

Egg production and growth rates of *Calanus euxinus* (Copepoda) in the Black Sea

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Egg production rates (EPRs) of Calanus euxinus were measured in the Black Sea during October 2000 and May 2001. EPRs were generally low, on average 1.7 eggs female⁻¹ day⁻¹ in October 2000 and 3.9 eggs female⁻¹ day⁻¹ in May 2001. The relationships between EPRs and gonad maturity, depth-integrated chlorophyll a (Chl a) and mean surface layer temperature were examined. The EPRs were not related to depth-integrated Chl a, but were negatively correlated with temperature. EPRs were strongly related to the proportion of mature females. Growth rates of C. euxinus were derived from the EPRs. The mean growth rate was 0.011 day⁻¹ in October 2000 and 0.03 day⁻¹ in May 2001. Growth rates were not significantly correlated with Chl a concentrations, but were negatively related to female weight and temperature.

INTRODUCTION

The calanoid copepod *Calanus euxinus* is a dominant secondary producer in the Black Sea, accounting for over one-third of the total zooplankton biomass (Vinogradov *et al.*, 1992). *Calanus euxinus* has an important role in transferring the organic matter from primary producers to the higher taxa. It is estimated that 14.5 and 9.5% of primary production was consumed by female *C. euxinus* in April and September 1995, respectively (Besiktepe *et al.*, 1998). *Calanus euxinus* is also the main food for a variety of commercially important fish species, e.g. sprat and anchovy, in the Black Sea (Sirotenko and Danilevsky, 1977; Sirotenko and Sorokalit, 1979; Avsar, 1993).

Most probably linked to predator avoidance, *Calanus* shows a normal diel vertical migration (DVM) pattern in the Black Sea (Vinogradov *et al.*, 1985, 1992; Besiktepe, 2001). Among the developmental stages, females, copepodite V (CV) and copepodite IV (CIV) show strong DVM; DVM occurs from the depth of the oxygen minimum zone to the surface. CV undergoes seasonal migration during summer and early autumn (during the warmer period) in the Black Sea. The whole CV population does not enter diapause at the same time, with around 50% of the CV population observed in the diapausing state in June, while only 13% of the population was in diapause in September (Besiktepe, 2001). Vinogradov *et al.* reported that 60–75%

of stage V remained at the lower limit of the oxygenated layer at night-time in August (Vinogradov *et al.*, 1990).

Calanus euxinus has been observed throughout the year, and population structure results have shown that the population was youngest (metanauplii, CI, CII and CIII) in April and December, whereas the oldest stages (CIV, CV and adults) made up >60% of the population in May, June and September (Besiktepe, 2001). Sazhina reported that the egg production rates (EPRs) of *C. euxinus* varied between 3 and 30 eggs female⁻¹ day⁻¹, with the maximum off the western Crimea in May 1992, and did not observe any egg production in the northwestern nearshore waters during May and September 1992 (Sazhina, 1996).

In this paper, we present the data on abundance, stage structure, gonad maturity and EPR of the *C. euxinus* population in the Black Sea, sampled on 6–17 October 2000 and 23–27 May 2001. Relationships between EPR and temperature, chlorophyll *a* (Chl *a*) and gonad maturity were explored. On the basis of the weight of eggs and females, we attempted to estimate weight-specific fecundity of *C. euxinus* in the Black Sea.

METHOD

Sampling took place in the Black Sea on two cruises conducted on 6–17 October 2000 and 23–27 May

2001. In October 2000, 12 stations located in the south-eastern part of the Black Sea and, in May 2001, eight stations located in the southwestern part of the Black Sea were visited (Figure 1).

Temperature, salinity and *in situ* fluorescence profiles were taken using a Seabird CTD with Chelsea fluorometers attached to it. Seawater samples were taken using a rosette of 5 L Niskin bottles attached to the CTD system. The Chl *a* concentration was used here as an index of phytoplankton concentration and, for Chl *a* measurements, seawater samples from different depths within the upper 50 m containing the euphotic layer were filtered through GF/F filters and stored at -20°C until analysis. Chl *a* concentrations were determined in 90% acetone extracts with a Hitachi F-3000 model fluorescence spectrofluorometer (IOC, 1994).

