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# Chronic Food Limitation of Egg Production in Populations of Copepods of the Genus *Acartia* in the San Francisco Estuary

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**ABSTRACT: Egg production of planktonic copepods is commonly measured as a proxy for secondary production in population dynamics studies and for quantifying food limitation. Although limitation of copepod egg production by food quantity or quality is common in natural waters, it appears less common or severe in estuaries where food concentrations are often high. San Francisco Estuary, California, has unusually low concentrations of chlorophyll compared to other estuaries. We measured egg production rates of three species of *Acartia*, which dominate the zooplankton biomass at salinity above 15 psu, on 36 occasions during 1999–2002. Egg production was determined by incubating up to 40 freshly collected individual copepods for 24 h in 140 ml of ambient water. Egg production was less than 10 eggs female$^{-1}$ d$^{-1}$ most of the year, but as high as 52 eggs female$^{-1}$ d$^{-1}$ during month-long spring phytoplankton blooms. Egg production was a saturating function of total chlorophyll concentration with a mean of 30 eggs female$^{-1}$ d$^{-1}$ above a chlorophyll concentration of 12 ± 6 mg chl m$^{-3}$. We take chlorophyll to be a proxy for total food of *Acartia*, known to feed on microzooplankton as well as phytoplankton. These findings, together with long-term records of chlorophyll concentration and earlier studies of abundance of nauplius larvae in the estuary, imply chronic food limitation of *Acartia* species, with sufficient food for maximum egg production <10% of the time over the last 25 yr. These results may show the most extreme example of food limitation of copepod reproduction in any temperate estuary. They further support the idea that estuaries may provide suitable habitat for *Acartia* species by virtue of other factors than high food concentration.**

## Introduction

Copepods are key consumers in aquatic food webs, and their species composition, feeding behavior, and population dynamics can have substantial effects on the transfer of energy to higher trophic levels (Runge 1988). A key component of population dynamics is egg production rate, which has been examined often in terms of growth rate, recruitment, and response to environmental conditions.

Because copepods do not molt once they reach adulthood, egg production rate has been considered the equivalent of growth rate in copepodites (Sekiguchi et al. 1980). Although this assumption ignores weight gain and loss in female copepods (Hirst and McKinnon 2001), most of the lifetime production of adult females is in the form of eggs. Egg production is more likely to be food limited than is somatic growth of juveniles (Peterson et al. 1991; Hirst and Bunker 2003), although possibly not nauplii (Calbet et al. 2000).

Recruitment depends on egg production and subsequent survival, which may be greatly reduced by factors internal or external to the eggs (Peterson and Kimmerer 1994). Internal factors may include reduced hatching success due to components of the female diet; there has been considerable discussion of the role of diatoms in reducing hatching success (e.g., Ianora and Poulet 1993; but see Irigoien et al. 2002). External factors include temperature (Ambler 1986), burial in sediments and possible predation there (Albertsson and Leonardsson 2000), and predation in the water column including cannibalism (Peterson and Kimmerer 1994). Secondary production of the adults is unaffected by egg survival.

Reproduction of copepods can vary with temperature, salinity, season, species, size, feeding, and mating history of the female, and quantity and quality of food (Williamson and Butler 1987; Jónasdóttir 1989; Kiørboe and Sabatini 1995; Kleppel et al. 1998). Some degree of limitation by food quantity has been reported in most studies in coastal and estuarine waters, although some studies have found saturated feeding in highly productive estuarine waters (e.g., Chesapeake Bay; White and Roman 1992). A general trend toward greater food limitation from estuaries to coastal waters to the open ocean should be expected simply

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by virtue of the gradient in phytoplankton and microzooplankton.

San Francisco Estuary, California, is somewhat anomalous among estuaries in having a generally low level of phytoplankton biomass and primary production (Cole and Cloern 1987). In this paper, we show that egg production of *Acartia hudsonica*, *A. tonsa*, and *A. californiensis* was chronically food limited during a 2.5-yr study in the lower San Francisco Estuary, and present evidence that food limitation has been chronic for several decades. Oligohaline waters of the estuary have undergone severe declines in chlorophyll concentration, particularly in summer (Kimmerer 2004). In the higher salinity waters where *Acartia* species are found, chlorophyll concentrations have always been low except during spring and sometimes fall blooms (Cloern 1996) and have not declined markedly (Kimmerer 2004).

The taxonomy of two of the three *Acartia* species is in question. Several species in the subgenus *Acartiura* previously identified as *A. clausi* have been redescribed. Bradford (1976) separated *A. hudsonica* from eastern North America and *A. omorii* from Japan from *A clausi*, found only in Europe. Ueda (1986a) described *A. hudsonica* from Japan and asserted that the Japanese and Atlantic populations could not be distinguished morphologically, and Ueda (1986b) found that *A. hudsonica* and *A. omorii* were reproductively isolated. Kimmerer (1993) found copepods morphologically indistinguishable from both *A. hudsonica* and *A. omorii* in Tomales Bay, about 80 km northwest along the coast from San Francisco Bay. We have also found copepods in the San Francisco Estuary that cannot be distinguished from Bradford's description of *A. hudsonica*, but are clearly neither *A. omorii* nor *A. clausi*. Molecular evidence suggests that copepods identified as *A. tonsa* on the east and west coasts of North America are distinct species (Caudill and Bucklin 2004), and ecological requirements appear very different. We continue to refer to these two species as *A. hudsonica* and *A. tonsa* until new species descriptions are available.

