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## EGG PRODUCTION AND HATCHING SUCCESS IN NORTH ADRIATIC SEA POPULATIONS OF THE COPEPOD *Acartia clausi*

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Egg production, fecal pellet production and hatching success are reported for *Acartia clausi* females sampled during three cruises in February 1997, 1998 and June 1997 at 20–24 stations along 4 transects in the North Adriatic Sea. Dramatically low hatching rates were recorded during both diatom bloom events in February as opposed to much higher rates during post-bloom conditions in June, even though *A. clausi* productivity during the bloom was apparently high. These results are discussed in the light of recent findings on the negative impact of diatoms on copepod reproductive potential.

**Keywords:** Copepods; Adriatic sea; Egg hatching; Egg production; Diatom

### INTRODUCTION

Among the mesozooplankton, copepods are dominant planktonic grazers, often representing 80–95% of the total zooplankton biomass in large parts of the ocean. These small crustaceans probably represent the world's most numerous animals grazing directly on the world's largest plant crop, the marine phytoplankton. Since copepods act as a "filter" or link between primary producers and fish (Runge, 1988), understanding copepod recruitment rates is fundamental to quantify flux rates of organic material from primary producers through the mesoplankton to higher trophic levels.

Variations in copepod recruitment rates are largely considered to depend on the concentration and quality of food available to adults and juveniles, which in turn depends on varying hydrographic conditions. The response of copepods to such variations should ultimately be reflected through major biological functions such as feeding and reproduction. However, to date there has been much debate as to whether changes in fecundity truly reflect seasonal changes in phytoplankton standing stocks. Whereas some field studies have reported strong correlations between egg production and chlorophyll concentrations (*e.g.* Laabir *et al.*, 1998), others have not (*e.g.* Ianora *et al.*, 1992). The poor correlations observed in many cases seem

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to denote that copepod fecundity may also be related to other food characteristics such as food quality (Ianora and Poulet, 1993) rather than to total chlorophyll *per se*.

There is also much debate, at present, on the factors affecting copepod mortality which is highest in the egg and early naupliar stages (Poulet *et al.*, 1995a). Under natural conditions at sea, this parameter has been shown to vary from 0–100% with mean seasonal values of about 30% in most sub-temperate areas (Ianora, 1998). In the laboratory, poor egg quality has been shown to depend on several factors, including female age (Ianora *et al.*, 1996), an absence of remating (Parrish and Wilson, 1978), an inefficiency in sperm fertilizability (Ianora *et al.*, 1999) or an inadequate diet (Poulet *et al.*, 1994; 1995b). Several studies have shown that low hatching success can also depend on the presence of anti-mitotic compounds such as those described for diatoms which block copepod embryogenesis (see Miralto *et al.*, 1999 and references therein).

To date, most studies on the negative impact of diatoms on egg hatching rates have been carried out in laboratory experiments and there is as yet limited information on the effect of diatoms *in situ*. The object of the present study was, therefore, to describe egg production rates and egg hatching rates during a natural diatom bloom event such as those that occur in the North Adriatic Sea in late winter, and/or early spring.

We show that egg mortality can vary enormously under natural conditions and not only in laboratory experiments. These results have major implications on copepod recruitment rates and for the modelling of flux rates of organic material through the pelagic food chain.

## MATERIALS AND METHODS

*Acartia clausi* egg production, fecal pellet production and egg hatching success were determined in February 1997, 1998 and June 1997 at 20–24 stations located along 4 transects in the northern Adriatic Sea (Fig. 1). These periods coincided either with strong diatom bloom events (February 1997 and 1998), when diatom concentrations reached  $10^3$  cells  $\text{ml}^{-1}$ , or post-bloom conditions in June when diatom concentrations were more relaxed ( $10^2$  cells  $\text{ml}^{-1}$ ) (Miralto *et al.*, 1999).

