Egg production by the calanoid copepod *Acartia tonsa* in the mesohaline Chesapeake Bay: the importance of food resources and temperature

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**ABSTRACT:** Egg production of *Acartia tonsa* females was measured simultaneously with grazing and other biological and physical parameters in the mesohaline portion of Chesapeake Bay, USA, during periods of 1987 and 1988. We hypothesized that egg production would be related to food abundance *in situ*, depending principally on phytoplankton in spring and microzooplankton in summer. Step-wise multiple regression analysis indicated that egg production (female C d⁻¹) was significantly correlated with temperature (parabolic transform), protozoan microplankton biomass, and the C:N ratio of suspended particulate matter. Egg production was not correlated with any measures of phytoplankton biomass, production or ingestion. Egg production was significantly higher at night while there was no observed diel trend in ingestion of phytoplankton by *A. tonsa*. The amount of carbon ingested as phytoplankton was adequate to support calculated growth and metabolic requirements of *A. tonsa* females roughly half the time. Carboy experiments were used to compare the relative amounts of phytoplankton and microzooplankton carbon ingested by *A. tonsa* in the bay on 2 occasions in May and August of 1988. Copepod carbon-specific ingestion rates on phytoplankton were low [5.5 μg C (mg C)⁻¹ h⁻¹] in May, but relatively high on microzooplankton [22.7 μg C (mg C)⁻¹ h⁻¹]. In August, microzooplankton were ingested at lower rates compared to May [7.2 μg C (mg C)⁻¹ h⁻¹] but phytoplankton were ingested at much higher rates [48.2 μg C (mg C)⁻¹ h⁻¹]. For both experiments, the total C ingested as phytoplankton and microzooplankton was sufficient to balance the calculated respiration and measured egg production requirements of *A. tonsa* females. From these results we conclude that microzooplankton can provide an important food source for estuarine copepods, and that temperature and microzooplankton rather than phytoplankton abundance may be the best indicators of *A. tonsa* reproductive potential in Chesapeake Bay.

**INTRODUCTION**

Reproduction rate of copepods has been shown to depend on temperature (McLaren 1965, Heinle 1969, Paffenhofer & Harris 1976), food quantity (Huntley & Boyd 1984) and the quality of available food (Checkley 1980a, b). The relative importance of these factors in controlling copepod growth and production can vary between species and location, and it may depend on recent feeding history. The goal of this study was to determine which factors control egg production of the dominant copepod species *Acartia tonsa* in Chesapeake Bay, USA, during summer.

Egg production by adult female copepods has been used as an index of growth since it is a relatively simple measurement (Marshall & Orr 1955). Egg production of *Acartia tonsa* has been related to food abundance and quality (Dagg 1977, Cahoon 1981, Durbin et al. 1983, Kiorboe 1989) and temperature (Sekiguchi et al. 1980, Uye 1981) in laboratory studies, and the concentration of chl a > 10 μm (Bellantoni & Peterson 1987), temperature and the amount of particulate nitrogen (Ambler 1982) in situ. Because egg production is an integrated response to recent feeding history, it may be more closely related to concentrations of food measured 12 to 24 h prior to egg laying (Stearns et al. 1989).
Protozoan microplankton are a potentially important food source in the size range of prey items selected by copepods. In laboratory experiments, copepods clear planktonic ciliates and heterotrophic dinoflagellates at rates equal to or greater than algae (Stoecker & Capuzzo 1990, and references therein). In addition, microzooplankton have been shown to provide up to 50% of the C ingested by *Acartia tonsa* (Gifford & Dagg 1988, Tiselius 1989). However, no information is presently available concerning the effect of microzooplankton ingestion on copepod egg production.

Chesapeake Bay is characterized by spring blooms of relatively large-cell phytoplankton species (principally diatoms and large flagellates), followed in summer by water column stratification, increasing water temperature, and high rates of primary production by phytoplankton < 20 µm in diameter (Malone et al. 1986, McCarthy et al. 1974). Under these conditions, we hypothesized that copepods would feed on larger phytoplankton cells available in the spring, and on microzooplankton when small algae are more abundant during summer.

