Intraspecific egg size variation and sperm limitation in the broadcast spawning bivalve *Macoma balthica*

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**A R T I C L E   I N F O**

Article history:
Received 14 June 2010
Received in revised form 8 October 2010
Accepted 14 October 2010

**Keywords:**
Stock-recruitment relationships
Life history theory
Sperm limitation
Sperm competition
Egg size

**A B S T R A C T**

Broadcast spawners are exceptionally suited and simple models for studying parental investment in offspring, because direct post-spawning investment is nonexistent. However, a comprehensive understanding of the large variation that exists in their egg sizes is still lacking. One of the main hypotheses states that variation in fertilization conditions underlies some of the egg size variation, as larger eggs are larger targets for sperm. Here, we test the hypothesis that egg size may be locally tuned to expected ambient sperm concentrations during fertilization. In accordance with the hypothesis, we find that in the bivalve *Macoma balthica* (L.) adult density as a proxy for sperm concentration correlates strongly (correlation coefficient — 0.87) with egg size in the field. Optimisation modeling confirms the negative relationship between optimal egg size and sperm concentration for *M. balthica* and this is independent of the fertilization model used. Discrepancies between models and observations remaining include larger egg sizes overall and a concave predicted relationship that is not obvious in the data. The results suggest that in *M. balthica* sperm limitation may play a role in fertilization success and in shaping egg size variation, and that locations with high population densities may make disproportionately large contributions to the next generation.

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**1. Introduction**

One of the central themes in the study of life history evolution is parental investment in offspring (Trivers, 1972). A principal trait in this respect is egg size. Marine broadcast spawning invertebrates (i.e., with external fertilization) have formed excellent empirical study systems, in which post-spawning maternal investment is necessarily entirely contained within the eggs themselves. This implies an important simplification of a complex problem that includes post-spawning or post-natal investment. In spite of this simplification, understanding natural egg size variation in broadcast spawners remains a challenge (Bernardo, 1996; Marshall et al., 2000; Levitan, 2006; Bode and Marshall, 2007; Marshall and Keough, 2008a,b).

Egg sizes in broadcast spawning taxa tend to vary considerably among (e.g. Lessios, 1987; Levitan, 2000; McEdward and Morgan, 2001) as well as within species (e.g. Lessios, 1987; Bertram and Strathmann, 1998; George, 1999; Miles et al., 2007; Phillips, 2007; Marshall and Keough, 2008a,b). Concepts based on optimality theory first and foremost explain egg size as the product of a trade-off with egg number (Vance, 1973a,b; Smith and Fretwell, 1974): females should always produce the maximum number of eggs that are, as a consequence, of minimal size for development, unless larger egg size conveys benefits that increase disproportionally with size. The two benefits of larger size to the offspring are higher fertilization probability and an increased chance of zygote survival. Sperm is necessary to start egg development in the majority of species and can be a limiting resource for broadcast spawning females (Levitan, 1993, 1995, 1998; Yund, 2000); however, sperm can also be too abundant and lead to polyspermy (Styan, 1998). A change in sperm availability could lead to a different optimal egg size (Levitan, 1993). In the case of sperm limitation there are strong indications that intensified sperm limitation should theoretically translate into a larger optimal target size (Jantzen et al., 2001; Podolsky, 2002, 2004; Luttikhuizen et al., 2004; Levitan, 2006), and this relationship should reverse in case of adverse effects of polyspermy (Styan, 1998). Larger target size may be achieved by increasing egg size, or, alternatively, by increasing the size of accessory structures such as jelly coats (Podolsky, 2004) or, chemically rather than physically, by increased secretion of chemottractants (Jantzen et al., 2001). Remarkably, the hypothesis that egg size varies intraspecifically with sperm limitation has not yet been directly tested (see also Levitan, 2006). However, Crean and Marshall (2008), having set out to test egg size plasticity in the ascidian *Styela plicata* in relation to sperm competition, reached the conclusion that sperm limitation might better explain their data.

Pleas for examining intraspecific in addition to interspecific patterns to test life history theories were made by Bernardo (1996) and several others (see references in Bernardo, 1996), because the transfer of interspecific patterns to the intraspecific level has often proven elusive. At the interspecific level, many factors (including phylogenetic, environmental, morphological, physiological) covary to...
produce patterns among groups that are well separated by space and time. Ideally, tests should take place at a level where selection may reasonably be assumed to take place. This is the case for the populations studied here, as gene flow as well as differential selection have been demonstrated to occur at this scale (Luttkhuizen et al., 2003a,b; Drent et al., 2004).