## Methods

We conducted 38 cruises from November 1999 to May 2002, visiting stations in San Pablo Bay (38°02′N, 122°22′W) and central San Francisco Bay (37°54′N, 122°25′W). Cruises were generally monthly except that we increased the sampling rate especially in Central Bay during periods when spring blooms were expected, particularly in April. At each station we measured temperature and salinity with a Seabird Model SBE-19 CTD. Samples were taken for chlorophyll analysis from the surface with a bucket and from mid depth and near bottom using Niskin bottles. A single net tow was taken with a 250-μm mesh, 0.5-m diameter net with a 1-l jar for a cod end, towed slowly at least 1 m below the surface. The sample was immediately diluted in a 20-l bucket filled with surface bay water and covered for transport to the laboratory. Additional water samples were taken with a bucket and reverse filtered through a 35-μm mesh screen to remove eggs, nauplii, and larger animals.

Chlorophyll samples were filtered on GF/F filters (total chlorophyll) or on 5-μm or 10-μm Nuclepore filters. Chlorophyll concentration was determined using a Turner Designs Model 10-AU fluorometer after extraction in 90% acetone. Data used here are either from surface samples (during interim cruises to Central Bay) or the means of 3 samples taken near surface, mid depth, and near bottom.

Individual females of *Acartia* spp. were sorted under a dissecting microscope and placed in 140-ml bottles of <35 μm filtered surface water from the same station, usually within 4 h of collection. The filtering probably removed some food organisms of *Acartia* spp., although the effect of that removal on egg production in the next 24 h was probably small. The target number for sorting was 40 females per station. To achieve that number quickly with minimal handling we did not attempt to determine the species of the copepods during sorting. The incubation bottles were placed on a shelf in a constant temperature room at a temperature setting close to ambient and a 12-h light-dark cycle. After 24 h, each bottle was examined to ensure the copepod was alive, the contents were rinsed through a 35-μm mesh screen, concentrated in a vial with neutral red stain, and preserved with 2–5% formaldehyde.

Samples were examined for the presence of a single stained female, the female was identified to species and measured, and eggs and nauplii were counted. During the initial sorting process, on some occasions additional organisms were apparently introduced to the samples; in addition, on a few occasions female copepods were missing from a vial and two were found in the next vial processed, presumably because they had stuck to the screen used to concentrate the samples. Samples in which any such irregularity was noted were excluded from the analysis of egg production. Egg production was calculated as the sum of eggs and nauplii in the remaining containers. We saw no egg membranes in any samples, which would have suggested cannibalism. Weight-specific egg production ($d^{-1}$) was calculated for *A. hudsonica* using egg carbon for *A. tonsa* from Ambler (1985) corrected to the mean egg diameter for *A. hudsonica* (70 ± 5, mean and SD, n = 37, compared to 73 for *A. tonsa*), or 28 ng C $egg^{-1}$. Female carbon was calculated from length using relationships in Uye (1982).

Egg production of *Acartia grani* varied during 24-h incubations in which the food concentration was changed from its preincubation values (Saiz et al. 1997). We followed the recommendation of Saiz et al. by incubating with water from the location where the copepods were sampled. We were concerned that settling of food could reduce egg production rate toward the end of the incubation period, so on three occasions we placed half of the incubation bottles on a plankton wheel to rotate at 1 rpm and half on the shelf. Bottles to be rotated were selected at random individually (one experiment) or assigned to a treatment in alternating groups of 10 with the first group assigned at random. Differences were determined using analysis of variance (ANOVA) of square-root transformed egg counts with sample (date and station) as one factor and treatment as the other, and also with *t* tests from individual cruises.

We conducted ancillary experiments to determine the influence of added food on egg production rate. Following Durbin et al. (1983), we placed several hundred copepods in 4-l beakers of ambient surface water to which we added cultured phytoplankton at 200–500 mg C $m^{-3}$ as estimated by cell measurements and counts, and using a volume to carbon conversion of 0.12 pg C $\mu m^{-3}$. Added phytoplankton was a mixture of roughly equal biomass of the cryptophyte *Rhodomonas salina* and the diatom *Skeletonema costatum* grown at approximately 17°C on a 12:12 light:dark cycle on f/2 medium with silicate added for diatoms. After 24 h we sorted copepods into 20 bottles following the procedure above, except that these bottles contained surface water to which fresh phytoplankton had been added at 200–500 mg C $m^{-3}$. ANOVA using the entire data set revealed significant interactions between food addition and sample, so comparisons between natural water and food added treatments were made separately by *t*-test for each sample. To compare egg production between diatom and nondiatom foods we also conducted a single incubation using the same methods with alternative food: 500 mg C $m^{-3}$ of either *R. salina*, *S. costatum*, or *Thalassiosira* sp., or a mixture of the latter two diatoms.

