

# Does temperature-influenced egg production predict the recruitment in the bivalve *Macoma balthica*?

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**ABSTRACT:** As in most populations of bivalves, year-to-year variation in recruitment is large in the tellinacean *Macoma balthica* (L.). During the period of observation (1973 to 1996), high densities of recruits (numbers of spat, 0-year-class, per m<sup>2</sup> in late summer) were observed after 3 severe winters (1979, 1985, and 1987) and also in 1991, which was a normal winter, whereas recruitment failed after all of the 5 mildest winters of the period of observation (1974, 1988, 1989, 1990, and 1995). As fecundity (the number of spawned eggs per female) also varies strongly in response to winter temperature in *M. balthica*, we studied to what extent the large year-to-year variation in recruitment can be explained in terms of temperature-influenced variation in fecundity. To this end, we related both mean annual egg numbers per female (fecundity) and per m<sup>2</sup> (egg density) to subsequent recruitment data during the 1973 to 1996 period in a population at Balgzand, a 50 km<sup>2</sup> tidal flat area in the southwestern part of the Dutch Wadden Sea. Water temperatures in winter influenced individual egg production (winter temperature was negatively correlated with fecundity) and, consequently, total egg production of the population (stock size was not related to winter temperature). Although a substantial part (37%) of the year-to-year variation in recruit densities could be explained by interannual variation in winter temperatures, only a minor part of recruitment variation (7%) was explained by variation in egg density. Thus, the numbers of adults and the total number of eggs spawned in a certain year are poor predictors of subsequent recruit abundance. The significant effect of winter temperature on recruitment cannot be explained by the winter-temperature-governed fecundity and total egg production.

**KEY WORDS:** *Macoma balthica* · Fecundity · Stock-recruitment relationship · Winter temperature · Stock size

## INTRODUCTION

An important topic in marine ecology is the still poorly understood interannual variation in recruitment of many marine species, including economically important fish and shellfish species. So far, different definitions for recruitment are in use. In fish ecology, the term recruitment is commonly used for the year-class strength at the fishable stage (Miller 1994). As a consequence, the period between spawning and recruitment can be very long, sometimes even years (Hancock 1973). In our study on bivalve ecology, we adopt the following definition: recruitment is the num-

ber of juveniles (spat, 0-year-class individuals, which can be distinguished from 1 yr old juveniles by their size and the lack of a year-ring), retained on a sieve with a mesh size of 1 mm, present per m<sup>2</sup> in the first summer after spring spawning. The period between spawning and recruitment is relatively short (3 to 5 mo) and the factors affecting recruitment success can be studied within a short period.

Variation in bivalve recruitment can be very large. Examples of long-term data series of recruitment success include the cockle *Cerastoderma edule* (L.) (Kristensen 1957, Beukema 1982, Möller & Rosenberg 1983, Ducrotoy et al. 1991, Beukema et al. 1993), the mussel *Mytilus edulis* (L.) (Beukema 1982, McGrorty et al. 1990, Beukema et al. 1993), the clam *Mya arenaria* (L.)

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(Beukema 1982, Möller & Rosenberg 1983), and the tellinaceans *Macoma balthica* (L.) (Beukema 1982, Beukema et al. 1998), *Scrobicularia plana* (da Costa) (Essink et al. 1991), and *Abra tenuis* (Wood) (Dekker & Beukema 1993). All these studies show that year-to-year differences of 2 to 3 orders of magnitude are not uncommon.

In fish, only a minor part of the interannual variability in recruitment can usually be explained by variability in adult stock size or egg numbers (Parrish 1973, Corten & Van de Kamp 1979). Data about the stock-recruitment relationship in shellfish and other marine invertebrates appear to be scarce (Hancock 1973) and show a lack of correlation between size of spawning stock and subsequent recruitment. An exception is the common cockle *Cerastoderma edule* (L.), for which a (weak) negative relationship between the stock, defined as the total number (Hancock 1973) or biomass of adult year classes (Van der Meer 1997), and recruitment was observed.

