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▶ **To cite this version:**

Erwan Saulnier, Anik Brind'Amour, Adrien Tableau, Marta M Rufino, Jean-Claude Dauvin, et al.. Seasonality in coastal macrobenthic biomass and its implications for estimating secondary production using empirical models. Limnology and Oceanography, 2019, 64 (3), pp.935-949. 10.1002/lno.11086 . hal-02126943

HAL Id: hal-02126943

https://normandie-univ.hal.science/hal-02126943

Submitted on 13 May 2019

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LIMNOLOGY
and
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ASLO

Limnol. Oceanogr. 64, 2019, 935–949
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doi: 10.1002/lno.11086

Seasonality in coastal macrobenthic biomass and its implications for estimating secondary production using empirical models

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Abstract

Macrobenthic secondary production is widely used to assess the trophic capacity, health, and functioning of marine and freshwater ecosystems. Annual production estimates are often calculated using empirical models and based on data collected during a single period of the year. Yet, many ecosystems show seasonal variations. Although ignoring seasonality may lead to biased and inaccurate estimates of annual secondary production, it has never been tested at the community level. Using time series of macrobenthic data collected seasonally at three temperate marine coastal soft-bottom sites, we assessed seasonal variations in biomass of macrobenthic invertebrates at both population and community levels. We then investigated how these seasonal variations affect the accuracy of annual benthic production when assessed using an empirical model and data from a single sampling event. Significant and consistent seasonal variations in biomass at the three study sites were highlighted. Macrobenthic biomass was significantly lower in late winter and higher in summer/early fall for 18 of the 30 populations analyzed and for all three communities studied. Seasonality led to inaccurate and often biased estimates of annual secondary production at the community level when based on data from a single sampling event. Bias varied by site and sampling period, but reached ~ 50% if biomass was sampled at its annual minimum or maximum. Since monthly sampling is rarely possible, we suggest that ecologists account for uncertainty in annual production estimates caused by seasonality.

Macrobenthic invertebrates are essential components of marine coastal ecosystems. They support key ecological functions such as bioturbation and nutrient recycling, and contribute substantially to energy flow from primary organic sources to upper trophic levels (Tumbiolo and Downing 1994; Reiss and Kröncke 2005; Bolam and Eggleton 2014). Secondary production of benthic macrofauna represents the incorporation of organic matter or energy per unit of time and area (Cusson and Bourget 2005). It integrates dynamic population processes such as recruitment, growth, and mortality, and biotic and abiotic interactions between populations and their environment. Hence, secondary production has been used as a useful integrative indicator of the trophic capacity, health, and functioning of marine ecosystems (Benke and Huryn 2010; Dolbeth et al. 2012).

Macrobenthic secondary production can be estimated using classic direct methods, based on measuring abundance and mean body mass of cohorts sampled at regular time intervals (Sprung 1993). It can also be assessed using empirical models, which predict production or the production-to-biomass (*P*:*B*) ratio from life history traits (mean body mass and life span) and biotic and abiotic variables (Dolbeth et al. 2005). Since classic direct methods are time-consuming (Robertson 1979), empirical models have been increasingly used to estimate macrobenthic production, especially in studies focusing on the production of an entire community of species (Burd et al. 2012; Beukema and

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Dekker 2013). Most empirical models use mean annual data (on biomass and body mass) to predict annual secondary production or the *P*:*B* ratio (Cusson and Bourget 2005). The *P*:*B* ratio is the ratio of annual production to mean annual biomass. A general method to estimate secondary production is thus to multiply the *P*:*B* ratio predicted by an empirical model by the mean annual biomass (Robertson 1979; Wong et al. 2011). Mean annual biomass is rarely estimated since it requires seasonal sampling that is expensive and time-consuming. Consequently, annual production estimates are often derived from a single measurement of biomass per year, which may differ from the annual mean. Indeed, many ecosystems show seasonal variations in abiotic (e.g., temperature) and biotic factors (e.g., food availability and predation) that drive species phenology and ultimately, population and community dynamics (Field et al. 2007; Passuni et al. 2016). In temperate marine coastal ecosystems, the biomass of macrobenthic species seems generally higher in late summer due to recruitment and individual growth, and lower in late winter due to natural mortality and weight loss (Beukema 1974; Zwarts and Wanink 1993; Coma et al. 2000). Therefore, estimating mean annual biomass and mean body mass using data from a single sampling event could lead to biased estimates of secondary production (Bolam and Eggleton 2014).

Several studies investigated effects of sampling design on estimation of secondary production (Cushman et al. 1978; Morin et al. 1987; Cusson et al. 2006). They showed that the choice of sampling period and frequency affect the estimation, and inappropriate choices can lead to high bias in production estimates. However, their estimates were based on simulations of a single population, mainly in freshwater ecosystems; more importantly, they used classic direct methods to calculate secondary production. To our knowledge, the effect of sampling period on production estimates of empirical models has been tested only by Beukema and Dekker (2013). These authors used an empirical *P*:*B* model (Brey 2001) to estimate production of a marine bivalve population (*Limecola balthica*) sampled twice per year (late summer and late winter). They showed that production estimates based on data from a single sampling event were biased, and this bias was even higher when data were collected in late summer. Yet, empirical models are ineffective at estimating production of a single population. Instead, they are recommended for estimating secondary production of an assemblage of species, since prediction error decreases greatly when the estimates of several populations are pooled (Brey 2001, 2012). Studies investigating seasonal variations in macrobenthic invertebrate communities generally focused on a few species or were restricted to abundance and species richness (Desroy and Retière 2001; Mucha et al. 2005). Those that quantified seasonal variations in macrobenthic biomass and production at the community level did not always identify a seasonal trend (Reiss and Kröncke 2005; Wong et al. 2011). Hence, whether the bias observed in production estimates of a single population persists at the community level and how the sampling period affects annual production estimates remain to be tested.

In this study, we used time series of macrobenthic data collected seasonally to address two main questions: (1) whether the biomass of coastal soft-bottom macrobenthic invertebrates shows significant seasonal variations at both population and community levels and (2) how biased and accurate the estimates of community secondary production from an empirical model are when macrobenthic data come from a single sampling event. Given the potential seasonal variability, the latter question quantifies the bias and accuracy at different periods of the year.

Materials and methods

Three subtidal macrobenthic communities were monitored for more than 20 yr at three fixed stations located along the French coast in the southern North Sea and western English Channel. These data sets were previously published, at least partially (Fromentin et al. 1997; Dauvin 1998, 2000; Ghertsos et al. 2000).

Study sites

All three sampling sites of this study are located on shallow, subtidal soft-bottom areas (Fig. 1). The two first sites, "Pierre Noire" (PN) and "Rivière de Morlaix" (RM), are located in the Bay of Morlaix, western English Channel. The PN site is a fine-sand macrobenthic community located at a depth of 17 m in the outer part of the bay (Dauvin 1998). The RM site is a muddy fine-sand community located at a depth of 10 m in the inner part of the bay, near the mouth of the Morlaix River estuary (Dauvin 2000). Both sites are influenced by temperate Atlantic waters, with sea bottom temperatures ranging from 9°C in winter to 15°C in summer (annual mean ± SD = 12.1°C ± 0.4). The third study site, "Gravelines" (GV), is a fine-sand macrobenthic community located at a depth of 10 m in the southern North Sea. The GV site has a continental climate characterized by relatively cold winters and warm summers (Ghertsos et al. 2000), with sea bottom temperatures ranging from 6°C in winter to 20°C in summer (annual mean ± SD = 12.9°C ± 0.6).

Data collection and selection

In the western English Channel, the PN site was sampled each month from 1978 to 1981, and then five times per year from 1982 to 1996 (March, June, August, October, and December). The RM site was sampled during the five same months from 1980 to 1996. In the southern North Sea, the GV site was sampled four times per year (January/February, March/April, June/July, and September/October) from 1989 to 2016.

The same sampling procedure was applied at the three study sites. Ten replicates were collected at each sampling event using a 0.1 m^2 Smith-McIntyre grab. Each sample was sieved through a 1 mm mesh sieve, and the material retained was fixed with a 10% buffered formaldehyde solution. In the laboratory, the organisms retained were identified to the

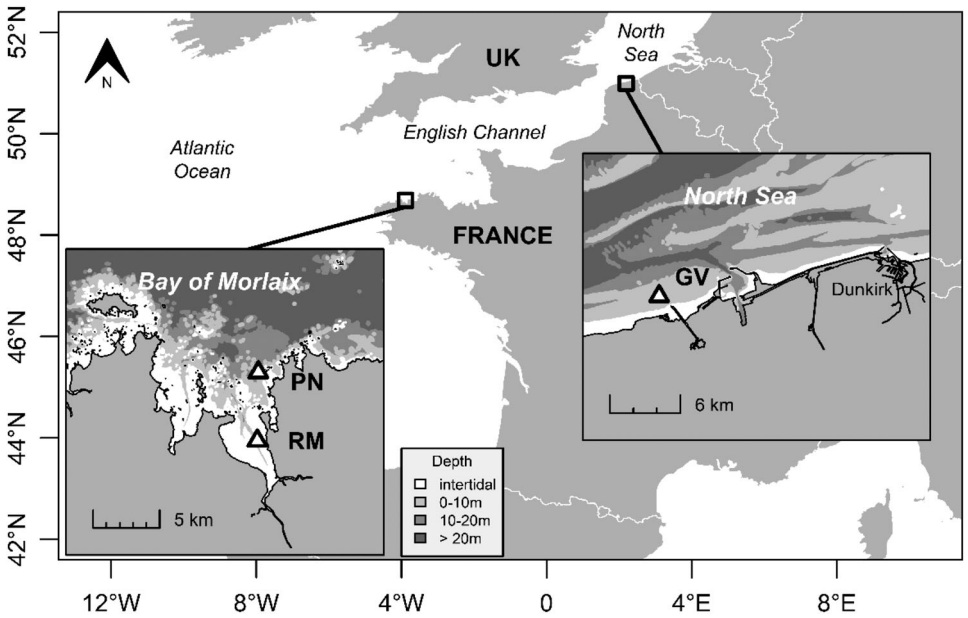


Fig. 1. Location of the three study sites: PN, RM, and GV (white triangles). The PN and RM sites are located in the Bay of Morlaix, in the western English Channel. The GV site is located in the southern North Sea. All sites are situated on a shallow, subtidal soft-bottom habitat. The same single fixed station was sampled at each site during the entire sampling period ($\sim$ 20 yr).

species level, counted, and weighed. Biomass per species was determined as dry mass (DM) at the PN and RM sites, and as ash-free dry mass (AFDM) at the GV site. Biomass in DM was converted to AFDM by applying conversion factors (Brey et al. 2010) to standardize the unit of biomass at the three sites. The 10 replicates were pooled for each station and the biomass expressed in g AFDM m^{-2} before data analysis.

