

Long-term variability in secondary production of an intertidal bivalve population is primarily a matter of recruitment variability

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Summary

1. The importance of recruitment processes in determining benthic population dynamics has received considerable interest among marine ecologists in the last two decades. Observational demographic studies, in which recruits were followed to and through the adult state, aimed to estimate whether the variation in the numbers of recruits is dampened by density-dependent post-recruitment processes. These studies revealed conflicting results on the importance of post-recruitment density dependence, but were performed over at most a few years.

2. Based on a study of the demography and growth of the bivalve *Macoma balthica* (L.) on an intertidal flat in the Dutch Wadden Sea for a period of almost 30 years, we explored the extent to which the among-cohort variability in recruitment was reflected in the secondary production (which results from the combined action of recruitment, mortality and growth) of the adult population.

3. Since growth in length was of the Von Bertalanffy type and post-recruitment instantaneous mortality rate was approximately constant for each cohort, production could be explicitly written in terms of the following parameters: recruit density, condition (ratio of mass to cubic length), Von Bertalanffy growth coefficient, asymptotic cubic length, and expected life span.

4. Decomposing the among-cohort variability in production in terms of the covariance matrix of these parameters revealed that most of the variance in production could be attributed to year-to-year variability in recruit density.

5. Small negative covariances between recruit density and asymptotic size and expected life span indicated weak density dependence after recruitment.

6. The major cause of temporal variation in abundance and production is inter-annual variation in recruitment and competition for resources seems to play a small role in affecting post-recruitment population density and production.

Key-words: *Macoma balthica*, population regulation, recruitment limitation, soft sediments.

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Introduction

Many populations living in marine benthic habitats have dispersive propagules. After spending some time in the water column, the surviving larvae try to settle on the sea floor. Such benthic populations are often characterized as open systems, i.e. it is assumed that the local adult stock has effectively no effect on the number of new individuals that try to settle in the local population. The question of whether the variability in larval supply, i.e. the numbers of potential settlers, is

maintained when the animals grow older, has attained considerable theoretical and empirical interest. This interest has focused on two points (Ólafsson, Peterson & Ambrose 1994; Booth & Brosnan 1995). The first point concerns the settlement process itself. Although the local stock may have little or no effect on the larval supply, the local adult population may influence the chance of a successful settlement for an individual larva. The second point, which is also the concern of the present paper, is to what extent density-dependent post-settlement processes dampen the variation in the numbers of successful settlers. In order to be more specific about what is meant by successful settler, it is useful to reiterate at this point the distinction between settlement and recruitment (Keough & Downes 1982;

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Connell 1985; Ólafsson *et al.* 1994). Settlement of larvae to the seafloor is an instantaneous process, and is in fact not measurable. Instead recruitment is measured, which is always defined in some practical way, for example as the density of post-larvae at some specific time (which in some studies may mean months after the settlement phase has been completed). Hence, recruitment is necessarily the integrative result of larval supply rate, settlement success and early post-settlement mortality.

Empirical studies, which have followed recruits to the adult state, have been mainly performed in invertebrate communities at intertidal rocky shores and in coral-reef fish communities (Doherty & Williams 1988; Menge & Farrell 1989; Booth & Brosnan 1995), and to a minor extent in soft-sediment communities (Ólafsson *et al.* 1994). Some of these studies showed only a weak relationship between densities of recruits and subsequent adult population size (Möller & Rosenberg 1983; Pfister 1995), but other studies revealed cases where the density of recruits was reflected in adult population density long after settlement (Jensen & Jensen 1985; Raimondi 1990). Most of the observational studies in which recruits are followed through to the adult stage were performed only over a few years, generally 2–3 years. Among the longest studies reported are the ones by Bertness *et al.* (1992) on barnacles, and McGrorty & Goss-Custard (1993) on mussels, both lasting 8 years.

Post-recruitment density dependence may appear in terms of increased mortality when the density of recruits is high. It may also arise in terms of reduced growth in length or a lowered condition (mass per cubic length) of individual animals. For example, Jensen (1993) observed a decrease in growth rate in the cockle *Cerastoderma edule* (L.) when recruitment densities were high. Together, recruitment, mortality and growth determine the secondary production of an adult population. Long-term observational studies in which both mortality and growth are followed through the adult population are virtually lacking, and most secondary production studies in the marine benthic habitat have been performed over relatively short periods (Möller & Rosenberg 1983; Brey & Hain 1992; Noda 1997), but see Beukema (1980).

We estimated the density, age structure, length and mass distribution of a benthic population of the bivalve *Macoma balthica* in the Western Wadden Sea, The Netherlands, over a time span of about 30 years. These long-term data on the demography and growth of this bivalve species allow us to explore whether density-dependent post-recruitment processes occur. We therefore describe the temporal variability in secondary production during the benthic life-phase in terms of the variability in recruit density, mortality and individual growth and in terms of their covariation. A negative covariation between recruit density and subsequent survival rate or growth indicates dampening of recruitment variability. We defined recruitment as the density of the 0-year class *M. balthica* at the end of the settlement period (i.e. at the end of their first winter). Basically,

this separates the highly mobile first life phase, including a pelagic phase, a first settlement at the lower intertidal zones, a gradual move to the higher zones and finally a second settlement at the lower zones, from the more-or-less sessile later part of life (Beukema 1993).