Here we present the results of an intraspecific test of the hypothesis that increased sperm limitation selects for larger egg sizes in the sedentary, broadcast spawning bivalve Macoma balthica (L.). This taxon, the Baltic tellin, is a circumpolar species of the northern hemisphere that lives in the shallow subtidal to the high intertidal, burrowed in mud or sand. It has a single spawning season per year in most places (Harvey and Vincent, 1989) and fertilization of its eggs, that bear no accessory structures, is external. The fertilized eggs develop for about three days without feeding and the larvae are planktotrophic (see Drent 2002). It occurs in a range of natural population densities of approximately 1–500 adult individuals per m² (see Bocher et al., 2007) and equal sex ratio (Caddy, 1967). Adult density may be regarded as an inverse measure of sperm concentration during external fertilization because with decreasing adult density, male density decreases similarly, and, all else being equal, the ambient sperm concentration during fertilization can be expected to be lower. We measured egg sizes in three different years at several locations and correlated this with population densities, predicting a negative correlation. Verification of the interpretation of the data is done by optimisation modeling, determining optimal egg size by maximizing expected reproductive success of female M. balthica as a function of sperm limitation.

2. Materials and methods

In early spring, at which time the eggs are ripe and the animals are ready for spawning (Caddy 1967; Honkoop et al., 1999), of three different years (1995, 1996 and 1999) we collected M. balthica using a grab and sieve from a boat (for subtidal sites) or a corer and sieve (for intertidal sites). In both 1995 and 1996 samples were taken at three intertidal sites, and in 1999 at two intertidal and three subtidal sites (see Table 1). Sampling sites were distributed over the western Dutch Wadden Sea and the adjacent North Sea (Fig. 1). The bivalves were individually induced to spawn by administering a temperature shock (see Table 1). This was done for a range of temperature of about 10 °C (Honkoop and van der Meer, 1997; Honkoop et al., 1999), of three

For 1995 and 1996, local adult density (number of individuals per m² with shell length exceeding 10 mm) at the time of spawning was obtained from the benthos monitoring database of J. Beukema and R. Dekker (Royal Netherlands Institute for Sea Research, see e.g. Beukema et al., 2002). In 1999, local adult density was estimated at the time of collection for our spawning experiments. Fitness (f) of individual females producing eggs of variable size was defined as the expected number of recruits per female and modeled as the product of number of eggs produced (n), fertilization probability per egg (p) and survival probability per zygote (s):

\[ f(x, y) = n(x) \cdot p(x, y) \cdot s(x) \]

where \( x = \) egg volume (mm³) and \( y = \) sperm concentration (µL⁻¹). Optimal egg size was found by maximizing \( f \). This was done for a range of sperm limitation.

![Fig. 1. Map showing sampling locations (triangles) of Macoma balthica in Dutch Wadden Sea and North Sea. Location numbers: see Table 1.](image)