The biomass of a few species with low abundance was unknown at the species level and thus excluded from the analyses. We also excluded large individuals belonging to the "megafauna" size class (e.g., *Asterias rubens*, *Atelecyclus rotundatus*, *Lutraria lutraria*) and species with a frequency of occurrence of < 5% over the entire time series. The remaining taxa represented 37 species at PN, 22 species at RM, and 46 species at GV, for a mean of 93% of the total biomass sampled at the three study sites.

Macrobenthic communities at PN and RM have clearly distinct faunal compositions despite the short distance between them (< 5 km). PN supports one of the richest benthic amphipod communities recorded in Europe (Dauvin 1998), which represents a mean of 21% of the community biomass over the studied period. These dominant *Ampelisca* spp. populations almost disappeared after the "Amoco Cadiz" oil spill in March 1978 but gradually recovered to their original state (Dauvin 1998). The RM community is dominated by a few polychaete species, mainly deposit feeders, and was affected only slightly by the oil spill (Dauvin 2000). We excluded data collected during and shortly after the oil spill at both sites, since this perturbation temporarily modified the structure and dynamics of the macrobenthic communities (Dauvin 1998). We retained data from 1980 to 1996. In 1991, the American jack-knife clam *Ensis directus* was recorded for the first time at GV and successfully settled in the area (Luczak et al. 1993; Luczak 1996). The biological invasion of *Ensis directus* deeply modified the structure and dynamics of the GV community until 1996 (Ghertsos et al. 2000). Thus, we retained data from 1997 to 2016 at GV, except for 2013, when inclement weather precluded winter sampling. Overall, the time series analyzed in this study covered 17 yr at PN and RM, and 19 yr at GV, with a sampling frequency of 4–5 times per year at each site.

Modeling the seasonal pattern in macrobenthic invertebrate biomass

We modeled the seasonal pattern in biomass of macrobenthic invertebrates at both population and community levels using generalized additive models (GAMs; Wood 2006). GAMs are a flexible extension of generalized linear models that allow for nonlinear modeling by making no a priori assumption about the shape of the response function. Application of GAMs to ecological data has rapidly increased, notably for modeling nonlinear trends in time series (e.g., Boyce et al. 2010; Curtis and Simpson 2014; Bunting et al. 2016).

Community level

We first investigated seasonal variations in macrobenthic biomass at the community level. The following Gaussian additive model was fitted to each data series:

$$\log(\text{Biomass}_{ijk}) = \beta_0 + \text{site}_k + f_{1,k}(\text{Year}_i) + f_{2,k}(\text{Month}_j) + \varepsilon_{ijk} \quad (1)$$

where Biomass_{ijk} is the biomass of the macrobenthic community observed in year i, month j at site k, β_0 is the model

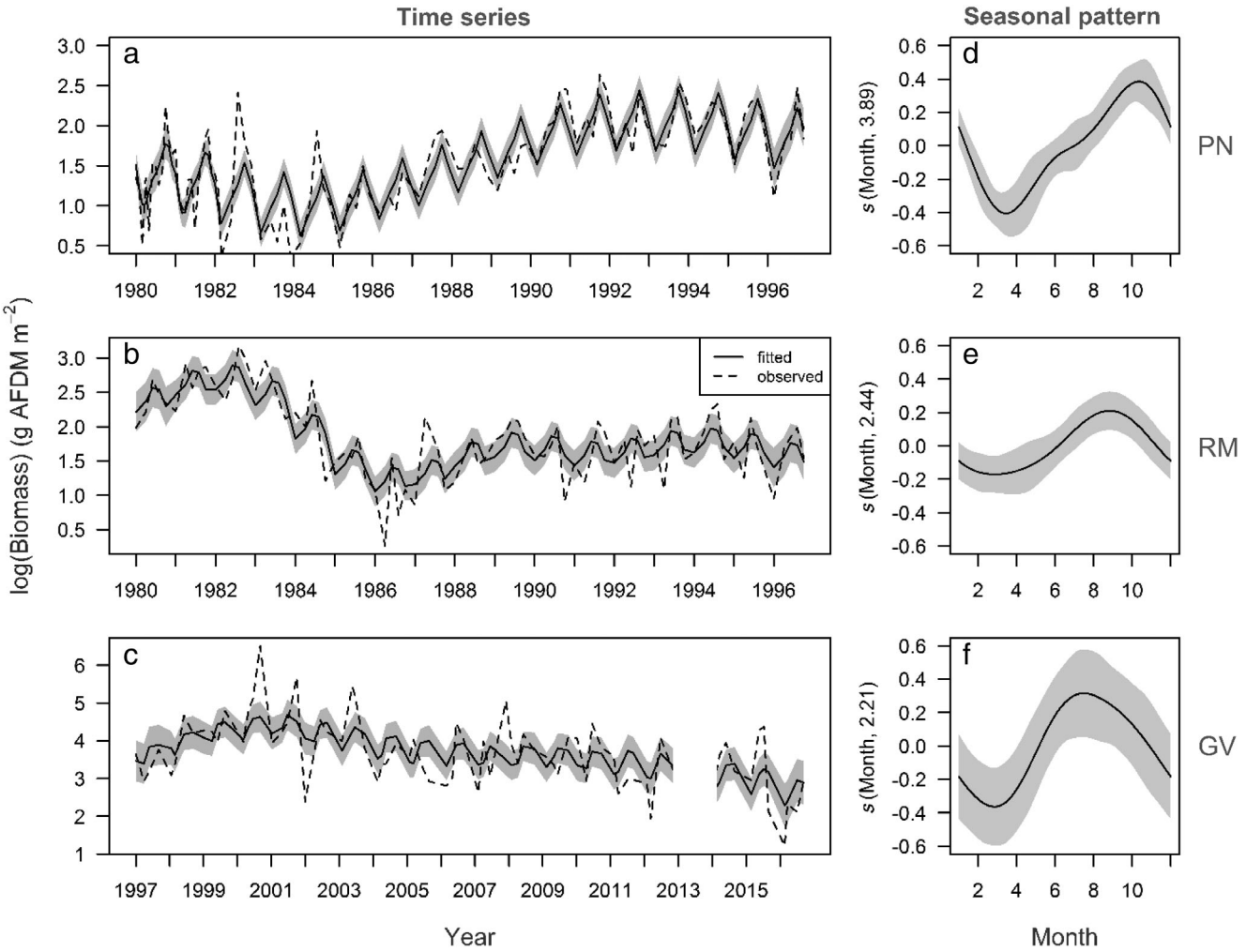


Fig. 2. Temporal variations in macrobenthic biomass on a log-scale at the community level. (**a–c**) Time series of observed biomass (dashed lines) and predicted biomass using a GAM (solid lines) at PN, RM, and GV, respectively. Shaded areas represent 95% confidence intervals of the fitted GAM. No sampling was performed in winter 2013 at GV. (**d–f**) Seasonal pattern in biomass modeled as a smooth function of the months at PN, RM, and GV, respectively. Estimated degrees of freedom for each smoother are given in parentheses on the *y*-axis label. Shaded areas represent approximate 95% confidence intervals.

intercept, site$_k$ is the study site fixed effect, $f_{1,k}(\text{Year}_i)$ is a smooth function of the years that represents the long-term trend, $f_{2,k}(\text{Month}_j)$ is a smooth function of the months that represents the seasonal pattern, and ε_{ijk} is mean-zero, normally distributed error with variance σ_k^2. Hence, the model estimates separate smoothers for the variables "Year" and "Month" for each study site. We used a natural log-transformation to reduce skewness of the data. We focused on the seasonal pattern in macrobenthic biomass, so we present mainly results of the fitted seasonal smoother f_2 (Fig. 2; *see* Supporting Information Fig. S1 for the fitted long-term smoother f_1). We also tested for pairwise differences in the seasonal pattern between sites (*see* Supporting Information for details).

