina* was not collected at station 3 during any part of the sampling period. This was the only marine species not appearing at the station.

Relative distributions of *P. polyphemoides*, *E. nordmanni*, and *E. spinifera* at station 3 seemed similar to patterns established at station 1. The major difference in the assemblages occurred with *E. spinifera*
Table 4. Physical data and species occurrences of marine cladocerans collected at station 3 from April, 1978 through March, 1979.

<table>
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</table>
which persisted in the Bay through the middle of August at station 3 and until the end of June at station 1. *P. polyphemoides* and *E. nordmanni* were both more abundant than *E. spinifera* which comprised less than 1.5% of the total cladocerans taken at the station during the sampling period.

Station 4 (Table 5) was the northernmost sampling station in the monthly scheme. The presence of *P. avirostris* was greatly decreased at this station (approximately 2% of the total cladocerans taken at the station). It seemed that station 4 delineated the lower salinity limit of the species, although factors such as predation and competition cannot be wholly eliminated in explaining the scarcity of *P. avirostris* at this station.

*P. polyphemoides* was observed at station 4 with little fluctuation in numbers throughout the year. The densities in the area were low (approximately 3% of total cladocerans taken at the station).

*E. nordmanni* and *P. intermedius* showed temporal distributions at station 4 similar to patterns established at earlier stations. Temperatures and salinities recorded were all within reported limits for the species. Relative abundances of the species spatially seemed to favor *P. intermedius* (2.3:1), however, *E. nordmanni* persisted for a longer period of time at the station.

*P. leuckarti* and *E. tergestina* occurred only rarely at station 4. These species collectively made up a small percentage of the total number of cladocerans taken at the station (less than 4%). Samples containing these species, however, exhibited a relatively large number of young (determined by size) specimens.

*E. spinifera* was not encountered in any of the samples collected at
Table 5. Physical data and species occurrences of marine cladocerans collected at station 4 from April, 1978 through March, 1979.

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<th>15 Jul</th>
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station 4. Although other factors such as predation, competition, lack of acceptable food supply, and so on may have also influenced the exclusion of this species, salinity may have been the primary limiting factor.

At station 5 (Table 6), P. avirostris, P. leuckarti, and E. spinifera were not detected in the plankton samples. Samples were not collected from the sediment to examine for the presence of resting eggs of these species.

_P. polyphehoides_ persists throughout the year in low concentrations (less than 5% of the total cladocerans taken at the station) at station 5. Another persistent occurrence pattern is demonstrated by _P. intermedius_. This species comprises almost 100% of the total number of marine specimens taken at this station. Mostly older females, some with resting eggs, were taken in samples from June through August. The abundance of the species was highly dependent upon the taxonomic classification used for species identification (Appendix A).

Specimens of _E. tergestina_ and _E. nordmanni_ were sparse at station 5. Older females were taken at the station, some having double resting eggs in the brood pouches. One male _E. nordmanni_ was also collected at this station. This male specimen was one of only three male cladocerans obtained during the entire sampling period.

The final station, number 6 (Table 7) was located near Hampton Roads, Virginia (figure 1) and provided the least saline environment considered in the temporal portion of the study. The only two marine species recorded in the area were _P. intermedius_ and _P. polyphehoides_. These species followed temporal patterns established at earlier stations during the sampling period. Cladoceran percentages of the total plankton taken from the station were low (approximately 10%). Freshwater
Table 6. Physical data and species occurrences of marine cladocerans collected at station 5 from April, 1978 through March, 1979.

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Table 7. Physical data and species occurrences of marine cladocerans collected at station 6 from April, 1978 through March, 1979.

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species were noted in the area and were often more abundant than marine copepod species collected at the station (1.2 to 1).

**Feeding Morphology Evaluation**

The modified mandibular index (MEI) used for separating groups of cladocerans into feeding categories was first tested on freshwater *Daphnia* species found in the Norfolk area whose feeding habits are well documented. Predictions from the MEI corresponded to the known feeding patterns for all species tested. Marine species, morphologically similar to the freshwater species examined, were categorized using the MEI and results are recorded in Table 8. Along with the edge analyses, Table 8 shows a listing of the mean lengths of all age groups in each of the species as determined by cumulative frequency analyses. It should be noted that each age class represents size relationships within the species and not necessarily between the species.

The MEI for all size groups of *P. avirostris* were well within the range established for filter feeders or herbivores (MEI less than 500). The labrum of this species appeared to be modified for piercing or sucking (Appendix B). Striations were visible in the labrum when specimens were stained and not cleared with KOH.

Auxiliary feeding appendages of *P. avirostris* have spines located at the basal ends of the first two thoracic limbs. These appendages were moderately setose with visible setules. Setules appeared to be closely packed. Thoracic limbs were all approximately the same length, extending slightly below the carapace in preserved specimens. Terminal segments of all thoracic appendages had a flattened, leaf-like appearance.

*P. polymemoides* also appeared to be an herbivore-filter feeder, according to the MEI. The second antennae and the first two thoracic
appendages were moderately setose with setules closely packed. The labrum was not distinctive, although spination patterns were apparent.