The stations were sometimes re-visited a few days later and replicates are referred to as a and b in Figures 1–5. At each station, adult female *Acartia clausi* were sorted from live

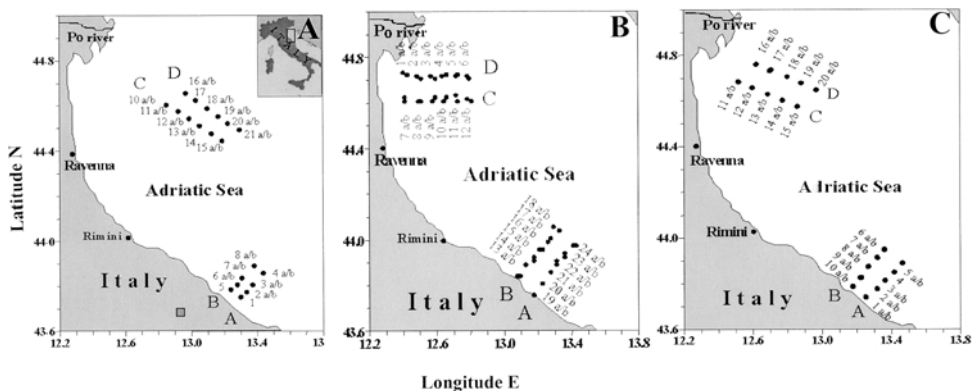


FIGURE 1 Station locations during (A) February 1997, (B) June 1997 and (C) February 1998. Stations visited only once are indicated by station number; those visited more than once are indicated as a and b where a indicates samples collected the first day and b those collected a few days later.