Zooplankton samples were collected with a Hensen net (mouth opening 70 cm, mesh size 300 μm) via vertical hauls from the depth of the 16.2 sigma theta density layer, where the anoxic water column begins, to the surface. Zooplankton from the first tow were preserved with 4% borax-buffered formaldehyde for stage identification and enumeration under a stereomicroscope. Zooplankton from the second tow were diluted into 5 L beakers filled with surface seawater. Among the zooplankton, female *C. euxinus* were sorted using a stereomicroscope for EPR experiments. The groups of 10 (occasionally 5 or 15) adult females were transferred to 2 L translucent bottles containing 56- μm -filtered

seawater from the depth of fluorescence maximum. Usually three replicate experimental bottles were prepared for each station. The experimental bottles were kept on deck in an incubator with sea surface water running through. The incubations were performed under the natural light cycle for 24 h. At the end of experiments, the contents of the bottles were filtered onto 56 μm sieves, and eggs and females were preserved with 4% buffered formaldehyde. The EPR was expressed as the number of eggs produced per female per day.

Owing to the nature of the cruise track, we visited almost half of the stations at night and another half in the daytime during both cruises. It would be better to sample during the morning or early afternoon so as to not to interfere with the night-time egg release period. However, we did not observe any statistically significant difference between EPR of females collected from night-time and daytime stations in October and May (*t*-test, $P > 0.05$).

Egg cannibalism is a potential source of error in the estimation of EPR. Empty egg shells in the experimental container are the traces of egg cannibalism. However, during our study we did not observe any empty shells in the experimental bottles. It is not certain whether *C. euxinus* ingests entire eggs; ingestion of entire eggs without leaving behind any identifiable trace has been reported for *Calanus finmarchicus* (Runge and Roff, 2000). If this event occurred in our experiments, then underestimation of the EPR could be possible.

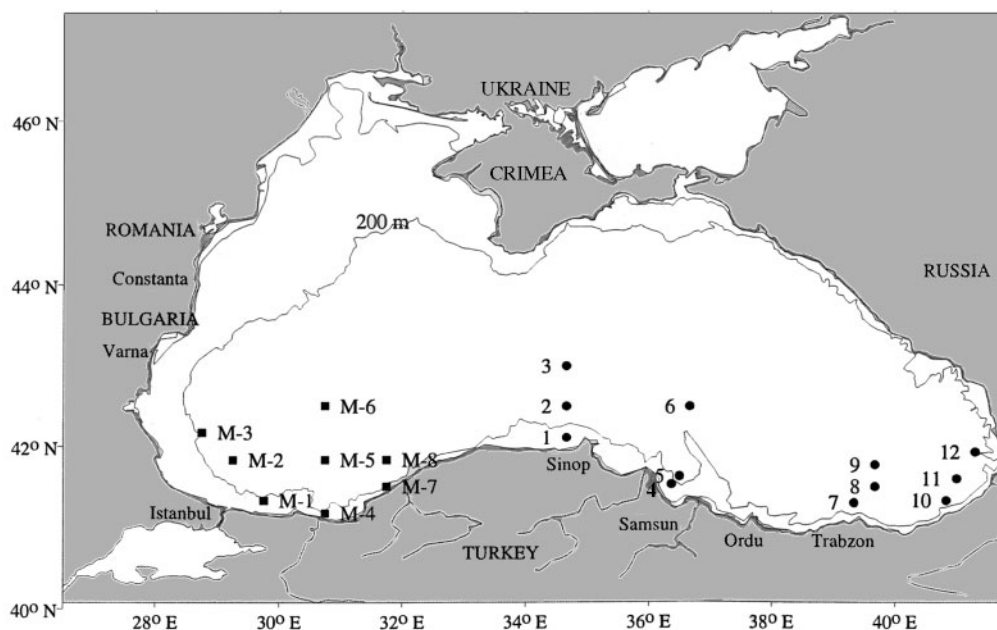


Fig. 1. Sampling stations visited during October 2000 (circles) and May 2001 (squares) in the Black Sea.