The mandibles appeared simple and possessed thirteen major cutting edges. The right and left mandibles were similar, although a slight groove appeared on the interior surface of the right mandible which was not apparent on the left mandible. Short spines covered the denticulations densely and decreased near the base. The maxillae were not conspicuous and appeared as flattened, spinose appendages. The first antennae were reduced with two to three sets of setae extending from each. The setae were approximately one and a half times the length of the first antennae.

Eva. tergestina had an index which indicated that the species should show omnivorous feeding habits. The mandibles were more complex than any of the previously described species (figure 9). Spines and spinules formed angles with the denticulations and decreased in number toward the bases of the major teeth. The labrum appeared subovoid with a broadening noticeable at the anterior end. Thoracic appendages showed strong endopodite spination and moderate exopodite setation. Setules were visible and appeared closely packed.

F. intermedius seemed to be in an intermediate area near the critical lower point for the separation of herbivore-filter feeders and omnivores. According to the strict interpretation of the index, this species should be considered an herbivore-filter feeder. Taking into account the standard deviation, however, it cannot be statistically separated from the omnivore category. The mandibles of the species did not seem as complex as the mandibles of E. tergestina (figure 9). Thoracic appendages were moderately setose and spinose compared to the other Bay species. The second antennae were approximately the same length as the morphological
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<td>19</td>
<td>0.542</td>
<td>683.1</td>
<td>62</td>
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<tr>
<td>4</td>
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<td>0.640</td>
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<td>117 - 945</td>
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<td>5</td>
<td>11</td>
<td>0.720</td>
<td>490.2</td>
<td>103</td>
<td>257 - 759</td>
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<tr>
<td><em>Evadne spinifera</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>27</td>
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<td>201</td>
<td>647 - 1397</td>
</tr>
<tr>
<td>3</td>
<td>21</td>
<td>0.549</td>
<td>1075.7</td>
<td>247</td>
<td>633 - 1277</td>
</tr>
</tbody>
</table>

Table 8. Summary of modified edges index analyses. Numbers under the species column indicate the age group. N is the number of individuals examined. Mean length has the units of mm.

*Length given is the mean morphological length.*
axis of the body. The first antennae seemed reduced with two to four sets of setae extending from each.

*P. intermedius* and *E. tergestina* were both found during the same time period in approximately the same areas. Although the two species were predicted to feed at the same level, there was a significant difference in the mean MEIs at all levels.

*P. leuckarti* was predicted to be a definite carnivore (MEI greater than 900). The mandibles appeared simple with three major teeth. There was little variation between the right and left mandibles. The labrum was slightly ovoid and spination patterns were obvious. The first antennae were reduced with three to five sets of setae extending from each. The second antennae were longer than the morphological length of the body for each size group. Large spines appeared along the basal and first two segments of the first thoracic appendage exopodites.

*E. nordmanni* should be considered carnivorous, according to the predictive index. The mandible could be divided into a major and minor tooth section. The major tooth area contained only the major tooth and its accompanying spines and spinules. The minor denticule area displayed an elongated basal area ending in a series of short teeth. First antennae were not elaborate. The second antennae and thoracic limbs were heavily spinated, setulation was not dense, setae were few in number, and spines appeared only on the interior surfaces of the exopodites.

Although *E. nordmanni* and *P. leuckarti* can both be classified as carnivorous, the species had significantly different mean MEIs at all age levels.

The final species examined in the study, *E. spinifera*, also seemed to be a carnivore. The mandibles were complex in comparison with other
Evadne species found in the Bay. There was a large spine-like projection on the interior surfaces of both the right and left mandibles, which may function to hold prey but was not considered as a cutting surface. Thoracic appendages were strongly spinose with little setation or setula­tion. The labrum was ovo-renate with rows of spinules concentrated in patterns at the medial depression. These spinules seemed angled towards the medial depression. The second antennae were approximately three fourths the morphological length of the specimens examined for all age groups. The first antennae were not elaborate.

Age classes within each species showed overall differences in feeding abilities. All age groups collected in the samples varied in abundance with time. Those species that overlapped temporally and spatially showed the most consistent differences in trophic abilities of all age groups.

Index Variations

MEI ranges for each age group of each species are given in Table 9. Table 9 also contains results of varying points of measurement for certain species. The results of all variations fall within the ranges found in the original MEI calculations.

Most variations appeared as differences in heights of the teeth, rather than in width calculations. Those species which were predicted to be carnivorous seemed to show the most variation in index due to selection of point from which to measure height parameters. This was not unexpected in that the 'carnivorous' species tended to show more pronounced denticulation.
Table 9. Summary of various methods for calculating MEI as shown in figures 6, 7, and 8. The (m1) refers to the methods in figure 6, the (m2) refers to methods in figure 7, and (m3) refers to methods in figure 8. The ranges given for the species represent magnitudes greater than observed for the 15 specimens. These ranges were taken from 36 of each species except E. spinifera for which 27 total specimens were considered. Standard deviations were rounded to the nearest whole number. Mean length has the units mm.

*Length given is the morphological length.