Table 1

<table>
<thead>
<tr>
<th>Year</th>
<th>Site</th>
<th>Position</th>
<th>( n ) females</th>
<th>Adult density (ind/m²)</th>
<th>Av. egg diameter (µm) (± se)</th>
<th>CV overall</th>
<th>CV among female</th>
</tr>
</thead>
<tbody>
<tr>
<td>1995</td>
<td>Balgzand A</td>
<td>S2°57.00'N 4°50.39'E</td>
<td>23</td>
<td>66</td>
<td>107.8 (1.19)</td>
<td>6.7</td>
<td>5.3</td>
</tr>
<tr>
<td></td>
<td>Balgzand B</td>
<td>S2°55.30'N 4°48.84'E</td>
<td>20</td>
<td>189</td>
<td>104.1 (0.81)</td>
<td>5.0</td>
<td>3.5</td>
</tr>
<tr>
<td></td>
<td>Balgzand C</td>
<td>S2°54.28'N 4°50.54'E</td>
<td>24</td>
<td>224</td>
<td>100.5 (0.49)</td>
<td>3.7</td>
<td>2.4</td>
</tr>
<tr>
<td>1996</td>
<td>Balgzand A</td>
<td>S2°57.00'N 4°50.39'E</td>
<td>46</td>
<td>73</td>
<td>108.5 (0.90)</td>
<td>7.3</td>
<td>5.6</td>
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<td>Balgzand B</td>
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<td>34</td>
<td>150</td>
<td>106.0 (0.82)</td>
<td>6.6</td>
<td>4.5</td>
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<tr>
<td></td>
<td>Balgzand C</td>
<td>S2°54.28'N 4°50.54'E</td>
<td>40</td>
<td>165</td>
<td>104.3 (0.76)</td>
<td>6.2</td>
<td>5.0</td>
</tr>
<tr>
<td>1999</td>
<td>Balgzand D</td>
<td>S2°55.36'N 4°49.15'E</td>
<td>11</td>
<td>22</td>
<td>107.0 (0.64)</td>
<td>2.7</td>
<td>1.9</td>
</tr>
<tr>
<td></td>
<td>Mok</td>
<td>S3°05.00'N 4°45.80'E</td>
<td>43</td>
<td>56</td>
<td>106.6 (0.47)</td>
<td>3.8</td>
<td>2.9</td>
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<tr>
<td></td>
<td>Molengat</td>
<td>S3°01.44'N 4°40.08'E</td>
<td>30</td>
<td>5</td>
<td>108.4 (0.88)</td>
<td>6.4</td>
<td>4.4</td>
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<tr>
<td></td>
<td>Terschelling</td>
<td>S2°27.13'N 5°25.00'E</td>
<td>7</td>
<td>150</td>
<td>105.5 (1.59)</td>
<td>4.9</td>
<td>5.0</td>
</tr>
<tr>
<td></td>
<td>Wierbalg</td>
<td>S2°56.00'N 4°57.05'E</td>
<td>29</td>
<td>115</td>
<td>106.7 (0.59)</td>
<td>3.9</td>
<td>2.9</td>
</tr>
<tr>
<td>overall</td>
<td></td>
<td></td>
<td>307</td>
<td></td>
<td>106.1</td>
<td>6.5</td>
<td>4.7</td>
</tr>
</tbody>
</table>
of natural population densities, where population density was used as a proxy for ambient sperm concentration during fertilization.

Number of eggs produced per female was modeled as the inverse of egg volume (i.e., assuming the nutrient concentration stays the same so that larger eggs contain more nutrients), assuming a trade-off between size and number of eggs in a brood as defined by Smith and Fretwell (1974), and scaled in such a way that the number of eggs produced per female remained below 40,000, which represents the upper limit in the field (Honkoop and van der Meer, 1997):

\[ n(x) = \frac{\alpha}{x} \]

where \( \alpha = 20.74 \) and represents the total volume of reproductive mass per female.

Fertilization probability was modeled according to three previously published fertilization kinetics models: Don Giovanni, in which a sperm continues to search after it hit an egg even if it led to a fertilization; Don Ottavio ‘solo’, in which a sperm attaches to the first egg it encounters and egg concentration is treated as constant; and Don Ottavio ‘tango’, in which egg and sperm concentration covary (Vogel et al., 1982; Luttikhuizen et al., 2004):

\[
\begin{align*}
\hat{p}_{\text{Giovanni}}(x,y) &= 1 - e^{-\alpha' y} \\
\hat{p}_{\text{OttavioSolo}}(x,y) &= 1 - e^{-\beta y(1-e^{-b y'})} \\
\hat{p}_{\text{OttavioTango}}(x,y) &= 1 - e^{-m(1-e^{-m y'})}
\end{align*}
\]

where \( x' \) is the egg surface area, \( c \) is a constant that is the product of the swimming speed and life span of spermatozoa, \( a \) is a constant that equals the sperm swimming speed times the fertilizable egg surface fraction divided by egg concentration, \( b \) is a constant that is the product of egg concentration and life span of spermatozoa, \( m \) is a constant that equals the sperm swimming speed times the fertilizable egg surface fraction, and \( n \) is a constant that equals life span of spermatozoa. In order to estimate the parameter values of these models, the relationship between sperm concentration and fertilization rate was estimated in 78 fertilization trials (see later discussion).