Most of the copepods were identified as *A. hudsonica*, but a variable proportion were *A. californiensis* or *A. tonsa*. This variation precluded the use of an ANOVA model to determine differences in egg production among species. For each experiment in which *A. hudsonica* was abundant (>10 of the 40 samples from a station), we converted individual egg production rates from the other two species to standardized values using the mean and standard deviation of egg production from *A. hudsonica*. We then used graphical analyses and *t*-tests to determine whether the means of these standardized values for *A. californiensis* and *A. tonsa* were different from zero, implying no difference in egg production rates between these species and *A. hudsonica*. The assumption underlying this approach is that egg production rates of the different species had similar error distributions; this is supported by the similarity of confidence intervals for egg production rates determined when each species was abundant (see results).

All statistical analyses were run using S-Plus 6.2 (Insightful Corp. Seattle, Washington). Assumptions underlying analyses were addressed by graphical analysis of residuals following each analysis. Egg production data were fitted to linear models including temperature and salinity and a rectilinear function of chlorophyll (i.e., linear in chlorophyll to a constant maximum). Data for all three *Acartia* spp. (when >10 in a sample) were included in this model since they seemed to have the same distribution (see results). Because residual analysis showed a trend toward increasing variance with increasing egg production rate, we fitted the egg production data using a general linear model with variance proportional to the mean squared (Venables and Ripley 1997). The break point for the rectilinear function was determined by first fitting only chlorophyll concentration to the egg production data and calculating the break point that minimized the sum of squared residuals in the general linear model. We then used a dummy variable equal to chlorophyll up to the break point and constant above the break point in the full model. Bootstrap sampling was used (n = 1000) to determine confidence limits of the break point, and the model was refit with values at those confidence limits to determine how robust the model was with respect to changes in the break point.

## Results

Temperature and salinity followed a seasonal pattern between the summer low flow period and the winter wet season (Fig. 1). The temperature difference between stations was 1–2°C in summer and less than that the rest of the year. Salinity was always lower in San Pablo Bay than in Central Bay, by about 5 psu on average. Salinity stratification from bottom to surface had a median of 1.7 psu and a range of 0 to 8.5 psu, with values from San Pablo Bay generally 1 psu higher than those from Central Bay.

Of the 39 cruises undertaken, three were unsuccessful (Table 1). In one case the constant temperature room failed during incubation. In two other cases (one from both stations, one from one station) copepods appeared sluggish during sorting, and all copepods were dead at the end of

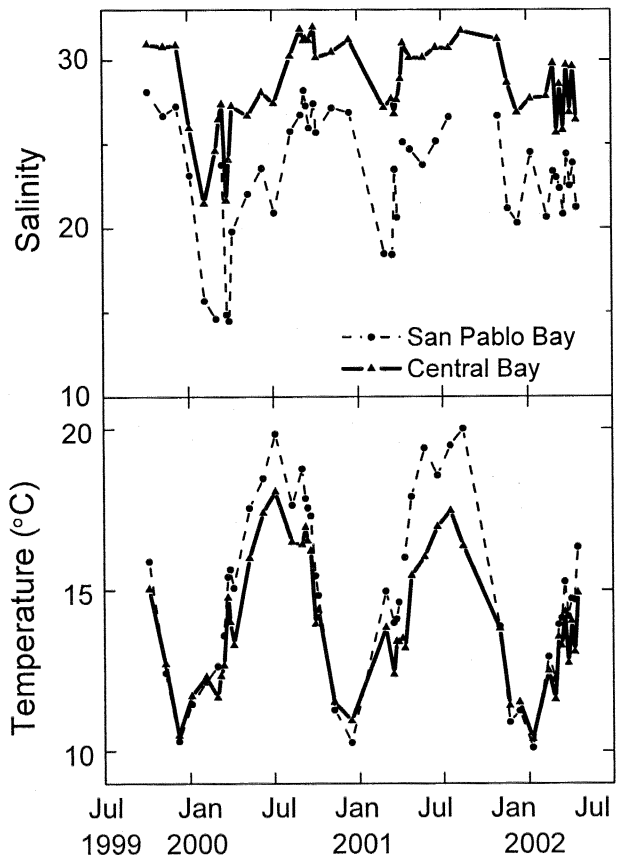


Fig. 1. Time series of water column mean salinity and temperature from CTD casts at the San Pablo Bay and Central Bay sampling stations. On some dates only the Central Bay station was sampled.

the incubation. There was no evidence of obvious problems in the containers such as low oxygen. These mortalities may have been due to the effects of toxic phytoplankton, and on both dates unusually large numbers of *Gymnodinium* sp. dinoflagellates were observed in phytoplankton samples, although we do not know if these were toxic. Among the other experiments, overall mortality rate was 1%. Of the copepods from all successfully completed incubations, 87% were *A. hudsonica*, 9% were *A. californiensis*, and 3% were *A. tonsa* (Table 1); none of the three species had clear seasonal distributions. Except where noted the discussion below refers only to data for *A. hudsonica*. The use of a plankton wheel had no effect on egg production measurements (ANOVA, $p > 0.5$ for all 3 dates, $p > 0.2$ for each date individually, minimum 65 df).