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Mean length*</th>
<th>Mean index</th>
<th>std. dev.</th>
<th>range</th>
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<td><em>Penilia</em></td>
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<tr>
<td>avirostris</td>
<td>15</td>
<td>0.621</td>
<td>78.5</td>
<td>11</td>
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<tr>
<td>2 (m1)</td>
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<td>0.732</td>
<td>110.7</td>
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<td>43 - 197</td>
</tr>
<tr>
<td>2 (m2)</td>
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<td>0.801</td>
<td>97.3</td>
<td>16</td>
<td>31 - 159</td>
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<td>2 (m3)</td>
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<td>0.907</td>
<td>115.6</td>
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<tr>
<td>Podon polyphemoides</td>
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<td>278.8</td>
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<td>98 - 407</td>
</tr>
<tr>
<td>1 (m2)</td>
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<td>259.5</td>
<td>47</td>
<td>36 - 401</td>
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<tr>
<td>1 (m3)</td>
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<td>35</td>
<td>934 - 1342</td>
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<tr>
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<td>1221.7</td>
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<td>697 - 1116</td>
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<tr>
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<tr>
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</tr>
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<td>1173.3</td>
<td>115</td>
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</tr>
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</table>
DISCUSSION

Primary factors which seemed to influence spatial distributions of cladocerans seasonally in the Chesapeake Bay proper were temperature and salinity. Although quantitative results were not established, the present study implied that temporal distributions for Bay species were directly correlative with temperature and salinity patterns. These observations did not refute the findings of previous studies. However, earlier reports failed to address the fact that many Bay cladoceran species overlap both temporally and spatially during periods of peak population density. Such occurrences are not usual in open ocean conditions and may introduce a competitive factor into distribution patterns.

Appearances of these species in high concentrations during the same spatial and temporal hypervolume warrants examination of the hypothesis that factors other than temperature and salinity influence population structures and movements within observed patterns of gross seasonal changes. Coexistence of morphologically similar species in relatively high numbers within the same area at the same time also suggests an inherent mechanism segregating the species precludes competitive exclusion.

Results from this study may be used to construct a case to support resource partitioning of food in the estuarine environment as one possible mechanism.

During the May cruise, *P. polyphemoides*, *E. nordmanni*, *E. spinifera*, *P. avirostris*, and *P. leuckarti* co-occurred temporally in the lower Bay. Relative concentrations of the species revealed that *E. nordmanni* was the most abundant species present at the time, although the peak reproductive period for the species had not yet occurred (Bryan, 1977).
Further discussion of the interactions of the various species must be prefaced by considering the validity of using the MEI and in the choice of age classes by cumulative frequency analyses.

Itoh's Index is based on the premise that there is a basic difference in the cutting edges of carnivores, omnivores, and herbivores. In reviewing his results (Itoh, 1970), it can be noted that in general the herbivore-filter feeding category displayed shortened teeth which were closely packed. This would indicate that herbivorous species present a grinding edge to food items. Carnivores appeared to show distinctly separate teeth which were relatively long in relation to the major dentification. The carnivore thus presented a tearing or chewing surface to food items. The omnivore appeared to possess some characteristics of both the carnivore and the herbivore, although teeth were not as distinctly separable into either category.

One major flaw in Itoh's Index is that no error bounds are given for discerning the various categories. By grouping several size classes of individuals into lump sums and by not allowing for variations in the sexes, the index may be somewhat misleading at critical points. For these reasons, an error analysis was applied to the index (figure 5; Table 9). By examining the ranges of the various categories in view of inherent error in the calculations, it becomes possible to use the index for predicting feeding habits with more confidence.

The second question mark in determining the validity of using the index as a predictive tool is the use of cumulative frequency curves to determine size classes. Generally, these curves are used in fishery statistics to determine size classes. Grussendorf (personal communication) suggested that crustaceans may prove ideal for use of the method.
because of their method of growth in distinctive stages. Plotting all values of body length for each species and then separating age groups by analysis of variance, make it possible to determine age groups with some degree of confidence. All groups in this study were tested and determined to be distinctly separate age groups.

Assuming that some degree of mathematical confidence can be placed in both the modified index and in the method for determining various age groups, it is possible to evaluate the relationships between and among the various species of cladocerans represented in Chesapeake Bay.

*E. nordmannii* was predicted to be carnivorous. However, the MEI value was not significantly different from the value determining omnivory at any of the age levels represented for the species. The secondary feeding appendages seemed to be of a raptorial nature, displaying little setation and heavy spination. The first and second thoracic appendages appeared to be cylindrical, which is characteristic of carnivorous species.

The only other strict carnivore found at the lower Bay stations during the May cruise was *E. spinifera*. The MEI calculated for this species was significantly different from the MEI calculated for *E. nordmannii* at any age level. Such a variation may suggest that these two species partition the trophic level. Since the calculation of the index depends upon the variations of the denticulations, it is not unlikely that the partitioning is achieved by prey selection or particle size selection. Such a possibility cannot be determined quantitatively from the present study.

*P. leuckarti* was predicted to be carnivorous in early growth stages and omnivorous as fully developed adults. The MEIs of the first age
groups were not significantly different from the MEIs of both groups of *E. spinifera*. The third *P. leuckarti* age group was significantly different from all *E. spinifera* and *E. nordmanni* age groups. *P. leuckarti* age groups had MEIs different from all age groups of *E. nordmanni*.