Gonad maturity was determined from the females used in EPR experiments. Females were stained in a borax carmine solution according to Niehoff and Hirche (Niehoff and Hirche, 1996). A simple classification for assessment of gonad maturity based on the presence of eggs in diverticula, ovary and oviducts was performed under an Olympus SZX12 model stereomicroscope as described in Kosobokova (Kosobokova, 1999).

Female growth rates (g_r ; as egg production) were derived using the equation described by Hirst and Lampit (Hirst and Lampit, 1998):

$$g_r = W_{\text{Egg}}/W_{\text{Female}}$$

where W_{Egg} is the carbon weight of eggs produced over 24 h and W_{Female} is the carbon weight of a female. Egg weights, as carbon, were predicted from the direct measurements of egg diameters, assuming a carbon content of $0.14 \times 10^{-6} \mu\text{g C } \mu\text{m}^{-3}$ (Huntley and Lopez, 1992). The female weights, as carbon, were predicted from dry weight by assuming carbon = 40% of dry weight (Kjørboe and Sabatini, 1994). The dry weights of females were predicted from the length–weight relationships of *C. euxinus*. Prosome lengths of individuals (from CI to adults) were measured using a stereomicroscope with an ocular micrometer. Individuals within the same length groups were washed in distilled water, placed in pre-weighed aluminum pans and dried at 55°C for 24 h; samples were then cooled in a desiccator for 6 h, and weighed. It should be noted that the length–weight relationship was determined using the individuals from preserved samples. Owing to the loss of weight during preservation, this relationship should be considered cautiously.

To describe the diel egg-laying pattern of *C. euxinus*, one experiment was performed at a station (30°48'80"E, 41°19'74"N) in the southern Black Sea in April 2003.

Seven females were placed individually into Petri dishes containing 50 mL of 56- μm -filtered seawater. They were incubated at 19°C under natural light regimes, and checked six times per day for observation of the diel egg production cycle.

RESULTS

The vertical profiles of temperature, salinity and Chl *a* from the stations are shown in Figure 2. A well-developed seasonal thermocline above 50 m was present during both cruises. Sea surface temperature was around 20 and 16°C in October and May, respectively. Sea surface salinity ranged from 17.5 to 18.2 in October and varied from 16.90 to 18.1 in May. Chl *a* was low during the cruises, $<1 \mu\text{g L}^{-1}$, and the Chl *a* maximum coincided with the thermocline or was within the mixed layer (Figure 2).

The late copepodite stage (CV) and females dominated the *C. euxinus* population, with average values of 1797 and 1202 ind. m^{-2} , respectively, in October (Figure 3). However, at some stations (Stations 4, 7, 8 and 10; see Figure 1) located in the coastal anticyclonic regions, young copepodite stages (CIIIs and CIIIs) outnumbered CV and females. The contribution of CIs to the young copepodite stages could be underestimated since the 300 μm mesh size used for collection of copepods might cause a loss during sampling. In October, a *C. euxinus* population with a high abundance of CV and females reflects typical characteristics for the population structure just after the summer diapausing period. In May, stages other than CIs and males made almost the same and important contributions to the population (Figure 3). Females always outnumbered males by an average factor of six or more during the sampling period. The dry weight of *C. euxinus* increased exponentially