TABLE 1. Summary of experiments. Total dates and incubations include one or both stations and are less than the sum of the dates and incubations from the two stations. See text for explanation of successful incubations and why some copepods were discarded.

| | San Pablo Bay | Central Bay | Total |
|---|---|---|---|
| Total sample dates | 35 | 32 | 39 |
| Incubations successful | 33 | 29 | 36 |
| Total bottles set up | 1272 | 1116 | 2428 |
| Total dead at end (of successful incubations) | 17 | 6 | 23 |
| Total discarded | 109 | 79 | 190 |
| Total used | 1146 | 1031 | 2215 |
| *Acartia hudsonica* | 968 | 929 | 1935 |
| *Acartia californiensis* | 152 | 54 | 206 |
| *Acartia tonsa* | 26 | 48 | 74 |

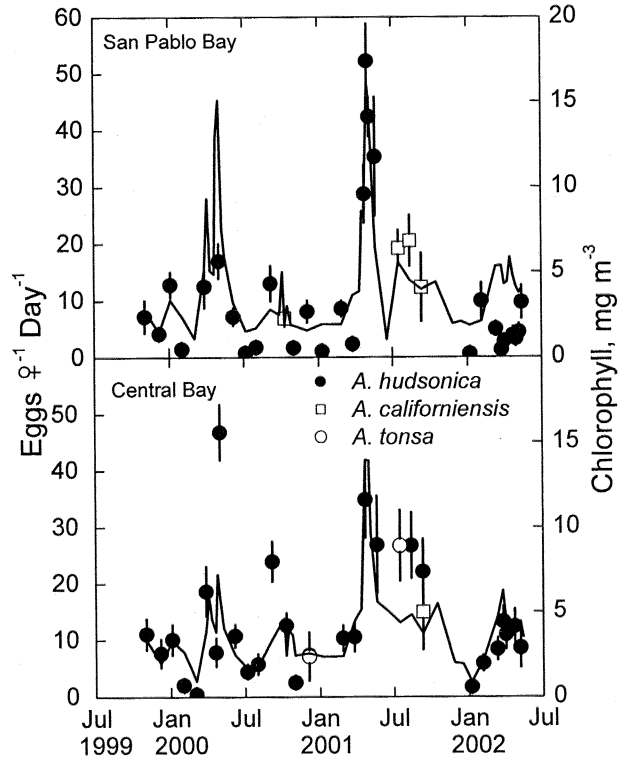


Fig. 2. Time series of chlorophyll concentration (solid line, right axis) and *Acartia* egg production rate with 95% confidence limits (symbols, left axis) for San Pablo Bay and Central Bay.

Chlorophyll concentration was low through most of the year except during two spring blooms that lasted about a month each in 2000 and 2001 (Fig. 2). The proportion of chlorophyll >5 and >10 μm had median values of 60% and 44%, respectively, and did not differ much between stations. The fraction of chlorophyll >10 μm was always above 66% (median 86%) when chlorophyll concentration exceeded 7 mg chl $m^{-3}$. The larger blooms were characterized by somewhat larger cells than the nonbloom periods, and the bloom organisms were mostly diatoms, usually dominated by *S. costatum* (Lassiter personal communication). Chlorophyll values from near surface samples were closely correlated with samples from mid depth or near bottom ($r = 0.93$ and 0.97, respectively, for total

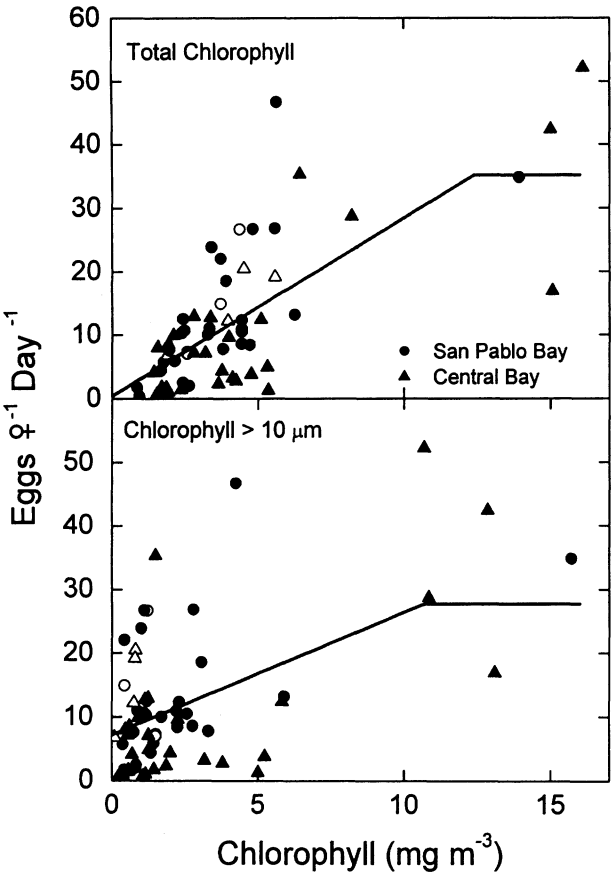


Fig. 3. *Acartia* spp. egg production rate versus total chlorophyll and chlorophyll size fractionated at 10 μm. Open symbols indicate *A. tonsa* or *A. californiensis*; closed symbols indicate *A. hudsonica*. Statistics for rectilinear function for total chlorophyll are given in Table 3. The line for this figure was determined using mean values of salinity and copepod length.

chlorophyll, 0.97 for chlorophyll >10 μm, n = 90 samples with data from all 3 depths).