Van Straalen (1985) and Aldenberg (1986) developed a framework that permits a general formulation of secondary production in terms of three characteristics: renewal (recruitment) rate, mortality and individual growth. They based their work on the standard demographic theory of age- and stage-structured populations in continuous time, mathematically framed in terms of partial differential equations (Metz & Diekmann 1986; De Roos 1995). In order to avoid the use of partial differential equations, with which many ecologists are not familiar, we frame the problem in terms of elementary probability theory. Next, we discuss the specific case of exponentially distributed life span and Von Bertalanffy growth. This case is relevant for our study population of *M. balthica*.

To summarize, by examining a long-term data series of the demography and growth of a bivalve population living in the intertidal soft-sediment habitat, we explore to what extent the temporal variability in secondary production can be explained by recruitment variability.

Theoretical framework

LIFE SPAN AND MASS AT DEATH

Suppose that the life span (age at death) of an individual is a continuous random variable X whose probability density function is given by $f(x)$, where $f(x) = 0$ when $x < 0$. The cumulative distribution function is

$$F(x) = \int_{t=0}^x f(t) dt \quad \text{eqn 1}$$

and the survival function is $S(x) = 1 - F(x)$.

The contribution of each individual to the production of the population can be defined as its mass at death. Now assume that the mass-age function (growth function) is a fixed monotonously increasing function $G(X)$, for which holds that $G(0) = W_0$ and $\lim_{x \rightarrow \infty} G(x) = W_{\infty}$. This means that the random variable mass at death W is a function $G(X)$ of age at death. Let

$$\frac{dG(x)}{dx} = g(x), \quad \text{or} \quad G(x) = W_0 + \int_0^x g(t) dt \quad \text{eqn 2}$$

Then, the cumulative distribution function of W is

$$F_w(w) = F[G^{-1}(w)] \quad \text{eqn 3}$$

and thus the probability density function of W is

$$\begin{aligned} f_w(w) &= \frac{dF_w(w)}{dw} = \frac{dF[G^{-1}(w)]}{dG^{-1}(w)} \frac{dG^{-1}(w)}{dw} \\ &= f[G^{-1}(w)] \frac{dG^{-1}(w)}{dw} \end{aligned} \quad \text{eqn 4}$$

or in a short-hand notation

$$f_w(w) = f(x) \frac{dx}{dw} = \frac{f(x)}{g(x)} \quad \text{eqn 5}$$

The expectation of the mass at death follows from

$$\begin{aligned} E(W) &= \int_{W_0}^{\infty} f_w(w) w dw = \int_0^{\infty} f(x) \frac{dx}{dw} G(x) dx \\ &= \int_0^{\infty} f(x) G(x) dx \end{aligned} \quad \text{eqn 6}$$

Defining production as the expectation of mass at death also provides a theoretical justification for the so-called 'removal summation' method for measuring production in the field, where for each age class

$$\left\{ x - \frac{\Delta x}{2}, x + \frac{\Delta x}{2} \right\} \quad \text{eqn 7}$$

the fraction of the population that dies at that particular age, which approximately equals $\Delta x f(x)$, is multiplied by the mass at death $G(x)$. Summation over all age classes leads to the following approximation for the production per individual: $\sum f(x) G(x) \Delta x$. Alternative methods to estimate production in the field can also be related to the expectation of mass at death $E(W)$: partial integration of

$$E(W) = \int_0^{\infty} f(x) G(x) dx \quad \text{eqn 8}$$

gives

$$E(W) = W_0 + \int_0^{\infty} S(x) g(x) dx \quad \text{eqn 9}$$

or, using $g(x) = dw/dx$ and $S_w(w) = S[G^{-1}(w)]$,

$$E(W) = W_0 + \int_{W_0}^{\infty} S_w(w) dw \quad \text{eqn 10}$$

where the integrals from the right-hand term are the basis of the 'growth-increment-summation' and 'Allen-curve' method, respectively (Rigler & Downing 1984). This shows that in principle these two latter methods only differ from the 'removal-summation' method in implicitly subtracting mass at birth from the expected mass at death. So, these two latter methods must either add mass at birth or take into account reproductive production in order to arrive at the total secondary production. Alternatively, the 'removal-summation' is sometimes used, but with subtracting mass at birth from the mass at death. Yet, in that case reproductive production must be explicitly added in order to arrive at the total production. See Van Straalen (1985) for further details. The expected lifetime production of a cohort (a group of individuals recruited at the same time) is the number of recruits multiplied by the expected mass at death $E(W)$.

EXPONENTIAL LIFE SPAN AND VON BERTALANFFY GROWTH

Assume that the instantaneous mortality rate $r(x) = f(x)/S(x)$ is constant: $r(x) = \lambda$. This means that the life

span X is exponentially distributed, with probability density function $f(x) = \lambda e^{-\lambda x}$, survival function $S(x) = e^{-\lambda x}$, and expected life span $E(X) = 1/\lambda$.

Assume further that growth is of the Von Bertalanffy type. Let $L(x)$ be the shell length at age x . Then

$$\frac{dL(x)}{dt} = \gamma(L_{\infty} - L(x)) \quad \text{eqn 11}$$

where γ is the Von Bertalanffy growth parameter and L_{∞} is the asymptotic length. A physiological basis for the Von Bertalanffy growth model has been provided by Kooijman (1993), whose dynamic energy budget (DEB) model reveals that under constant food conditions growth is of the Von Bertalanffy type.