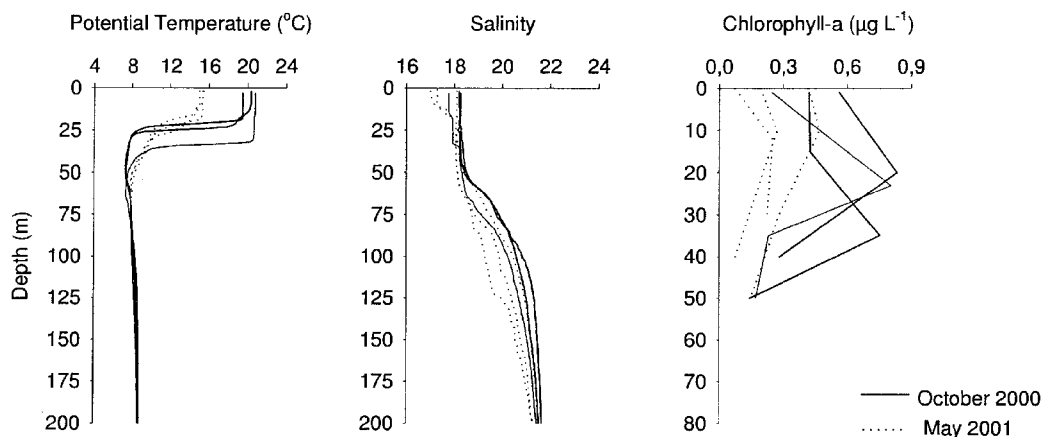


Fig. 2. Vertical profiles of temperature, salinity and Chl *a* concentrations in October 2000 (solid lines) and May 2001 (dashed lines) in the Black Sea. Data from three stations were chosen as representatives of the sampling period.

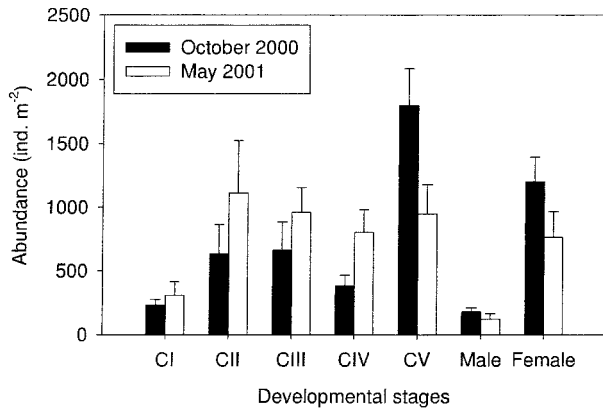


Fig. 3. Abundance of *C. euxinus* stages in October 2000 and May 2001 in the Black Sea.

with prosome length (from CI to adults). The length-weight regressions are shown in Figure 4.

EPRs, depth-integrated Chl *a* and mean surface layer temperature (calculated as the mean temperature above the thermocline) are shown in Figure 5. EPR of *C. euxinus* varied between the stations and was generally higher in May 2001 than in October 2000. EPR were very low, ranging from 0 to 9.5 (average 1.7 ± 2.3) and from 1.04

to 8.7 (average 3.9 ± 1.9) eggs female⁻¹ day⁻¹ in October 2000 and May 2001, respectively.

Depth-integrated Chl *a* concentrations were generally higher in October than those in May. Depth-integrated Chl *a* varied from 13.2 to 36.8 mg m⁻² in October (average 24.4 mg m⁻²), and varied from 9.4 to 24 mg m⁻² (average 15.1 mg m⁻²) in May (Figure 5). The EPR was independent of depth-integrated Chl *a* (Spearman rank correlation, $P > 0.05$). However, a significant negative correlation was found between EPR and mean surface layer temperature, and temperature explained only 28.9% of the variance in EPR (Figure 6).

The variation in EPR in *Calanus* was also explained by the endogenous factors, e.g. gonad development stages. EPR should be closely related to the proportion of mature females during the incubation period. We used reproductive stage identification described by Kosobokova (Kosobokova, 1999), who described seven reproductive stages of *Calanus gracialis* from the White Sea, and reported that the females in the mature stage (stage 4, with the largest oocytes) are in spawning condition. Figure 7 shows the relationship between EPR and the proportion of females in mature stages in experimental bottles. The relationship was described well by a power model, and the proportion of mature females explained 54.3% of the variance in EPR.