Egg production rate covaried with chlorophyll concentration throughout the study (Fig. 2). Egg production rate of *A. hudsonica* was elevated during blooms, but was also high during some nonbloom periods, particularly when chlorophyll was moderately high in July through September 2001. Egg production rate of the other *Acartia* spp. was similar to that of *A. hudsonica* when they co-occurred (*t*-test, $p > 0.05$, 72 df for *A. californiensis* and 42 df for *A. tonsa*). On four dates in San Pablo Bay and one in Central Bay, *A. hudsonica* was insufficiently abundant for a reliable estimate of egg production. Egg production rates by the other species on those occasions fell within the scatter of points in Fig. 2, also suggesting no difference in egg production among these three species.

Weight-specific egg production rate of *A. hudsonica* averaged for each date ranged from 0.6% to 70% $d^{-1}$ with a mean of 20% $d^{-1}$. Copepod cephalothorax length was variable among dates (mean ± SD = 0.74 ± 0.08 mm for all copepods) and weakly related to temperature [Length = 0.88 − (0.007 ± 0.006)Temperature, 95% CL, $r^2 = 0.17$, 34 df]; length varied only from 0.81 to 0.74 mm from the minimum to the maximum temperature.

TABLE 2. Empirical model of egg production as a function of total chlorophyll, salinity, and copepod total length (62 df). The break point in the broken line function was determined from 1,000 bootstrap samples; the remaining parameters were then determined using a generalized linear model with the mean break point value. Parameter estimates were within the stated confidence limits for all values of the break point within its 95% confidence limits. The factor f(Chlorophyll) is a saturating function equal to total chlorophyll concentration up to a maximum, then constant at the maximum equal to the break point (see Fig. 3).

| Factor | Parameter ± 95% Confidence Limits | *t* statistic | p |
|---|---|---|---|
| Break point | 12.5 ± 6.1 | – | – |
| Intercept | −29 ± 6.3 | −9.25 | <0.0001 |
| f(Chlorophyll) | 2.8 ± 0.5 | 10.4 | <0.0001 |
| Salinity | 0.56 ± 0.16 | 6.9 | <0.0001 |
| Length | 15.6 ± 5.6 | 5.5 | <0.0001 |

Egg production for all species together was related to chlorophyll concentration through a saturating function (Fig. 3). The relationship of egg production to chlorophyll was tightest for total chlorophyll and weaker for size-fractionated chlorophyll. Exploratory analysis showed that salinity and size of the copepods were linearly related to egg production rate, but that temperature was not. A general linear model including salinity, copepod total length, and the rectilinear function of chlorophyll provided a good fit to the data, with a coefficient of determination of 0.63 (Table 2). Although the confidence limits on the break point were wide, the parameters determined using the generalized linear model were not sensitive to variation in the break point.

Egg production did not consistently increase in treatments with added food compared with those in natural food (Table 3). Even at relatively low egg production the addition of phytoplankton did not always stimulate more rapid egg production. The experiment comparing alternative foods (*S. costatum*, *Thalassiosira* sp., and *R. salina*) indicated diatoms resulted in egg production rates at least as high as *R. salina* (Table 4).

## Discussion

The egg production model indicated a strong effect of chlorophyll, a positive effect of copepod length, and a positive effect of salinity, meaning that low salinity coincided with reduced egg production. This is in contrast to a strong influence of

TABLE 3. Results of experiments with added food. For each date and station the mean egg production rate (number of replicates) is given for copepods incubated with natural food and for those incubated with added food. The difference in egg production rate (added − natural) is given with 95% confidence limits.

| Month/Year | Station | Natural Food | Added Food | Difference |
|---|---|---|---|---|
| 3/2001 | Central | 10 (38) | 15 (16) | 5 ± 5 |
| 4/2001 | San Pablo | 29 (39) | 12 (16) | −17 ± 8 |
| 4/2001 | Central | 34 (40) | 9 (20) | −25 ± 10 |
| 5/2001 | San Pablo | 42 (39) | 20 (18) | −22 ± 7 |
| 8/2001 | San Pablo | 21 (40) | 31 (18) | 10 ± 9 |
| 8/2001 | Central | 28 (39) | 25 (20) | −3 ± 8 |
| 9/2001 | Central | 19 (37) | 11 (12) | −7 ± 7 |
| 1/2002 | San Pablo | 0.6 (34) | 4.7 (12) | 4 ± 3.5 |
| 1/2002 | Central | 1.8 (35) | 8.9 (18) | 7 ± 2 |