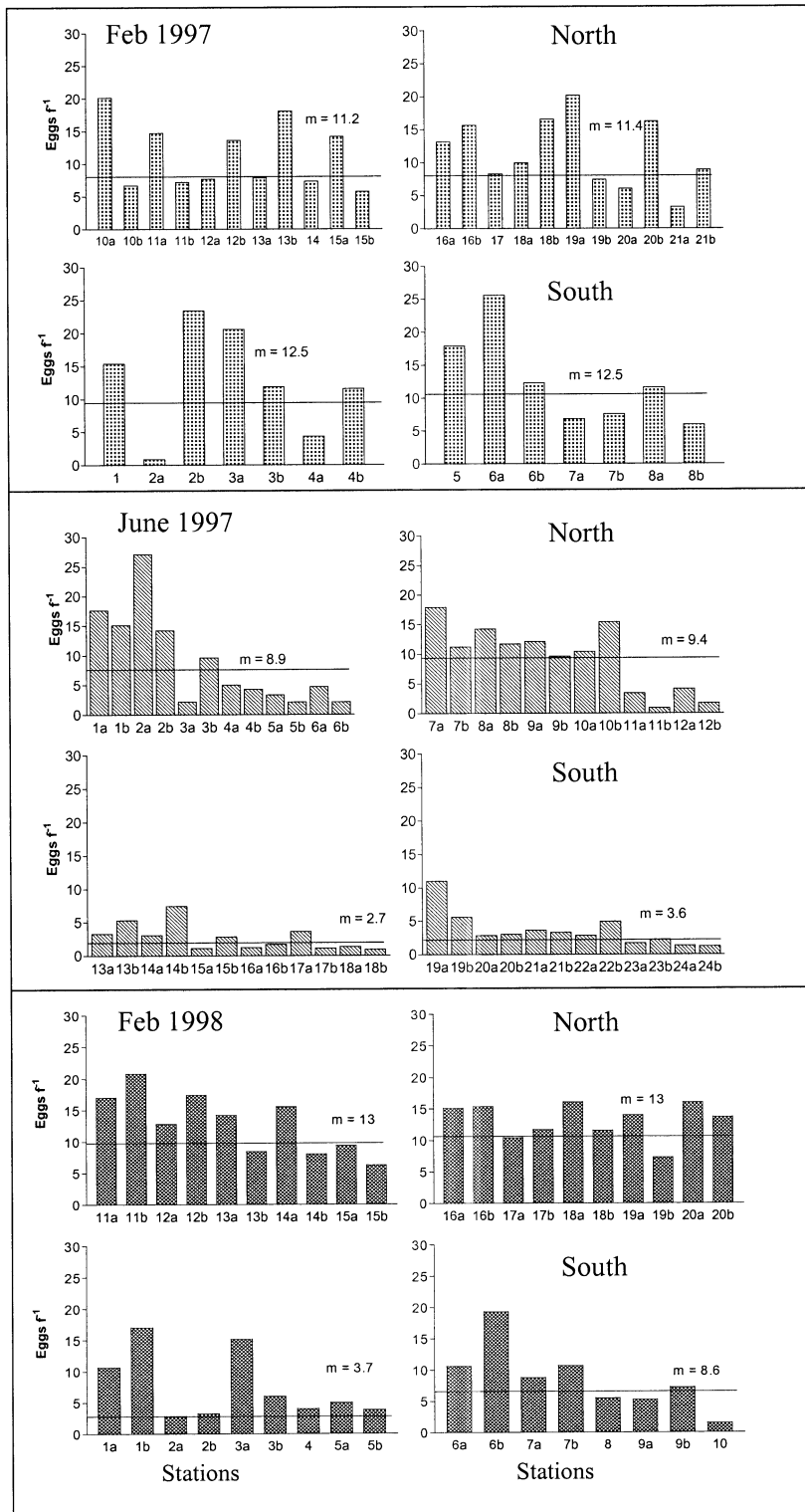


FIGURE 2 *Acartia clausi* egg production rates female<sup>-1</sup> day<sup>-1</sup> at different stations sampled in