Integration leads to $L(x) = L_{\infty}(1 - e^{-\gamma x})$ and $G(x) = \phi L_{\infty}^3 (1 - e^{-\gamma x})^3$, where the so-called condition parameter ϕ relates cubic shell length to mass (and hence incorporates both the specific density, relating volume to mass, and a shape coefficient relating cubic shell length to volume). The expected mass at death is

$$E(W) = \int_0^{\infty} f(x) G(x) dx = \int_0^{\infty} \lambda e^{-\lambda x} \phi L_{\infty}^3 (1 - e^{-\gamma x})^3 dx \quad \text{eqn 12}$$

which equals (see the Appendix)

$$E(W) = \phi L_{\infty}^3 \left(\frac{\gamma \cdot 2\gamma \cdot 3\gamma}{(\gamma + \lambda) \cdot (2\gamma + \lambda) \cdot (3\gamma + \lambda)} \right) \quad \text{eqn 13}$$

Thus, if the life spans of individuals from cohort i are identically distributed and if these individuals follow the same growth trajectory, the expected lifetime cohort production (per unit area) equals

$$p_i = \mu_i \phi_i L_{\infty,i}^3 \left(\frac{\gamma_i \cdot 2\gamma_i \cdot 3\gamma_i}{(\gamma_i + \lambda_i) \cdot (2\gamma_i + \lambda_i) \cdot (3\gamma_i + \lambda_i)} \right) \quad \text{eqn 14}$$

where μ_i is the initial cohort density.

Study area and life history

STUDY AREA

Balgzand is a tidal-flat area in the westernmost part of the Wadden Sea, The Netherlands. The area ranges from a coastal area above mean-tide level with silty sediments to a low exposed area close to low-tide level (80 cm below mean-tide level) that emerges a few hours at most and only when strong easterly winds prevail. The area that regularly emerges is about 45 km² in extent. More details are given in Beukema (1988) and Beukema *et al.* (1993).

LIFE HISTORY

The bivalve *Macoma balthica* is one of the most common macrobenthic species on the tidal flats in the Wadden Sea. The adult stage occurs at high densities (tens or hundreds per m²) on nearly all tidal flats (Beukema 1976; Dankers & Beukema 1983). Initial settlement of post-larvae in spring, at a size of approximately 280 µm, takes place mainly in the lower half of the intertidal

(Günther 1991; Armonies & Hellwig-Armonies 1992; Beukema 1993). Some weeks later, the juveniles, with a shell length between 1 and 10 mm, occur in maximal numbers on the higher tidal flats, above mean-tide level (Dankers & Beukema 1983; Günther 1991; Armonies & Hellwig-Armonies 1992; Beukema 1993). In the subsequent winter most animals move again to the middle and lower zones, where they will spend the rest of their life (Beukema 1989; Beukema 1993).

Methods

SAMPLING AND DATA SELECTION

Between 1970 and 1998, 12 randomly selected stations, each in the form of a 1-km long transect, have been sampled at the tidal flats of Balgzand each year in late winter (March). The geographical position of each station has been determined by a starting point and a wind direction, which were randomly chosen from a grid of geographical coordinates and a set of angles, respectively. One station was not taken into account in the present paper, because it rarely emerges. At each station 50 cores of 0.019 m² were taken at a regular distance of 20 m between two cores. All cores were taken to a depth of 30 cm and immediately washed through a 1-mm sieve. Shells of *M. balthica* were aged by counting the narrow dark year-rings due to interruption of growth (Lammens 1967). Numerical density Y , biomass density B , and average length L were determined for each age-class (0–4 and 5+) separately. Only data for the cohorts born in the years 1969–92 (which could be followed from age class 0 up to age class 5) were used. More details of the sampling procedure are given in Beukema (1974).

In the remaining part of the paper, all biomass data refer to ash-free dry biomass. In the present analysis, the term recruitment refers to the abundance of the zero-year class at the first sampling occasion, i.e. at the end of their first winter.

ESTIMATING THE PRODUCTION PARAMETERS FOR EACH SITE-COHORT COMBINATION

For each cohort $i = 1969, \dots, 1992$, at each site $k = 1, \dots, 11$, non-linear regression was used to estimate the Von Bertalanffy length growth curve

$$E(L_{ijk}) = L_{\infty,ik} [1 - \exp(-\gamma_{ik} x_{ijk})] \quad \text{eqn 15}$$

where L_{ijk} is the average length and x_{ijk} the age of animals from cohort i , age-class $j = 0, \dots, 4$, site k . The 0-groups were not exactly 1 year old at the time of sampling. Age was therefore given by $x_{ijk} = j + \tau$, where the parameter τ gives the relative length of the growth period between birth and the first sampling occasion. The parameters asymptotic length $L_{\infty,ik}$, Von Bertalanffy growth coefficient γ_{ik} , and the length of the first period τ , were estimated by least squares minimization.

Similarly, for each cohort, at each site, log-linear Poisson regression was used for estimating the survival curve

$$\log E(Y_{ijk}) = \mu_{ik} - \lambda_{ik} x_{ijk} \quad \text{eqn 16}$$

where Y_{ijk} is the density of animals for cohort i , age-class $j = 0, \dots, 4$, site k . The parameters initial cohort density μ_{ik} and mortality rate λ_{ik} were estimated by maximizing the Poisson likelihood, which is equivalent to minimizing the deviance (McCullagh & Nelder 1989).