To further understand the factors that control copepod production in estuaries, we present results from measurements of egg production, ingestion of phytoplankton and microzooplankton by the copepod *Acartia tonsa*, and measurements of hydrographic parameters taken 2 successive years in Chesapeake Bay.

**METHODS**

**Egg production experiments.** Shipboard egg production experiments with *Acartia tonsa* females were carried out during cruises to the mesohaline reach of Chesapeake Bay (37°41' N, 64°15' W). Experiments were run on 4 dates from May to August 1987 and 9 dates spanning the period May to October 1988. Copepods used in the experiments were collected in a 200 µm mesh, 0.5 m diameter plankton net fitted with a closed cod-end towed obliquely through the surface mixed layer. After the tow, cod-end contents were gently diluted and transferred into 2 l plastic beakers. *A. tonsa* adult females were identified under a stereoscopic microscope (dim light for night-time incubations) and 3 to 4 copepods were gently picked by pipet and placed into egg production chambers pre-filled with 200 µm screened surface water. Chambers were then placed into an incubator containing flowing surface water (Fig. 1) for 2 consecutive 12 h (12 night:12 day) or one 24 h incubation. Chambers containing only 200 µm screened water were incubated along with treatment chambers to correct for eggs and small nauplii added with the water.

At the end of the experimental period, chambers were removed from the incubator and the water allowed to drain, concentrating copepods on the first mesh and eggs on the bottom mesh (Fig. 1). Both copepods and eggs were washed into sample jars with filtered bay water, the condition of females noted (immobile opaque individuals were considered dead and not included in egg production rate calculations), and the samples preserved in 5% buffered formalin. In the laboratory, adult female and egg length were determined using a microscope, digitizing pad and computer image-analysis system. Egg carbon was estimated using the conversion factor 0.0305 µg C egg−1 (Ambler 1982). Female carbon was calculated from an equation derived by drying and weighing different stages of preserved *Acartia tonsa* (allowing for 30% shrinkage due to preservation in formalin) and assuming a carbon to dry weight ratio of 0.32:

$$C_f = 3.04 (L^{1.81})$$

where $C_f$ is the biomass in µg C female−1 and $L$ = length in mm ($r^2 = 0.64, SE_{slope} = 0.399$).

**Grazing experiments.** Copepod grazing of phytoplankton was measured simultaneously during all egg production experiments. Copepods were collected as described above and 20 to 60 late-stage copepodites (Stages CIV to CVI) >200 µm gently transferred to six 1 l polycarbonate bottles containing 200 µm screened bay water. For experiments run in 1987, phytoplankton were pre-labelled for 1 h under fluorescent light with 14C-bicarbonate before adding copepods (Daro 1980,
White & Roman: *Acartia tonsa* egg production in Chesapeake Bay

Roman et al. 1988a). Once copepods were added, the bottles were placed in light (day) or dark (night) incubators with flow-through bay water. During 1988 phytoplankton were labelled after adding copepods (Daro 1978). A combination of $^3$H-methylamine and $^{14}$C-bicarbonate was added in daylight incubations while $^3$H-methylamine alone was used for dark incubations. $^3$H-methylamine is an ammonium analog taken up by phytoplankton in both light and dark (Balch 1985) which gives grazing rates similar to those obtained using $^{14}$C-bicarbonate ($s = 42$, $r^2 = 0.80$; White & Roman 1991). This method eliminates the need to pre-label phytoplankton for nighttime feeding measurements.

Incubation times were short (15 to 60 min) to reduce the transfer of label through herbivorous protozoa to copepods. After incubations, copepods were washed on a 200 μm sieve with 0.22 μm filtered bay water (FBW). Washed copepods and particulate matter were collected on 12.0 and 3.0 μm polycarbonate filters respectively and their activity analyzed by liquid scintillation counting.

