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The commonly applied Brey model to estimate benthic secondary production cannot be used for communities dominated by large bivalves

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ABSTRACT

The Brey model to calculate secondary production from data on biomass and mean individual weight is widely used, but so far it has not been tested for communities in which one or a few species dominate. On the base of a long-term (tens of years) data series on estimates of densities, biomass, mean individual weights and annual production of the most important bivalve species (together accounting for about 60% of the zoobenthic biomass) in a vast tidal-flat area, we compared production values obtained by two methods: the weight-increment summation method and the Brey model. In 4 out of the 5 studied bivalve species, the Brey estimates were on average substantially lower than the direct estimates. As a consequence, the Brey method seriously underestimated the production of the entire bivalve community in about half of the years. In 10 out of the 28 years, the Brey estimates were even less than half of the actual bivalve production. The one species (*Limecola balthica)* with a satisfactory match between the two methods was (as contrasted to the 4 other species: *Cerastoderma edule, Mytilus edulis, Mya arenaria, Ensis leei*) characterized by low annual weight increments and the simultaneous presence of many year classes, none of them strongly dominating. As secondary production of the studied ecosystem is dominated by the group of large bivalves, Brey estimates for such bivalve-dominated systems are inadequate for a study of their functioning.

1. Introduction

Estimation of secondary production is an important tool for better understanding of ecosystems (Dolbeth et al., 2012). Unfortunately, secondary production of an entire community cannot easily and cheaply be determined. It asks for a laborious procedure of frequent measurements of numbers and weights of all constituent populations for a long period. As a shortcut, Brey (1990, 2001, 2012) presented a model to calculate secondary production of benthic invertebrates that circumvents this procedure. Instead, he proposed to estimate the ratio P/B of production P to biomass B from the mean weight of individuals observed from a limited number of samplings. The heavier the individuals, the lower the P/B ratio. From a huge number (>1000) of published results on such population parameters as number, biomass and production he built a multi-parameter model for an average log-log relationship of P/B with mean individual weight.

Simplified: at any weight, the P/B value in the model is an average of published values for a taxonomic group (such as molluscs, worms, etc.). Actually, observed values for individual species may represent a wide range, resulting in P values that differ substantially from the Brey-based ones. For an entire community, however, the positive and negative species differences with the Brey values generally more or less compensate each other. As a result, the difference between direct and Brey estimates for the P of the entire community is invariably less extreme. However, it may be expected that extreme over- or underestimates in species with a dominating biomass contribution cannot be compensated fully by the remaining species, representing lower shares in biomass.

The Brey model has extensively been used to estimate production of communities of benthic invertebrates (e.g. Bolam et al., 2010 and several other examples enumerated in Beukema and Dekker, 2013). However, the use of the model was frequently based on single (one--season) samplings rather than on multiple-season samplings and annual means (as prescribed by Brey). Such limitation to a single sampling may cause serious bias (Beukema and Dekker, 2013, Saunier et al. 2019). In temperate coastal ecosystems, macrozoobenthic biomass is generally much lower in winter than in summer (Beukema, 1974, Saunier et al. 2019).

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So far, the Brey model has not rigorously been tested. The literature shows conflicting evidence for its reliability. Brey (1990, 2012) evaluated the model outcomes by comparisons with published results from the weight-increment summation method. Satisfactory outcomes of such tests for marine communities are reported both in Brey (1990): 3 out of 4 comparisons with studies by the Warwick group (Buchanan and Warwick, 1974; Warwick and Price, 1975; Warwick et al., 1978; Warwick and George, 1980) as well as in Dolbeth et al. (2005), who studied 2 communities in 2 years. For individual species, the differences found between the results of the 2 methods were frequently large, but they were invariably much smaller for the sums of the species. Very small community differences were found in 7 out of the 8 above comparisons: from <1 to 11% in 3 of the 4 comparisons by Brey (1990) and from 4 to 10% in the 4 comparisons by Dolbeth et al. (2005). Thus, 7 out of 8 comparisons yielded results inspiring confidence. On the other hand, Brey (2012) added 2 more comparisons with substantial differences between measured and model-estimated community values. Further, Petracco et al. (2012) showed that the Brey model performed only moderately, underestimating production of sandy beach macrofauna. A similar conclusion was reached by Mistri et al. (2001) for a community dominated by one bivalve species. They rightly warned that the Brey method should be used with utmost care, as its use may lead to misleading estimates in certain cases, e.g. in communities dominated by one species with extraordinarily high biomass (like mussel beds). In the present paper, we add examples similar to the Mistri one, again for a community dominated by a low number of bivalve species. Our examples are based on comparisons for a large number of years.