The condition parameter ϕ_{ik} , the individual mass to cubic shell length ratio, was estimated for each cohort i , at each site k , by

$$\phi_{ik} = \frac{\sum_{j=1}^5 (B_{ijk}/L_{ijk}^3)}{\sum_{j=1}^5 Y_{ijk}} \quad \text{eqn 17}$$

where the biomass density B_{ijk} represents the individual mass W_{ijk} multiplied by the numerical density Y_{ijk} . The 0-group was left out, as the biomass density and length measurements were much less accurate for this group than for the older age classes. The applied estimator approximates the unweighted average over all individuals.

ESTIMATING AMONG-COHORT VARIABILITY IN INITIAL DENSITY

For each cohort i the mean initial density $\hat{\mu}_i$ was estimated by averaging over all sample sites. The estimated among-cohort variance $\text{var}(\hat{\mu}_i)$, based on all $m = 24$ cohorts, not only incorporates the variability of the underlying densities but it also contains the (spatial) sampling error. A two-way Analysis of Variance model with one observation $\hat{\mu}_{ik}$ per cell and with site and cohort as the two random factors, was therefore used to estimate the among-cohort variance component $\hat{\sigma}_c^2$, which reflects the true variability of the underlying densities (Sokal & Rohlf 1981; McArdle 1995). This leads to

$$\hat{\sigma}_c^2 = \text{var}(\hat{\mu}_i) - \frac{\hat{\sigma}^2}{n} \quad \text{eqn 18}$$

where $\hat{\sigma}^2$ is the estimator of the sampling variance:

$$\hat{\sigma}^2 = \frac{\sum_i \sum_k (\hat{\mu}_{ik} - \hat{\mu}_i - \hat{\mu}_k + \hat{\mu})^2}{(m-1)(n-1)} \quad \text{eqn 19}$$

CLUSTER SAMPLING

For the individual-related parameters (mortality rate, growth and condition parameters) each year a cluster sampling strategy was used. The randomly selected sites were the primary units and the individuals were the secondary units. The estimators were chosen accordingly (Thompson 1992; pp. 113–117). For example, for each cohort, the mean condition parameter was estimated by

$$\hat{\phi}_i = \frac{\sum_{k=1}^n Y_{i,k} \hat{\phi}_{ik}}{\sum_{k=1}^n Y_{i,k}} \quad \text{eqn 20}$$

where

$$Y_{i,k} = \sum_{j=0}^5 Y_{ijk} \quad \text{eqn 21}$$

The sampling variance of this estimator is approximately estimated by (ignoring the finite population correction)

$$\text{var}(\hat{\phi}_i) = \frac{n}{n-1} \frac{\sum_{k=1}^n Y_{i,k}^2 (\hat{\phi}_{ik} - \hat{\phi}_i)^2}{\left(\sum_{k=1}^n Y_{i,k} \right)^2} \quad \text{eqn 22}$$

As an alternative the bootstrap (for each cohort, sites were re-sampled 150 times) was used to estimate the sampling variance of $\hat{\phi}_i$.

Here again, the estimator of the among-cohort variance contains the sampling variance. Unfortunately, no standard theory is available to correct for this. We used the analogue of the above mentioned Analysis of Variance procedure to get an indication of the magnitude of the sampling variance,

$$\hat{\sigma}^2 = \frac{(mn)^2}{(m-1)(n-1)} \frac{\sum_i \sum_k Y_{i,k}^2 (\hat{\phi}_{ik} - \hat{\phi}_i - \hat{\phi}_k + \hat{\phi})^2}{\left(\sum_i \sum_k Y_{i,k} \right)^2} \quad \text{eqn 23}$$

ESTIMATING PRODUCTION AND ITS VARIABILITY IN TERMS OF THE UNDERLYING PARAMETERS

For each cohort i production p_i was estimated by

$$p_i = \mu_i \hat{\phi}_i L_{\infty}^3 \left(\frac{\gamma_i \cdot 2\gamma_i \cdot 3\gamma_i}{(\gamma_i + \lambda_i) \cdot (2\gamma_i + \lambda_i) \cdot (3\gamma_i + \lambda_i)} \right) \quad \text{eqn 24}$$

The within-cohort sampling variance was estimated by the bootstrap (150 re-samples). The variance of $\log p$ can be split up in terms of the covariance matrix of the logarithms of the three parameters μ , ϕ , L_{∞}^3 , and the term between brackets, using the similarity

$$\text{var}(\sum \log x_u) = \sum \text{var}(\log x_u) + 2 \sum_u \sum_{v < u} \text{cov}(\log x_u, \log x_v) \quad \text{eqn 25}$$

Hence, the sum of all elements of this covariance matrix equals $\text{var}(\log p)$.

If the differences between γ and λ are small, the complicated term between brackets can be approximated by the much simpler expression $\gamma_i/(4\lambda_i)$ (see the Appendix). This would enable a more convenient (though approximate) decomposition of the variance of $\log p$ in terms of the covariance matrix of the logarithms of μ , ϕ , L_{∞}^3 , γ and $1/\lambda$. Recall that $1/\lambda$ is equivalent to the expected life span.