the North Adriatic in February and June 1997, and February 1998.

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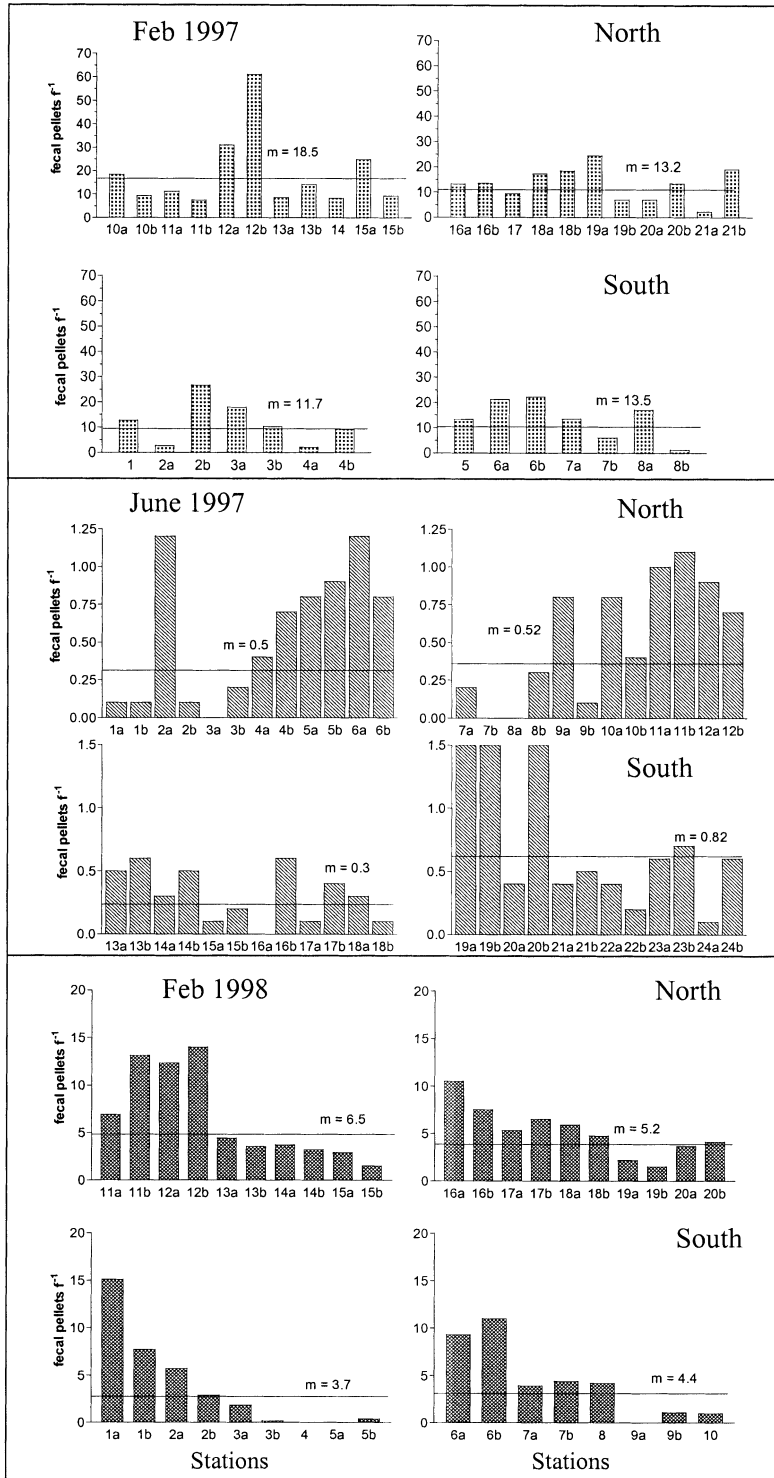