Clearance of phytoplankton [ml (mg copepod C)$^{-1}$ h$^{-1}$] was calculated using the equations of Daro (1978), and converted to carbon ingested [μg phytoplankton C (mg copepod C)$^{-1}$ h$^{-1}$] multiplying by phytoplankton carbon. A conversion factor for phytoplankton carbon-to-chlorophyll of 51 was derived from the slope of a regression of total particulate organic carbon (POC) and chl a data collected during the study [POC = 235 + 51(chl a), $n = 13$, $r^2 = 0.48$, SE = ±16]. In this calculation, we assumed: (1) the y-intercept represents non-phytoplankton carbon and (2) that this value varies independently of phytoplankton carbon (Strickland 1960, Banse 1977). Although this technique has been criticized in situations where the above assumptions are grossly violated (Banse 1977), we feel it provides a relatively efficient method of estimating phytoplankton carbon in situ. Notice that the ratio of 51 used by us is high, but in the range of values obtained for phytoplankton collected from natural populations and laboratory cultures (23 to 79 for mixed phytoplankton, Parsons et al. 1977; 30 to 51 for *Proorocentrum mariae-lebouriae* collected from Chesapeake Bay surface water, Harding & Coats 1988).

**Property measurements.** Temperature, salinity and chl a depth profiles were determined using a pump-CTD-fluorometer system (Malone & Ducklow 1990). To convert the fluorescence measurements to chl a, chlorophyll samples collected from the surface and bottom were analyzed by fluorometer after acetone extraction (Parsons et al. 1984). The chlorophyll size fraction >10 μm was determined by pre-screening water with 10 μm Nitex. Particulate carbon and nitrogen were determined for pump water collected on pre-combusted GF/F glass fiber filters and measured by a Control Data 240 HA analyzer. Microzooplankton (oligotrich and tintinnid ciliates and heterotrophic dinoflagellates >10 μm in diameter) were collected by Niskin bottle. The bottle contents were mixed by inverting the bottle and replicate 150 ml whole water samples preserved in 2% glutaraldehyde. Subsample volumes were adjusted to settle 300 individual protozoa in settling chambers for enumeration with a Zeiss inverted microscope. Abundances of major taxonomic and size groupings were converted to biomass assuming spherical shape (cylindrical for tintinnids) and using literature-derived carbon to volume ratios (Table 1).

**Carboy experiments.** Experiments to estimate ingestion of microzooplankton by copepods were run on 2 cruises to the Chesapeake Bay during May 12 and August 11, 1988. Water was collected from the surface by bucket and gently reverse-filtered through a 64 μm nitex screen into acid-washed, 10 l polycarbonate carboys. Two control carboys contained only 64 μm screened bay water. Two treatment carboys contained only 64 μm screened bay water. Two treatment carboys contained screened water with Stages CIV to CV1 *Acartia tonsa* added at 2 to 5x in situ concentrations (May) to 179 (August) 1$^{-1}$; copepods were collected and separated as described above for egg production experiments. Carboys were incubated for 24 h in flow-through deck incubators covered with neutral density screen (roughly 60% ambient light) during day and black plastic at night.

Time-series samples were collected by gently inverting the carboys several times to mix contents, and then pouring 1200 ml from each into 2 l plastic beakers. One sample from each carboy was taken for chl a, particulate C and N, and for microzooplankton abundance. Microzooplankton >10 μm in replicate subsamples were settled in Utermöhl chambers (7 to 15 ml), and

<table>
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<th>Category</th>
<th>Cell diameter (μm)</th>
<th>Conversion factor (μg C μm$^{-2}$)</th>
<th>Mean cell radius (μm)</th>
<th>Cell carbon (ng C cell$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
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<td></td>
<td>20–50</td>
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<td>17.5</td>
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<td></td>
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</tr>
<tr>
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<td>90$^{c}$</td>
<td>10</td>
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</tr>
<tr>
<td>Heterotrophic dinoflagellates</td>
<td>&gt;20</td>
<td>120$^{d}$</td>
<td>9</td>
<td>0.844</td>
</tr>
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</table>