The above contrasting results of model testing (only 7 out of the total of 12 comparisons yielded a satisfactory correspondence between direct and Brey estimates) give every reason for further testing of the performance of the Brey model for specific communities and particularly to study why there is sometimes a serious lack of correspondence. The availability of a long-term (several decades) data series on macrozoobenthic populations monitored in a vast tidal-flat area (Beukema and Dekker, 2020) offers a unique opportunity to compare for several years the observed values of "real" production (as obtained by the weight-increment summation method) with Brey-calculated estimates. We limit this study to bivalves, in which production estimates were relatively easily obtained by the presence of year marks on the shells, allowing a classification of the sampled individuals into year classes (enabling the monitoring of numbers and weights of groups born in the same year for long periods). In the studied community, bivalves accounted for a large proportion (more than half) of the zoobenthic biomass. We not only discuss differences between our direct production estimates and those from the Brey model, but enumerate particularly the characteristics of communities in which the Brey model is failing. We state for what type of communities the Brey model does yield satisfactory results.

2. Methods

We obtained direct estimates on annual production by the weight-increment summation method (Van der Meer et al., 2005), using twice-annual (samplings in March and August) data on numerical densities (n m^{-2}) and biomass (g AFDM m^{-2}, ash-free dry mass) found by long-term (tens of years) sampling at 15 permanent stations on Balgzand, a 50-km^2 tidal-flat area in the westernmost part of the Wadden Sea, the Netherlands. Details are published in a number of earlier papers on production measurements in *Cerastoderma edule* (Beukema and Dekker, 2006), *Mytilus edulis* (Beukema and Dekker, 2007), *Limecola balthica* (Dekker and Beukema, 2007; Beukema and Dekker, 2013) and *Ensis leei* (Dekker and Beukema, 2012). So far, results on similar research on *Mya arenaria* are unpublished. In the 1970s, the 5 bivalve species studied accounted together for 97% of the bivalve biomass and for 62% of the total zoobenthic biomass of 26.6 g AFDM m^{-2} on the tidal flats of the Dutch Wadden Sea (Beukema, 1976). Nowadays, on the Balgzand tidal flats, these percentages amount to 92 and 60%, respectively, at a total biomass of 36.4 g AFDM m^{-2} (Beukema and Dekker, 2020). Such high shares of big bivalves are not unique for the Balgzand area, but appear to be typical for tidal flats all over the Wadden Sea (Dankers and Beukema, 1983; Compton et al. 2013; Schückel et al., 2015). Similar dominance of bivalves was observed also in other coastal waters (Möller & Rosenberg, 1983).

The data on numbers and biomass were collected in late winter and late summer, the times of minimal and maximal biomass, respectively (Beukema, 1974). Annual production estimates refer to the March–March periods. The share of young-of-the-year in production was not included, as we did not succeed in estimating their production with sufficient precision (it would have required much more frequent sampling in spring and summer). We checked the effect of omitting recruit production (by adopting equality of their production to their summer biomass, a minimum estimate) and found a negligible effect on the difference between our direct estimates and the (recalculated) Brey values. For the annual means of individual weights of the animals of >0.9 y old, we averaged the weights found in March and August.

Brey-calculations of the annual production of these 5 bivalves followed the multi-parameter model (version 4-04) of Brey (2001), which we simplified to:

$$\log P/B = -0.52 - 0.238 \log W,$$

in which W is the mean individual weight expressed in g AFDM (see Beukema and Dekker, 2013 for further details on the simplification and the conversions). Because later versions of the Brey model showed highly similar relationships between P/B and W, we used the frequently applied version 4-04 in Brey (2001).