One of the factors which seems to influence variation in recruitment is winter temperature. For a number of bivalve species, relatively successful recruitment has been reported after cold winters, whereas recruitment after mild winters usually fails. Among these species are *Mytilus edulis* (Beukema 1982, 1992a, Jensen & Jensen 1985, McGroarty et al. 1990, Young et al. 1996), *Cerastoderma edule* (Kristensen 1957, Hancock 1973, Beukema 1982, 1992a, Möller & Rosenberg 1983, Jensen & Jensen 1985, Yankson 1986, Ducrottoy et al. 1991, Young et al. 1996), *Mya arenaria* (Beukema 1982, 1992a, Möller & Rosenberg 1983, Jensen & Jensen 1985), and *Macoma balthica* (Beukema 1982, 1992a, Jensen & Jensen 1985).

In the present study, we present detailed data on the egg number-recruitment relationship in the Balgzand (The Netherlands) population of the bivalve *Macoma balthica*. Data on numbers and biomass of aged specimens of this population have been collected since 1970 at 15 tidal-flat Wadden Sea stations (Beukema 1974, 1988). It has already been shown that there is no correlation between the stock size of this population, defined as the total *M. balthica* ash-free dry mass per m<sup>2</sup>, and subsequent recruitment (Van der Meer 1997). In an earlier study, the dependence of fecundity (number of spawned eggs per female) in *M. balthica* on its body mass and shell size was established (Honkoop & Van der Meer 1997). Taking these variables into account, we modify the relevant index of adult stock size to total number of eggs produced per m<sup>2</sup> (i.e. egg density). Using this index we examine the stock-recruitment relationship to determine how far the interannual variation in *M. balthica* recruitment can be explained by year-to-year variation in egg production.

In earlier studies it was shown that variation in fecundity in *Macoma balthica* and *Cerastoderma edule* can be very large, and that winter temperature is one of the main factors influencing variation in individual egg production (Honkoop & Van der Meer 1997, 1998); low winter temperatures appear to have a positive effect on fecundity. Thus, winter temperature seems to affect both individual egg production and subsequent recruitment in a similar way. Therefore, the following question arises: are egg production and recruitment closely connected and can winter temperatures thus explain a significant part of the variation in recruitment via temperature-induced variation in fecundity? To answer this question, we estimated which part of the year-to-year variation in egg density and recruitment can be explained by variation in winter temperature.

## MATERIALS AND METHODS

**Study area and monitoring.** Each year, since 1970, benthic invertebrates have been quantitatively sampled at the Balgzand, a 50 km<sup>2</sup> tidal-flat area in the southwestern part of the Dutch Wadden Sea. Mostly twice a year, in March and August, 15 fixed sites scattered over the whole area were sampled: 12 transects 1 km in length (each with 50 sub-sampling points) and 3 squares of 900 m<sup>2</sup> (each with 18 sub-sampling points). At each sub-sampling point a core with a known area was taken from the sediment down to a depth of 20 cm. The cores were washed through a sieve with a mesh size of 1 mm, and all animals were sorted, identified, counted, dried and incinerated. Numbers and biomass are expressed per m<sup>2</sup>. For further details about the sampling method see Beukema (1974, 1988). At each site the following variables were measured or calculated for *Macoma balthica*: (1) shell length (mm), each individual was aged, by counting year-rings, and measured to the nearest mm, using a calliper; (2) density (m<sup>-2</sup>), for each year-class (6 year-classes), which is defined as a group of individuals born in the same year (individuals older than 5 yr were pooled into the same year-class); (3) body mass index (BMI) within each year-class for each mm-class, i.e. ash-free dry mass per cubic shell length (mg cm<sup>-3</sup>); and (4) recruitment, which is defined as the number of spat (0-year-class individuals, no year-ring) retained on a 1 mm mesh-size sieve in August. Annual recruitment data are available from 1973 up to and including 1996 (n = 24 yr). The year 1991 was exceptional in the Dutch Wadden Sea with respect to the density of filter-feeding bivalves, the adult body masses, and the recruitment of some bivalve species (Beukema & Cadée 1996). Because 1991 was such an outlying year we did not use data from this one year in our statistical analyses.

Water temperatures were obtained from measurements of surface water in the Marsdiep, the neighbouring major tidal channel; each day at 08:00 h the water temperature was measured to the nearest 0.1°C. The winter water temperature is defined as the mean of the daily measurements in January, February, and March in each year.