temperature and a slight negative effect of salinity (down to 10 psu) on egg production of *A. tonsa* in a Texas estuary (Ambler 1985). The abundance of all *Acartia* spp. in the San Francisco Estuary declines at salinity <15 psu (Ambler et al. 1985; Kimmerer and Orsi 1996), and below that value we never collected enough adults for egg production measurements. Molecular data indicate that the *A. tonsa* populations on the West Coast and those on the East and Gulf Coasts are distinct species (Caudill and Bucklin 2004), supported by the difference in distribution and egg production with regard to salinity and temperature. The same may be true for *A. hudsonica* populations between the East and West Coasts (Carrillo et al. 1974).

We infer food limitation from the data points below the inflection in the fitted curve in Fig. 3. Chlorophyll concentration exceeded this value in only 9 (6%) out of a total of 146 samples taken. Although the inflection point has a wide confidence interval, chlorophyll concentration exceeded the lower 95% confidence limit of the inflection point in only 17 samples (12%).

The data for total chlorophyll allowed for a better fit to the egg production rates than the size-fractionated chlorophyll data (Fig. 3). Many other studies have shown that size-fractionated chlorophyll (>5 to 20 μm) is a better predictor of egg production than total chlorophyll, presumably because of higher feeding efficiency on larger particles (e.g., Runge 1985; Peterson et al. 1991). The better fit with total chlorophyll in our data could be due to greater error variance in the size-fractionated data, but the within-site (across-depth) correlations were actually somewhat higher for size-fractionated than total chlorophyll, suggesting that size fractionation added no additional variance to chlorophyll concentration.

A more likely explanation of the better fit of egg production to total chlorophyll is that feeding and egg production are responding not to the phytoplankton blooms themselves, but to blooms of microzooplankton that respond to the high phytoplankton biomass (Rollwagen Bollens and Penry 2003). *Acartia* spp. can consume microzooplankton and should be considered omnivores (Kleppel et al. 1991). Grazing rates of *Acartia* spp. were highest on ciliates in the San Francisco Estuary during spring 2000, except during the phytoplankton bloom when they consumed large quantities of diatoms (Rollwagen Bollens and Penry 2003). We did not have the resources to determine the abundance of microzooplankton.

TABLE 4. Results of a single experiment using alternative cultured food taxa.

| Taxon | Number of Copepods | Egg Production Rate (mean ± 95% CL) |
|---|---|---|
| *Rhodomonas salina* | 13 | 20 ± 10 |
| *Skeletonema costatum* | 16 | 24 ± 8 |
| *Thalassiosira* sp. | 17 | 21 ± 9 |
| *S. costatum* and *Thalassiosira* sp. | 17 | 23 ± 8 |

Even more than ingestion, egg production depends on a high and diverse food quality, probably because of dietary components required for reproduction (Kleppel et al. 1998). It seems likely that both the residual variance in our egg production model and the mixed response to added food are the result of variability in food quality and in particular taxonomic composition. Copepods fed unialgal diets often produce fewer eggs when the diet consists of diatoms than on other diets such as dinoflagellates (Ianora and Poulet 1993) or cryptophytes (*Rhodomonas* sp., Koski et al. 1998). Long-term culture of *A. tonsa* was possible on a diet of *Rhodomonas* (Stoettrup et al. 1986), although we have been unable to obtain more than moderate egg production rates on *Rhodomonas*, and have been unable to rear *Acartia* spp. on this species alone. We also found diatoms to be as suitable as *Rhodomonas* for producing eggs (Table 4).

Our experiments with added food were perplexing. The concentration may have been inadequate for saturation of egg production in some experiments, but in all cases when base egg production was low there should have been some stimulation. The failure to find a consistent increase in egg production with additional food means that we are forced to rely on the weaker inference available from the relationship between egg production rate and chlorophyll. Alternative explanations for variable egg production cannot be ruled out, but these (e.g., age of the females, mating history) are unlikely to covary with chlorophyll concentration. The distribution of egg production rates among individual copepods indicated that few copepods were reproductively inactive (Kimmerer unpublished data).

TABLE 5. Food limitation inferred from this study and from selected relationships of egg production to chlorophyll in the literature for species of *Acartia*, *Centropages*, *Calanus*, and *Temora*. Data were obtained from Peterson (personal communication) or digitized from published graphs, and a rectilinear function relating egg production rate to chlorophyll was fitted to the data as described for the data in this study. Size refers to either total chlorophyll (T) or mesh size at which chlorophyll was fractionated. The break point k is the chlorophyll value at which egg production becomes saturating, and $EPR_k$ is the saturated egg production, i.e., with chlorophyll >k. For each of these parameters, columns give the percent of samples with values exceeding the parameter and the median ratio of the data to the parameter as a percent. Data from Frost (1985) were normalized for body size, and chlorophyll was calculated as the mean for the water column. Data from Runge (1985) were calculated from his Fig. 12 using the maximum egg production rate in his Fig. 4 for scaling. In Kiørboe and Nielsen (1990) chlorophyll values were picked off the contour plot from above the halocline (their Fig. 1) and calculated by regression on fluorescence corresponding to egg production data (their Fig. 2).