Female growth rates, derived from egg production experiments (g_r), ranged from 0 to 0.065 day⁻¹ (the mean value was 0.011 ± 0.017 day⁻¹) in October and from 0.009 to 0.067 day⁻¹ (the mean value was 0.03 ± 0.018 day⁻¹) in May. When we looked for correlations between female weight-specific fecundity and depth-integrated Chl *a*, temperature and body carbon weight (CW), we found significant negative correlations between growth and CW and mean surface layer temperature; however, no relationship was observed between growth and depth-integrated Chl *a* (Figure 8).

The diurnal difference in the EPR of *C. euxinus* is shown in Figure 9. *Calanus euxinus* showed nocturnal egg-laying behavior in the Black Sea. The same fecundity pattern has been recorded for the other *Calanus* spp. from other regions (Marshall and Orr, 1972; Runge and Plourde, 1996).

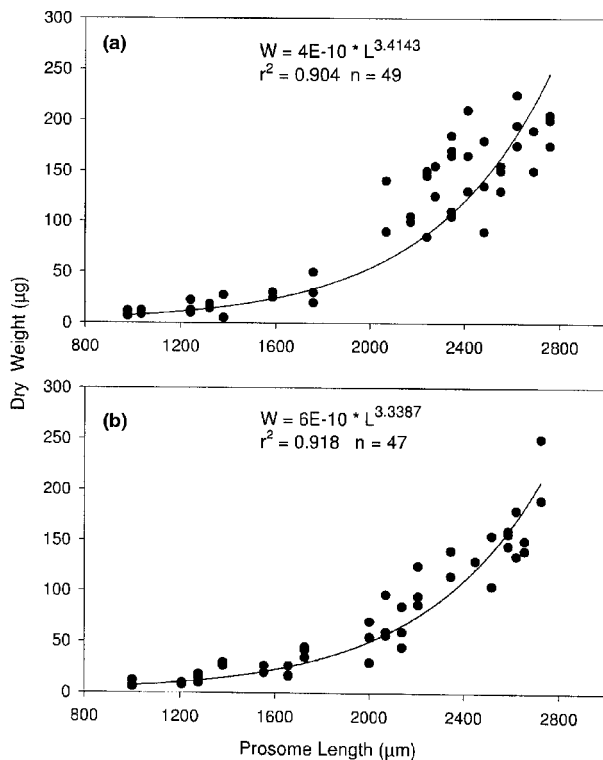


Fig. 4. Length-weight relationships for *C. euxinus* in October 2000 (a) and May 2001 (b) in the Black Sea.

DISCUSSION

The main purpose of the present study was to contribute to the knowledge of the reproductive and growth pattern of *C. euxinus* in the Black Sea. The overall mean of EPR of *C. euxinus* observed in this study was low and fell at the lower range reported earlier for the *Calanus* in the Black Sea. On average, egg production was 1.7 eggs female⁻¹ day⁻¹ in October 2000 and 3.9 eggs female⁻¹ day⁻¹ in May 2001. Arashkevich *et al.* observed that the mean EPR of *C. euxinus* was 5.3 eggs female⁻¹ day⁻¹ in September–October 1996

