1996

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Available at: http://dx.doi.org/10.3354/meps139095
Ecology and life history traits of the benthopelagic mysid *Boreomysis oparva* from the eastern tropical Pacific oxygen minimum zone

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**ABSTRACT:** The ecology and life history traits of *Boreomysis oparva*, a recently described benthopelagic mysid, were examined from the seamount Volcano 7 which penetrates into the oxygen minimum zone. In the near-bottom waters, *B. oparva* was very abundant at the lower summit in the oxygen minimum zone (<0.2 ml O₂ L⁻¹). It decreased in abundance with increasing depth and increasing oxygen at the flank and was absent from the base of Volcano 7. Length distribution of free-living stages was continuous, from 4 to 26 mm, and similar at the lower summit and flank. This and the presence of larvae of all stages suggest continuous rather than seasonal reproduction. Reproductive females with developing larvae were more abundant at the lower summit than the flank. This new oxygen minimum zone mysid has relationships of egg volume and clutch size to female body length similar to other meso- and bathypelagic mysids.

**KEY WORDS:** Life history traits - Oxygen minimum zone - Deep-sea mysids - *Boreomysis oparva* - Seamounts

**INTRODUCTION**

Life history studies focus on coadapted traits as tactics to solve ecological problems (Stearns 1976). Environmental factors affect the reproductive success of parents by influencing the fitness of offspring and, thus, the evolution of life history traits. Factors that limit the energy available to organisms have the greatest effect on life history traits and the distribution of energy between traits. Comparative studies within taxa allow for predictions to be made from trends of life history traits. For example, brood volume and body volume of oceanic pelagic crustaceans tend to be correlated with each other (Mauchline 1988). Since female mysids (Superorder Peracarida) have lamellae in which developing larvae are carried, it is possible to study some life history traits of deep-sea mysids. In Mysidacea, meso- and bathypelagic species have relatively fewer and larger eggs than shallower-living species (Mauchline 1973, 1980, Wittmann 1984). Also the egg size tends to remain a constant proportion of body size for all meso- and bathypelagic mysids. Life history traits of a species limited by oxygen have not previously been examined with respect to these trends.


Midwater oxygen minimum zones (OMZs), which exist in all the world's oceans, are especially prominent in the eastern Atlantic off NW Africa, in the northern
Indian Ocean and in the eastern tropical Pacific (Kamykowski & Zentara 1990). In these regions, OMZs reach to about 1000 m depth and the oxygen concentration decreases to less than 0.2 ml O₂ l⁻¹. The concentration of oxygen influences plankton distributions, species composition and species assemblages in the OMZ (Vinogradov & Voronina 1962, Longhurst 1967, Brinton 1979, Weikert 1980, Saltzman 1995). At the lower interface of OMZs, biological and biogeochemical activities are elevated (Wishner et al. 1995).

The new mysid species *Boreomysis oparva* (Crustacea: Mysidacea) was discovered on a seamount in the eastern tropical Pacific (Saltzman & Bowman 1993). This inactive seamount, Volcano 7, protrudes up into the prominent OMZ. At the seamount summit, distinct faunal zones of the benthic and near-bottom communities appeared to be related to the oxygen concentration (Wishner et al. 1990, 1995, Levin et al. 1991). Between 750 and 770 m, a physiological boundary, related to the oxygen gradient, separated communities. Above the boundary, benthic megafaunal abundances were low, although meiofauna and sediment bacteria abundances were high. Tens of meters below the boundary, the near-bottom zooplankton, including *B. oparva*, and benthic megafauna and macrofauna were more abundant than usual in the deep sea. This paper examines the ecology and life history traits of *Boreomysis oparva* in relation to the OMZ at Volcano 7.

**METHODS**

The study site, Volcano 7, rises from a depth of 3400 m to its summit at 730 m. Zooplankton samples were collected in November 1988 from the submersible DSRV ‘ALVIN’ operated by the RV ‘Atlantis II’ at 13–14° N, 102–103° W. A total of 10 dives were made: 4 to the summit (724 to 908 m), 3 to the flank (1162 to 1339 m) and 3 to the base (2944 to 3112 m) of the seamount.