The above observations lend support to the premise that endemic species such as *E. nordmanni* and *P. leuckarti* may be forced to concentrate on different parts of the trophic level to permit coexistence over time. *E. spinifera* has not yet become established in the lower Bay as a permanent part of the plankton. This species may serve as an invader on estarine food resources.

In most environments, saturation levels have not been reached with respect to invading species. Coupling this idea with the suggestion that extinction may not be a common event in the estuary, it can be conjectured that *E. spinifera* may fill a trophic gap between *E. nordmanni* and *P. leuckarti*. By appearing only at short intervals, *E. spinifera* may initiate circumstances which could lead the endemic species to displace feeding habits in areas of extreme temporal and spatial overlap. Another alternative to this premise is that *E. spinifera* does not exist long enough in the area to force further separation of the trophic habits of the endemic species and thus can exist only as an infrequent invader upon habitat resources. Partitioning of these environment could be a compromise between the selective pressures to displace and the disadvantages to displacing. When three or more species have interactions, it is possible that selective pressure to displace one competitor may increase competition with the other competitor. This may describe the situation with *E. nordmanni*, *P. leuckarti*, and *E. spinifera* assemblages found in the lower Bay. These factors should be examined more closely.
to determine possible evolutionary consequences of geographic variation imposed by temporal and spatial interactions.

The problem surrounding determination of interactions between and among populations have received much attention in the past thirty years. There have been several complete reviews of theoretical population interactions (Schoener, 1974; Pianka, 1976).

Considerations of competition, resource partitioning, and coexistence have dominated ecological thought in apparent attempts to decipher patterns observed in species diversity (Hutchinson, 1961). Species diversity has been operationally defined in the present study to mean the number of cladoceran species present in a population complex.

Factors which have been known to affect diversity of such complexes in other species include 1) time, 2) spatial heterogeneity, 3) competition, 4) predation, 5) climatic stability, 6) productivity, and 7) combinations of the preceding factors (Pianka, 1974). The concepts of competition and resource partitioning encompass most of these factors.

In viewing competition as a shaping force in cladoceran assemblages, there is an a priori assumption that abundance of a resource, in this case food, is in some way limiting. Coexistence could be permitted under competitive interactions only if the common resource is partitioned in some manner (MacArthur and Levins, 1967).

Reviewing the interactions of the three cladoceran species found concurrently in the lower Bay, it seemed appropriate to accept the concept of resource partitioning to explain cladoceran distributions within seasonal patterns observed in Chesapeake Bay. By accepting this premise, one of the problems underlying this study could be explained.

The problem deals with the incongruity of taxonomic descriptions of
the various species from different geographical locations. Prior to the present study, no significant differences in taxonomic characteristics between conspecifics located in different geographic settings with varying species compositions were recorded. Comparing keys from various locations around the world, it was discovered that distinguishing taxonomic characteristics seemed inconsistent. An explanation for such discrepancies is provided by the concepts of resource partitioning and competitive interactions in that character displacement is a common phenomenon in limited, co-occurring populations (e.g. Darwin's finches, Lack, 1947). Descriptions may hold true for each of the localities and yet not be consistent from one location to another. Since the Chesapeake Bay is the only area in the world where seven marine cladoceran species occur simultaneously, character displacement may be more evident in trophically related species. Compounding the likelihood of character displacement in marine cladocerans is the almost unique form of reproduction exhibited by all known marine species.

A specialized form of parthenogenesis known as paedogenesis has allowed cladocerans to reach high densities in short periods of time. At least three generations can be readily identified in a single female. Fertility of females is known to change with major shifts in environmental conditions, especially in connection with food availability. It is thought that generally the greatest fertility occurs in older females and this study confirms that observation. There is a positive correlation between female body length and the number of eggs or embryos (Onbe, 1978).

Causes of the shift from parthenogenetic to sexual reproduction: are not known for marine cladoceran species. The percentage of sexual
females has been associated with abrupt environmental changes, although records of stimuli initiating changes vary specifically and geographically. Such differences may be due to numerous types of sampling equipment and techniques used by various workers in making initial observations of patterns. The present study indicated that the number of sexual individuals increased near the end of the peak density period. The number of females with resting eggs seemed to increase as population numbers decreased, although the number of males did not seem to increase.

Resting eggs appeared consistently in older females with few exceptions. There are no reports of numbers of offspring that one female can reproduce in one season, but observations during this study suggest that population clones may be common.

Clone conditions could allow rapid incorporation of displaced morphological characteristics into species confined to the lower Bay. Observation of Podon species with various eye colors lends support to the contention that clones may exist. Patches of specimens with eye colors ranging from dark black to red apparently exist throughout the year.

Background information for the case of resource partitioning in the E. nordmanni, E. spinifera, and P. leuckarti complex is suppositional with little direct evidence for quantitative support. Examining the records of cladoceran distributions temporally and spatially, similar patterns emerge for other species complexes.

P. avirostris and P. polyphemoides appeared together at the lower Bay stations during the May study although both were predicted to be in the herbivore-filter feeder category. Secondary feeding appendages of both species affirm that both are herbivores or filter feeders. The first categories of P. avirostris were significantly different from all
groups of *P. polyphemoides* and from the oldest group of *P. avirostris*. The mean MEI for the third age group of *P. avirostris* was not significantly different from all groups of *P. polyphemoides*, although the body sizes of the groups varied greatly.