Population level

To (1) explore potential similarities and differences in the seasonal pattern between species and study sites and (2) investigate whether some key species drive the seasonality in macrobenthic communities, we then modeled the seasonal pattern in biomass at the population level. Here, a population refers to a species observed at one site. We focused on the 10 dominant species (by biomass) at each site (30 populations). They represent a mean of 78%, 91%, and 86% of total biomass at PN, RM, and GV, respectively. All the populations selected had a frequency of occurrence of ≥ 70%, which implies they were sufficiently sampled to properly model both the seasonal pattern and the long-term trend. We fitted to each data series the following Gaussian additive model:

$$\log(\text{Biomass}_{ijp}) = \beta_0 + \text{population}_p + f_{1,p}(\text{Year}_i) + f_{2,p}(\text{Month}_j) + \varepsilon_{ijp} \quad (2)$$

where Biomass$_{ijp}$ is the biomass of macrobenthic population p observed in year i and month j, β_0 is the model intercept,

population_p is the population fixed effect, $f_{1,p}(\text{Year}_i)$ is a smooth function of the years that represents the long-term trend, $f_{2,p}(\text{Month}_j)$ is a smooth function of the months that represents the seasonal pattern, and ε_{ijp} is mean-zero, normally distributed error with variance σ^2. The model estimates separate smoothers for the variables "Year" and "Month" for each population.

GAM-based methods provide a flexible framework to separate any seasonal pattern from the long-term trend and to test the significance of this pattern. Here, the p values of both models correspond to the null hypothesis of no long-term trend or seasonal pattern in the time series. The GAMs were built using the package *mgcv* (version 1.8–17: Wood 2006, 2011) of R statistical software (version 3.3.3: R Core Team 2017). The smoothness parameters were estimated using the restricted maximum likelihood (REML) method, which tends to be more robust than the generalized cross validation method (Wood 2011). We used a thin-plate regression spline for the long-term smoother f_1 and a cyclic-cubic regression spline for the seasonal smoother f_2, which implies continuity from December to January, as recommended for cyclic responses (Wood 2006). We checked model assumptions of normality, homogeneity, and independence of the residuals by visual inspection (*see* Supporting Information Figs. S2, S3, S6, S7).

Estimating production-to-biomass ratio and production

We estimated annual secondary production P of each species using the empirical model developed by Brey (2012). This model uses artificial neural networks (ANN) to predict P:B from three continuous parameters (mean body mass M in Joules, mean annual bottom water temperature in °C, depth in m) and 17 categorical parameters (taxonomic, functional, and environmental parameters, and a marker for commercial exploitation). All categorical parameters are binary (0 or 1). The model is implemented in an Excel spreadsheet freely available at http://www.thomas-brey.de/science/virtualhandbook/ (version 01–2012, downloaded on 28 March 2017).

To estimate each species' mean body mass M, we divided its mean annual biomass by its mean annual abundance and converted it to Joules using energy densities (kJ g^{-1}) from a global database of conversion factors (Brey et al. 2010). When no conversion factor was available at the species level, we used the conversion factor for the next higher taxonomic rank. Information about taxonomy and functional traits used as input parameters were collected from the literature and online resources, including the Integrated Taxonomic Information System database (https://www.itis.gov/), the Biological Traits Information Catalogue of The Marine Life Information Network (http://www.marlin.ac.uk/biotic/), and the World Register of Marine Species (http://www.marinespecies.org) (last accessed on 04 May 2018). The marker for commercial exploitation was always set to zero since no species has been commercially exploited at the three study sites. Depth was previously reported (Fromentin et al. 1997). We estimated mean annual temperature from time series of sea bottom temperature recorded monthly or bimonthly at a fixed station near each study site (Dauvin et al. 1989; Conq et al. 1998; Woehrling et al. 2005).

We used the Brey (2012) model for three reasons. First, the models developed by Brey (2001, 2012) are used more frequently than other empirical models to estimate secondary production (*see* Fuhrmann et al. 2015; Tableau et al. 2015; Degen et al. 2016 for recent examples). Second, they perform as well or better than others in predicting P:B and P (Cusson and Bourget 2005; Dolbeth et al. 2005; Petracco et al. 2012). Third, they can be used to predict secondary production in a wide range of marine and freshwater ecosystems using easy-to-measure abiotic and biotic parameters (Brey 2012). Conversely, many other empirical models are restricted to certain taxonomic groups (Cartes et al. 2002) or ecosystem types (Morin and Bourassa 1992) or require life span as input (Cusson and Bourget 2005), which is difficult to determine accurately (Brey 2012; Beukema and Dekker 2013).

The models developed by Brey (2001, 2012) are based on the empirical relationship between P:B and the mean individual body mass M of macrobenthic invertebrates (Schwinghamer et al. 1986). We used Brey's (2012) ANN model rather than his multiple linear regression model (Brey 2001) since the ANN approach shows slightly but significantly better performance in predicting P:B and P of macrobenthic communities (Brey et al. 1996; Brey 2012).

Model outputs are a P:B for each species. We calculated P by multiplying P:B by the biomass B of the respective species. We then calculated P of the macrobenthic community by summing the production of all species:

$$P = \sum_{i=1}^{n} B_i \times (P:B)_i, \text{with } i \text{ the species index.}$$

We first calculated annual production estimates using the annual mean of individual mean body mass $\overline{M}$ and biomass $\overline{B}$ of each species, as required (Dolbeth et al. 2005; Beukema and Dekker 2013). These production estimates were used as a reference and thus were implicitly assumed to have no error.

Then, we mimicked the procedure usually followed by users of the Brey model by calculating annual production based on data from a single sampling event (e.g., March, June, August, October, or December). We used mean annual sea temperature in all cases, since it is usually known, even when biological data come from a single sampling event (e.g., Fuhrmann et al. 2015). Estimating P:B requires filling an Excel spreadsheet for each study site and sampling scenario (monthly data or annual mean data). Overall, we estimated 5384 P:B ratios, equivalent to 246 spreadsheets, which would have been extremely time-consuming to fill iteratively using Excel. Instead, we implemented the Brey (2012) model in R to optimize the procedure and calculated all production estimates

directly in the R environment (R code and associated data supplied as Supporting Information).

Assessing the effect of sampling period on production estimates

A good estimator should be unbiased (the difference between the predicted and the "reference" value is null on average) and accurate (estimates as close as possible to the "reference" value; Walther and Moore 2005). Here, we estimated how accurate a single measurement of M and B per year is to predict annual production of macrobenthic communities. Although we investigated seasonal variations in biomass at both population and community levels, we calculated bias and accuracy only at the community level, since empirical models are known to provide inaccurate estimates of P for a single species but robust estimates for an assemblage of species (Brey 2001, 2012). For each sampling period, we calculated the proportional error (PE, also called relative error or deviation), defined as $\mathrm{PE} = (\hat{\theta} - \theta)/\theta$, where $\hat{\theta}$ represents the estimated value and θ the reference value of P, which is based on annual mean $\overline{M}$ and $\overline{B}$. We then calculated the median proportional error (MPE) of P estimates to measure bias and the median absolute proportional error (MAPE) to measure accuracy (Ono et al. 2015; Anderson et al. 2017). At PN and RM, we estimated bias and accuracy for each sampling month. At GV, sampling months varied slightly among years (e.g., April instead of March, June instead of July) and were thus grouped by 2-month periods to estimate bias and accuracy.

Results

Seasonal patterns in biomass of macrobenthic invertebrates

Seasonal patterns at the community level

Biomass of the macrobenthic communities showed a strong, significant, and consistent seasonal pattern at the three study sites, characterized by a minimum value in late winter and a maximum value in summer/early fall (Fig. 2; Table 1). Seasonal patterns at RM and GV did not differ significantly under this model ($p > 0.05$, Supporting Information Table S1). Conversely, that at PN differed significantly from the other two in both timing and amplitude ($p < 0.05$, Supporting Information Table S2). Biomass fell to its minimum in late winter at all sites (March), but its maximum occurred earlier at GV (July) than at RM (September) or PN (October). Moreover, the amplitude of the seasonal pattern was lower at RM than at the other two sites, with a mean predicted max: min biomass ratio of 1.46, 1.86, and 2.12 at RM, GV, and PN, respectively (back-transformed estimates; *see* Supporting Information Table S3 for monthly estimates of the seasonal smoother on a log scale at each site). Seasonal variations were also less regular at GV and RM than at PN, as shown by the poorer fit to the data and the larger 95% confidence interval of the seasonal smoother, especially at GV (Fig. 2).

Table 1. Outputs of the GAM fitted to long-term data series of macrobenthic community biomass for three sites (PN, RM, and GV) on a log-scale (model 1, $n = 262$, adjusted $R^2 = 0.798$). df, degrees of freedom. Significance of the smoothers is indicated by: $^{**}p < 0.01$; $^{***}p < 0.001$.

Explanatory variable	Estimated df	F	p value	
$s(\mathrm{Year})_{\mathrm{PN}}$	5.224	29.938	$< 2.0 \times 10^{-16}$	***
$s(\mathrm{Year})_{\mathrm{RM}}$	7.952	19.442	$< 2.0 \times 10^{-16}$	***
$s(\mathrm{Year})_{\mathrm{GV}}$	5.282	9.395	4.27×10^{-8}	***
$s(\mathrm{Month})_{\mathrm{PN}}$	3.892	9.116	4.95×10^{-15}	***
$s(\mathrm{Month})_{\mathrm{RM}}$	2.444	3.418	0.0001	***
$s(\mathrm{Month})_{\mathrm{GV}}$	2.209	1.462	0.0015	**

Nevertheless, the model 1 successfully explained a large part of the variability in the data (adjusted $R^2 = 0.798$). The factor "site" was not significant as a fixed effect and thus not included in the final model. No temporal structure was left in the residuals (Supporting Information Fig. S3), as expected, because the two temporal smooth effects accounted for temporal autocorrelation. The biomass of each macrobenthic community also showed a significant but different long-term trend at each study site (Table 1, Supporting Information Fig. S1).