Mysids were collected with a multiple opening-closing 8 net system modified for the submersible (Wishner & Meise-Munns 1984, Wishner & Gowing 1987). Nets of 183 μm mesh, with mouth openings of 40 x 40 cm, were towed 1 to 5 m above the bottom. From the 8 net system, 4 sets of duplicate samples were collected during each dive. Three pairs of nets were open for about 15 min, filtering 26 to 275 m³ of water (median of 73 m³) and trapping the mysids in the cod end when closed. Specimens were killed with MS-222 (2 g l⁻¹) in situ and preserved in 4% buffered formalin on board, or preserved in situ with glutaraldehyde. Mysids collected in the cod end and net were combined for all analyses.

In situ environmental parameters (temperature, conductivity, pressure, and time) were recorded with a Seacat CTD attached to the submersible. Dissolved oxygen in the near-bottom water of the seamount at each site was determined from water collected in Niskin bottles attached to the submersible. Oxygen concentration was measured by a modification of the Winkler titration method for low oxygen (Carritt & Carpenter 1966). Particulate organic carbon (POC) in the water from the same bottles was determined with CHN measurements using a Carlo Erba 1106 Elemental Analyzer (Wishner et al. 1995). Time series measurements of temperature from moored current meters with temperature probes were described by Wishner et al. (1995). In the water column above and around Volcano 7, temperature, salinity, and dissolved oxygen were measured with an SBE 19 Seacat CTD Profiler. Data from 31 CTD casts defined the physical structure of the water column, especially the extent of the OMZ (Wishner et al. 1990, 1995, Levin et al. 1991).

Abundance of *Boreomysis oparva* in each sample was determined from the total number of free-living mysids (defined as mature and immature individuals) collected in the cod end and the net. Damaged and partial specimens were included for abundance estimates. The ratio of females to males was determined using total counts of specimens with sexual traits (lamellae, the plate like process of the brood pouch, for females and developed pleopods for males).

The developmental stages (larvae) of mysids, which are carried by the females in their brood pouch, were not included in abundance calculations. Some larvae were found intact in female brood pouches. Most larvae were found free in the samples but had most likely been lost from the female’s brood pouch during collection. Larvae were separated into 3 stages as defined by Jepson (1965) and Mauchline (1980). Briefly, Stage I were egg-like, Stage II had yolk above the eyes, attached to the carapace, and Stage III had more developed legs and little yolk above the eyes. Gravid females were females observed with at least one larva intact in their brood pouches.

Body length was measured using the Zeus video-based image analysis system (Estep & MacIntyre 1989). For free-living mysids, total length was measured from the tip of the rostrum to the end of the telson. The diameter for Stage I larvae and the total length for Stage II and Stage III larvae were measured. The lengths of specimens from several nets were not measured because they were either destroyed in analysis of feeding rates or gut.
RESULTS

Oxygen availability

Oxygen concentration was less than 0.5 ml O\textsubscript{2} l\textsuperscript{-1} at median depths of 72 to 1302 m and less than 0.1 ml O\textsubscript{2} l\textsuperscript{-1} at median depths of 288 to 1077 m (Fig 1). The minimum concentration of oxygen was found between 700 and 900 m and appeared to oscillate vertically over 30 m, probably with a semi-diurnal tidal cycle (Levin et al. 1991, Wishner et al. 1995, L. S. Mullineaux unpubl.). The seamount summit protrudes into the OMZ. Near-bottom oxygen concentration on the seamount increased with increasing depth. However, tidal displacement of water passing over the seamount probably caused periodic variation in oxygen concentration at any particular site on the summit (Levin et al. 1991, Wishner et al. 1995). Temperature-depth and temperature-oxygen relationships in the pelagic realm were compared with time series temperature records on the seamount summit (from moored current meters). They revealed that benthopelagic fauna above 800 m were exposed to lower oxygen concentrations more often than those below 800 m (Wishner et al. 1995). At 830 m, exposure to minimum oxygen was less than 0.1 ml; over 9 d, while at 730 m, exposure to minimum oxygen occurred more than 65% of the time.