*P. avirostris* has not become established as an integral part of the Bay plankton and may function as a resource invader. *P. avirostris* appeared to be a superior competitor for food resources over *P. polyphemoides* if the relative number of specimens collected in each sample reflects competitive ability. In relation to cladocerans, the assumption that ratios represent environmental and competitive responses is not unreasonable. Since *P. polyphemoides* is endemic in the lower Bay, another factor must be limiting the distribution of *P. avirostris* into the area. A likely limiting factor is salinity. *P. avirostris* tolerates a lower limit of 12.5 ppt while *P. polyphemoides* can survive and reproduce in areas where the salinity is 4.3 ppt.

MEI differences for the first age groups of *P. avirostris* and *P. polyphemoides* may imply that the trophic level is divided into subcomponents. Since the MEI is a reflection of the mandibular cutting surfaces, it is not unreasonable to assume that different types of particles are consumed by animals within the same trophic level. If this assumption is correct, interspecific competition between *P. avirostris* and *P. polyphemoides* for food resources may be lessened.

During peak densities, a larger percentage of the total cladoceran population is made up of individuals of the younger age groups. If these individuals of *P. avirostris* are interacting with adult individuals of *P. polyphemoides*, the latter species may be able to compete adequately for resources in the environment by avoiding first order competition.
during vulnerable early growth stages.

Further penetration into the upper Bay by any marine species was recorded for *E. nordmanni*. It was collected in samples up to station 818 where salinities were 15 ppt and temperatures were 8°C (Table 1), both of which were well within tolerance ranges recorded for the species. Although temperatures and salinities should not have limited further penetration up the Bay, the animals were not found in May samples. No other records of marine species penetrating further into the Bay have been reported. This suggests that factors other than temperature and salinity influence the intrusion of *E. nordmanni* into the upper Bay during peak population densities.

*P. polyphemoides*, an herbivore-filter feeder, was recorded up to station 804 in a distribution pattern similar to *E. nordmanni*. This species should have been able to tolerate lower salinities and temperatures encountered at more northern stations, although the species were not collected at these stations during the May cruise.

One possible explanation for the relative exclusion of these two euryhaline species from areas within the lower tolerance limits of the species could be that freshwater or brackish water species become dominant in the upper Bay.

*Leptodora kindtii* which is considered a freshwater species is found commonly in the upper Bay (Table 1). Previous investigators recorded the presence of the species in brackish areas, but concluded that its appearance was correlated with heavy river run-off. The species was found living in areas where salinities were 6.4 ppt. Upon discovery of specimens in the samples, live samples were observed under a dissecting microscope to determine if the specimens were live at capture. Live
and dead animals were observed. Cursory gut content examinations suggested that the animals ingested brackish water copepod species. Further investigations into the tolerance ranges of this 'freshwater' species may prove useful in understanding the absence of marine species in the brackish upper Bay.

Temporal distributions appeared to follow patterns similar to spatial distributions found along the axis of the Bay. At station 1 (figure 2), all known marine species common to the Bay were collected during the year-long sampling period. A complex consisting of P. avirostris, P. leuckarti, E. spinifera, and E. nordmanni was found at this station during May and continued through June at which time, another species, P. intermedius became incorporated into the group.

P. intermedius was predicted to be either an herbivore-filter feeder or omnivore. The first age groups of this species were not significantly different from the transition point delineating the two trophic levels. The MEI of the species as a whole is significantly different from all other age groups of the species complex. It is one of only two omnivores predicted by the MEI.

As the summer progressed, P. leuckarti, E. spinifera, and E. nordmanni disappeared from the plankton at station 1 and were replaced by E. tergestina. The index for this species indicated that it should be omnivorous. This would allow E. tergestina to exploit two feeding levels and thus partially fill the subcomponent levels vacated by the three carnivores.

At station 1, E. tergestina, P. avirostris, and P. intermedius were the only cladocerans present from June to October. In November, E. tergestina was absent from samples collected at this station. The remaining
were predicted to be herbivore-filter feeders. Other species were most likely eliminated from the area due to changes in the physical environment, although changes in food availability may have contributed to population declines in the area. The number of resting eggs observed inside specimens of *E. tergestina* increased during September, suggesting that conditions prompting production of males appeared near September.

In September, *E. nordmanni* and *P. polyphemoides* appeared at station 1 in relatively small numbers. *E. nordmanni* was predicted to be a carnivore. However, the species cannot be statistically separated from the omnivore category. The tendency towards omnivory may have permitted this species to exploit both plant materials and small zooplankton before other strict carnivores could become re-established in the area. As *P. polyphemoides* becomes established in the area, *E. nordmanni* could be forced to compete more actively with the carnivorous species.

In March, *P. polyphemoides*, *E. nordmanni*, and *P. leuckarti* appeared in the samples taken at station 1. The ratio of *E. nordmanni* to other cladocerans began to decrease as these species moved into the area, although small population cells were still found at the station (less than 1% of total cladocerans taken).