Seasonal patterns at the population level

Similar to those at the community level, a significant and consistent seasonal pattern was observed in 18 of the 30 populations analyzed in this study (Table 2). Seasonality was detected across a wide range of taxonomic groups (annelids, crustaceans, bivalves, and gastropods) and trophic guilds (suspensivores, deposivores, carnivores, and scavengers). The model 2 explained a large part of the variability in the data (adjusted $R^2 = 0.731$).

The seasonal pattern in biomass had the same general shape as that observed at the community level for all the populations that showed significant seasonal variations (Fig. 3, Supporting Information Fig. S5). However, they differed greatly in amplitude and, to a smaller extent, in timing. Minimum biomass was almost always recorded in late winter (March–April), unlike peak biomass, which varied from early summer (June–July) to late summer/early fall (September–October).

Interestingly, these differences were observed among sites even for the same species. This feature is well illustrated by the three dominant species that were present at all sites (Fig. 3). For instance, the seasonal pattern of *Nephthys hombergii* was significant at GV but not significant at PN and RM. *Abra alba* showed a peak biomass slightly earlier but significantly higher at RM than at PN and GV. Finally, the seasonal pattern of *Lanice conchilega* at GV differed greatly in both amplitude and timing from that observed at the other two sites. At GV, this species exhibited a seasonal pattern with

Table 2. Relative biomass (mean percentage of total biomass of the community) and seasonality of the 10 dominant species at three study sites (PN, RM, and GV). Seasonality refers to the significance of a seasonal pattern in biomass modeled as a smooth function of the months, using a GAM (model 2, $n = 2415$, adjusted $R^2 = 0.731$), and indicated by: ns, nonsignificant; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

Site	Species	Relative biomass (%)	Seasonality
PN	*Nephtys hombergii*	27	ns
	Tritia reticulata	16	*
	Ampelisca armoricana	10	**
	Abra alba	8	ns
	Ampelisca sarsi	7	**
	Pseudopolydora pulchra	4	***
	Marphysa bellii	4	*
	Lanice conchilega	3	**
	Aponuphis bilineata	2	ns
	Euclymene oerstedii	2	**
RM	*Nephtys hombergii*	25	ns
	Lanice conchilega	20	ns
	Melinna palmata	13	ns
	Euclymene oerstedii	12	ns
	Notomastus latericeus	10	ns
	Pagurus bernhardus	5	**
	Abra alba	4	***
	Pseudopolydora pulchra	4	***
	Chaetozone setosa	4	***
	Thyasira flexuosa	1	*
GV	*Tritia reticulata*	19	ns
	Ensis directus	19	ns
	Abra alba	17	**
	Lanice conchilega	15	***
	Owenia fusiformis	7	ns
	Lagis koreni	4	***
	Notomastus latericeus	3	*
	Ophiura albida	3	ns
	Nephtys hombergii	3	*
	Limecola balthica	3	*

one of the highest amplitudes recorded among all populations analyzed in the present study (Supporting Information Fig. S5). For instance, in 2003, biomass of *Lanice conchilega* decreased from 147 g AFDM m^{-2} to 2 g AFDM m^{-2} from July to October, and its density from 6649 individuals m^{-2} to 11 individuals m^{-2} during the same period. The peak biomass observed for *Lanice conchilega* in July was synchronous with the peak biomass recorded at the community level at GV.

Biomass of the 12 remaining populations showed either no seasonal variation, modeled by a flat seasonal smoother in model 2 (e.g., *Lanice conchilega* at RM, Fig. 3e), or a weak seasonal pattern that was nonsignificant at $\alpha = 0.05$ (e.g., *Abra alba* at PN, $p = 0.096$, Fig. 3a, Supporting Information Fig. S5). We found no evidence of clear differences in seasonal pattern among taxonomic groups or feeding guilds. Evidence for a long-term trend in biomass was found for 25 of the 30 macrobenthic populations analyzed ($p < 0.05$).

Estimating the bias and accuracy of production estimates for each sampling period

Annual production estimates were inaccurate and generally biased when based on data from a single sampling event per year. Inaccuracy (MAPE) varied by the month of sampling from 14% to 47% at PN, 15% to 26% at RM, and 42% to 58% at GV, without any clear seasonal pattern (Supporting Information Table S4). Conversely, bias (MPE) showed a clear pattern at all study sites, following the seasonal variations in macrobenthic biomass (Fig. 4): high and negative in late winter (underestimation of P), close to zero when the sampled biomass was close to mean annual biomass (e.g., in December at PN and June at RM), and high and positive in summer/early fall (overestimation of P) (Supporting Information Table S4). If community biomass was sampled at its annual minimum, underestimates of P reached 47%, 25%, and 58% at PN, RM, and GV, respectively. Conversely, if biomass was sampled at its annual maximum, overestimates of P reached 46%, 23%, and 29% at PN, RM, and GV, respectively (Supporting Information Table S4). We found that bias could differ significantly among sites even for the same sampling month. For instance, P estimates based on data collected in August were slightly underestimated at PN (MPE = −7%) but significantly overestimated at RM (MPE = 23%). Both bias and inaccuracy were lower at RM than at the other two sites (Fig. 4, Supporting Information Table S4).

The long-term trend in annual production was consistent whether estimates were based on late-winter biomass (annual minimum), summer biomass (annual maximum), or mean annual biomass (the reference) (Fig. 5), except at GV with late-winter biomass. Indeed, the extremely high values and strong interannual variability of annual benthic production observed at GV when the estimates were based on summer or mean annual biomass were not detected with late-winter biomass, notably from 1998 to 2003.

Discussion

Using time series of macrobenthic data seasonally collected in temperate marine coastal ecosystems, we found evidence that biomass of macrobenthic invertebrates showed consistent and significant seasonal variations at both population and community levels, across a wide range of species. These seasonal variations resulted in inaccurate and often biased estimates of secondary production when the estimation was based on data collected during a single period of the year, which is often the case in macrobenthic studies (Reiss et al. 2009; Bolam and Eggleton 2014; Fuhrmann et al. 2015).

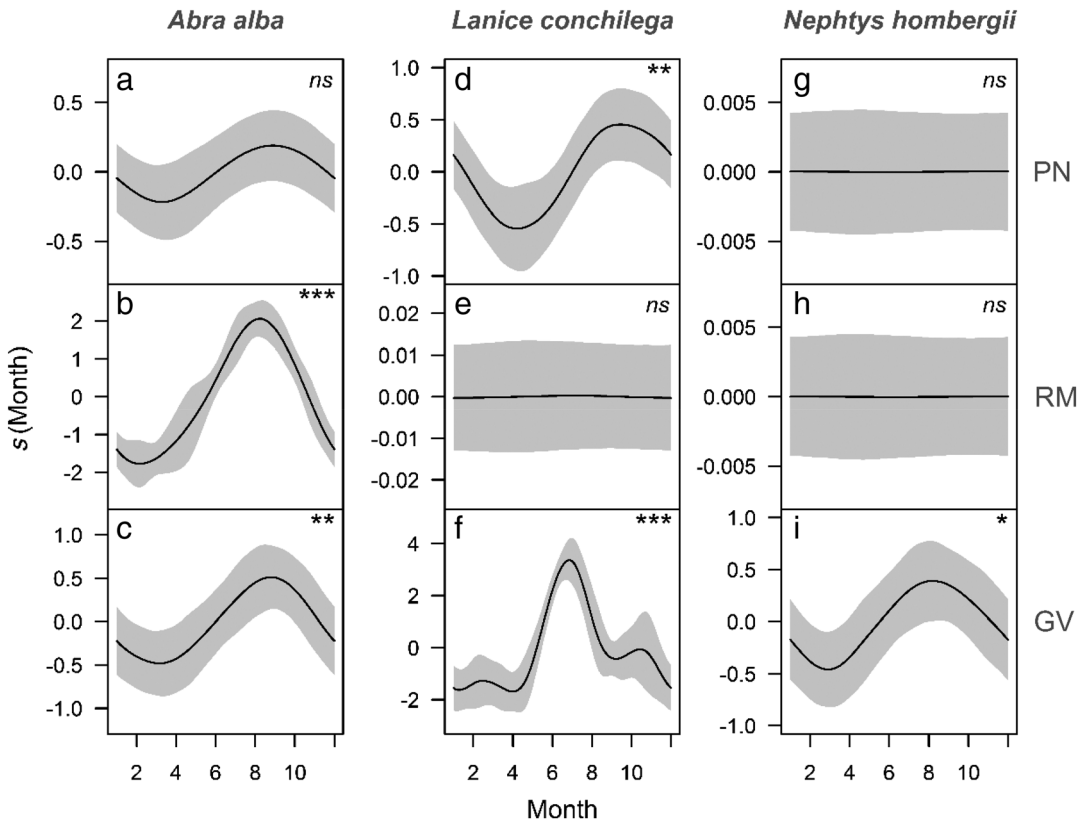


Fig. 3. Seasonal pattern in biomass on a log-scale at the population level for the three dominant species present at all sites: *Abra alba* (**a–c**), *Lanice conchilega* (**d–f**), and *Nephtys hombergii* (**g–i**) at PN, RM, and GV, respectively. Seasonal patterns were modeled as a smooth function of the months using a GAM. Shaded areas represent approximate 95% confidence intervals. Significance of the smoothers is indicated by ns, nonsignificant ($p > 0.05$); *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$. Note the different scale on the *y*-axis among species and sites.