Abundance and distribution

No mysids were collected above 770 m in the least-oxygenated waters at the upper summit. Just below 770 m, at 775 to 825 m on the lower summit, Boreomysis oparva was abundant (up to 114.3 per 100 m\textsuperscript{3}) and was found in almost all samples (Fig. 2, Table 1). The oxygen concentration was slightly higher and POC was lower at the lower summit than at the upper summit (Saltzman 1995, Wishner et al. 1995). B. oparva was an order of
Table 1. *Boreomysis oparva*. Abundance and frequency of occurrence in the near-bottom waters of Volcano 7. Abundances are reported in number per 100 m³. 'With zeros' refers to the inclusion of zero abundance samples and 'without zeros' refers to the exclusion of these samples in calculating the mean abundance. Gender ratio and percent immature were computed with the total number of males, females, and immatures at each depth zone. Immature mysids were mysids without sexual traits but not larvae.

<table>
<thead>
<tr>
<th>Samples with <em>B. oparva</em></th>
<th>Lower summit</th>
<th>Flank</th>
<th>Lower summit &amp; flank</th>
</tr>
</thead>
<tbody>
<tr>
<td>% with <em>B. oparva</em></td>
<td>26 of 28</td>
<td>15 of 24</td>
<td>41 of 52</td>
</tr>
<tr>
<td>Total</td>
<td>93</td>
<td>63</td>
<td>78</td>
</tr>
<tr>
<td>Females</td>
<td>75</td>
<td>33</td>
<td>56</td>
</tr>
<tr>
<td>Average abundance</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total, with zeros</td>
<td>34.1 ± 3.0</td>
<td>2.8 ± 3.9</td>
<td>19.6 ± 27.1</td>
</tr>
<tr>
<td>Total, without zeros</td>
<td>36.7 ± 29.6</td>
<td>4.5 ± 4.0</td>
<td>24.9 ± 28.3</td>
</tr>
<tr>
<td>Females, with zeros</td>
<td>10.3 ± 10.4</td>
<td>0.6 ± 1.2</td>
<td>5.8 ± 9.0</td>
</tr>
<tr>
<td>Median abundance</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>With zeros</td>
<td>36.8</td>
<td>1.6</td>
<td>5.4</td>
</tr>
<tr>
<td>Without zeros</td>
<td>40.4</td>
<td>3</td>
<td>11.2</td>
</tr>
<tr>
<td>Maximum abundance</td>
<td>114.3</td>
<td>14.8</td>
<td>114.3</td>
</tr>
<tr>
<td>Gender and stage distribution</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female: male ratio</td>
<td>2.8</td>
<td>1.7</td>
<td>2.7</td>
</tr>
<tr>
<td>Percent immature</td>
<td>64</td>
<td>72</td>
<td>65</td>
</tr>
</tbody>
</table>

Abundances of *Boreomysis oparva* were not significantly different in samples collected simultaneously in paired nets. The abundance difference between paired samples was the same for both 15 min tows and 1 h tows (t-test, p < 0.05). The abundance differences between paired samples were greater at the lower summit (18.2 ± 20.5 per 100 m³) than at the flank (4.0 ± 3.6 per 100 m³) (Mann-Whitney U-test, p < 0.05).

Two other *Boreomysis* species occurred in the near-bottom water at the lower summit (Table 2). Sixteen specimens of *B. californica* and 1 specimen of an unidentified *Boreomysis* sp. were collected in 1 sample. *B. oparva* was less abundant than *B. californica* in this sample. In the paired sample collected at the same time, only *B. oparva* was found. In this single species sample, *B. oparva* (12.7 per 100 m³) was only slightly more abundant than in the sample with both *B. oparva* and *B. californica* (11.5 per 100 m³).

At both the lower summit and the flank, female *Boreomysis oparva* outnumbered the males with female:male ratios of 2.8 and 1.7 respectively (Table 1). Overall, 65% of the specimens were immature and their gender could not be determined; these were not included in the sex ratio.

Length distribution

Free-living *Boreomysis oparva* ranged in total length from about 4 to 25.9 mm. The 3 largest specimens were mature males. Length distribution of free-living *B. oparva* did not show separation of size classes (Fig. 3A). Frequency of length categories was evenly distributed for mid-sized mysids of 10 to 20 mm at the

Table 2. *Boreomysis* species other than *Boreomysis oparva* that were collected on and around Volcano 7. The near-bottom sample from an ALVIN tow also contained *B. oparva*. Pelagic samples were collected with a MOCNESS above the flank of Volcano 7 (methods in Saltzman 1995).