| | | | k (mg chl $m^{-3}$) | | | $EPR_k$ (eggs $female^{-1}$ $d^{-1}$) | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Size | n | k | % >k | Median % chl/k | $EPR_k$ | % >$EPR_k$ | Median % EPR/$EPR_k$ | Source |
| *Acartia* | | | | | | | | | |
| *A. hudsonica* | T | 56 | 12 ± 6 | 6 | 27 | 35 | 7 | 24 | This study |
| *A. clausi* | T | 112 | 0.6 | 67 | 141 | 13 | 32 | 64 | Tiselius et al. (1991, Fig. 6) |
| *A. clausi* | 8 | 11 | 2.6 | 27 | 76 | 42 | 18 | 84 | Kiørboe et al. (1990, Fig. 8) |
| *A. clausi* | 11 | 14 | 4.2 | 21 | 56 | 3 | 21 | 53 | Kiørboe and Nielsen (1990, Fig. 3) |
| *A. hudsonica* | 10 | 23 | 5.1 | 13 | 27 | 18 | 22 | 57 | Peterson (personal communication, Long Island Sound) |
| *A. tonsa* | T | 52 | 15 | 23 | 81 | 37 | 25 | 68 | Durbin et al. (1983) |
| *A. longiremis* | 11 | 8 | 1.5 | 12 | 54 | 10 | 25 | 62 | Peterson et al. (1991, Table IV) |
| *Centropages* | | | | | | | | | |
| *C. hamatus* | T | 118 | 0.7 | 61 | 130 | 22 | 32 | 69 | Tiselius et al. (1991, Fig. 6) |
| *C. typicus* | 11 | 8 | 1.5 | 12 | 54 | 98 | 38 | 94 | Peterson et al. (1991, Table IV) |
| *C. typicus* | 10 | 23 | 3.9 | 13 | 36 | 73 | 13 | 36 | Peterson (personal communication, Long Island Sound) |
| *Calanus* | | | | | | | | | |
| *C. agulhensis* | 11 | 112 | 35 | 7 | 12 | 6 | 7 | 13 | Peterson and Hutchings (1995) |
| *C. pacificus* | T | 22 | 3.8 | 14 | 38 | 22 | 32 | 18 | Frost (1985, Fig. 7) |
| *C. pacificus* | 5 | 15 | 9.9 | 27 | 65 | 43 | 20 | 77 | Runge (1985, Fig. 12) |
| *C. finmarchicus* | T | 12 | 0.8 | 17 | 19 | 30 | 17 | 4 | Hirche and Bohrer (1987, Fig. 4) (60 m depth) |
| *C. finmarchicus* | 11 | 8 | 0.7 | 62 | 115 | 31 | 38 | 95 | Peterson et al. (1991, Table IV) |
| *Temora* | | | | | | | | | |
| *T. longicornis* | 8 | 11 | 2.6 | 27 | 75 | 28 | 36 | 61 | Kiørboe et al. (1990, Fig. 8) |
| *T. longicornis* | 11 | 13 | 4.5 | 15 | 49 | 18 | 23 | 74 | Kiørboe and Nielsen (1990, Fig. 3) |
| *T. longicornis* | 11 | 8 | 0.5 | 88 | 179 | 7 | 38 | 84 | Peterson et al. (1991, Table IV) |
| *T. longicornis* | 10 | 41 | 3.4 | 24 | 41 | 41 | 15 | 46 | Peterson (personal communication, Long Island Sound) |

Although food limitation of copepod egg production appears common in nature (Hirst and Bunker 2003), we are aware of few cases in which the frequency of food limitation has been so great. Several examples from the literature, selected only for the availability of sufficient data to fit egg production to chlorophyll data, show that while food limitation is commonly detected in studies of egg production in estuarine and coastal waters, rarely is its degree or frequency as great as shown here (Table 5). Only examples for *Calanus* spp. had lower median egg production rates as a fraction of the saturated values. Median egg production rates for *Acartia* spp. from other studies were 53–84% of the saturated values.

Many reports have indicated food limitation in *Acartia* spp. on some occasions (e.g., Lonsdale et al. 1996). Most reports of long-term studies of egg production of *Acartia* spp. from estuaries indicate that food limitation is infrequent or absent (e.g., White and Roman 1992 for *A. tonsa* in Chesapeake Bay). *A. tonsa* egg production was unrelated to chlorophyll concentration in Mobile Bay (McManus and Foster 1998). Egg production of *A. tonsa* in the Los Angeles Harbor varied with temperature and with food quantity at high temperature (Kleppel 1992). In Narragansett Bay, *A. tonsa* was food limited in summer (Durbin et al. 1983), but *A. hudsonica* was at most weakly food limited during the winter–spring bloom (Durbin et al. 1992). This trend for increasing food limitation with increasing temperature may be common (Hirst and Bunker 2003). The relatively low temperatures in the San Francisco Estuary (Fig. 1) are in a range where food limitation should not be frequent (Hirst and Bunker 2003).