Survival was modeled according to Levitan (2000), after Vance (1973a), a model developed to describe survival rate \( s \) and development time \( T \) for facultative planktotrophic larvae:

\[ s(x) = e^{-pT} \]

where \( p \) equals mortality rate (day\(^{-1}\)):

\[ T = \left( \frac{x_p}{x} - 1 \right) + T_{fp} \]

where \( x_p \) and \( T_{fp} \) the volume and time needed to develop throughout the pelagic period and metamorphose intosettling competence without feeding, are here interpreted as the maximum volume and minimum time needed to develop from zygote to metamorphosis for an obligate planktotroph such as the study species. The rationale behind this model is that size at metamorphosis is constant and that the effect of smaller egg size is a longer pelagic development time. Constant size at metamorphosis is a reasonable assumption for M. balthica (Drent, 2002), at least for a given level of food conditions (Ros et al., 2007).

For finding optimal egg sizes, ambient sperm concentration \( y \) during fertilization was calculated as a function of adult density \( d \) (m\(^{-2}\)):

\[ y = \frac{0.5 \cdot d \cdot g}{v} \]

where \( g \) equals the average number of sperm produced per male (see later discussion) and \( v \) equals the volume (\( \mu l \)) of water in which fertilization takes place (here assumed to be a water layer of 5 cm).

Fertilization trials consisted of exposing a batch of freshly spawned eggs from a single female to freshly spawned sperm of known concentration from a single male. Spawning induction followed procedures described above. Gamete suspensions were gently mixed and left standing overnight, by which time fertilized eggs can be easily distinguished from unfertilized ones by their multicellularity (Luttikhuizen and Pijnacker, 2002), which was visualized under a binocular microscope for about 150 eggs per batch. For estimating the average number of sperm produced per male, 209 males were induced to spawn. Sperm concentration \( S \) was quantified using optical density \( D \) at 660 nm, and the relationship between optical density and concentration calibrated by counting trials using both a hemocytometer and a flowcytometer: \( S = 2.57 \cdot 10^3 (n = 10, \text{linear regression } R^2 = 0.969) \).

3. Results

The average diameter of eggs produced by M. balthica females was strongly negatively correlated with adult density (Fig. 2, Table 1), with a correlation coefficient of \( r = -0.867 \) (Pearson correlation coefficient, \( P < 0.001 \)). Analyzed as a linear relationship between egg size and population density, 75% of the variation in average egg diameter is explained by local adult density (linear regression, \( n = 11, R^2 = 0.75, P < 0.001 \)).

Variation in egg diameter was considerable, both between samples, within samples and within females. The overall coefficient of variation (CV) of egg diameter was 6.5% (\( N = 7414 \) eggs); CV among all females was 4.7% and within females 3.6% (\( N = 307 \) females). At the within-population level, CV averaged 5.2% overall (\( N = 674 \) eggs on average), and 3.9% among females (\( N = 27.9 \) females on average). The among-population variance in egg size contributed significantly to variation in average egg size among females (ANOVA, \( df = 10, F \text{-ratio} = 7.08, P < 0.001 \)) and amounted to a variance component of 18.2% (i.e., variation among females within populations amounted to 81.8%).

Fertilization kinetics models fitted well to the data obtained from fertilization trials (Fig. 3, Table 2), although male or female identity and/or the particular male–female combination seemed to contribute to variation in fertilization success. Individual males produced on average 3.36 \( \times 10^8 \) sperm upon spawning induction (Table 2).

Similar to observed egg size, predicted optimal egg size was also negatively correlated with adult density (Fig. 4A). The three different fertilization kinetics models gave similar predictions, with the Don Giovanni model predicting the largest optimal egg size and the Don Ottavio ‘tango’ model smallest optimal egg size. Differences between the Don Ottavio ‘solo’ and ‘tango’ models were marginal. At the parameter values used and population densities examined, realized
fertilization success ranged from 1 to 3% at a population density of 1 adult per m², to 75%, 95% and 89% for the Don Giovanni, Don Ottavio ‘solo’ and Don Ottavio ‘tango’ models, respectively, at a density of 250 individuals per m² (Fig. 4B).

4. Discussion

The data presented here represent the first direct empirical test at the intraspecific level of the hypothesis that sperm limitation exerts a selection pressure on egg size in marine broadcast spawning invertebrates. The hypothesis is corroborated by the data. Population density of adults is used as a proxy for ambient sperm concentrations during external fertilization and a strong negative correlation between egg size and local adult density was observed (Fig. 2). It is important to rely on intraspecific tests of life history theories (Bernardo 1996 and references therein), and it is for this reason that the test presented here gives empirical substance to the earlier, to a large extent theoretical, treatment of the topic of sperm limitation and egg size (e.g., Styan, 1998; Podolsky, 2002, 2004; Luttikhuizen et al., 2004; Levitan, 2006).