$^{a}$Conversion factors were obtained from: $^{b}$Putt & Stoecker (1989); $^{c}$Heinbokel (1978); $^{d}$Strathmann (1967). Carbon conversions were corrected for shrinkage due to preservation with 2% glutaraldehyde (Choi & Stoecker 1989).
enumerated with an inverted microscope. Clearance rate [ml (mg copepod C)\(^{-1}\) h\(^{-1}\)] was calculated by integrating the average change in cell density for the 2 replicate treatment carboys over all time periods, and correcting for growth of prey in control carboys (Frost 1972). Carbon ingested [\(\mu g\) C (mg copepod C)\(^{-1}\) h\(^{-1}\)] was calculated from clearance rates and estimates of biomass for each functional size category of microzooplankton (Table 1).

RESULTS

Egg production

Egg production rate was variable both within and between sample dates, and only the highest and lowest measured rates were significantly different (95 % confidence level; Fig. 2). Rates did not vary linearly with temperature or phytoplankton carbon in either year, but did track microzooplankton carbon > 20 \(\mu m\) during 1988. These results are supported by separate simple least squares regression analyses of egg production against individual environmental parameters (non-transformed), with only the regression model containing microzooplankton significant (Table 2).

Because biological processes often respond to changes in environmental parameters non-linearly, we examined the relationship between egg production and transformed field data. Egg production and temperature data show that these rates generally increased with temperature up to 27 °C, but were reduced at higher temperatures (Fig. 2) indicating a polynomial or curved function may better represent the relationship between them. In addition, egg production should also have a nonlinear response to increases in food concentration, reaching a maximum level at some critical concentration and not increasing beyond that (Checkley 1980b, Kjærboe et al. 1985). Transformations used to linearize the relationship between egg production and independent variables are shown in Table 2.

Some of the variables considered in the single variable regression analyses may act simultaneously (but independently) to affect egg production. Therefore, we used step-wise multiple linear regression analysis to examine the effects of several variables on egg production at once. Since microzooplankton were not collected during 1987, only data from the 9 sampling dates in 1988 were included in the multiple regression analysis.

The multiple linear regression model utilizing transformed temperature data gave results different from the single variable regression analyses. Significant variables were selected by step-wise factor analysis (Sokal & Rolf 1981). The polynomial temperature function accounted for the most variation in egg production, although both microzooplankton biomass and C:N ratio were also significant (Table 3). Egg production was not closely related to chlorophyll in either the simple or multiple regression analysis.

Table 2. *Acartia tonsa*. Results of simple least squares regression of copepod egg production vs different environmental parameters measured simultaneously in Chesapeake Bay during 1987 and 1988. Variables consist of either raw or transformed data with operation shown: \(T\) = temperature (°C); whl chl = chl a from GF/F filters (\(\mu g\) l\(^{-1}\)); chl > 10 = chl a > 10 \(\mu m\) (\(\mu g\) l\(^{-1}\)); mz = microzooplankton carbon > 10 \(\mu m\) (\(\mu g\) l\(^{-1}\)); C:N = carbon-to-nitrogen ratio of suspended particulate matter; S = stratification parameter [\(A_{w} - A_{m}\) \(\times\) mixed depth \(^{-1}\)]; \(l_{p}\) = ingestion of phytoplankton [\(\mu g\) phytoplankton C (mg copepod C\(^{-1}\) h\(^{-1}\)]; \(aT\) = polynomial equation relating temperature and egg production; n = no. of observations