<table>
<thead>
<tr>
<th>Species</th>
<th>Stage</th>
<th>No. ind</th>
<th>Abundance (no. per 100 m³)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Near bottom, 816–988 m</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. californica</em></td>
<td>Immature female</td>
<td>1</td>
<td>0.37</td>
</tr>
<tr>
<td>(Ortmann, 1894)</td>
<td>Immature male</td>
<td>1</td>
<td>0.37</td>
</tr>
<tr>
<td><em>Boreomysis sp. 1</em></td>
<td>Immature male</td>
<td>14</td>
<td>5.22</td>
</tr>
<tr>
<td></td>
<td>Immature female</td>
<td>1</td>
<td>0.37</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>6.34</td>
<td></td>
</tr>
</tbody>
</table>

| **Pelagic, 795–995 m** |                        |         |                           |
| *Boreomysis sp. 2*    | Female                 | 2       | 0.18                      |
| (B. atlantica or B. hansenii) |                | 1       | 0.09                      |
| Female                | 1                      | 0.28    |
| Immature female       | 3                      | 0.46    |
| Immature male         | 5                      | 0.46    |
| Total                 |                        | 1.01    |                           |

| **Pelagic, 995–1142 m** |                        |         |                           |
| *B. curtirostris*      | Female                 | 1       | 0.14                      |
| (Burrstein & Tchindonova, 1958) |            |         |                           |
Saltzman. Ecology and life history of Boreomysis oparva

A. Length Distribution of B. oparva

B. Length Distribution of Larvae

C. Length Distribution of female B. oparva

Fig. 3. Boreomysis oparva. Length distribution in the near-bottom waters of Volcano 7. (A) Free-living mysids at the summit and flank (523 mysids). Each interval is 0.5 mm. (B) Larval mysids at the summit and flank areas combined (67 Stage I, 435 Stage II and Stage III). (C) Female mysids, with and without larvae in their brood pouches, at the summit and flank (91 females).

lower summit, suggesting continuous growth and reproduction. Evidence of even distribution was not as strong at the flank. This was the result of a smaller sample at the flank. Smaller size categories were less common at the flank.

Larvae (all stages) ranged in size from 0.8 to 5 mm. The Stage I larvae ranged in size from 0.82 to 1.61 mm (Fig. 3B). The low frequency of larvae in the 1.5 to 2.0 mm range was due to round Stage I larvae developing laterally rather than spherically into Stage II larvae. Stages II and III overlapped in the 3.5 to 4.0 mm size class. Larvae are probably released as free-living mysids at 4 to 5 mm. A comparison between the lower summit and flank is not presented because a total of only 7 larvae was collected at the flank.

Females began to show lamellae when longer than 16 mm (Fig. 3C). The mean length of all females was 20.6 ± 1.5 mm. Females made up 72% of the mysids in the 20 to 22 mm class. Twelve females from the lower summit were observed carrying larvae. The mean length of a gravid female (20.3 ± 1.5 mm) was nearly the same as for all females.

Reproductive life history traits

Boreomysis oparva were members of a reproducing population. At the lower summit, 7% of the females were observed with larvae in their brood pouches. Each gravid female had only 1 stage of larva, and all 3 stages of larvae were found in brood pouches and free in the samples. The mean observed clutch size of females with greater than 3 larvae was 8.5 larvae per female with a range of 5 to 12 larvae per female. The maximum observed clutch size was 12 Stage II larvae in a 23.29 mm female. The smallest mysid observed with a clutch was 18.13 mm and had 7 Stage III larvae. At the flank, none of the females were gravid.

DISCUSSION

Volcano 7 penetrates into the OMZ of the eastern tropical Pacific. At the summit, between 750 and 770 m, it has been hypothesized that a physiological boundary separates the zooplankton communities; the upper and lower summit both had coarse-grained sediments, organic matter availability was high and constant, and oxygen concentration increased only slightly across the boundary (Wishner et al. 1990, 1995, Levin et al. 1991). The vertical distribution of the new species Boreomysis oparva was from slightly deeper than the region of the physiological boundary downslope to the flank, from about 770 m to at least 1340 m (but above 3000 m). The vertical distributions of most mysid species are unknown (Mauchline & Murano 1977).