SOME SYSTEMATIC ERRORS IN THE PRODUCTION ESTIMATES

The production equation given above should yield post-recruitment production: mass at death summed over all animals that have been recruited into the benthic population. Pre-recruitment production (where the mortality rate is much higher) is not taken into account. However, for mathematical convenience the equation was obtained by integrating the mass at death equation

$$E(W) = \int_0^{\infty} f(x) G(x) dx = \int_0^{\infty} \lambda e^{-\lambda x} G_{\infty} (1 - e^{-\gamma x})^3 dx \quad \text{eqn 26}$$

from zero instead of from the age at recruitment. So, post-recruitment production will be slightly overestimated. Yet, numerical integration revealed that the error was negligibly small, i.e. in the order of $50 \mu\text{g m}^{-2}$, compared to a mean post-recruitment production of about 1.6 g m^{-2} . Another systematic error is due to the fact that condition estimates are only based on late-winter values. Intra-annual variation in condition is not taken into account. Since the condition in late winter is rather low, production will be underestimated. However, this holds for all years and the among-cohort variability, in which we were mainly interested, may not be affected too much.

Results

GROWTH, SURVIVAL AND CONDITION

The Von Bertalanffy growth model was fitted for each of the 256 cohort (24) by site (11) combinations separately (but with a general parameter τ) and revealed an overall goodness-of-fit of $R^2 = 1 - \text{RSS}/\text{TSS} = 0.98$, where RSS is the residual sum of squares ($\text{RSS} = 532$ d.f. = 776), and TSS the total sum of squares ($\text{TSS} = 27515$, d.f. = 1304). The standard error of the estimate (which is the square root of the residual mean square and indicates the magnitude of the residual variation) equalled 0.83 mm . The length of the first growing period τ was estimated at 0.64 years with a 95% confidence interval ranging from 0.611 to 0.662 years. The estimated parameters asymptotic length $\hat{L}_{\infty ik}$ and Von Bertalanffy growth coefficient $\hat{\gamma}_{ik}$ varied, apart from a few outliers, between 15 and 25 mm , and between 0.4 and 0.8 a^{-1} , respectively.

Survival curves were fitted separately for each cohort-site combination. The overall deviance, a measure of the goodness-of-fit related to the likelihood, was 2345 (d.f. = 792). Apart from a few outliers, the estimated initial cohort densities $[\hat{\mu}_{ik}]$ and mortality rates $\hat{\lambda}_{ik}$ were in the range 10 – 300 m^{-2} and 0.2 – 0.8 a^{-1} , respectively. Simpler models (e.g. initial cohort density and mortality rate are only site dependent) fitted significantly less well, although the model in which the site \times cohort \times age interaction was left out (and thus assuming that the mortality rate can be modelled by a site effect plus a cohort effect only) also yielded a reasonable fit in terms of deviance (Table 1).

Table 1. Deviance D of various log-linear models relating survival to site and cohort effects. All models assume that density decreases exponentially with age, except for the last model in which density decreases exponentially with age $^\alpha$, where α is the Weibull parameter

Model	d.f.	D
Constant	1319	47101
Age	1318	31648
Age + site + site:age	1298	26481
Age + cohort + cohort:age	1272	17010
Age + site + site:age + cohort + cohort:age	1252	11852
Age + site + site:age + cohort + cohort:age + site:cohort	1022	3649
Age + site + site:age + cohort + cohort:age + site:cohort:age	1022	7158
Age + site + site:age + cohort + cohort:age + site:cohort + site:cohort:age	792	2345
Age $^\alpha$ + site + site:age $^\alpha$ + cohort + cohort:age $^\alpha$ + site:cohort + site:cohort:age $^\alpha$	791	2333

Table 2. Mean, among-cohort variance, variance component, coefficient of variation and the cross-correlation coefficient with production, of the various production parameters: initial cohort density μ (m $^{-2}$), condition ϕ (kg m $^{-3}$), asymptotic length L_∞ (mm), Von Bertalanffy growth coefficient γ (a $^{-1}$), mortality rate λ (a $^{-1}$), and production p (g m $^{-2}$). $n = 24$

Parameter	Mean	Variance	Variance component	Coefficient of variation	Cross-correlation
Initial cohort density μ	88.0	4.94 10 3	4.33 10 3	0.80	0.89
Condition ϕ	8.26	0.410	0.367	0.08	0.18
Asymptotic length L_∞	20.1	1.36	1.12	0.06	-0.12
Growth coefficient γ	0.567	6.46 10 $^{-3}$	4.82 10 $^{-3}$	0.14	0.27
Mortality rate λ	0.493	1.51 10 $^{-2}$	1.05 10 $^{-2}$	0.25	0.20
Production p	1.58	1.02	0.93	0.64	1.00

Overall annual survival rate was rather similar among the six age classes. Average densities (averaged over all cohorts and sites) were 59.1, 34.3, 20.4, 14.1, 7.7 and 11.2 animals per m 2 , for the six age classes, respectively. This indicates an overall annual survival of 58%, 60%, 69%, and 54%, respectively, for the first four age classes. The density of the 5 + age class was 146% of the density of the 4 years age class. This number points to an annual survival of 59% for the older (5 +) age classes (using the series

$$\sum_{n=0}^{\infty} p^n = \frac{1}{1-p} \text{ for } |p| < 1 \text{ gives } Y_{5+} = \frac{p}{1-p} = Y_4 \quad \text{eqn 27}$$

where p is the annual survival) and thus fits in the general pattern of an annual survival of about 60%. The assumption of age-independent mortality (and hence an exponential distribution of the life span) was tested by fitting a Weibull distribution model, whose survival function is given by