Seasonality in biomass of macrobenthic invertebrates

Our results indicated that the three macrobenthic communities showed significant seasonal variations, in accordance with the annual pattern generally described in temperate coastal soft-bottom ecosystems, in both timing (lower biomass in late winter, higher biomass from early summer to early fall) and amplitude. At the community level, biomass amplitudes (ratio of annual maximum to annual minimum biomass) lay in the same order of magnitude as those reported for other temperate coastal soft-bottom ecosystems: 1.86 (Beukema 1974) and 1.98 (Zwarts and Wanink 1993) for macroinvertebrate assemblages of the Dutch Wadden Sea; and 2.0 for suspension feeders and 2.5 for deposit feeders in the Chesapeake Bay, U.S.A. (Baird and Ulanowicz 1989). This seasonal pattern is considered to be induced by the combination of abiotic (e.g., temperature) and biotic factors (e.g., food availability and predation). Increasing temperatures, photoperiod, and nutrient availability in spring result in an increase in primary production that fuels upper trophic levels (Townsend et al. 1992; Wiltshire et al. 2008), including macrobenthic invertebrates. The biomass increase observed from late winter to late summer for most macrobenthic taxa is basically a combination of recruitment and somatic growth. The relative contribution of each component to the overall increase seems to vary among taxa and study sites. For instance, the increase in macrobenthic biomass within intertidal flats of the Dutch Wadden Sea was attributed mainly to somatic growth (Beukema 1974; Zwarts and Wanink 1993), whereas recruitment appeared to contribute more at the present study sites, particularly at GV (Luczak 1996; Ghertsos et al. 2000). Conversely, the decline observed from early fall to late winter was likely related to weight loss (Beukema and De Bruin 1977; Beukema et al. 2014) and natural mortality, including predation (Baird and Ulanowicz 1989). Indeed, the three study sites are nurseries for juvenile fish (Dauvin 1998; Amara et al. 2001), which may apply strong predation pressure on macroinvertebrates during summer (Virnstein 1977; Pihl 1985).

The analyses carried out at the population level shed light on the differences in seasonal pattern observed at the community level among the three sites. For instance, the lower amplitude at RM was related to the absence of a seasonal pattern in biomass of the five dominant species (Table 2). Regarding timing, differences among the communities can be explained at least partly by their taxonomic compositions. The earlier peak of biomass observed at GV is directly related to seasonal variations in the polychaete *Lanice conchilega*, whose biomass

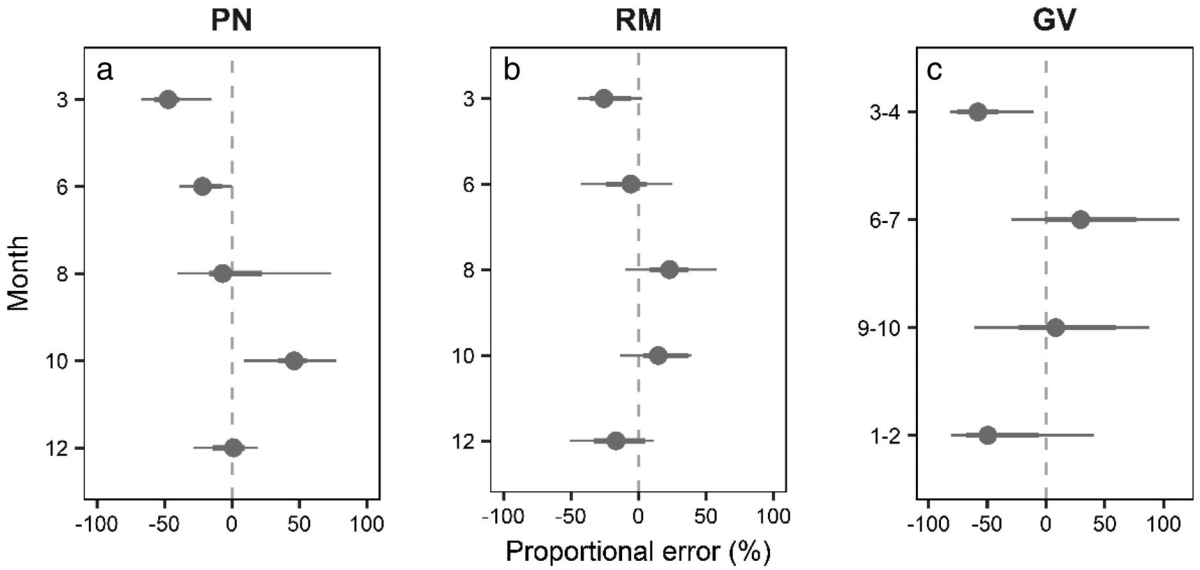


Fig. 4. Proportional error (PE) of production estimates based on data from a single sampling event, according to the month of sampling at PN (**a**), RM (**b**), and GV (**c**). Dots represent median values of PE, used here as a measure of bias. Thick lines represent 25% and 75% quantiles of inter-annual variability in PE, while thin lines represent 10% and 90% quantiles. At GV, sampling months varied slightly among years and were thus grouped by 2-month periods to estimate the bias. PE estimates from January/February sampling at GV were plotted at the bottom of the plot to facilitate comparison with the PE estimates from December sampling at PN and RM.

peaked in early summer (Fig. 3f). Excluding this species from the community model confirmed its importance as a driver of the seasonal pattern: peak biomass was thus delayed and fit better to the pattern of the other two sites (Supporting Information Fig. S4). This study also stressed the ephemeral nature of *Lanice conchilega* (Zühlke 2001; Callaway et al. 2010). Its population dynamics at GV are characterized by low biomass throughout the year except in early summer during recruitment, which produces extremely high biomass (Fig. 3). Previous studies showed that *Lanice conchilega* can modify the structure and inter-annual dynamics of benthic communities (Dauvin 2000; Callaway 2006; De Smet et al. 2015). Here, we showed that it can also affect the seasonal pattern of the entire community in both amplitude and timing. This ephemeral nature also illustrated why seasonal variations in the GV community appeared less consistent than those in the other two communities (Fig. 2). Indeed, each major peak biomass observed in the GV time series (in 2000, 2001, 2003, 2007, and 2015) followed a massive recruitment of one or more species with a bentho-pelagic life cycle, including *Lanice conchilega*, *Abra alba*, and *Lagis koreni*. Local climatic and hydrodynamic conditions have been suggested to induce such variations in the recruitment success of these species (Dewarumez et al. 1993; Fromentin and Ibanez 1994; Ghertsos et al. 2000). The exact causes of the steep decline in biomass following massive recruitment events remain unknown, but it is likely related to density-dependent processes (Frid et al. 1996; Philippart et al. 2003; Henderson et al. 2006). The biomass variations observed at GV may have been magnified by less regular sampling than at the other two sites.

The significant seasonal variations observed at the community level suggest that at least a few dominant species show a consistent seasonal pattern, even though the pattern may differ among species or may not be significant for all of them. This assumption was confirmed by the analysis at the population level, with 60% of the populations analyzed exhibiting a significant seasonal pattern (Table 2, Supporting Information Fig. S5). Although the pattern was relatively consistent among species, it differed in timing and even more in amplitude. These differences may be related to different life history strategies, but why some species exhibited a significant seasonal pattern at one site but not another remains unknown. Differences in seasonality among taxonomic groups or trophic guilds may exist, but they were not revealed in our study.

In this study, we focused on seasonal variations in macrobenthic invertebrates in temperate coastal soft-bottom ecosystems. It is worth noting that the seasonal pattern in macroinvertebrates may change with physical or geographical variables such as substratum type, depth, and latitude. For instance, the taxonomic composition of soft-bottom communities differs greatly from that of hard-bottom communities (Asmus 1987; Wong et al. 2011), which can be dominated by a single species (e.g., oyster reef, mussel bed). Since our results revealed that seasonality in biomass differs among species, the corresponding seasonal pattern in a hard bottom may differ significantly at the community level from those quantified in this study. Similarly, seasonal variations in abiotic factors (e.g., temperature and nutrient inputs) are dampened in deep offshore areas (Hessler and Sanders 1967), suggesting that the seasonal pattern may be weaker in such ecosystems. Conversely, comparing our estimates

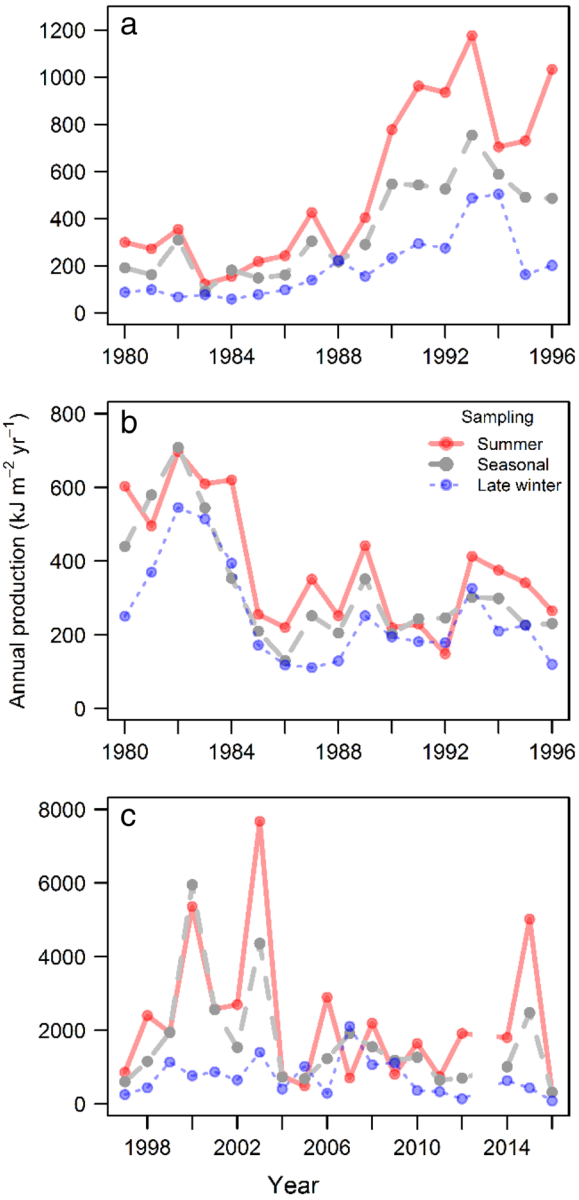


Fig. 5. Temporal trend in annual benthic production estimates at PN (**a**), RM (**b**), and GV (**c**), according to sampling period and frequency. Annual production (*P*) estimates were based on summer biomass (single annual sampling, solid red line), mean annual biomass (seasonal sampling, dashed gray line), or late winter biomass (single annual sampling, dotted blue line). Graphs present *P* estimates based on summer data collected when the biomass was at its annual maximum, which differed among sites (PN: late summer, RM: mid-summer, GV: early summer). Annual minimum biomass was always recorded in March at all sites (late winter). No sampling was performed in winter 2013 at GV. Note the different scale on the *y*-axis among sites.