At station 2 (figure 2) the highest salinity conditions were observed. This station was the only location outside the Bay proper. *P. avirostris* had been recorded at the station year-round in previous reports. This species is an oceanic species which has become a transient part of the Bay plankton. Circulation patterns near the Bay mouth most likely have facilitated the dispersion of the species into the Bay. The MEI for the species indicated that it was herbivorous. Reports from the literature affirm the herbivorous habits of the species.
The MEI is less than 100, suggesting that the mandibular surface is nearly flat. Appearance of the secondary feeding appendages and the relatively low MEI suggest that this species may feed on small particles which may not be utilized by a majority of other Bay herbivores.

In June, *P. polyphemoides* and *E. spinifera* were collected at station 2. These species appeared in low densities compared to *P. avirostris*. *E. spinifera*, a carnivore according to the MEI, should not have had interactions related to food gathering with the other species found at the station through the end of June. In July, *P. leuckarti* appeared at the station and *E. nordmanni* disappeared from the collections. The appearance of *P. leuckarti*, a carnivore according to the predictions of the MEI, may have directly contributed to the displacement of *E. nordmanni*. Feeding experiments under controlled laboratory conditions will be necessary to support this conjecture.

In August, *E. tergestina*, an omnivore was recorded at station 2. *E. spinifera* and *P. polyphemoides* were not present at the station near the end of August. *P. intermedius*, another omnivore, appeared at the station briefly near the end of August and into the first part of September. After October, only *P. avirostris* remained in the samples collected. Although a succession pattern of herbivores, omnivores, and carnivores can be established from distribution records at this station, the influence of temperature and salinity changes can also explain the patterns of distributions. The association patterns of the species could be interpreted differently, although this interpretation appears to support the hypothesis of resource partitioning.

Distribution patterns for all species found at station 3 were similar to those encountered at station 1. This could be a result of similarities
in the physical environments of the stations. The major changes in the species represented appeared in relative abundances of the various groups and in the distribution of *E. spinifera*. *E. spinifera* appeared to show a northward movement pattern throughout the sampling period. More sampling in a broad pattern is needed to ascertain whether the pattern observed is a migratory movement of the species into the Bay.

At station 4, the salinity level dropped to around 15 ppt. This drop probably affected the distribution of some species, such as *P. avirostris* and *E. spinifera*, which are usually considered oceanic species. *P. polyphemoides*, one of the more euryhaline and eurythermal of the marine cladoceran species, appeared to be phytophagous or filter feeding according to the MEI. Other filter feeders such as *P. avirostris* and *P. intermedius* were present at the station only rarely. The combination of salinity limits and the inability to coexist with a ubiquitous species may have led to the elimination of these filter feeders from station 4.

*P. polyphemoides* appeared to dominate samples taken throughout the sampling period at station 5. *P. intermedius*, an omnivore, was collected from June through August at this station, somewhat decreasing the seasonal distribution pattern observed at stations 1 and 3. The only other marine cladocerans found at the station were *E. nordmanni* and *E. teregestina*, two carnivores, which did not overlap temporally in appearance. It is possible that food availability coupled with inability to tolerate conditions at lower range limits excluded these predators from reaching peak population densities at station 5.

Station 6 provided the lowest salinity conditions of any of the lower Bay stations. *P. polyphemoides* was the only marine species represented at the station in large numbers (greater than 95% of total
cladocerans taken at the station). The temporal occurrence of this species decreased slightly from the previous stations. This decrease could be contributed to by sampling problems encountered in the area throughout the period. The only other marine species represented at the station was *P. intermedius* which appeared in low densities from June through August.

Overall cladoceran distribution patterns observed in the lower Bay seemed to be influenced by salinity and temperature factors, while the seasonal microstructures of the distributional patterns appeared to be affected by other factors such as competitive interactions and resource partitioning.

*Morphological Analyses*

The use of the MEI provides a mathematical basis to predict feeding habits of marine species without relying upon gut analyses and determination of organisms found in conjunction with marine species in plankton tows. Although the two previously mentioned methods have inherent problems unique to each, it is not the intention of this study to suggest that use of the MEI is flawless.

Problems encountered in applying the MEI are primarily in the subjectivity of measuring. Positioning of specimens appeared to be extremely important in making initial calculations. Since the mandibles of all marine cladocerans are three dimensional, further modification of the MEI formulae to consider the third dimension may be necessary. Use of both scanning and electron micrographs may enable modification and fine tuning of the MEI which light microscopes cannot provide.

In an attempt to point out the problems in using the MEI, a study on variations in calculations related to points of measurement was conducted.
This study revealed that overall measurements were statistically within the same ranges as the values determined in the actual study, although variation in the measurements and the standard deviations were much greater. The error incurred by slight angular changes sometimes increased deviation an order of magnitude (Table 9).

Other problems which occurred in dealing with the MEI were the separation of species into age groups and the determination of the boundaries for each feeding group.

By using cumulative frequency analyses for age groups, a certain margin of error was artificially introduced to the MEI calculations. The original index was supposedly calculated from only adult animals, disregarding the size differences. In applying the index to various size groups, it may be necessary to introduce a scaling factor. Such a factor would have to be determined by examining the morphological relationships of various age (size) groups whose feeding habits were well documented. The age groups were separated into categories at the 95% confidence level.

The underlying bases for separation of the groups into age categories depended upon the normality of distributed sizes in the populations examined. Although the method has been used on non-normally distributed populations (Cassie, 1950), the reliability of the categories can be correlated to normality of the populations examined.