$$S(x) = e^{-(\lambda_{ik}x)^\alpha} \quad \text{eqn 28}$$

where the Weibull parameter α ($\alpha > 0$) indicates whether the mortality rate increases with age ($\alpha > 1$) or decreases with age ($0 < \alpha < 1$) (Kooijman 1993). The exponential distribution, where the mortality rate is constant, is a special case of the Weibull distribution, when $\alpha = 1$. The Weibull model fitted slightly better than the exponential model, but the difference in scaled deviance was small ($D/\sigma^2 = 4.04$, d.f. = 1), and when compared with $\chi^2_{1,0.05} = 3.84$, only marginally significant ($P = 0.045$). The estimate of the Weibull parameter was indeed close to one: $\hat{\alpha} = 0.89$; with a 95%

confidence interval that ranged from 0.790 to 0.997. For reasons of parsimony, the exponential distribution model seems a reasonable choice.

Most of the condition estimates $\hat{\phi}_{ik}$ were in the range 7–9 kg m $^{-3}$.

AMONG-COHORT VARIABILITY

Of all five parameters (initial cohort density, condition, asymptotic length, Von Bertalanffy growth rate, and mortality rate), initial cohort density showed the highest variability between cohorts (Table 2, Fig. 1). The coefficient of variation of initial cohort density was about 0.80, whereas the second highest was 0.25 for mortality rate (Table 2). Initial cohort density also had the highest cross-correlation coefficient with production, $r = 0.89$ (Table 2).

For all five parameters the estimated within-cohort sampling variance contributed only a relatively small part of the among-cohort variance, and consequently the estimated among-cohort variance component was only slightly smaller than the estimated among-cohort variance (Table 2). Similarly, bootstrap replicates suggested that the estimated correlations between parameters, using cohort means, were only to a minor extent the result of within-cohort sampling error (Fig. 2). This implies that the estimated among-cohort variances and covariances, which follow below, were not too much distorted by sampling errors.

The complicated term $\gamma 2\gamma 3\gamma[(\gamma + \lambda)(2\gamma + \lambda)(3\gamma + \lambda)]^{-1}$ from the production equation could be reliably approximated by the much simpler expression $0.25 \cdot \gamma 1/\lambda$ (see also the Appendix). The correlation coefficient