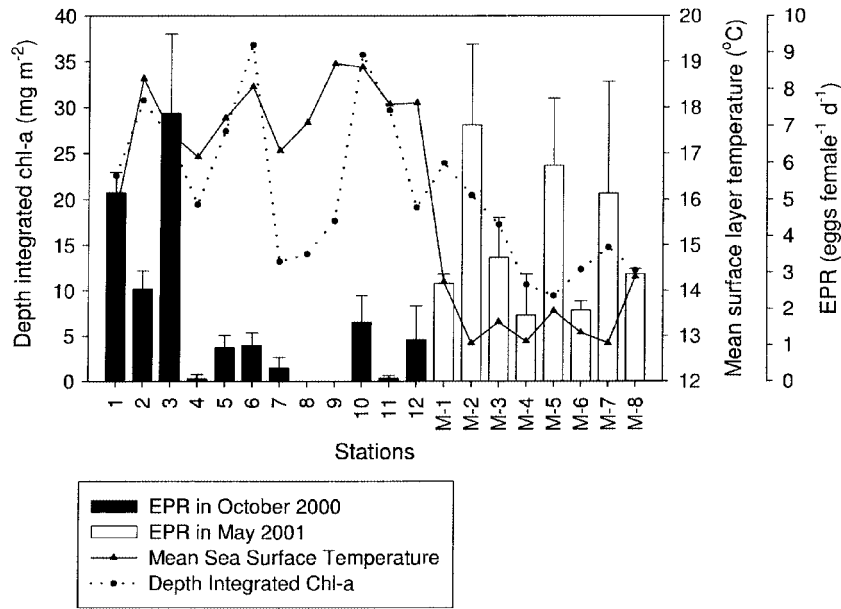


Fig. 5. Depth-integrated Chl *a* (0–50 m), mean surface layer temperature (mean temperature above the thermocline) and EPR of *C. euxinus* females from the stations visited in October 2000 (1–12) and May 2001 (M-1–M-8) in the Black Sea.

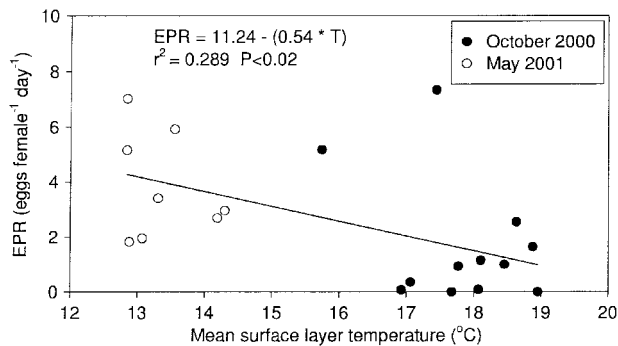


Fig. 6. EPRs of *C. euxinus* as a function of the mean surface layer temperature in the Black Sea.

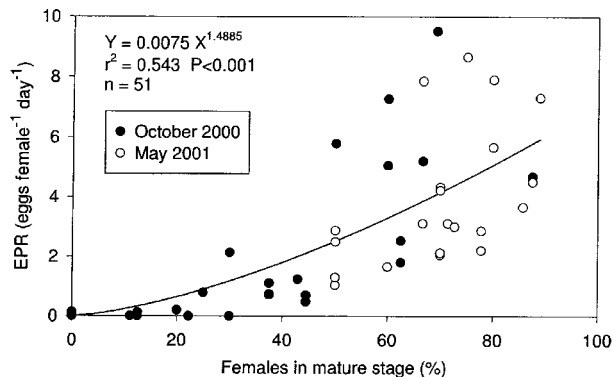


Fig. 7. Relationship between EPR and proportion of *C. euxinus* females with mature gonads in the Black Sea.

for the southern part of the Black Sea (Arashkevich *et al.*, 1998). However, in the Northern Black Sea, the EPR of *Calanus* were in the range of 15 and 30 eggs female⁻¹ day⁻¹ in May 1992, whereas they were 3 and 7 eggs female⁻¹ day⁻¹ in September 1992 (Sazhina, 1996).