At times, less than 20 animals represented an entire age group. It may be difficult to argue that such a small sample can represent a group adequately since the molting process of crustaceans causes changes in size in a discontinuous manner. Genetic as well as other factors could influence the total amount of change seen in each patch.
CONCLUSIONS AND IMPLICATIONS

1. Overall seasonal patterns of cladoceran distributions are associated with temperature and salinity changes in both the Chesapeake Bay estuary and the open ocean. Microdistributional patterns within gross seasonal patterns may be influenced by species associations or interactions. The intrusion of marine cladoceran species into the upper Bay regions may be limited by interactions with freshwater or brackish water species.

2. Calculations of a modified mandibular index can be used to separate marine cladocerans into distinctive feeding types, although the diets of these species are not known empirically. Incorporating error analyses into the mandibular index forces some groups into transition areas in which feeding methods are questionable. Confirmation or denial of predicted habits should be examined in controlled experiments.

3. Feeding modes and resource partitioning may explain distribution patterns of marine cladocerans appearing coincidentally in time and space during peak population densities. Invasion of species into the Bay may suggest that saturation of the environment with respect to exemic intrusion has not been achieved. Invading species appear in the Bay 'proper' in lower densities than observed outside the Bay mouth.

4. Reports of taxonomic variation of species which are geographically isolated may be related to character displacements which result from populational interactions. Such displacements appeared most often in species which exhibited closely related trophic abilities and which also were found at peak densities in the same time and space hypervolume.

5. The almost unique form of reproduction utilized by marine cladocerans allows for a strong likelihood that clones are formed during parthenogenetic phases. Cloning may contribute to propagation of character displacements. The appearance of red-eyed individuals and black-eyed individuals found in Chesapeake Bay is heretofore unrecorded in the literature. Genetic implications of cloning and parthenogenesis in marine cladocerans have not been explored for any known species.


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APPENDIX A

Phylum: Arthropoda  
Class: Crustacea  
Subclass: Branchiopoda  
Superorder: Diplostraca  
Order: Cladocera  
Suborder: Eucladocera  

Superfamily: Sidoidea Brooks (=Ctenopoda Sars)  
Family: Sididae Baird  
1. Penilia avirostris Dana (=Penilia schmackeri Richard)  
Superfamily: Polyphemoidea Brooks (=Onychopoda Sars)  
Family: Podonidae Mordukai-Boltovskoi  
2. Podon polyphemoides Leuckart  
3. Podon intermedius Lilljeborg  
4. Podon leuckarti Sars  
5. Evadne nordmanni Loven  
6. Evadne tergestina Claus  
7. Evadne spinifera Sars  

There has been some discussion on the removal of Podon polyphemoides from the genus Podon and the establishment of a separate genus Pleopis, which was originally used by Dana in 1852 to describe all Podon. Although there is some agreement among workers that a separate genus should be made, morphological evidence has not been clearly delineated for the separation. The latest suggestion is that P. polyphemoides and E. tergestina be placed in the new genus and other Podonidae remain in the genus Podon.

Because of the unstable nature of the newer nomenclature and taxonomy, I have chosen to retain the older classifications for the purposes of this paper.
Taxonomy

Of the 420 known species of cladocerans, almost 95% are found only in freshwater. The remaining 5% are primarily estuarine, with a few species considered to be truly oceanic. The bivalve shape of the carapace, which is distinctive to the group, is folded and not hinged. In cladocerans, the carapace never covers the head, but may cover the body and limbs.

In general, filter-feeding forms have leaf-like appendages which are at least partially concealed by the carapace, while the more raptorial forms have appendages which are sparsely setated and which are exposed from beneath the carapace.

The first antennae of marine species are reduced and have few setae. The second antennae are usually well developed. These appendages are biramous and function primarily in locomotion (personal observation) and secondarily in feeding.

The following is a working taxonomic key for the identification of marine cladoceran species observed in the Chesapeake Bay:

1a. Neck region distinguishable. No nuchal organ. - - - - - - 2
1b. No apparent neck region. Nuchal organ obvious. - - - - - - 3

2a. Exopodite of the first thoracic limb has 1 seta -- Podon leuckarti.
2b. Exopodite of the first thoracic limb has more than 1 seta - 4

3a. Thoracic limbs appear leaf-like and are covered by carapace - Penilia avirostris.
3b. Thoracic limbs cylindrical - - - - - - - - - - - - - - - - 5

4a. Second antennae have 4 segments. Mandibles have 13 cutting edges -- Podon polyphemoides.
4b. Second antennae have 5 segments. Mandibles have 9 major cutting edges -- Podon intermedius.

5a. Exopodites of thoracic limbs have formulae 2-3-3-1 -- Evadne tergestina.
5b. Exopodites of thoracic limbs do not have formulae 2-3-3-1.

6a. Abdomen apexes into a spine-like projection. Setae on first four exopodites have 2-2-2-1 formulae. Evadne spinifera.