The numbers of years with sufficiently precise data available varied between the species: 37 in *C. edule* and *L. balthica,* 36 in *M. edulis*, 29 in *M. arenaria* (this species was not sampled deep enough in the early years) and only 14 in *E. leei* (this species became sufficiently numerous regularly only by 2005 and in a few earlier years).

3. Results

3.1. Brey calculations compared with direct data

In 4 out of the 5 studied bivalve species, we found serious (on average mostly >50%) and statistically significant (mostly $p < 0.01$) underestimates of production values obtained by application of the Brey model (Table 1). Only in *Limecola balthica*, the difference between the means of direct and Brey-calculated estimates were non-significant and small. For the totals of bivalve production (sums of P values of the 5 species), mean Brey-estimates were significantly lower (by about 40%) than direct ones. The numbers of annual underestimates of these sums were substantially (by an order of magnitude) higher than the numbers of overestimates by the Brey method. Thus, real bivalve production was on average 2 to 3 times higher than Brey-calculated production and underestimates by Brey calculations were many times more frequent than overestimates. The Brey method underestimated actual production in particular in years with high production values (Fig. 1). Consequently, the year-to-year variation in P values calculated by the Brey method was lower than the between-year variation in the actual P values (Fig. 1).

As there are no indications that production by non-bivalves was higher in years with strong underestimates of the Brey calculations of bivalve production, the deficits of the Brey bivalve estimates will have been passed fully to estimates of the total secondary production of the ecosystem.

3.2. Comparison of relevant characteristics of the 5 species

To explain the difference found between the results in *Limecola balthica* (showing roughly correct Brey estimates) with those in the other

Table 1
Comparisons between annual estimates of secondary production P for populations of 5 bivalve species obtained by two methods: a direct one (based on twice-annual measurements during 14–37 years at 15 sampling stations of numbers, biomass B and mean individual weights) and calculations with the Brey model. The data are for the recent 14 years in which *Ensis leei* had become abundant and for all 28 years of the 1987–2015 (except 1990) period (when *Mya arenaria* was correctly sampled), respectively (in 1990 an estimate for *Mytilus edulis* was impossible*)*. The separate estimates for *Cerastoderma edule* and *Limecola balthica* refer to the 37 years of the 1979–2015 period, for *M. edulis* for these years minus 1990, for *M. arenaria* for 1987–2015 and for *E. leei* for 1992, 1993, 1995, 1997, 2005–2012, and 2014–2015. Significance of ratio difference from 1.0 indicated by * or ** ($p < 0.05$ or < 0.01, sign test with N pairs). Nr gives the numbers of over- and underestimates of the Brey calculation as compared to the direct estimate.

	C. edule	*M. edulis*	*M. arenaria*	*L. balthica*	*E. leei*	Sum	
N annual comparisons	37	35	29	37	14	14	28
Direct	5.8	3.5	8.9	1.4	5.9	26.5	22.0
Brey	3.3	1.1	4.3	1.9	1.7	12.8	11.7
Ratio	0.58**	0.32**	0.48**	1.34	0.29*	0.48**	0.53**
Nr overestimates	9	7	4	24	2	1	4
Nr underestimates	28**	28**	25**	13	12*	13**	24**