<table>
<thead>
<tr>
<th>Variable</th>
<th>n</th>
<th>(r^2)</th>
<th>p-value</th>
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</tr>
<tr>
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<tr>
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</tr>
<tr>
<td>C:N</td>
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<td>0.20</td>
</tr>
<tr>
<td>S</td>
<td>13</td>
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<td>0.96</td>
</tr>
<tr>
<td>(l_{p})</td>
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<td>0.09</td>
<td>0.31</td>
</tr>
<tr>
<td>(aT)</td>
<td>9</td>
<td>0.73</td>
<td>0.003**</td>
</tr>
<tr>
<td>log chl</td>
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</tr>
<tr>
<td>log mz</td>
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<td>0.03*</td>
</tr>
<tr>
<td>log (l_{p})</td>
<td>9</td>
<td>0.02</td>
<td>0.72</td>
</tr>
</tbody>
</table>

*Significant \(r^2\), ** highly significant \(r^2\)

![Graph](image-url)
Ingestion of phytoplankton

The weight-specific ingestion rate of phytoplankton by copepods (I_p = μg phytoplankton C (mg copepod C)^{-1} h^{-1}) varied by season with rates generally high during summer, but low during May of both years and October 1988 (Fig. 3). Variability was highest between late May and early June 1988 (Fig. 3). Unlike egg production, log I_p was directly correlated with temperature (r^2 = 0.67, p<0.01) and therefore could not be considered in the multiple regression model. However, results of partial correlation analysis (Sokal & Rolf 1981) show that log I_p accounts for little if any of the variation in egg production when considered with the transformed temperature data (partial correlation coefficients: aT - bT^2 = 0.66, log I_p = 0.16, n = 11). Taken together with the results of the regression analyses, these findings indicate that phytoplankton abundance and ingestion are poor predictors of Acartia tonsa egg production in Chesapeake Bay.

Egg production (EP) was not closely correlated with log I_p, as a function of time of day or depth in the water column. We made separate night and day measurements of egg production together with I_p on 8 occasions (Fig. 4). Although egg production was significantly higher at night on 7 of 8 dates sampled, the ratio of I_p day: I_p night was variable, and frequently there was no difference in I_p (Fig. 4A). Egg production was better correlated with log I_p measured 12 h previously (i.e. EP night vs log I_p day, r^2 = 0.69) than with I_p measured simultaneously (i.e. EP night vs log I_p night, r^2 = 0.41), indicating a time lag between ingestion and egg production. For the same dates, egg production was poorly correlated with chlorophyll measured both simultaneously (r^2 = 0.12) and 12 h previously (r^2 = 0.05).

On May 19, 1988, ingestion and egg production were measured with Acartia tonsa and water collected from both 10 m in the chlorophyll maximum (CM = 22.3 μg chl a l^{-1}) and the surface (CM = 10.9 μg chl a l^{-1}). Egg production was significantly higher (outside 95% confidence limits) in CM water compared with surface water. In contrast I_p was not significantly different (p = 0.05) between surface and CM water (Fig. 5).

To determine whether ingestion of phytoplankton could balance the carbon requirements of Acartia tonsa females during our study, we compared temperature-specific respiration and growth rate (defined as measured egg production) with measured ingestion rates (Table 4). Growth rate was calculated using the equation:

\[ G = EP \times C_f \]  

where G = growth rate (μg C female^{-1} d^{-1}); EP = fraction of female carbon produced as eggs per day (d^{-1}); and C_f = female carbon (μg C female^{-1}). Carbon demand due to respiration was estimated for Acartia tonsa using a relationship derived from Conover (1956: Fig. 20):

\[ R = C_f K (0.543 T + 0.25) \]  

where R = respired carbon (μg C female^{-1} d^{-1}); T = temperature (°C); and K includes factors converting oxygen volume and
Fig. 4. *Acartia tonsa*. Comparison of nighttime and daytime rates of (A) phytoplankton ingestion and (B) egg production by adult female copepods measured on different dates in Chesapeake Bay. Error bars = SE of mean.

Dry weight to carbon units (12 mg C/22.4 ml O2; Parsons et al. 1977) and hours to days. The respiratory quotient is assumed to equal 1. Since female biomass did not differ by more than 21% during our study, respiration was treated as a simple linear, rather than logarithmic, function of biomass.