6b. Abdomen does not have spine-like projection. Setae formulae are 2-2-1-1. Evadne nordmanni.
Descriptions

The genus *Podon* was originally described by Lilljeborg in 1853 as belonging to the family Polyphemoidae previously described by Baird in 1850. Primary diagnosis for *Podon polyphemoides* was taken from a later account by Lilljeborg (1901). Before the name of *polyphemoides* was standardized, the animal was referred to as *E. polyphemoides* (Leuckart, 1859), *Pleopsis minutus* (Sars, 1851), *P. mecznikovii* (Czerniavski, 1862), and *P. minutus* (DeGuerne, 1887; Stenroos, 1895). The name *Podon polyphemoides* was first used by Poppe (1888). Investigators previously using other names for the species began to accept *Podon polyphemoides* as a primary name for their synonymous species (Sars, 1890; Nordquist, 1891; Kramer, 1894; Apstein, 1901; Behning, 1912; Gibitz, 1922; and Rammner, 1930). Today there is some controversy as to whether *P. polyphemoides* actually belongs to the genus *Podon* (Gieskes, 1971c).

*Podon leuckarti* has not been described in as much detail as *P. polyphemoides*. Relative lack of knowledge relating to the etymology of the name may be due to the fact that most of the early history was described in Russia and is extremely difficult to obtain. Early descriptions given by Kuttner (1911) and Manuilova (1964) recounting Kuttner's description are commonly used as key references for identification of the species. *P. leuckarti* is recorded and reported in the Bay area by Bosch and Taylor (1968) and appears restricted to the lower Bay regions.

*Podon intermedius* is not clearly traceable through early literature. It appears that Lilljeborg (1900) first identified and named the species, although it had been described and recorded as another species in 1877 (Claus). Its presence in the Atlantic Ocean has been known for several years (Cleve, 1900; Apstéin, 1919; Jorgensen, 1933; Stephensen, 1938;

Bryan and Grant (1974) were the first to describe and report the species in the Chesapeake Bay area.

**Evadne nordmanni** was first described by Loven in 1835. Later accounts were given by many authors (Goodsir, 1843; Baird, 1850; Leydig, 1860; Sars, 1962; Nordquist, 1891; Stenroos, 1895; Lilljeborg, 1901; Behning, 1912; Kajdiz, 1912; and Rammner, 1930). More recent records of the species are given by Bainbridge (1958), Eriksson (1974), and in the Chesapeake Bay by Bosch and Taylor (1968) and Bryan (1977).

Claus (1862) first described *Evadne tergestina* as *Evadne mediterranea*. There was one report that this animal would be named *Evadne aspinosa* (Kramer, 1894), although there was no universal acceptance of this name. Earliest reports of *E. tergestina* dealt primarily with the distribution of the animal with very little reference to the ecology of the organisms (DeGuerne, 1887; Hansen, 1899; Juday, 1907; Schweiger, 1912; Kajdiz, 1912; Gibitz, 1922; and Rammner, 1931). Reports of the species in the Bay area were given by Bosch and Taylor (1968) and Bryan (1977).

*Penilia avirostris* appears to be the only Ctenopod cladoceran which may be considered to be truly marine. Earliest reports of the species are from Kramer (1894). Distributions and descriptions are reported by Sudler (1901), Leder (1915), Marukawa (1921), Rammner (1933), Steuer, (1933), Lochhead (1936-1937), Motoda and Anraku (1952), and Gaino (1971). DellaCroce (1964) was the first to report the species in the Bay area. Subsequent reports suggest that *P. avirostris* is confined to the lower Bay and may exist in the Bay in large numbers for short periods of time (Bryan, 1977).
The derivation of the name *Evadne spinifera* began with the original description by Lilljeborg (1853) and was distinguished as a species in a study performed by Muller (1868). A synonymous name for the species was given by Claus (1862) as *E. mediterranea*. Another name which was mistakenly given to the species was *E. spinosa*, although the mistake was rectified in an article by Hansen (1899) before the error was highly publicized. The species is found primarily in warmer regions, even though it is not strictly limited to such waters. Bryan (1977) recorded the species in Chesapeake Bay.
APPENDIX B

The following illustrations were made using an M20 Wild microscope equipped with a camera lucida. The illustrations are arranged in the following order: *P. avirostris*, *E. tergestina*, *E. nordmanni*, and *E. spinifera*. 
Figure A. Representative feeding appendages of *P. avirostris*.
1. second antenna, 2. first antenna, 3. maxillule, 4. labrum.
Figure B. *Podon polyphemoides*. 1. second antenna, 2. labrum, 3. first thoracic appendage, 4. antennule, 5. second thoracic appendage, 6. third thoracic appendage, 7. fourth thoracic appendage.
Figure C. *Evadne tergestina*. 1. first thoracic appendage, 2. second thoracic appendage, 3. third thoracic appendage, 4. fourth thoracic appendage. Each length given represents 0.005 mm.
Figure D. *Eudadne nordmanni*. 1. second antenna, 2. antennule, 3. first thoracic appendage, 4. second thoracic appendage, 5. third thoracic appendage, 6. fourth thoracic appendage. Unless otherwise indicated, measured lengths represent 0.005 mm.
Figure E. *Evadne spinifera*. 1. first thoracic appendage, 2. second thoracic appendage, 3. third thoracic appendage, 4. fourth thoracic appendage. Measured lengths represent 0.005 mm.