The only other empirical test of an intraspecific relationship between egg size and fertilization kinetics was in the broadcast spawning ascidian Styela plicata (Crean and Marshall, 2008). There, the relationship between egg size (and other gamete traits) and adult density was tested in light of the possibility of sperm competition. The authors reached the conclusion that the overall data could also be in line with sperm limitation rather than with sperm competition. For example, total egg size increased significantly in response to an experimental reduction of adult population size (Crean and Marshall, 2008). Eggs in S. plicata consist not only of an ovicell but include follicle cells and ovicell area actually decreased in the mentioned treatment. Nevertheless, total egg size reflects the target size for sperm and, as such, the data for S. plicata match the data presented here for M. balthica. In natural environments a combination of influences, including maternal resources, sperm limitation, sperm competition and polyspermy, probably play a role simultaneously in determining gamete traits of broadcast spawning taxa (the ancestral state). With regard to the fertilization-related influences, it may be noted that the only two tests to date (Crean and Marshall 2008 and the present study) are consistent with an effect of sperm limitation.

4.1. Verification of interpretation using models

Model predictions carried out here verify the interpretation of the correlation between population density and egg size as an adaptive response to fertilization conditions, as predictions and observations are qualitatively similar; theoretical optimal egg size in M. balthica is also dependent on population density, regardless of which fertilization kinetics model is used (Fig. 4A). While predictions and observations match in a qualitative sense, a difference lies in the fact that the concave relationship that is theoretically predicted (Fig. 4A) is not observed in the data (Fig. 2); the steepest dependence on adult density is found at lower densities in the predictions, but at

Table 2

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Unit</th>
<th>Value</th>
<th>References</th>
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</thead>
<tbody>
<tr>
<td>(a)</td>
<td>mm²</td>
<td>20.74</td>
<td>Honkoop and van der Meer (1997)</td>
</tr>
<tr>
<td>(c)</td>
<td>mm</td>
<td>0.03158</td>
<td>estimated here</td>
</tr>
<tr>
<td>(a)</td>
<td>mm²/(s·µL)</td>
<td>0.1248</td>
<td>“</td>
</tr>
<tr>
<td>(b)</td>
<td>µL·s</td>
<td>0.6764</td>
<td>“</td>
</tr>
<tr>
<td>(m)</td>
<td>mm/s</td>
<td>3.537</td>
<td>“</td>
</tr>
<tr>
<td>(n)</td>
<td>s</td>
<td>0.02645</td>
<td>“</td>
</tr>
<tr>
<td>(p)</td>
<td>day⁻¹</td>
<td>0.1</td>
<td>Drent (2002), Bos et al. (2007)</td>
</tr>
<tr>
<td>(x_0)</td>
<td>mm²</td>
<td>0.007987</td>
<td>“</td>
</tr>
<tr>
<td>(T_0)</td>
<td>day</td>
<td>3</td>
<td>“</td>
</tr>
<tr>
<td>(g)</td>
<td>none</td>
<td>3.36·10⁸</td>
<td>estimated here</td>
</tr>
</tbody>
</table>

Fig. 3. Fitting fertilization kinetics models to experimental fertilization trials in Macoma balthica. Dots: experimental results of fertilization percentage of eggs in well-mixed sperm suspensions of known concentration. Broken line: fitted Don Giovanni model, sperm continue searching after fertilizing an egg. Line: fitted Don Ottavio ‘solo’ model, sperm remain with the first egg hit. Dotted line: fitted Don Ottavio ‘tango’ model, similar but egg and sperm concentration covary.

Fig. 4. (A) Model predictions of optimal egg size in Macoma balthica in relation to local adult density. (B) Fraction of eggs fertilized under the model conditions examined.
higher densities in the observations. Also, predicted egg sizes are larger (diameter approximately 120–165 μm) than observed egg sizes (100–110 μm). At present we can only speculate as to the cause of these differences. First, the scatter in the data is too substantial to reject a concave model with certainty. Second, the model is a considerable simplification of the highly dynamic process of external fertilization; e.g., gamete dilution was here modeled as a perfect mixing process while in effect turbulence and diffusion play important roles, and gamete behavior is more complex in reality, also, and includes aspects such as clustering and sinking. Third, a number of factors other than sperm limitation may be expected to have been involved in producing the observed egg sizes, including climate, habitat, etc. (Honkoop and van der Meer, 1997, 1998; Honkoop et al., 1998); not knowing the underlying mechanisms makes further speculation premature. Finally, it seems likely that there are intrinsic (e.g., genetic) limits to how large an egg can become so that sperm limitation can only be a driver of egg size to a certain extent.