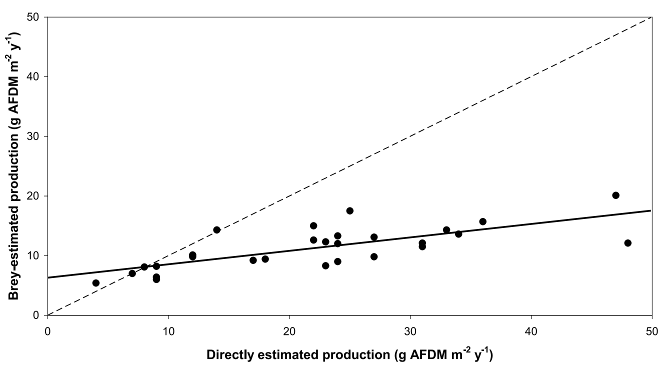

Fig. 1. Annual values of bivalve production P (sums of the 5 species *Cerastoderma edule, Mytilus edulis, Mya arenaria, Ensis leei,* and *Limecola balthica*) on Balgzand (means of observations at 15 sampling stations) as estimated in 2 ways: (horizontal axis) the direct method of weight-increment summation and (vertical axis) calculations by the Brey model (using annual means for biomass and mean individual weight). One point for each of the 28 years 1987–1989 plus 1991–2015. Full line indicates best linear relationship, dashed line shows equal values for the 2 methods. Full line: P-Brey = 0.2253 P-direct + 6.305.

studied bivalve species (generally showing Brey estimates that were far below the true values), we present in Fig. 2 as an example the data on the relationship between P/B and mean individual weight as found in *Cerastoderma edule*. Like the relationship described by Brey (1990), who compared results of (mostly 1-year) studies in a high number of different bivalve species, we found within this one species a similar negative relationship between multiyear values of P/B and mean individual weight. We found similar relationships in the other 4 species studied. In

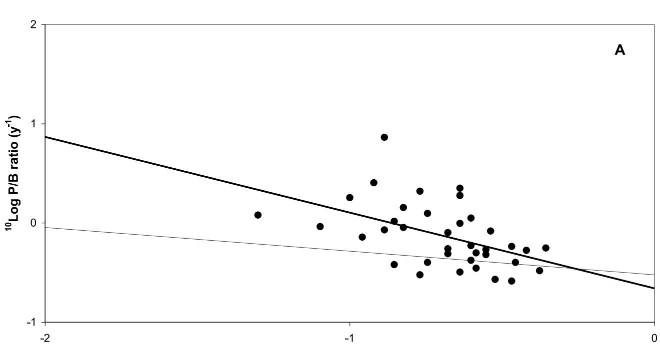

Fig. 2. The relationships (at ^{10}log scale) between annual P/B values (in y^{-1}) and mean individual weight (w, in g AFDM) in the *Cerastoderma edule* population on Balgzand for the years 1979–2014: Full line for best fit, dotted line for Brey-model relationship. Brey relationship: $^{10}\log P/B = -0.52 - 0.24\ ^{10}\log w$; best fit for Fig. 2: $^{10}\log P/B = -0.66 - 0.76\ ^{10}\log w$.

C. edule, by far most of the observed P/B values were above the Brey-calculated ones (represented by the dashed lines in Fig. 2). This was particularly so in all years when the annual mean weight of the individuals was <0.2 g AFDM (Fig. 2). At higher mean weights, observed P/B values were closer to the Brey-calculated ones. Thus, underestimates by Brey calculation became more frequent as mean weight of the individuals was lower, i.e. when the proportion of small (young) individuals was higher. The years with low mean weights (of <0.2 g AFDM for the entire year) were characterized by a high (usually >80%, on average 90%, $n = 15$ out of 37) proportion of about 10 months old spat. Higher mean weights occurred in all years with invariably <70% of spat at the start of the growing season (on average 30%, $n = 22$). Such years were generally characterized by the presence of individuals belonging to a number of different year classes. Years with populations consisting for >85% of spat invariably led to P/B values of >1.

Two other species (*Mytilus edulis* and *Ensis leei)* which also frequently showed far too low Brey-calculated P/B and P values (Table 2) had similar characteristics in their population composition as shown in Fig. 2 for *C. edule*: strongest underestimates of P/B in years with low mean individual weights, several years (about one third of the years) with numerical dominance of spat-sized individuals at the start of the growing season and substantial weight gain of these animals in the growing season (amounting on average to 0.29 and 1.1 g AFDM for *M. edulis* and *E. leei*, respectively). In contrast, *M. arenaria* showed minor underestimates in Brey calculations and relatively few years with spat