On roughly half of the sampling dates, ingestion of phytoplankton ($I_p$) alone was not sufficient to meet the carbon requirements for growth and respiration of female *Acartia tonsa* [$I_p/(G+R) < 1.0$]. This shortfall occurred infrequently during summer, often in May of both years and during October 1988 (Table 4). Egestion was not measured, so ingestion rates used in the comparison were not corrected for assimilation efficiency. Therefore, actual carbon assimilated by *A. tonsa* to balance growth and metabolism may be 10 to 50% less than ingested (Kieboe et al. 1985).

**Carboy experiments**

There was a clear difference between sample dates in the proportions of microzooplankton and phytoplankton consumed by late stage *Acartia tonsa* copepodes. Microzooplankton had high growth rates and were cleared at the highest rates in the carboys during the August experiments (Fig. 6). However, cell densities were higher initially in May (Fig. 6; $t = 0$ h), while copepod densities in carboys were $3x$ higher in August, so that ingestion of microzooplankton by individual copepods was highest in May (Table 4). Phytoplankton accounted for only 19% of the carbon ingested by individual *A. tonsa* in May, when most of the carbon was ingested as microzooplankton (Table 4). In August, the reverse was true with over 80% of the carbon being ingested as phytoplankton and the remainder as microzooplankton. When ingestion of microzooplankton is considered together with phytoplankton, total carbon ingested by *A. tonsa* females exceeds their calculated requirements for growth and respiration (Table 4).

**DISCUSSION**

The environmental factor most closely correlated with egg production in our study was temperature. Our observation that a nonlinear polynomial function of temperature was more closely related to egg production than untransformed temperature data is interesting but not without precedent. Laboratory experiments have shown that egg production of *Acartia hudsonica* (Sekiguchi et al. 1980), *A. clausi* and *A. steuri* (Uye 1981), and *A. tonsa* (Heinle 1969, Ambler 1982)
Table 4. *Acartia tonsa*. Individual growth, respiration and ingestion rates of copepod females collected in Chesapeake Bay.

Growth ($G$) was measured as egg production, respiration ($R$) was estimated from temperature ($T$) and body weight (see text) and ingestion of phytoplankton ($I_p$) and microzooplankton ($I_{mz}$) by copepods was measured in shipboard experiments. Daily C requirement is defined as $G + R$. The relation $I_p/(G + R)$ is an index of C uptake vs requirement: assuming an 80% assimilation efficiency, a value $< 1.25$ indicates C deficit, $> 1.25$ superfluous feeding.

<table>
<thead>
<tr>
<th>Date</th>
<th>$T$ (°C)</th>
<th>$G$</th>
<th>$R$</th>
<th>$G + R$</th>
<th>$I_p$</th>
<th>$I_{mz}$</th>
<th>$I_p / (G + R)$</th>
<th>$(I_p + I_{mz}) / (G + R)$</th>
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<td></td>
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<td></td>
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</tbody>
</table>

In contrast to egg production, ingestion of phytoplankton tracked temperature directly with the highest values occurring at the highest temperatures. The relationships between temperature, measured egg production and ingestion rates, and estimated respiration rate are summarized for this study in Fig. 7. In general, egg production and respiration exceeded ingestion of phytoplankton at low temperatures, while ingestion was in excess of demand at high temperatures. For lower temperatures, the apparent carbon deficit is probably made up by ingestion of microzooplankton (as it was during May of 1988) or detritus (Roman 1984). At temperatures above $25$ °C, the decoupling of ingestion and egg production may result from damaging effects of elevated temperature on enzymes or alteration of the viscosity of lipids involved in oogenesis (Hochachka & Somero 1984). This should result in a redirection of ingested carbon towards respiration, a condition not satisfied by Eq. (3) (Fig. 7). Respiration does exceed egg production at the highest temperatures observed, but not enough to account for measured ingestion (Fig. 7). If the assimilation efficiency of *Acartia tonsa* changes by less than a factor of 2 with increased temperature (Kierboe et al. 1983), then a
lower associated cost of digestion and assimilation

Pre-screening particles tended to increase the portion efficiently (Nival 1976, Berggreen et al. 1988).