of seasonal amplitude in biomass to estimates from the literature suggests no difference between intertidal (Beukema 1974; Zwarts and Wanink 1993) and subtidal areas (Baird and Ulanowicz 1989; present study), but more research is needed to confirm this observation. Finally, environmental seasonality (e.g., solar irradiance and vertical mixing) changes with latitude, being generally stronger at high latitudes and weaker at low latitudes (Walther et al. 2002; Field et al. 2007). This results in different seasonal patterns in primary production among ocean regions (Boyce et al. 2010) and likely affects seasonality in macrobenthic biomass and secondary production. In polar regions, seasonality of benthic organisms has received little attention due to sampling challenges during winter (ice cover). Consequently, macrobenthic annual biomass and production estimates in (sub)-polar ecosystems were based on spring or summer sampling in most studies (e.g., Kędra et al. 2013; Fuhrmann et al. 2015), although evidence for a strong seasonal pattern in macrobenthic community biomass was recently found in an Arctic fjord (Pawłowska et al. 2011).

Bias and accuracy of production estimates

Although previous studies suggested that calculating secondary production from empirical models using data collected during a single period of the year may lead to inaccurate estimates of annual production (Beukema and Dekker 2013; Bolam and Eggleton 2014), this hypothesis had never been tested at the community level, and the bias potentially induced by seasonal variations never quantified. This is likely due to the scarcity of time series of macrobenthic biomass collected on a seasonal basis, particularly at the community level, since macrobenthic survey and laboratory analyses are time consuming. The three long-term data sets analyzed in this study offered a unique opportunity to explore seasonal variations in biomass of macrobenthic invertebrates and to assess how these variations affect estimates of secondary production.

Our findings for macrobenthic communities emphasized what was previously found for a single bivalve population (Beukema and Dekker 2013): (1) secondary production estimates derived from empirical models (e.g., Brey model) change significantly according to the season of data collection and (2) these production estimates are inaccurate and clearly biased if biomass is sampled at its annual minimum (late winter) or annual maximum (early summer/early fall) in temperate coastal ecosystems. Given the significant seasonal patterns in biomass, we expected to find inaccurate and biased estimates of secondary production, since biomass and secondary production are correlated (Plante and Downing 1989). Indeed, although *P*:*B* estimates may exhibit seasonal variations opposite to those in biomass from spring to late-summer (Beukema and Dekker 2013), the amplitude of seasonal variations in *P*:*B* was in average eight times lower than the amplitude of seasonal variations in biomass (Supporting Information Fig. S8). Thus, the variations in annual *P* estimates with the period of sampling were almost entirely driven by seasonal variations in biomass. Similarly, the lower bias at RM came as no surprise, since bias in production is proportional to the amplitude of the seasonal pattern, which was lower at RM (Fig. 2). More interestingly, we provided estimates of the bias and inaccuracy induced by the seasonality, and we suggest that their orders of magnitude (bias up to ~ 50%) be kept in mind when

comparing production estimates from different studies and/or study sites, especially if sampling did not occur during the same period of the year. It is worth noting that production estimates are also sensitive to temperature data used as input (Brey 2012). Consequently, the bias and the inaccuracy of production estimates would be even higher if one uses sea bottom temperature recorded during the survey instead of mean annual temperature as it is required, particularly during winter and summer. For instance, using monthly sea temperature in late-winter (March) instead of mean annual sea temperature would increase the bias by 8% on average in the present study. When sampling occurs only once but always at the same period in studies focusing on temporal or spatial variation in annual macrobenthic production (Bolam et al. 2010), or along a gradient of anthropogenic pressure (Reiss et al. 2009), we can expect that the bias is approximately the same among years or sites and that relative estimates of *P* are sufficient to detect such variations. Precaution is needed, however, since we showed that bias in *P* estimates differed between two close sites (< 5 km between PN and RM) sampled during exactly the same month. Our results also highlighted that temporal variations in annual production may be underestimated if *P* estimates are based on late-winter data. In addition, the uncertainty in annual production estimates due to seasonality has to be accounted for in studies comparing production of macrobenthic prey to energy requirements of their predators (juvenile fish, crustaceans; Tableau et al. 2015; Jung et al. 2017), and more generally, in studies focusing on energy flows between macrobenthic fauna and upper trophic levels (Kuipers et al. 1981). Indeed, absolute estimates of *P* are required in such studies, and the conclusions (e.g., whether prey availability limits production of their predators) may change with the period of sampling.

For a bivalve population of the Dutch Wadden Sea, Beukema and Dekker (2013) recommended using late-winter rather than late-summer data to calculate annual production estimates using the Brey model if no more than one annual sample could be taken. Our results from three subtidal macrobenthic communities in the southern North Sea and western English Channel (France) do not support this recommendation at the community level, since the bias in *P* estimates based on late-winter data (March) was as high or even higher than that estimated for the other sampling seasons (Fig. 4, Supporting Information Table S4). Indeed, no single sampling period could be identified as the "best" one for calculating *P* estimates using Brey's empirical model: the "fine-scale" seasonal variation of the bias was site-specific (e.g., *P* estimates from December data were biased at RM but unbiased at PN). Nevertheless, the general pattern was consistent among the three study sites. Consequently, we recommend that sampling twice per year—in late winter and late summer—would likely improve *P* estimates of temperate coastal macrobenthic communities. We tested this hypothesis, and found that *P* estimates averaged for late winter (March) and late summer (September–October) were more accurate at all sites, and unbiased at two of the three sites (Supporting Information Fig. S9). Quantifying the uncertainty in *P* estimates from empirical methods is challenging. Generally, *P* estimates from a cohort-based method are used as the "reference" and compared to *P* estimates from empirical models (e.g., Dolbeth et al. 2005). Here, we deemed this approach inappropriate for the question we addressed. Time series of seasonal biomass data for multiple species associated with corresponding *P* estimates using a cohort-based method are lacking. Instead, *P* estimates of the Brey (2012) model calculated from the mean annual biomass of each species were used as a reference and thus assumed to be known without error. Obviously, this assumption is false, and our reference estimates are not as accurate as assumed here. However, as mentioned, empirical models have high prediction error for a single species, but one that decreases greatly when estimates of several populations are pooled (Brey 2001, 2012). In addition, even *P* estimates from cohort-based methods may be inaccurate, for instance due to sampling error, which is commonly high in macrobenthic studies (Morin et al. 1987; Schlacher and Wooldridge 1996; Schoeman et al. 2003). Hence, the "true" value of *P* remains unknown, and the "reference" value, which generally depends on the purpose of the study, remains the choice of the modeler. Finally, it remains useful to know, for a given empirical method, the range of uncertainty related to the period of data collection. Here, we provided an estimate of the uncertainty for the Brey model, one of the most frequently used methods to estimate secondary production of a community of species (Beukema and Dekker 2013).

Although we limited analysis to the Brey (2012) model, we consider our findings robust and easily generalizable to most empirical methods for estimating secondary production. Indeed, empirical models either require mean annual biomass as input and predict *P* directly (Brey 1990; Morin and Bourassa 1992; Tumbiolo and Downing 1994) or predict *P*:*B*, which needs to be multiplied by mean annual biomass to calculate *P* (Robertson 1979; Cusson and Bourget 2005; Brey 2012). Using *P*:*B* ratios from the literature to estimate secondary production (e.g., Wong et al. 2011) is subject to the same constraints. Therefore, all empirical methods are affected by seasonal variations in biomass of macrobenthic invertebrates, and the uncertainty due to seasonality must be accounted for in studies based on a single sampling event, regardless of the method used. However, the order of magnitude of the bias and the inaccuracy of production estimates calculated in the present study hold true for temperate coastal soft-bottom ecosystems, but may vary greatly by substratum type (e.g., hard bottom, seagrass meadow), depth, and latitude. This is particularly true for polar and equatorial ecosystems, which display different environmental seasonality.