Table 2
Some characteristics of the populations of the 5 bivalve species studied. Data are 15-station averages found in late winter at Balgzand. First 2 columns: observed mean annual P/B values and between brackets calculated Brey values, separately for 2 wt classes for mean weights of all individuals of < and >0.1 g AFDM. Next 2 columns show numbers of years with population within these classes. Following column: numbers of years when spat contributed >80% of total numbers in population. Last column: mean weight increment (in g AFDM) during growing season of the individuals with a weight of <0.1 g AFDM at the start of the season. Sources: * Beukema et al. (2017), ** Dekker and Beukema (2012), *** Dekker and Beukema (2007).

	Mean P/B (y^{-1}) in years with		nr years with		nr years with	weight gain in
	w < 0.1 g	w > 0.1 g	w < 0.1	w > 0.1	spat >80%	individuals of <0.1 g
C. edule	4.8 (0.7)	0.8 (0.5)	16	21	12	0.27 g*
M. edulis	3.4 (0.6)	1.0 (0.4)	16	20	12	0.29 g*
M. arenaria	1.4 (0.6)	0.8 (0.4)	3	26	5	0.26 g*
E. leei	9.8 (0.6)	2.3 (0.4)	5	13	6	1.1 g**
L. balthica	0.6 (0.7)	no data	37′	0	0	0.03 g***

dominance. As contrasted to the three species *C. edule, M. edulis* and *E. leei*, population of *M. arenaria* generally consisted of many year classes: on average 7.2. In *C. edule* this number was 4.5, in *M. edulis* 4.4, in *E. leei* only 2.8 (for the years when this species had become numerous).

The data for *L. balthica* were in strong contrast with the above data for the other species (Table 2). In all 37 years, mean individual weights in populations in this species were well below 0.1 g AFDM (in fact below 0.04 g AFDM). On an annual basis, there was little difference between mean values of observed and Brey calculated P/B values (see Beukema and Dekker, 2013 for details). The under- and overestimates by Brey calculations occurred in roughly equal frequency. In this species, proportions of 10-months-old spat were nearly always below 70% and never above 80%. In all years, several year classes were simultaneously present (on average no less than 7.8). Seasonal weight gain was so low (on average 0.03 g AFDM per individual) that annual mean individual weights of the entire population never exceeded 0.1 g AFDM.

Summarizing: underestimates in Brey values were most serious in species with frequent dominance of spat (leading to low mean individual weights) and few year classes being simultaneously present. Spat dominance was not a rare phenomenon in 4 of the 5 species. Among the 29 years with observations in all 4 species about such dominance (Table 2), no less than 14 showed dominance (>80% spat) in at least 1 species. There were 4 years with simultaneous dominance in 2 species, 3 with 3 and 1 with 4.

4. Discussion

The Brey method yielded serious underestimates of production in 4 out of the 5 most important (as to biomass contribution) bivalve species on the Wadden Sea tidal flats. The only exception was *Limecola balthica* with on average similar estimates by the direct and Brey method (Table 1, see also Beukema and Dekker, 2013). In the other species, the underestimates by Brey calculation were substantial (first column of Table 2). This was particularly so in years with a high proportion of small individuals. However, for populations dominated by larger (older) individuals in these 4 species, results of Brey calculations still proved to be on average serious underestimates (second column of Table 2). Several reasons may have contributed to the satisfactory estimates by the Brey method in *L. balthica* as contrasted to those in the other studied species: there were more year classes simultaneously present in this one species than in the others, there was never strong dominance of spat-sized animals, and adult animals remained relatively small, leading to mean individual weights of <0.1 g AFDM in all years (Table 2). As contrasted to this species, the other 4 species were characterized by more rapid initial growth, high adult weights, extremely strong year classes recruited in some years, and fewer year classes being simultaneously present. These 4 species are suspension-feeders and show a life strategy that differs from that of the (predominantly) deposit-feeder *L. balthica* (r-versus K-strategists). Levinton (1972) already stated that suspension-feeders show greater fluctuations in population size than deposit-feeders. Warwick (1982) substantiated this view and added some examples of the shares of the species present in total production in waters around the British Isles. In 3 out of the 4 examples, production was dominated by 1 suspension-feeding bivalve. Möller & Rosenberg (1983) found dominance in biomass and production of 2 species of suspension-feeding bivalves in 4 out of 6 years in Swedish coastal waters. Thus, communities with a bivalve-dominated composition like the tidal-flat community we studied appear to be not uncommon. For reliable production estimates in such ecosystems, the tedious procedures extensively outlined in Van der Meer et al. (2005) should be followed.