Temperature and food concentrations are the major environmental factors controlling copepod reproductivity (Durbin *et al.*, 1983; Runge, 1985; Stearns *et al.*, 1989). In the present study, the EPR was independent of depth-integrated Chl *a*. Temperature seems to play a major role in the EPR of *C. euxinus* in the Black Sea during the study periods. Although this negative effect of temperature on egg production may seem reasonable because *C. euxinus* is described as a cold water species (Boltovski, 1969), this negative influence has to be considered cautiously because, similarly, Harris *et al.* observed a negative influence of temperature on egg production of *Calanus helgolandicus* from the English Channel (Harris *et al.*, 2000). When Harris *et al.* removed the hottest months with dinoflagellate blooms from their data set, this negative effect of temperature on egg production of *C. helgolandicus* disappeared. This indicates that egg production is some composite function of temperature and resources. Unfortunately, we do not have phytoplankton taxonomic composition measurements. Thus, to obtain a more precise picture of factors affecting the egg production of *C. euxinus* in the Black Sea, a comprehensive series of measurements containing phytoplankton taxonomic composition over different seasons should be carried out.

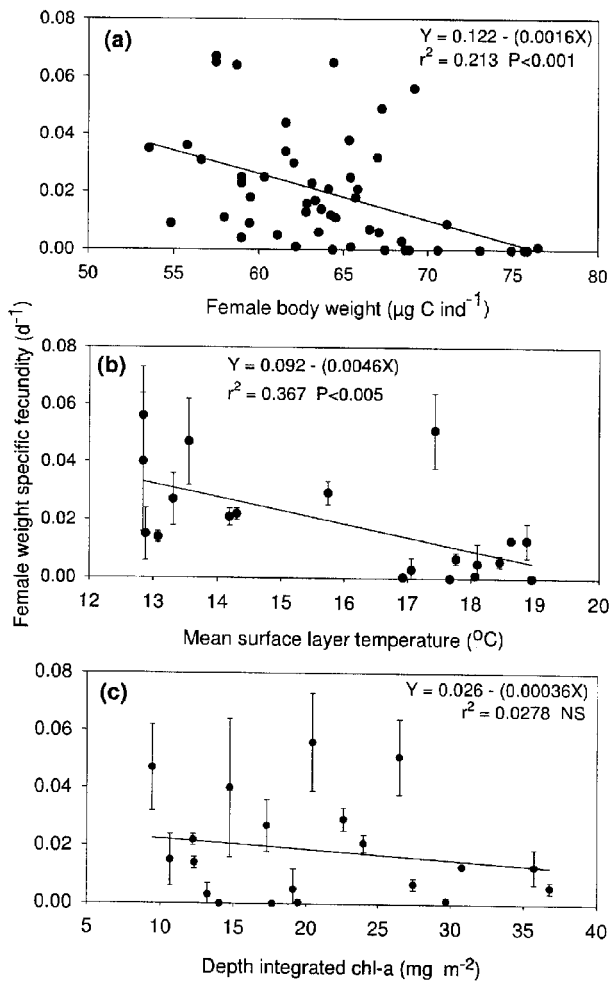


Fig. 8. Female weight-specific fecundity of *C. euxinus* as a function of female body weight (a), mean surface layer temperature (b) and depth-integrated Chl *a* (c) in the Black Sea. NS, not significant.

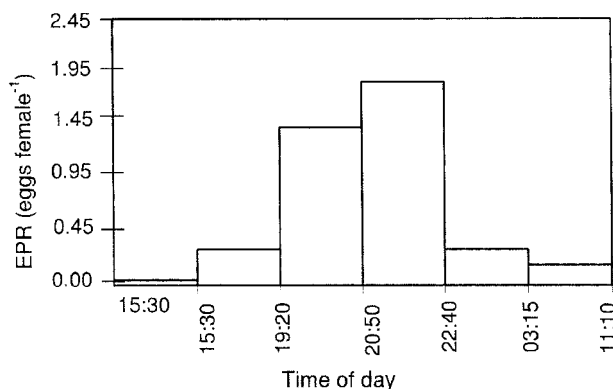


Fig. 9. Diel spawning behavior of *C. euxinus* in the Black Sea.