FIGURE 3 *Acartia clausi* fecal pellet production female<sup>-1</sup> day<sup>-1</sup> at different stations sampled in the North Adriatic in February and June 1997, and February 1998.

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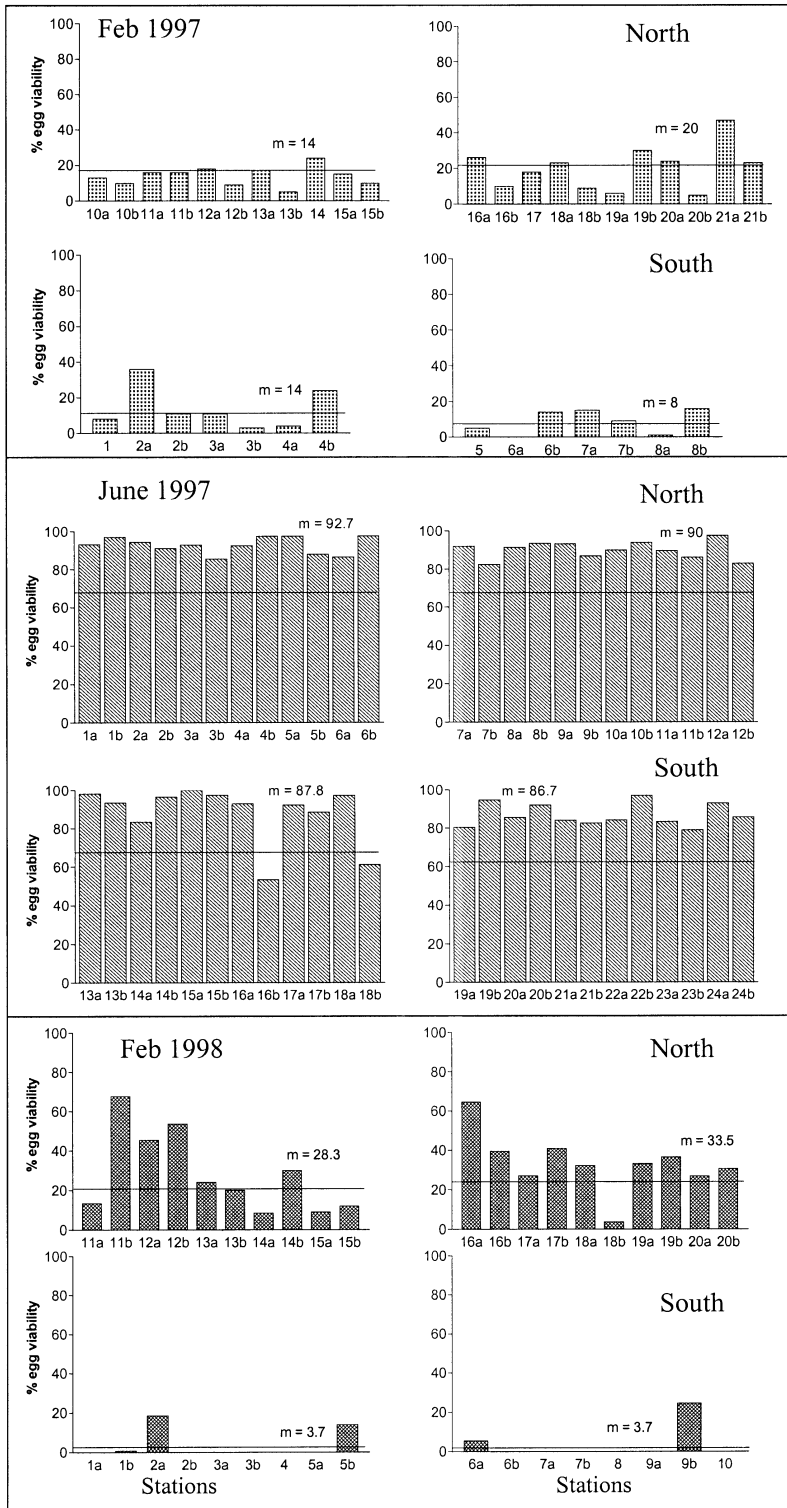