The main aim of estimating secondary production is to get an insight in the functioning of an ecosystem. To this aim, the estimate should be representative. Unfortunately, nearly all published results of Brey estimates of secondary production refer to only 1 or a few years. We found a high between-year variability in the estimates of total secondary production by bivalves (horizontal axis in Fig. 1; see also Beukema and Dekker, 2019). Therefore, single-year estimates appear to be of little value to characterize the functioning of an ecosystem such as the intertidal flats of the Wadden Sea. Only averaged values for a period of some 4 or 5 years might yield a representative estimate, as shown for single bivalve species in Beukema and Dekker (2006) and in Dekker and Beukema (2007). For a determination of long-term trends, even much longer data series are indispensable (Beukema and Dekker, 2020).

There are a few more examples of multi-year secondary-production estimates. Buchanan et al. (1974) observed a remarkable stable production for 4 years in a subtidal North Sea community of deposit feeders. Möller et al. (1985) found a 4-fold variation in infaunal production during a 6-year study in Swedish waters. At 1 of the 2 sites where Maurer et al. (1992) estimated secondary production for 2 years, the highest annual value was more than 4 times higher than the lowest one (at the other site, the annual values were equal). Dolbeth et al. (2005) published estimates for 2 years in 2 systems. The larger year estimates were 1.6 and 1.9 times the smaller ones. So, great differences between annual estimates in the same system were also found in other systems than on the tidal flats we studied. Another shortcoming of published Brey estimates is that they were frequently based on data gathered in a single sampling season instead of the prescribed annual average, leading to a bias (Beukema and Dekker, 2013; Saulnier et al., 2019).

5. Conclusions

The Brey model is widely accepted, though the results of published available tests are far from consistent: 5 out of the 12 published tests showed poor correspondence between the Brey production estimate and the measured values (see Introduction). Nevertheless, the Brey model is frequently used. It is the best of the available shortcuts (Dolbeth et al., 2005).

Mistri et al. (2001) already warned that Brey calculations might lead to misleading estimates in certain cases, e.g. in communities dominated by one species with an extraordinarily high contribution to biomass, such as mussel beds. The present paper corroborates this view and provides evidence that the warning by Mistri et al. (2001) was right. The community we studied was dominated by a few bivalve species with high biomass and highly irregular and frequently high annual recruitment (Beukema and Dekker, 2014) and this led to serious underestimates of its production in most years by the Brey method. In the examples Brey (1990) showed in order to check his calculations, a dominating (>50% of total biomass) suspension-feeding bivalve species was present in 2 cases (communities 3 and 4) and in both cases the Brey estimate was an underestimate. Generally, the other species (all or nearly all deposit-feeding species) could not completely compensate for the serious underestimate caused by the dominating suspension-feeding bivalve. In the community we studied, the situation was similar: the underestimate of the bivalve production as well as the share of bivalves in total biomass were frequently very high, excluding an ability of other species to compensate.

Thus, the Brey method appears to be impracticable in communities dominated by one or a few species characterized by irregular recruitments, rapid growth of spat to high adult weights, resulting in biomass dominance in part of the years (1 year after a highly successful recruitment). We conclude that the Brey model can be fruitfully used only for multi-species communities in which none of the species seriously dominates as to biomass. It is easy to check (by rank-production curves as in Warwick, 1982) whether or not the Brey model will probably yield a reliable estimate of secondary production.

CRediT authorship contribution statement

J.J. Beukema: Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Writing – original draft. **R. Dekker:** Data curation, Validation, Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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