4.2. Intraspecific egg size variability

Life history theory of propagule size recognizes the many ways in which trade-offs between father, mother, offspring and environment interact to produce variation in propagule size among and within mothers, populations and species (Steams, 1992; Bernardo, 1996; Ramirez-Lodra, 2002; Roff, 2002). Quantifying the distribution of propagule size variation over these levels is, in spite of its relevance for addressing central life history questions, not standard procedure (Bernardo, 1996; Marshall and Keough, 2008a) though some information of this kind is available. The level of variability in egg diameter observed here for M. balthica is very similar to that observed for other marine invertebrates with external fertilization and planktotrophic larvae. In a recent review, Marshall and Keough (2008b) show that the coefficient of variation (CV) of egg sizes among females within populations averages 4.2% for planktotrophs with external fertilization. Egg size CV is known for one other Macoma species, namely M. michelii (Kennedy et al., 1989) and is in fact identical to the CV reported here for M. balthica: 3.9%. For comparison, egg diameter CV in lecithotrophic species is larger than in planktotrophs and averages 7.1% for species with external fertilization (N = 21) (Marshall and Keough, 2008b). Interestingly, the amount of within-population variation in egg size was found to be smaller in species with external than in those with internal fertilization for lecithotrophic species, but not for planktotrophic species (Marshall and Keough, 2008b). Of course, if local fertilization conditions are important factors in determining egg size, then among-population variation, not within-population variation, is expected to be higher in species with external fertilization than in those with internal fertilization, but sufficient data to test this expectation are still lacking (Bernardo, 1996). In this study on M. balthica, ~18% of total variance in egg diameter could be attributed to the between population level; this is very comparable to the ~25% reported for offspring size of the bryozoan Watersipora subtorquata (Marshall and Keough, 2008a). One important point to be gained from these examples is that an appreciable, if not major part of offspring size variation appears to occur at levels below the population level (see also Miles et al., 2007; Phillips, 2007). Possibly, bet hedging, the idea that unpredictable environments select for genotypes that produce phenotypically variable offspring (for a review see Philipp and Seger, 1989), plays a role, making females with high levels of variation in egg size more successful under many different population densities.

4.3. Population dynamical effects

Concern has been growing that exploitation of marine taxa to critically low densities may hamper population recovery, in the case of broadcast spawners due to reduced fertilization success (Myers et al., 1995; Pfister and Bradbury, 1996; Lundquist and Botsford, 2004). The correlation between population density and egg size we observed is consistent with sperm limitation and this may have implications for our understanding of population dynamics of M. balthica and similar taxa. Zygote and subsequent recruit density should not be seen only as a function of total stock size — in addition, the distribution of stock densities is important; i.e., is the stock distributed over a large area with low density or, instead, patchily, contained in few patches of higher density; the latter would be more favorable for recruitment.

Population density and its variation are thus predicted to play a role in determining the number of zygotes produced, a notion which is part of the member/vagrant hypothesis (Sinclair, 1987; Sinclair and Illes, 1988) which states that population dynamics cannot be understood without knowledge on spatial distribution of a species in all its various life stages. It would increase our understanding of year-to-year variation in recruitment success if such spatial factors are taken into account (e.g., Claereboudt, 1999; Marelli et al., 1999; Wahle and Peckham, 1999; Dowling et al., 2004; Lundquist and Botsford, 2004).

Temporal variation in marine invertebrate stocks is high and this variability is poorly understood (van der Meer et al., 2001; Eckert, 2003). We suggest that incorporating spatial stock density variation will improve our understanding of the dynamics of natural populations and also of commercially exploited species (see Dowling et al., 2004 for an example). Locations with high density are expected to make disproportionally large contributions to the next generation and acknowledging this may be helpful for the management of natural resources.

Acknowledgements

We thank J. van der Meer, S. Saraiva and T. Piersma for discussions, J. Beukema and R. Dekker for generously providing density data from their long-term monitoring data base, and four anonymous referees for their helpful comments. This work was partly supported by three NWO grants: a PIONIER grant to T. Piersma, an NOP grant to JD and PH and a MEERVOUD grant to PL [RH]

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