**Calculation of egg production.** To estimate the number of eggs spawned by an individual female with a standard shell length of 1.5 cm, the following relationships were used:

(1) total body mass  $m$  (mg) is proportional to cubic length:

$$m = c \cdot l^3 \quad (1)$$

where  $l$  = shell length (cm) and  $c$  = BMI (mg cm<sup>-3</sup>).

(2) based on the relationship described by Honkoop & Van der Meer (1997), the number of spawned eggs per adult female,  $y$  (fecundity), is related to the difference between total body mass ( $c l^3$ ) and minimal (structural) body mass for any egg production ( $\beta l^3$ ) (i.e. the minimum body mass, excluding stores, necessary for a functional normal life; Van der Meer & Piersma 1994) of the female individual.

Hence:

$$y = \alpha \frac{l^3}{s^3} (c - \beta) \quad (2)$$

where  $\beta$  = structural body mass in BMI units (mg cm<sup>-3</sup>),  $\alpha$  = number of spawned eggs per BMI unit for a standard individual of 1.5 cm shell length (cm<sup>3</sup> mg<sup>-1</sup>), and  $s$  = shell length of a standard female (cm).

Values for  $\alpha$  (7739),  $\beta$  (43314/7739 = 5.6), and  $s$  (1.5 cm) were given by Honkoop & Van der Meer (1997).

Additional assumptions were:

(3) if  $c < 5.6$ , egg production was set to zero (thus excluding negative values for fecundity);

(4) only females >10 mm reproduce (reproduction rarely occurs at smaller shell lengths; Caddy 1967, Gilbert 1978, pers. obs.);

(5) on average, half of the adult population (all individuals except the 0-year-class) are females (Caddy 1967, De Wilde & Berghuis 1976, Gilbert 1978, Brousseau 1987).

Then, total egg production  $x_j$  in year  $j$  is:

$$x_j = \sum_{i=1}^{15} \sum_{k=1}^6 \frac{n_{ijk}}{2} y_{ijk} = \sum_{i=1}^{15} \sum_{k=1}^6 \frac{n_{ijk}}{2} \alpha \frac{l_{ijk}^3}{(1.5)^3} (c_{ijk} - \beta) \quad (3)$$

where  $i$  = sampling site,  $k$  = year-class,  $n_{ijk}$  = number of adults larger than 10 mm for site  $i$ , year  $j$ , and year-class  $k$ ,  $c_{ijk}$  = average BMI for site  $i$ , year  $j$ , and year-class  $k$ ,  $l_{ijk}$  = average length for site  $i$ , year  $j$ , and year-class  $k$ ,  $y_{ijk}$  = number of spawned eggs by a female for site  $i$ , year  $j$ , and year-class  $k$ .

## RESULTS

### Winter water temperature and egg production

Using average March BMI values of each year-class at each station, individual egg production  $y$  for a standard female with a shell length of 1.5 cm was calculated for each year (using Eq. 2). A negative relationship between winter water temperature and individual egg production  $y$  was observed, in accordance with previous experiments (Honkoop & Van der Meer 1997, 1998). Variation in mean winter (January–March) temperature explained 68% of the total among-years variance in (log-transformed) egg numbers produced by a single standard *Macoma balthica* ( $p < 0.0001$ ,  $R^2 = 0.68$ ; Fig. 1A).

Total egg production (estimated with Eq. 3) also depended on the numbers of reproducing females (as well as their age and size distribution). Linear regression of (log-transformed) total egg production against winter water temperature (Fig. 1B) revealed a negative relationship, but the explained variance was much lower ( $R^2 = 0.23$ ,  $p < 0.05$ ). Yet, relating subsequent (log-transformed) recruitment to winter water temperature (Fig. 1C) revealed a somewhat better fit ( $R^2 = 0.37$ ,  $p < 0.01$ ).

### Egg production and subsequent recruitment

*Macoma balthica* recruitment at Balgzand was low during most years of the study period, except for a few years with relatively large recruitment, viz. 1979, 1985, 1987, and 1991 (Fig. 2A).