References

Amara, R., P. Laffargue, J. M. Dewarumez, C. Maryniak, F. Lagardère, and C. Luzac. 2001. Feeding ecology and growth

of O-group flatfish (sole, dab and plaice) on a nursery ground (Southern Bight of the North Sea). J. Fish Biol. **58**: 788–803. doi:10.1111/j.1095-8649.2001.tb00531.x

Anderson, S. C., and others. 2017. Improving estimates of population status and trend with superensemble models. Fish Fish. **18**: 732–741. doi:10.1111/faf.12200

Asmus, H. 1987. Secondary production of an intertidal mussel bed community related to its storage and turnover compartments. Mar. Ecol. Prog. Ser. **39**: 251–266. doi:10.3354/meps039251

Baird, D., and R. E. Ulanowicz. 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. Ecol. Monogr. **59**: 329–364. doi:10.2307/1943071

Benke, A. C., and A. D. Huryn. 2010. Benthic invertebrate production—facilitating answers to ecological riddles in freshwater ecosystems. J. North Am. Benthol. Soc. **29**: 264–285. doi:10.1899/08-075.1

Beukema, J. J. 1974. Seasonal changes in the biomass of the macro-benthos of a tidal flat area in the Dutch Wadden Sea. Neth. J. Sea Res. **8**: 94–107. doi:10.1016/0077-7579(74)90028-3

Beukema, J. J., and W. De Bruin. 1977. Seasonal changes in dry weight and chemical composition of the soft parts of the tellinid bivalve *Macoma balthica* in the Dutch Wadden Sea. Neth. J. Sea Res. **11**: 42–55. doi:10.1016/0077-7579(77)90020-5

Beukema, J. J., and R. Dekker. 2013. Evaluation of Brey's production/biomass model on the basis of a long-term data set on a clam population. Mar. Ecol. Prog. Ser. **489**: 163–175. doi:10.3354/meps10409

Beukema, J. J., G. C. Cadée, R. Dekker, and C. J. M. Philippart. 2014. Annual and spatial variability in gains of body weight in *Macoma balthica* (L.): Relationships with food supply and water temperature. J. Exp. Mar. Biol. Ecol. **457**: 105–112. doi:10.1016/j.jembe.2014.04.003

Bolam, S. G., C. R. S. Barrio-Frojan, and J. D. Eggleton. 2010. Macrofaunal production along the UK continental shelf. J. Sea Res. **64**: 166–179. doi:10.1016/j.seares.2010.02.003

Bolam, S. G., and J. D. Eggleton. 2014. Macrofaunal production and biological traits: Spatial relationships along the UK continental shelf. J. Sea Res. **88**: 47–58. doi:10.1016/j.seares.2014.01.001

Boyce, D. G., M. R. Lewis, and B. Worm. 2010. Global phytoplankton decline over the past century. Nature **466**: 591–596. doi:10.1038/nature09268

Brey, T. 1990. Estimating productivity of macrobenthic invertebrates from biomass and mean individual weight. Meeresforsch **32**: 329–343.

Brey, T. 2001. Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2. [accessed 2018 May 4]. Available from http://www.thomas-brey.de/science/virtualhandbook/

Brey, T. 2012. A multi-parameter artificial neural network model to estimate macrobenthic invertebrate productivity and production: Macrobenthic production model. Limnol. Oceanogr.: Methods **10**: 581–589. doi:10.4319/lom.2012.10.581

Brey, T., A. Jarre-Teichmann, and O. Borlich. 1996. Artificial neural network versus multiple linear regression: Predicting P/B ratios from empirical data. Mar. Ecol. Prog. Ser. **140**: 251–256. doi:10.3354/meps140251

Brey, T., C. Müller-Wiegmann, Z. M. C. Zittier, and W. Hagen. 2010. Body composition in aquatic organisms — a global data bank of relationships between mass, elemental composition and energy content. J. Sea Res. **64**: 334–340. doi:10.1016/j.seares.2010.05.002

Bunting, L., P. R. Leavitt, G. L. Simpson, B. Wissel, K. R. Laird, B. F. Cumming, A. St. Amand, and D. R. Engstrom. 2016. Increased variability and sudden ecosystem state change in Lake Winnipeg, Canada, caused by 20th century agriculture. Limnol. Oceanogr. **61**: 2090–2107. doi:10.1002/lno.10355

Burd, B. J., T. A. Macdonald, and A. van Roodselaar. 2012. Towards predicting basin-wide invertebrate organic biomass and production in marine sediments from a coastal sea. PLoS One **7**: e40295. doi:10.1371/journal.pone.0040295

Callaway, R. 2006. Tube worms promote community change. Mar. Ecol. Prog. Ser. **308**: 49–60. doi:10.3354/meps308049

Callaway, R., N. Desroy, S. F. Dubois, J. Fournier, M. Frost, L. Godet, V. J. Hendrick, and M. Rabaut. 2010. Ephemeral bioengineers or reef-building polychaetes: How stable are aggregations of the tube worm *Lanice conchilega* (Pallas, 1766)? Integr. Comp. Biol. **50**: 237–250. doi:10.1093/icb/icq060

Cartes, J. E., T. Brey, J. C. Sorbe, and F. Maynou. 2002. Comparing production biomass ratios of benthos and suprabenthos in macrofaunal marine crustaceans. Can. J. Fish. Aquat. Sci. **59**: 1616–1625. doi:10.1139/f02-130

Coma, R., M. Ribes, J.-M. Gili, and M. Zabala. 2000. Seasonality in coastal benthic ecosystems. Trends Ecol. Evol. **15**: 448–453. doi:10.1016/S0169-5347(00)01970-4

Conq, C., J.-C. Dauvin, and J.-C. Lorgeré. 1998. Température et salinité de l'eau de mer au large de Roscoff de 1991 à 1997. Cah. Biol. Mar. **39**: 207–212.

Curtis, C. J., and G. L. Simpson. 2014. Trends in bulk deposition of acidity in the UK, 1988–2007, assessed using additive models. Ecol. Indic. **37**: 274–286. doi:10.1016/j.ecolind.2012.10.023

Cushman, R. M., H. H. Shugart, S. G. Hildebrand, and J. W. Elwood. 1978. The effect of growth curve and sampling regime on instantaneous-growth, removal-summation, and Hynes/Hamilton estimates of aquatic insect production: A computer simulation. Limnol. Oceanogr. **23**: 184–189. doi:10.4319/lo.1978.23.1.0184

Cusson, M., and E. Bourget. 2005. Global patterns of macroinvertebrate production in marine benthic habitats. Mar. Ecol. Prog. Ser. **297**: 1–14. doi:10.3354/meps297001

Cusson, M., J.-F. Plante, and C. Genest. 2006. Effect of different sampling designs and methods on the estimation of secondary production: A simulation. Limnol. Oceanogr.: Methods **4**: 38–48. doi:10.4319/lom.2006.4.38

Dauvin, J.-C. 1998. The fine sand *Abra alba* community of the Bay of Morlaix twenty years after the Amoco Cadiz oil spill. Mar. Pollut. Bull. **36**: 669–676. doi:10.1016/S0025-326X(98)00058-7

Dauvin, J.-C. 2000. The muddy fine sand *Abra alba–Melinna palmata* community of the Bay of Morlaix twenty years after the Amoco Cadiz oil spill. Mar. Pollut. Bull. **40**: 528–536. doi:10.1016/S0025-326X(99)00242-8

Dauvin, J.-C., M. Joncourt, D. Latrouite, and G. Raguénès. 1989. Température et salinité de l'eau de mer au large de Roscoff de 1983 à 1987. Cah. Biol. Mar. **30**: 5–10.

De Smet, B., and others. 2015. Biogenic reefs affect multiple components of intertidal soft-bottom benthic assemblages: The *Lanice conchilega* case study. Estuar. Coast. Shelf Sci. **152**: 44–55. doi:10.1016/j.ecss.2014.11.002

Degen, R., L. L. Jørgensen, P. Ljubin, I. H. Ellingsen, H. Pehlke, and T. Brey. 2016. Patterns and drivers of megabenthic secondary production on the Barents Sea shelf. Mar. Ecol. Prog. Ser. **546**: 1–16. doi:10.3354/meps11662

Desroy, N., and C. Retière. 2001. Long-term changes in muddy fine sand community of the Rance Basin: Role of recruitment. J. Mar. Biol. Assoc. U.K. **81**: 553–564. doi:10.1017/S0025315401004234

Dewarumez, J. M., A. Belgrano, J. Craeymeersch, S. Duquesne, C. Heip, D. Hilde, and M. Vincx. 1993. Influence de la circulation des masses d'eaux dans la dynamique du peuplement *Abra alba* de la Baie sud de la Mer du Nord. J. Rech. Oceanogr. **18**: 1–4.

Dolbeth, M., A. I. Lillebø, P. G. Cardoso, S. M. Ferreira, and M. A. Pardal. 2005. Annual production of estuarine fauna in different environmental conditions: An evaluation of the estimation methods. J. Exp. Mar. Biol. Ecol. **326**: 115–127. doi:10.1016/j.jembe.2005.05.010

Dolbeth, M., M. Cusson, R. Sousa, M. A. Pardal, and Y. T. Prairie. 2012. Secondary production as a tool for better understanding of aquatic ecosystems. Can. J. Fish. Aquat. Sci. **69**: 1230–1253. doi:10.1139/f2012-050

Field, I. C., C. J. Bradshaw, H. R. Burton, and M. A. Hindell. 2007. Differential resource allocation strategies in juvenile elephant seals in the highly seasonal Southern Ocean. Mar. Ecol. Prog. Ser. **331**: 281–290. doi:10.3354/meps331281

Frid, C. L. J., J. B. Buchanan, and P. R. Garwood. 1996. Variability and stability in benthos: Twenty-two years of monitoring off Northumberland. ICES J. Mar. Sci. **53**: 978–980. doi:10.1006/jmsc.1996.0121

Fromentin, J. M., and F. Ibanez. 1994. Year-to-year changes in meteorological features of the French coast area during the last half-century-examples of 2 biological responses. Oceanol. Acta **17**: 285–296.