FIGURE 4 *Acartia clausi* percentage of egg viability at different stations sampled in the North Adriatic in February and June 1997, and February 1998.

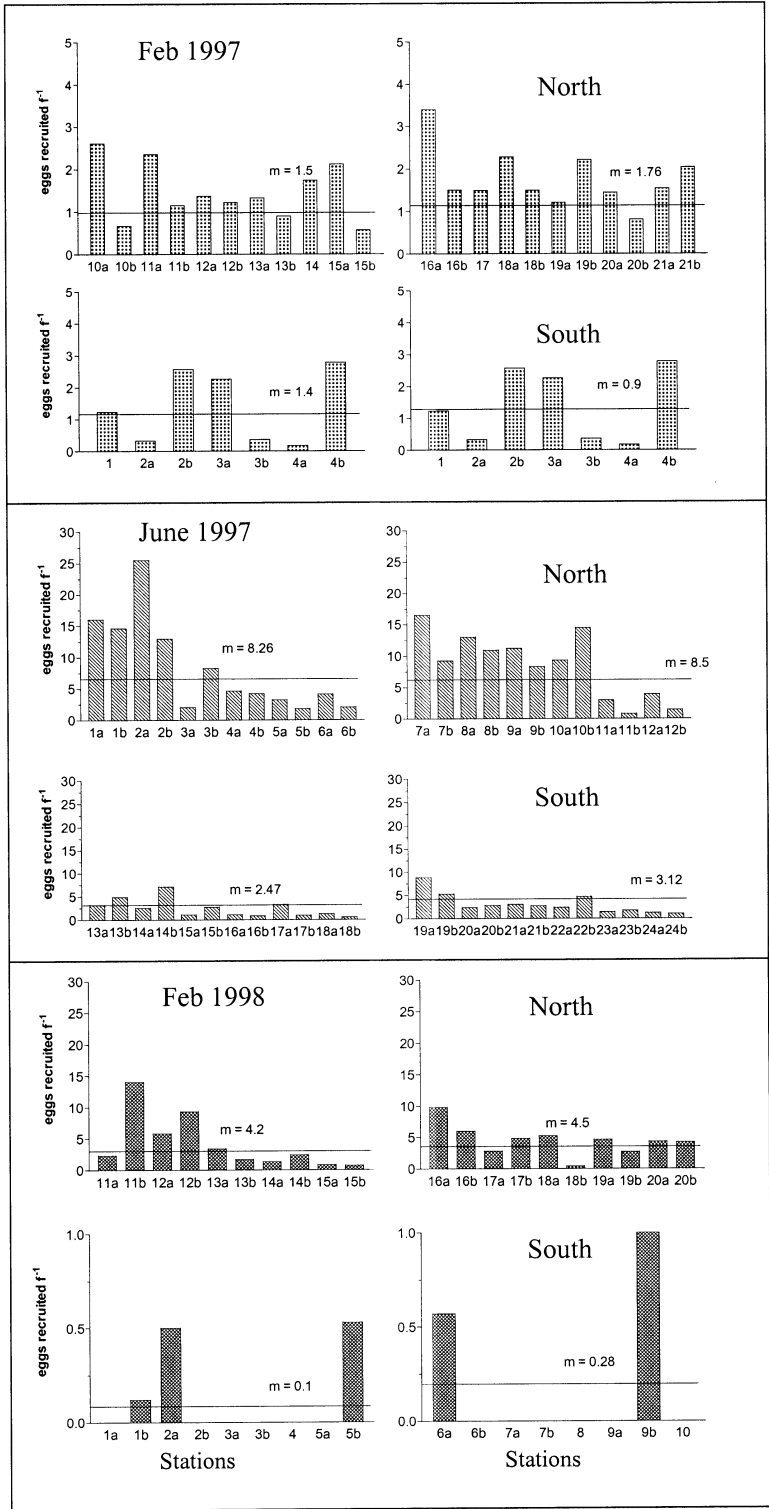


FIGURE 5 Potential number of *Acartia clausi* eggs female<sup>-1</sup> day<sup>-1</sup> recruited into the population based on female fertility and on egg mortality (see text).

plankton samples collected by oblique surface (0–50 m) tows with an open 200  $\mu\text{m}$  Nansen net. Depending on the station and abundance of females, from 3–20 females were incubated individually in 50 ml tissue culture flasks containing 50  $\mu\text{m}$  filtered seawater with a natural phytoplankton assemblage.

After 24 h, females were removed from flasks, and eggs and fecal pellets were counted with an inverted microscope. After an additional 48 h, samples were fixed with 4% formaldehyde and hatching success was determined by counting the number of hatched nauplii.

## RESULTS

Egg production rates were higher in February than June in both 1997 and 1998 (Fig. 2). Mean values ( $m$ ) ranged from 11.2–12.5 eggs female<sup>-1</sup> day<sup>-1</sup> ( $f^{-1} d^{-1}$ ) in February 1997 (mean of 11.9 eggs  $f^{-1} d^{-1}$  for the 4 transects) and 3.7–13 eggs  $f^{-1} d^{-1}$  in February 1998 (mean of 9.6 eggs  $f^{-1} d^{-1}$  for the 4 transects). Mean values in June ranged from 2.7–9.4 eggs  $f^{-1} d^{-1}$  with mean values of 6.2 eggs  $f^{-1} d^{-1}$  for the four transects. No clear spatial trend was apparent between northern (C and D) and southern (A and B) transects. Higher values were generally recorded in northern transects.

Fecal pellet production showed a similar pattern to egg production rates (Fig. 3). Highest values occurred in February of both years when values ranged from 11.7–18.5 fecal pellets  $f^{-1} d^{-1}$  in 1997 (mean of 14.2 fecal pellets  $f^{-1} d^{-1}$  for the 4 transects) and 3.7–6.5 fecal pellets  $f^{-1} d^{-1}$  in 1998 (mean of 5 fecal pellets  $f^{-1} d^{-1}$  for the 4 cruises). Much lower values were recorded in June 1997 when production was one order of magnitude less than in February 1997 and 1998 (mean of 0.53 fecal pellets  $f^{-1} d^{-1}$  for the 4 cruises).