In most years fecundity amounted to values between 10000 and 20000 spawned eggs per standard 1.5 cm female, but in some years it was roughly twice this amount (1985, 1986, 1987, 1991, and 1996) (Fig. 2B).

Egg density per year, which also depends on adult density (Fig. 2C), showed a somewhat larger variation among years (Fig. 2D), with approximately an order of magnitude difference among years. Survival of eggs to recruits (recruit/egg ratio) varied between 0.0001 and 0.001 and showed an almost continuous decrease throughout the study period (Fig. 2E).

Only 7% of the interannual variation in (log-transformed) numbers of recruits could be explained by variation in (log-transformed) egg density (Fig. 3). The estimate of the regression slope was much lower than 1 ( $b = 0.31$ ,  $SE = 0.24$ ), which implies that high egg production results in low survival of eggs to recruits.

Thus, although variation in winter water temperature accounts for a relatively large part (37%) of variation in recruitment, this cannot be explained by temperature effects on egg production, as only 7% of the

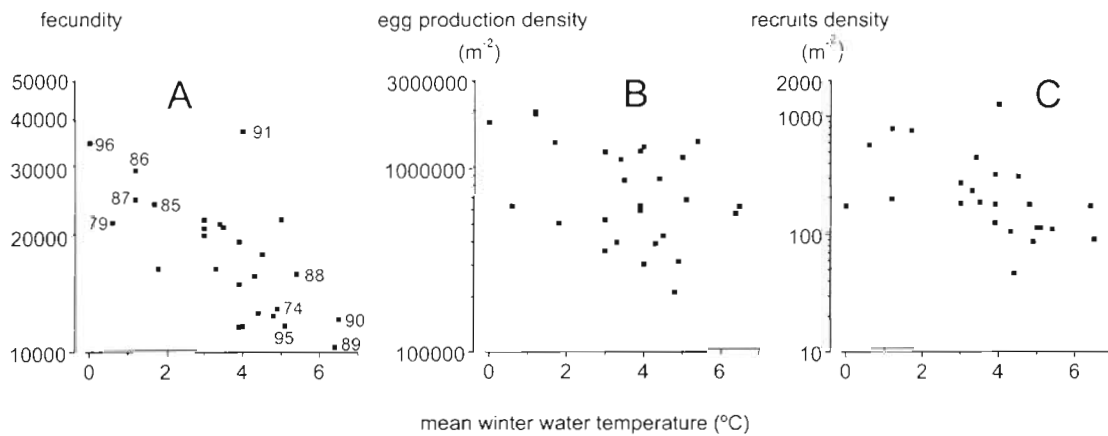


Fig. 1 *Macoma balthica*. Relationships between winter water temperature (mean water temperature of the January–March period) and log-scaled (A) individual egg production at Balgzand of a standard female with a shell length of 15 mm, (B) total egg production at Balgzand, and (C) recruit numbers at Balgzand. The numbered points in (A) refer to 5 cold winters (1979, 1985, 1986, 1987, and 1996), 5 mild winters (1974, 1988, 1989, 1990, and 1995), and the exceptional year 1991

variation in recruitment could be attributed to (temperature-related) variation in egg density. The effect of winter water temperature operates on survival from egg to recruit.

## DISCUSSION

### Stock-recruitment relationship

A study of a stock-recruitment relationship such as the present one for the *Macoma balthica* population at Balgzand has its inherent limitations, primarily because it is an open system that has been studied. Therefore, it is not certain that all Balgzand recruits originated from eggs of this population. It might be that (1) part of the eggs were produced by nearby populations and (2) eggs of the Balgzand population contributed to recruitment somewhere else (e.g. the North Sea). A real distortion of the relationships shown is not expected, as (1) the other populations will have experienced similar winter temperatures, and (2) their densities will have fluctuated similarly to those of the Balgzand population (Desprez et al. 1991, Beukema et al. 1996).

Fecundity of *Macoma balthica* is highly variable and depends on body mass and shell length (Honkoop & Van der Meer 1997, 1998). Therefore, these 2 factors have to be taken into account when calculating total numbers of eggs produced. To this end we used a previously described relationship (Honkoop & Van der Meer 1997). The total number of eggs spawned is not exactly equivalent to the product of the fecundity of a standard individual times the overall female stock size, as variation in age and size distribution are ignored. However, 92% of

the variance in total egg number [as calculated using Eq. (3), which takes into account differences in age and size distribution] was explained by this simple approximation, leaving only 8% to be explained by annual differences in age and size distribution.