Population characteristics of Boreomysis oparva changed downslope. Abundances were higher at the lower summit, associated with the lower OMZ interface, than at the flank. In addition, reproductive strategies (i.e. sex ratio, clutch size) appeared to differ between animals at the lower summit and flank. These differences may be related to the distance from the lower OMZ interface, oxygen concentration and fluctu...
Mysids often live in aggregations, some as breeding aggregations and others as schools, during certain periods of their life cycles (Mauchline 1980). Because each sample was taken over a variety of microenvironments (altitude, slope, substrate type), it was not possible to determine any preference from these samples.

![Diagram](image-url)

**Fig. 4. Boreomysis oparva.** The relationship between total average body length (raised to the third power) of females and (A) average egg volume, (B) average clutch size and (C) brood volume: (*) from averages of observed meso- and bathypelagic mysids (Mauchline 1973, 1980); [l] the observed mean of *B. oparva* with error bars. Error bars represent the average difference between calculated value of the mean ± 1 SD deviation of the observed values. Regression lines are from equations reported by Mauchline (1980), based on species where greater than 100 broods were observed and averaged for each species individually. Egg volume is the volume of an average Stage I larva assuming a spherical shape.
The variation in abundance between simultaneously collecting nets may be explained in several ways. (1) Mysids which were distributed in small groups or swarms may have very specific altitude and/or substrate preferences. (2) Patchiness may be smaller than the distance between nets and distributed unevenly. (3) The submersible often traversed steep slopes, with the inboard net close to the bottom and the outboard net farther away, causing the samples to be collected from different altitudes.

Reproductive life history trait comparisons

Comparisons of reproductive traits of mysids have been made in several studies (Mauchline 1973, 1980, 1988, Wittmann 1984, Clark & Threlfall 1993). The relationship between egg volume and body length for Boreomysis oparva appears to fit the relationship found by Mauchline (1980) for meso- and bathypelagic mysids (Fig. 4A). There appears to be a minimum size of egg, which seems to influence the size at emergence from the female brood pouch (Mauchline 1980). Post-emergence larvae are unable to swim until they molt and may be subject to predation or cannibalism. This molt takes place within hours of emergence (Mauchline 1980). Thus, it is likely that there is a minimum viable size of emerging larvae (Mauchline 1988).

Clutch size is another ecologically important life history trait. The observed clutch size in relation to body length of Boreomysis oparva was compared with that of other meso- and bathypelagic mysids (Fig. 4B). The regression coefficient was not significant for meso- and bathypelagic mysids (r = 0.39) (Mauchline 1973), yet B. oparva seems to fit with other observations. Observed clutch size in all meso- and bathypelagic mysids is a conservative estimate since loss of larvae is quite common.

Brood pouches of Mysidacea are made of 2, 3, or 7 overlapping pairs of lamellae attached to their thoracic legs. Species of the sub-order Lophogastrida and several genera of the sub-order Mysida, including Boreomysis, have 7 pairs of lamellae. The Lophogastrida include many meso- and bathypelagic species. Seven lamellae as opposed to 2 or 3 may provide more volume for developing larvae, yet larvae may be more easily lost. Loss of larvae from the brood pouch is not just a sampling concern, but a real problem for gravid females. Behavioral patterns show that females provide care to the larvae. Lateral movement of the lamellae in a rhythmic manner provides oxygen to the larvae (Mauchline 1980). This behavior probably causes accidental loss of larvae. Females have been observed in the laboratory replacing or 'adopting' lost larvae back into their brood pouch (Mauchline 1980, Wittmann 1984).

In natural populations, females have been observed with 'adopted' larvae in their brood pouches (Wittmann 1976).

Brood volume, the product of clutch size and egg volume, is also directly related to body length, raised to the third power, for all epi-, meso- and bathypelagic mysids (Mauchline 1973, 1980). From these comparisons, Boreomysis oparva, a benthopelagic mysid, looks like a typical mesopelagic species (Fig. 4). Oxygen limitation does not appear to disrupt the general relationships between these life history traits.