In spite of lower Chl *a* concentrations in May 2001 than in October 2000, the EPR was higher in May. The higher EPR in May seems mainly to be a result of the

numbers of reproductively active females. On average, 71% of the females in May and only 34% of those in October were mature. The low numbers of reproductively active females may reflect the poor food conditions, rather than the stage of development of the population, where the females are young and have not had time to mature. In October, at some stations EPR were zero or near zero, most of the females at these stations were reproductively immature, and the percentage of mature females was only 8–17%. Previous studies have shown a significant relationship between EPR and proportion of mature females (percentage of females in GS4) (Runge, 1987; Niehoff and Hirche, 1996; Campbell and Head, 2000).

Our growth rate estimates are based on measurements of EPR over 24 h incubation, and with the assumption that adult somatic growth is negligible. We found a low growth rate, an average of 0.011 day⁻¹ in October and 0.03 day⁻¹ in May. Egg production is not necessarily a measure of growth rate in copepods. Egg production is a common method to estimate growth in copepods, but this may not be the ideal approach since it may cause some biases. Using the literature data, Hirst and McKinnon explored whether there is an increase or decrease in adult body weight over the incubation period, concluding that growth is underestimated or overestimated using the EPR without correcting for adult body weight changes (Hirst and McKinnon, 2001).

There has recently been published a global analysis of growth in marine copepods (Hirst and Bunker, 2003). Hirst and Bunker established a global empirical equation for estimating the growth rate of copepods as a function of temperature, Chl *a* and body weight (see their table 6). Their equation for adult broadcasters assumes a positive relationship between growth and temperature and Chl *a* concentrations, but in our study we found negative correlations between growth and temperature. However, Chl *a* (using both depth-integrated Chl *a* and the Chl *a* concentrations from the depth of fluorescence maximum where the depth of incubation water collected) did not show any significant relationship with growth. Therefore, the application of Hirst and Bunker's (Hirst and Bunker, 2003) global model equation for adult broadcasters to the Black Sea may cause inaccurate results. However, considering the higher variability in their plots, adult weight-specific fecundity versus temperature (see their figure 1A) and adult weight-specific fecundity versus Chl *a*, particularly at low Chl *a* levels (see their figure 3A), we have attempted to apply their global model to our data. Our total Chl *a* concentrations collected from the depth of fluorescence maximum were within their low Chl *a* (0 to <2 µg Chl *a* L⁻¹) categorization. We found that their equation 78%

overestimated (predicted average growth 0.02) growth in October and 61% underestimated (predicted average growth 0.012) growth in May. Our median values (0.0054 for October and 0.0245 for May) are statistically different from the median values (0.0198 for October and 0.0098 for May) of growth predicted from Hirst and Bunker's (Hirst and Bunker, 2003) equation. These contradictory findings are not certainly related to the difference in food availability, because it is certain that *C. euxinus* was under food-limited conditions in both sampling periods.

We did a simple test to examine food limitation. The EPR of female *C. euxinus* were measured in both seawater from the depth of the fluorescence maximum and seawater from the depth of the fluorescence maximum enriched with a diatom, *Thalassiosira weissflogii* (addition was $\sim 198 \mu\text{g C L}^{-1}$). Food enrichment experiments were conducted at two stations with three replicates each in October 2000 and May 2001. Incubations were run for 2 days, and egg production was determined on day 2. EPRs in enriched water were enhanced considerably over those in ambient water. The average increase in EPR due to food enrichment was between 50 and 480% in October 2000, and between 76 and 300% in May 2001. Thus, this response to food enrichment provides evidence that *C. euxinus* was food limited on the southern part of the Black Sea in October 2000 and May 2001.

ACKNOWLEDGEMENTS

We gratefully appreciate the cooperation and help of the staff at the RV 'Bilim' during the cruises. This study was supported by METU-AFP-99-06-01-01, NATO-SfP-971818 ODBMS and TUBITAK-YDABCAG 100Y014 projects. We wish to thank two anonymous referees for their helpful comments and contributions.

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Received on December 2, 2003; accepted on January 30, 2004; published online on February 26, 2004