Egg viability was very low in February of both years as compared to June 1997 (Fig. 4). Mean values ranged from 8–20% hatching success in February 1997 (mean of 14% for the 4 transects) and 3.7–33.5% hatching success (mean of 17.3% for the 4 transects) in February 1998. Lower hatching success was recorded in southern transects in both February 1997 and 1998. Much higher values were recorded in June 1997 with values ranging from 86.7–92.7% hatching success (mean of 89.3% for the 4 transects).

Due to the enormous seasonal variability in hatching success and the low number of viable eggs in February, we recalculated female egg production rates considering only the number of hatched nauplii that were potentially recruited to the adult population:

$$\text{eggs} \cdot f^{-1} \cdot d^{-1} \cdot \% \text{viable eggs} = \text{eggs recruited} \cdot f^{-1} \cdot d^{-1}$$

These values are reported in Figure 5 illustrating that the eggs recruited in June 1997 were much higher than those recruited in February of both years even though egg production rates were much higher in February 1997 and 1998 (Fig. 2).

## DISCUSSION

Our results show that hatching success in *Acartia clausi* can oscillate dramatically during and after strong diatom bloom events. In February of both years, very high egg mortality (>80%) coincided with a bloom of *Skeletonema costatum* and *Pseudonitzschia delicatissima* which reached concentrations of  $10^3$  cells  $\text{ml}^{-1}$  (see Miralto *et al.*, 1999). On the contrary, egg mortality was minimal (<15%) in June when the composition of the phytoplankton was more diversified and the grazing impact of copepods on diatoms was more relaxed.



It is interesting to note that the diatom bloom suppressed copepod population growth even though copepod productivity during the bloom was apparently high. Maximum egg and fecal pellet production occurred during February of both years indicating that animals were better fed in this period than in June. Notwithstanding this, recruitment rates in June were at least double those in February (see Fig. 5). Copepod recruitment rates were therefore more favorable in post-bloom conditions, when the microbial food web was probably established, than during the diatom bloom, as also suggested for *Calanus finmarchicus* (and fish larvae feeding on *Calanus finmarchicus*) in the Gulf of St. Lawrence (Runge and de Lafontaine, 1996).

The most likely cause of high egg mortality was the presence of anti-mitotic compounds in diatoms blocking copepod embryogenesis. Miralto *et al.* (1999) have, in fact, recently isolated three low molecular weight aldehydes responsible for this cell blockage not only in copepod and sea urchin embryos but also in human adenocarcinoma cells. The same authors have also shown that although diatom blooms trigger an increase in egg production rates by the copepod *Acartia clausi*, mean egg hatching success during these blooms was only 12% and 24%, respectively, compared to 90% during the summer when diatom concentrations were lower.

What implications does this have on copepod secondary production and recruitment rates in the Adriatic Sea? The major implication is that secondary production, based on the measurement, in a given species, of the 3 variables ( $E$  = fecundity of females,  $Bf$  = biomass of females, and  $V$  = hatching success) and expressed by two simple equations: Production  $P = E \cdot Bf$  and Recruitment  $R = E \cdot Bf \cdot V$  (see Poulet *et al.*, 1995a), was probably very low during the diatom bloom in the winter of both years. Although females were apparently more fertile in this period, the potential number of eggs recruited per female was only ca. 1.4 eggs  $f^{-1}d^{-1}$  in February 1997 and 2.3 eggs  $f^{-1}d^{-1}$  in February 1998 as compared to 5.6 eggs  $f^{-1}d^{-1}$  in June 1997. Considering that *Acartia clausi* adult female population stocks were also very sparse in February (data not shown), the potential productivity of the population was minimal in winter and the flux of organic material was inefficiently transferred from primary producers through the mesozooplankton to higher trophic levels. These results challenge the traditional view of the beneficial role of diatoms in the pelagic food web.

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