Life history traits of Boreomysis oparva are similar to those of other Boreomysis species (Table 3). B. oparva has smaller Stage I larvae but larger Stage III larvae than B. tridens, a bathypelagic species. Growth rate or minimum viable size at emergence may be reasons for this difference. The clutch is considerably smaller for B. oparva than for most other Boreomysis species reported. Clark & Threlfall (1993) reported that B. nobilis, a cold-water near-bottom species, has a larger brood volume and egg volume in relation to its body volume than expected for epipelagic and coastal mysids from Mauchline's (1980) relationships. They suggested that this is because egg size is related to temperature (Wittmann 1984).

<table>
<thead>
<tr>
<th>Species</th>
<th>Body length of female (mm)</th>
<th>Range of clutch size (larvae/female)</th>
<th>Stage I length (mm)</th>
<th>Stage II length (mm)</th>
<th>Stage III length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Boreomysis oparva</td>
<td>20.6 ± 1.5</td>
<td>5 - 12</td>
<td>1.1 ± 0.1</td>
<td>3.5 ± 0.5</td>
<td>4.4 ± 0.5</td>
</tr>
<tr>
<td></td>
<td>(17.2 - 24.3)</td>
<td></td>
<td>(0.8 - 1.6)</td>
<td>(2.0 - 4.5)</td>
<td>(2.3 - 5.6)</td>
</tr>
<tr>
<td>B. arctica</td>
<td>20 - 28</td>
<td>3 - 44</td>
<td>0.8 - 1.1</td>
<td></td>
<td>3.9</td>
</tr>
<tr>
<td>B. megalops</td>
<td>15 - 20</td>
<td>9 - 18</td>
<td>0.7 - 0.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B. microps</td>
<td>35.1 ± 1.6</td>
<td>20 - 25</td>
<td>1.6 ± 0.1</td>
<td>-7.5 - 8.0</td>
<td></td>
</tr>
<tr>
<td>B. tridens</td>
<td>20 - 28</td>
<td>27 - 35</td>
<td>1.9 - 2.1</td>
<td>3.8 - 3.9</td>
<td></td>
</tr>
</tbody>
</table>

Table 3. Life history traits of Boreomysis spp. (as mean ± SE or range). For Boreomysis oparva, observed clutch size is reported and range of lengths is included in parentheses. Data for other species compiled by Mauchline (1973, 1980, 1986) and Clark & Threlfall (1993).
5.7°C water had smaller larvae than B. nobilis from −1.3 to 2.2°C water. The trend in temperature-size differences between these 2 species is consistent with the relationship described by Wittmann (1984).

New species remarks

Finding a new species at Volcano 7 is not surprising because near-bottom deep-sea zooplankton have not been well studied in general and especially not on seamounts (Kaufmann et al. 1989). Furthermore, the high percentage of endemic species suggests that seamounts are sites with a high incidence of speciation (Wilson & Kaufmann 1987, Rogers 1994). Seamounts may enhance speciation through isolation (Wilson & Kaufmann 1987) or may act as stepping stones for dispersal (Hamilton 1956, Newman 1986).

All the Mysidacea found in the Volcano 7 area were Boreomysis spp. In the benthopelagic zone, there were a total of 3 species of Boreomysis and, in the pelagic zone, there were 2 additional species (Table 2). Many Boreomysis spp. are considered meso- or bathypelagic from pelagic sampling, though most species of Mysidacea live in close association with the ocean bottom (Fossa 1985, Kaartvedt 1985). One of the important morphological features of Boreomysis is 7 pairs of lamellae in the females. Since larvae are provided with oxygen by the female moving the lamellae, Boreomysis spp., or other genera with 7 pairs of lamellae, may be able to provide more oxygen to their larvae. This is especially important for species living within the oxygen minimum zone.

Acknowledgements. I thank all the scientists, the captain, and the crew who participated and helped in this cruise. Thank you to K. F. Wishner for providing the specimens for analysis and reviewing this manuscript and to C. J. Ashjian for teaching me to use the Zeus system. This work was funded in part by NSF grants OCE-8608846, OCE-8716564, and OCE-8720193.

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This article was submitted to the editor

Manuscript first received: October 10, 1995
Revised version accepted: March 4, 1996