Enhanced the quality of the food available to copepods. It from cells too small or too big for copepods to handle.

The presence of microzooplankton may have enhanced the quality of the food available to copepods. It has been suggested that a diet rich in N may have a lower associated cost of digestion and assimilation.
(specific dynamic action) in _Acartia tonsa_, resulting in more ingested material available for growth (Kiorboe et al. 1985). Microzooplankton (ciliates and heterotrophic dinoflagellates) generally have a lower C:N ratio than phytoplankton and may contain other chemical constituents such as fatty acids essential for copepod egg production (Stoecker & Capuzzo 1990). Microzooplankton biomass was the only variable significantly related to egg production independent of temperature. Therefore, when the C:N ratio of total particulate matter is low, and/or when microzooplankton are abundant, _A. tonsa_ in Chesapeake Bay should respond by increasing production.

Analysis of _Acartia tonsa_ carbon requirements showed that ingestion of phytoplankton alone provided an adequate source of nutrition during summer, but fell short of _A. tonsa_ demand in May and October. Results of the May carboy experiment support this conclusion and indicate that ingestion of microzooplankton can provide the necessary carbon difference. This result was contrary to our expectation that copepods would feed primarily on diatoms during spring and shift their preference to microzooplankton during summer as the phytoplankton becomes dominated by smaller cells (McCarthy et al. 1974, Van Valkenburg & Flemer 1974, Malone et al. 1986).

_Acartia tonsa_ does not become dominant in Chesapeake Bay until May (Brownlee & Jacobs 1987), after the spring bloom and during the ‘bloom crash’ when much of the phytoplankton biomass is located at depth (Malone et al. 1988). This coincides with a peak in the abundance of heterotrophic dinoflagellates at depth in the bay (E. Lessard pers. comm.) and _A. tonsa_ probably relies on this food resource in May. In support of this, we found higher _A. tonsa_ egg production at depth in May, even though _I_p_ is higher in surface waters.

Since we did not measure _I_p_ in October, we do not know the source of extra nutrition supporting egg production then. It is possible that copepods rely on microzooplankton or detritus (Roman 1984) to make up the estimated carbon deficit occurring at that time.

Stearns et al. (1989) found a strong nocturnal signal for both egg production and ingestion of phytoplankton by _Acartia tonsa_ in 2 different estuaries. They attributed strong nocturnal egg laying to an endogenous rhythm but could not separate it from ingestion. In contrast, egg production and ingestion of phytoplankton by _A. tonsa_ were not closely linked in time during this study; egg production was usually higher at night while ingestion rate showed no consistent day-night pattern. The behavior may be linked to vertical migration patterns in _Acartia_ which often migrate to surface waters at night (Tiselius 1988). _A. tonsa_ vertically migrate in Chesapeake Bay under certain conditions (Roman et al. 1988b). The survival of nauplii may be enhanced if eggs are released and hatched in surface waters rather than at depth, especially during summer when deep waters of the bay are anoxic (Officer et al. 1984).

Egg production of _Acartia tonsa_ in Chesapeake Bay is correlated with several factors that vary in relative importance with season. In summer, _A. tonsa_ egg production appears to be inhibited when temperature exceeds 27 °C. At the other sampling times, egg production seems to be limited by a combination of temperature and the absence of high quality food, calling into question the usefulness of using simple size-fractionated chl_a measurements to characterize potential food resources of _A. tonsa_ (but see Bellantoni & Peterson 1987). Microzooplankton are clearly important to _A. tonsa_ production in May and probably provide a nutritional supplement, if not the primary source of carbon at other times in the bay. In Chesapeake Bay where potential food resources are often plentiful and temperature varies seasonally, _A. tonsa_ egg production rates can be approximated to the first order using temperature alone. Accounting for more variation requires characterizing a number of subtle differences in the quality of their food environment.

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