The lack of significant correlation between total egg number and recruitment (Fig. 3) and the observation of an increasing adult density throughout the studied period (Fig. 2C) imply that there must be a negative relationship between adult densities and survival of eggs to recruits. The opposing trends shown in Fig. 2C & 2E illustrate this point. It is not clear whether this relationship is based on an effect of the adults on survival of eggs, larvae, or post-larvae. In several species such a relationship has been shown (*Macoma balthica*: Bachelet 1986, Bonsdorff et al. 1996; *Cerastoderma edule*: Kristensen 1957, André & Rosenberg 1991, André et al. 1993; *Mya arenaria*: André & Rosenberg 1991) but a possible direct mechanism has been suggested only in *C. edule*, in which the adults inhaled their own offspring (André et al. 1993).

### Winter temperature and recruitment

Recruitment after mild winters during the period of observation (Figs. 1C & 2A, solid triangles) was consistently low. In these years, fecundity was invariably low (Fig. 2B), but adult densities happened to be high in most years (Fig. 2C), resulting in egg numbers which were generally not particularly low (Fig. 2D). Survival of eggs to recruits in these years was always relatively low (Fig. 3). This may have been due to predation by juvenile shrimps *Crangon crangon*, important predators on post-larval (i.e. early spat) *Macoma balthica*

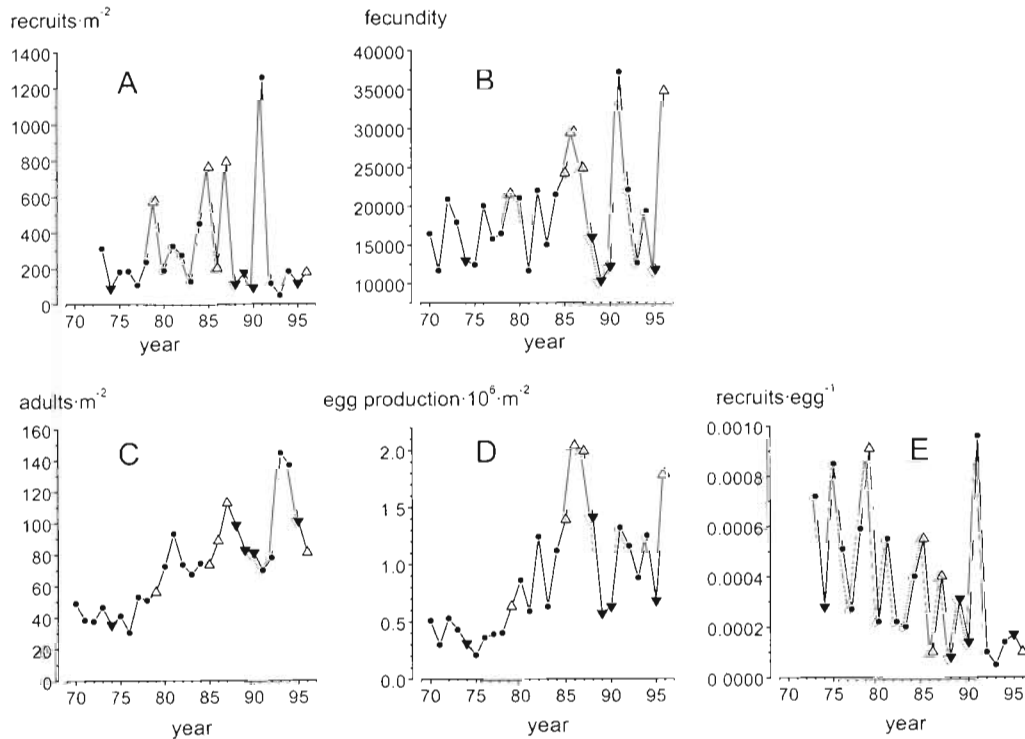


Fig. 2. *Macoma balthica*. Annual variability of some population characteristics. (A) Average number of recruits per m<sup>2</sup> on the tidal flats of Balgzand in August of each of the years 1973 to 1996, (B) number of eggs spawned by a standard *M. balthica* with a shell length of 15 mm for each year in the period 1970 to 1996, (C) density of reproducing individuals (thus males+ females) per m<sup>2</sup> for the same period, (D) calculated egg production per m<sup>2</sup> for the same period, and (E) survival from egg to recruit for the 1973 to 1996 period. (Δ) The 5 years with cold winters (mean January–March water temperature <1.8°C), (▼) the 5 years with mild winters (mean January–March water temperature >4.8°C) during the 1970 to 1996 period