Primary production in San Francisco Estuary is low (Cole and Cloern 1987). Chlorophyll concentration from the U.S. Geological Survey long-term monitoring program in San Pablo, Central, and South Bays from 1977 through early 2004 infrequently exceeded the lower 95% confidence limit of the inflection point of the egg production

TABLE 6. Summary of chlorophyll data from U.S. Geological Survey sampling in three regions of San Francisco Estuary, 1977–2004 (San Pablo Bay was not sampled in 1982–1987). For each region the samples were aggregated by month and the percentage of samples exceeding the threshold was calculated; the percentages were then averaged across months. This eliminated bias due to sampling that emphasized spring blooms. Data from http://sfbay.wr.usgs.gov/access/.

| Region | Total Samples | Percentage of Samples by Month | |
|---|---|---|---|
| | | >6.4 mg chl $m^{-3}$ | >12.5 mg chl $m^{-3}$ |
| San Pablo | 545 | 10.0 | 2.0 |
| Central | 1,081 | 9.6 | 3.2 |
| South | 4,148 | 16.9 | 7.6 |

relationship in Table 2 and exceeded the estimated inflection point in only 2–8% of samples (Table 6).

Data from 1978–1981 on abundance of *Acartia* nauplii in San Francisco Estuary confirm this picture of infrequent pulses of copepod production (Hutchinson 1982; Ambler et al. 1985; Cloern 1996). Nauplii were most abundant during times when chlorophyll concentration exceeded 5 mg chl $m^{-3}$ (Fig. 4). Together with the consistent pattern of low chlorophyll concentrations, these results suggest that chronic food limitation has been a feature of *Acartia* populations in more saline regions of this estuary for at least 25 yr. This contrasts with the situation in the brackish regions of San Francisco Estuary, where food concentrations and abundance of some copepods decreased sharply in the late 1980s (Kimmerer and Orsi 1996).

Several theories have been advanced to explain the dominance by *Acartia* spp. in the copepod biomass in higher salinity waters of temperate estuaries, having to do with elevated food supplies, depressed salinity, shallow depth allowing recruitment from resting eggs, and altered predatory environment. Reduced feeding rate of *Acartia* spp. at lower food concentrations in offshore waters (Paffenhöfer and Stearns 1988) may imply that some *Acartia* spp. are abundant in estuaries and not in adjacent shelf waters because of the greater abundance of food. Reduced salinity favors egg production (Ambler 1985) and survival of nauplii (Tester and Turner 1991) of *A. tonsa* from eastern North America, indicating a requirement for estuarine habitat. *Acartia* spp. often dominate the mesozooplankton in temperate marine bays where food concentrations are not particularly high and salinity not depressed (Kimmerer and McKinnon 1989; Ueda 1991). *A. tonsa* on the West Coast of North America reproduces well and is most abundant at high salinity (e.g., Uye and Fleminger 1976; Kleppel 1992; Kimmerer 1993). The ability of *Acartia* spp. to produce resting eggs may enable them to weather unfavorable periods in shallow regions (Uye and Fleminger 1976). Our results,

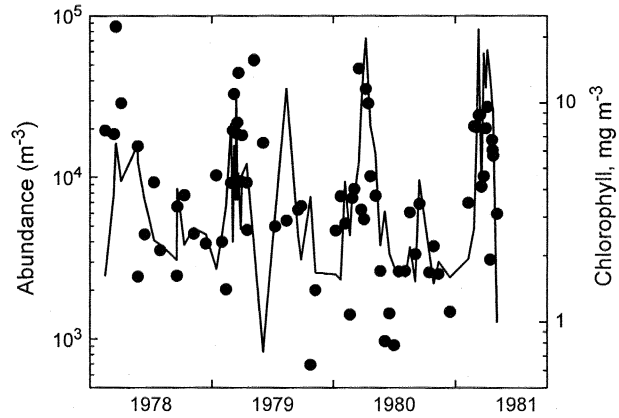


Fig. 4. *Acartia* spp. Time series of chlorophyll concentration (lines) and abundance of nauplii (circles) from south San Francisco Bay during 1978–1981. Data for chlorophyll from U.S. Geological Survey (http://sfbay.wr.usgs.gov/access/quality.html) and abundance of nauplii from Hutchinson (1982).

showing that *Acartia* can remain the biomass dominant, without seasonal disappearance, at moderate to high salinity, even when chronically underfed, also suggest that the dominance of *Acartia* may result from other attributes of marine bays and estuaries besides food, salinity, and benthic refuges. Many bays and estuaries have a reduced diversity of modes of planktivory, with dominance by fish that may result in dominance of the plankton by smaller, more cryptic zooplankton species or those with strong escape responses to visual predators (Kimmerer and McKinnon 1989; Kimmerer 1991; Ueda 1991). *Acartia* spp. may simply be able to exploit a variety of attributes of estuaries, and the key attribute may differ among estuaries.

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