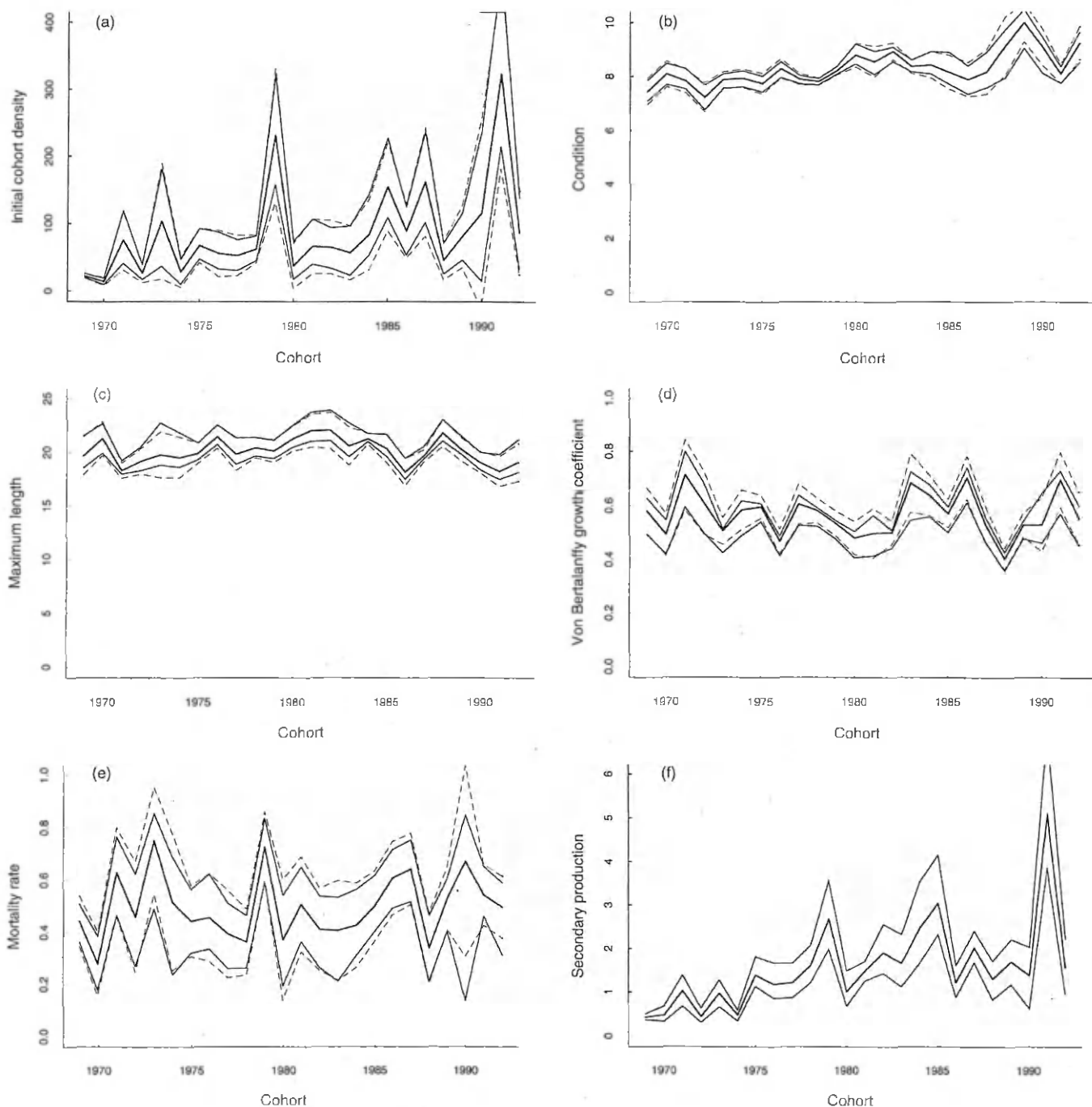


Fig. 1. For each cohort ($i = 1969, \dots, 1992$) estimated means (thick solid line), including 95% confidence intervals based on a first order Taylor approximation (dashed lines) or on a bootstrap sample (thin solid lines), of: (a) initial cohort density μ (m^{-2}); (b) condition ϕ (kg m^{-3}); (c) asymptotic length L_{∞} (mm); (d) Von Bertalanffy growth coefficient γ (a^{-1}); (e) instantaneous mortality rate λ (a^{-1}); (f) secondary production p (g m^{-2}).

between both terms was 0.996. This result implies that the among-cohort variance of production can be (approximately) decomposed in terms of the covariance matrix of the log-transformed parameters initial cohort density, cubic asymptotic length, condition, Von Bertalanffy growth coefficient and expected life span (Table 3). The reliability of the approximation is confirmed by the equivalence between the sum of all elements of the matrix, which equalled 0.3827, and the variance of log production, which was equal to 0.3826. The estimated covariance matrix revealed that the

variability of log production was mainly determined by the variability of log initial cohort density (Table 3). Yet, the variability of log initial cohort density, which was 0.52, was larger than the variability of log production (which was 0.38). Thus, the variability in log initial cohort density was not entirely reflected in the variability in log production, but was slightly lowered by the negative elements in the covariance matrix. The lowest covariances were those between log initial cohort density and log expected life span (-0.12) and between log initial cohort density and log cubic asymptotic length (-0.041) (Fig. 2).

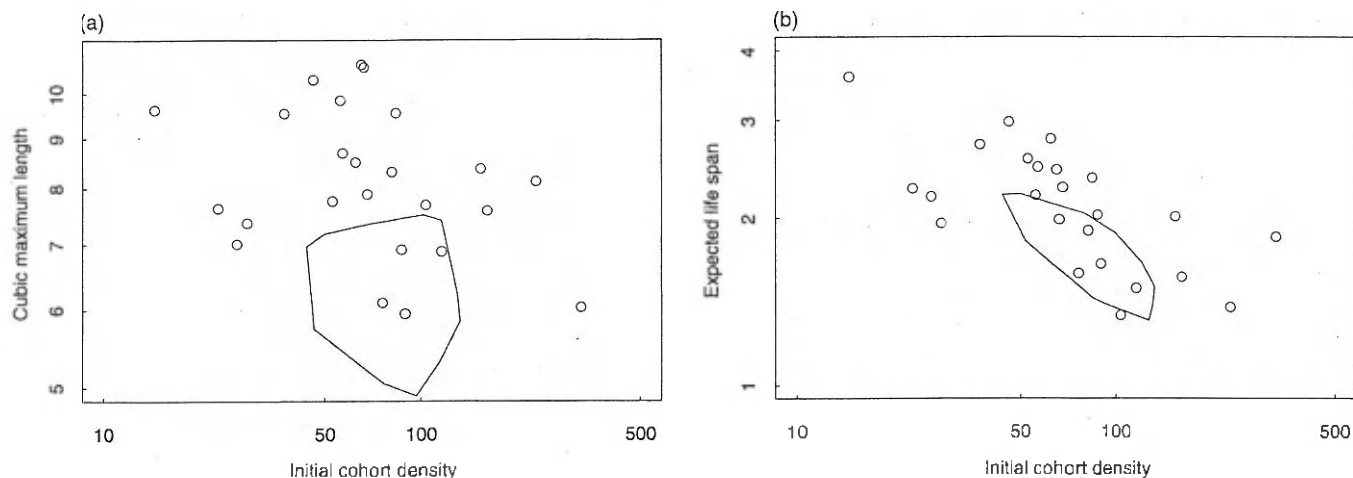


Fig. 2. (a) Cubic asymptotic length L_{∞}^3 (cm³); and (b) expected life span $1/\lambda$ (a), vs. initial cohort density μ (m⁻²) for each cohort, $n = 24$; logarithmic scales. For one cohort the convex hull containing 150 bootstrap samples is plotted to indicate the reliability of the estimates.

The obvious measure for post-recruitment abundance is initial cohort density multiplied by expected life span. The accompanying covariance matrix, which contains the variance of log initial cohort density (0.52), the variance of log expected life span (0.06), and their covariance (-0.12), is a subset of the matrix of all production parameters (Table 3). A similar result as for post-recruitment production was therefore obtained for post-recruitment abundance: its variability was mainly determined by recruit density, but slightly dampened by the negative covariance between density and life span.