(Beukema et al. 1998) that generally appear on tidal flats earlier in springs after mild than after cold winters (Beukema 1992b).

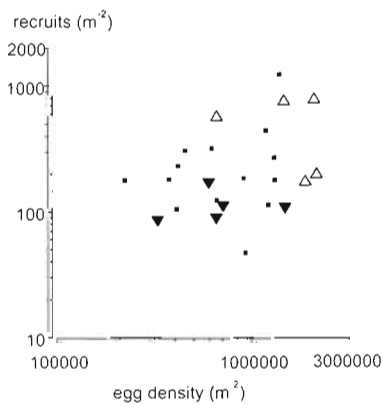


Fig. 3. *Macoma balthica*. Relationship (log-scales) between the total number of eggs produced per m<sup>2</sup> in spring and the number of recruits per m<sup>2</sup> observed in the following August. Each data point represents one year during the 1973 to 1996 period. (Δ) The 5 years with the coldest winters (mean January–March water temperature <1.8°C), (▼) the 5 years with the mildest winters (mean January–March water temperature >4.8°C) during the 1970 to 1996 period

Recruitment after cold winters (Figs. 1C & 2A, open triangles) was less consistent, being high after 3 out of the 5 years with a cold winter (1979, 1985, and 1987), and low after the others (1986 and 1996). In 1986, low recruitment can possibly be explained by shrimp summer density which was the highest observed during the studied period, ~210 ind. m<sup>-2</sup>, which is on average twice as high as in other years. Why recruitment success was low after the severe winter of 1996 is not known. An exceptionally high recruitment was observed in the summer of 1991: it was the highest observed in the studied period and followed high fecundity values in spring (Fig. 2B), but a close-to-average total egg production (Fig. 2D). The year 1991 was exceptional in several ways. Due to intensive bottom-fishery activities and 3 successive years of recruitment failure in almost all large filter-feeding bivalves (particularly the important species *Cerastoderma edule* and *Mytilus edulis*), bivalve stocks were exceptionally low in late 1990 and in early 1991. This resulted in increased food supply—phytoplankton densities are significantly reduced at high filter-feeding densities (Prins et al. 1995)—and therefore high body mass values for reproducing *Macoma balthica*

(Beukema & Cadée 1996). Moreover, shrimp densities in spring 1991 were exceptionally low,  $\sim 25$  ind.  $m^{-2}$  (Beukema et al. 1998).

Fecundity was significantly negatively correlated with winter temperature (Fig. 1A), resulting in a large percentage of the variation in egg production being explained by variation in water temperature (Fig. 1B). However, the relationship between winter temperature and recruitment (Fig. 1C) cannot be directly explained from temperature-determined differences in egg production. Egg density was weakly correlated with recruit numbers (Fig. 3) and only a small percentage (7%) of the variation in recruitment was explained by temperature-influenced egg production. This suggests that the temperature-influenced variation in recruit numbers (Fig. 1C) must have been caused by temperature-affected variation in factors other than egg numbers. One possibility is the predation by juvenile shrimps *Crangon crangon* and juvenile shore crabs *Carcinus maenas*. It has been shown that both shore crabs and shrimps arrive earlier on the tidal flats and, moreover, crabs arrive in higher numbers after a mild than after a cold winter (Beukema 1991, 1992b). Also, the density of juvenile shrimps in spring was significantly positively correlated with the temperatures of the preceding winter (Beukema et al. 1998). Although almost nothing is known about the intensity and timing of predation, this process may have decisively affected survival of all early life stages (eggs, larvae, and post-larvae) and may have overruled the effects of initial egg numbers.

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