Discussion

The recognition of the importance of recruitment processes in determining benthic population and community dynamics, granted by Thorson almost a half-century ago (Thorson 1950; Thorson 1966), has received a renewed interest among ecologists (Young 1987). The literature on recruitment limitation in marine soft-sediment systems was reviewed by Ólafsson *et al.* (1994). They concluded that sufficient information is available to show that post-settlement processes (such as recruitment inhibition by adult invertebrates, predation, and food limitation) play a significant role in population regulation of soft-sediment benthos and that recruitment limitation is not the dominant determinant of temporal patterns in this system. However, they also admitted that no definite study of even a single

population is available to partition pattern generation into pre- and post-settlement processes.

We used demographic and growth data of a single intertidal bivalve population, obtained over a much longer period than usual. Combining these data with a modelling approach we were able to quantitatively partition the among-cohort variability in some relevant characteristics of the post-recruitment population (such as abundance and secondary production) in terms of pre-recruitment (reflected in the variance in recruit density) and post-recruitment (reflected in all other variances and covariances) processes. In accordance with the conclusion of Ólafsson *et al.* (1994), negative covariances were obtained between recruit density on the one hand and maximum cubic length and expected life span on the other hand. These results point to density-dependent growth and survival, which may be related to post-recruitment processes such as food limitation, competition for other resources, and predation. Nevertheless, the temporal variation in abundance and production was to a much greater extent attributable to the annual variability in recruitment. This might imply that in poor-recruitment years post-recruitment population density and production were limited to less than their full potential.

In previous studies the importance of post-recruitment regulation was generally based on observed correlations between post-recruitment density and growth and/or survival (often in a spatial context) or on

Table 3. Covariance matrix of the log-transformed production parameters: initial cohort density μ (m⁻²), condition ϕ (kg m⁻³), cubic asymptotic length L_{∞}^3 (mm³), Von Bertalanffy growth coefficient γ (a⁻¹), and expected life span $1/\lambda$ (a). $n = 24$

	μ	ϕ	L_{∞}	γ	$1/\lambda$
Initial density μ	0.519				
Condition ϕ	0.012	0.006			
Cubic length L_{∞}^3	-0.041	0.005	0.030		
Growth coefficient γ	0.023	-0.005	-0.017	0.020	
Life span $1/\lambda$	-0.120	0.001	0.025	-0.009	0.062

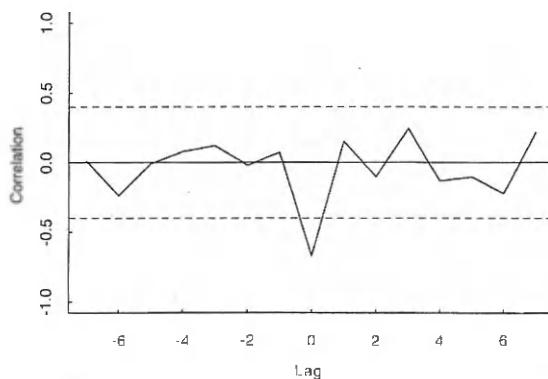


Fig. 3. Cross-correlation function of log initial cohort density μ (m^{-2}) and log expected life span $1/\lambda$ (a).

experimental tests (always in a spatial context) in which densities of the benthic fauna were manipulated (Ólafsson *et al.* 1994). These studies have indeed provided evidence for the existence of post-recruitment regulation, but we think that an analysis of long-term data, as presented here, is a prerequisite to quantify to what extent density-dependent post-settlement processes truly dampen the temporal variation in the numbers of recruits in the field. It should also be stressed that studies of spatial variation in recruitment do not necessarily tell too much about the amount or about the causes of temporal variation. Spatial variation might to a great extent be related to variability in local habitat quality for settling larvae, whereas temporal variation in recruitment might be strongly related to fluctuating conditions in the pelagic environment.

The data that we have used allowed the application of a relatively simple production model (for each cohort a constant instantaneous mortality rate, which appeared to be in the same order of magnitude as the Von Bertalanffy growth coefficient), with the advantage that the variability in log production could be decomposed in terms of the underlying parameters in a rather straightforward manner. Data for other species (or for the same species but including data from the mobile first life-phase) might require more complicated models (e.g. including the assumption of age-dependent mortality). Production variance can then be decomposed by means of a first-order Taylor approximation of the variance of a non-linear function.

We used cohorts as the units of observation, but the cohorts overlapped in time. The interval between cohort arrivals was 1 year, which is smaller than the average adult life span, which equalled about 2 years. So individuals from one cohort may affect individuals from another cohort, which is not reflected in the correlation between parameters as presented above. However, inspection of the auto- and cross-correlation functions for all parameters showed no clear patterns (e.g. Figure 3). No significant auto-correlations occurred, except for the log-transformed condition parameter ϕ , which showed a significant but weak (and hardly interpretable) autocorrelation of 0.49 at lag one. The

lack of auto-correlation also strengthens the validity of the estimates of the covariances and cross-correlation coefficients at lag zero (Chatfield 1989).

Summing up, our results stress the importance of processes during the early mobile life phase of *M. balthica*. Yet, keeping in mind our practical definition of recruitment (which integrates larval supply rate, success of first and second settlement, and early post-settlement mortality), they do not necessarily imply that pre-settlement processes dominate. A previous study on the variability in early post-first-settlement mortality has indeed indicated density dependence (Beukema 1982). Future studies on the population dynamics of this bivalve species should therefore emphasize the early life-phase.

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