Fromentin, J. M., F. Ibanez, J.-C. Dauvin, J. M. Dewarumez, and B. Elkaim. 1997. Long-term changes of four macrobenthic assemblages from 1978 to 1992. J. Mar. Biol. Assoc. U. K. **77**: 287–310. doi:10.1017/S002531540007168X

Fuhrmann, M. M., T. Pedersen, V. Ramasco, and E. M. Nilssen. 2015. Macrobenthic biomass and production in a heterogenic subarctic fjord after invasion by the red king crab. J. Sea Res. **106**: 1–13. doi:10.1016/j.seares.2015.09.003

Ghertsos, K., C. Luczak, J.-M. Dewarumez, and J.-C. Dauvin. 2000. Influence of spatial scales of observation on temporal change in diversity and trophic structure of fine-sand communities from the English Channel and the southern North Sea. ICES J. Mar. Sci. **57**: 1481–1487. doi:10.1006/jmsc.2000.0916

Henderson, P. A., R. M. Seaby, and J. R. Somes. 2006. A 25-year study of climatic and density-dependent population regulation of common shrimp *Crangon crangon* (Crustacea: Caridea) in the Bristol Channel. J. Mar. Biol. Assoc. U. K. **86**: 287–298. doi:10.1017/S0025315406013142

Hessler, R. R., and H. L. Sanders. 1967. Faunal diversity in the deep-sea. Deep-Sea Res. Oceanogr. Abstr. **14**: 65–78. doi:10.1016/0011-7471(67)90029-0

Jung, A. S., R. Dekker, M. Germain, C. J. Philippart, J. I. Witte, and H. W. van der Veer. 2017. Long-term shifts in intertidal predator and prey communities in the Wadden Sea and consequences for food requirements and supply. Mar. Ecol. Prog. Ser. **579**: 37–53. doi:10.3354/meps12263

Kędra, M., P. E. Renaud, H. Andrade, I. Goszczko, and W. G. Ambrose. 2013. Benthic community structure, diversity, and productivity in the shallow Barents Sea bank (Svalbard Bank). Mar. Biol. **160**: 805–819. doi:10.1007/s00227-012-2135-y

Kuipers, B. R., P. De Wilde, and F. Creutzberg. 1981. Energy flow in a tidal flat ecosystem. Mar. Ecol. Prog. Ser. **5**: 215–221. doi:10.3354/meps005215

Luczak, C. 1996. Dynamique du recrutement au sein du peuplement à *Abra alba* dans la baie sud de la Mer du Nord: Approche systémique. Ph.D. thesis. Univ. Lille I.

Luczak, C., J.-M. Dewarumez, and K. Essink. 1993. First record of the American jack knife clam *Ensis directus* on the French coast of the North Sea. J. Mar. Biol. Assoc. U. K. **73**: 233–235. doi:10.1017/S0025315400032768

Morin, A., T. A. Mousseau, and D. A. Roff. 1987. Accuracy and precision of secondary production estimates. Limnol. Oceanogr. **32**: 1342–1352. doi:10.4319/lo.1987.32.6.1342

Morin, A., and N. Bourassa. 1992. Modèles empiriques de la production annuelle et du rapport P/B d'invertébrés benthiques d'eau courante. Can. J. Fish. Aquat. Sci. **49**: 532–539. doi:10.1139/f92-063

Mucha, A. P., M. T. S. Vasconcelos, and A. A. Bordalo. 2005. Spatial and seasonal variations of the macrobenthic community and metal contamination in the Douro estuary (Portugal). Mar. Environ. Res. **60**: 531–550. doi:10.1016/j.marenvres.2004.12.004

Ono, K., and others. 2015. The importance of length and age composition data in statistical age-structured models for marine species. ICES J. Mar. Sci. **72**: 31–43. doi:10.1093/icesjms/fsu007

Passuni, G., and others. 2016. Seasonality in marine ecosystems: Peruvian seabirds, anchovy, and oceanographic conditions. Ecology **97**: 182–193. doi:10.1890/14-1134.1

Pawłowska, J., M. Włodarska-Kowalczuk, M. Zajączkowski, H. Nygard, and J. Berge. 2011. Seasonal variability of meio-and macrobenthic standing stocks and diversity in an Arctic fjord (Adventfjorden, Spitsbergen). Polar Biol. **34**: 833–845. doi:10.1007/s00300-010-0940-7

Petracco, M., R. S. Cardoso, T. N. Corbisier, and A. Turra. 2012. Secondary production of sandy beach macrofauna: An evaluation of predictive models. Estuar. Coast. Shelf Sci. **115**: 359–365. doi:10.1016/j.ecss.2012.10.002

Philippart, C. J., H. M. van Aken, J. J. Beukema, O. G. Bos, G. C. Cadée, and R. Dekker. 2003. Climate-related changes in recruitment of the bivalve *Macoma balthica*. Limnol. Oceanogr. **48**: 2171–2185. doi:10.4319/lo.2003.48.6.2171

Pihl, L. 1985. Food selection and consumption of mobile epibenthic fauna in shallow marine areas. Mar. Ecol. Prog. Ser. **22**: 169–179. doi:10.3354/meps022169

Plante, C., and J. A. Downing. 1989. Production of freshwater invertebrate populations in lakes. Can. J. Fish. Aquat. Sci. **46**: 1489–1498. doi:10.1139/f89-191

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Available from https://www.R-project.org/

Reiss, H., and I. Kröncke. 2005. Seasonal variability of infaunal community structures in three areas of the North Sea under different environmental conditions. Estuar. Coast. Shelf Sci. **65**: 253–274. doi:10.1016/j.ecss.2005.06.008

Reiss, H., and others. 2009. Effects of fishing disturbance on benthic communities and secondary production within an intensively fished area. Mar. Ecol. Prog. Ser. **394**: 201–213. doi:10.3354/meps08243

Robertson, A. I. 1979. The relationship between annual production: Biomass ratios and lifespans for marine macrobenthos. Oecologia **38**: 193–202. doi:10.1007/BF00346563

Schlacher, T. A., and T. H. Wooldridge. 1996. How sieve mesh size affects sample estimates of estuarine benthic macrofauna. J. Exp. Mar. Biol. Ecol. **201**: 159–171. doi:10.1016/0022-0981(95)00198-0

Schoeman, D. S., M. Wheeler, and M. Wait. 2003. The relative accuracy of standard estimators for macrofaunal abundance and species richness derived from selected intertidal transect designs used to sample exposed sandy beaches. Estuar. Coast. Shelf Sci. **58**: 5–16. doi:10.1016/S0272-7714(03)00038-6

Schwinghamer, P., B. Hargrave, D. Peer, and C. M. Hawkins. 1986. Partitioning of production and respiration among size groups of organisms in an intertidal benthic community. Mar. Ecol. Prog. Ser. **31**: 131–142. doi:10.3354/meps031131

Sprung, M. 1993. Estimating macrobenthic secondary production from body weight and biomass: A field test in a non-boreal intertidal habitat. Mar. Ecol. Prog. Ser. **100**: 103–109. doi:10.3354/meps100103

Tableau, A., H. Le Bris, and A. Brind'Amour. 2015. Available benthic energy coefficient (ABEC): A generic tool to estimate the food profitability in coastal fish nurseries. Mar. Ecol. Prog. Ser. **522**: 203–218. doi:10.3354/meps11121

Townsend, D. W., M. D. Keller, M. E. Sieracki, and S. G. Ackleson. 1992. Spring phytoplankton blooms in the absence of vertical water column stratification. Nature **360**: 59–62. doi:10.1038/360059a0

Tumbiolo, M. L., and J. A. Downing. 1994. An empirical model for the prediction of secondary production in marine benthic invertebrate populations. Mar. Ecol. Prog. Ser. **114**: 165–174. doi:10.3354/meps114165

Virnstein, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. Ecology **58**: 1199–1217. doi:10.2307/1935076

Walther, B. A., and J. L. Moore. 2005. The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. Ecography **28**: 815–829. doi:10.1111/j.2005.0906-7590.04112.x

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature **416**: 389–395. doi:10.1038/416389a

Wiltshire, K. H., A. M. Malzahn, K. Wirtz, W. Greve, S. Janisch, P. Mangelsdorf, B. F. Manly, and M. Boersma. 2008. Resilience of North Sea phytoplankton spring bloom dynamics: An analysis of long-term data at Helgoland Roads. Limnol. Oceanogr. **53**: 1294–1302. doi:10.4319/lo.2008.53.4.1294

Woehrling, D., A. Lefebvre, G. Le Fèvre-Lehoërff, and R. Delesmont. 2005. Seasonal and longer term trends in sea temperature along the French North Sea coast, 1975 to 2002. J. Mar. Biol. Assoc. U. K. **85**: 39–48. doi:10.1017/S0025315405010805h

Wong, M. C., C. H. Peterson, and M. F. Piehler. 2011. Evaluating estuarine habitats using secondary production as a proxy for food web support. Mar. Ecol. Prog. Ser. **440**: 11–25. doi:10.3354/meps09323

Wood, S. N. 2006. Generalized additive models: An introduction with R. Chapman and Hall/CRC.

Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J. R. Stat. Soc. Ser. B Stat. Methodol. **73**: 3–36. doi:10.1111/j.1467-9868.2010.00749.x

Zühlke, R. 2001. Polychaete tubes create ephemeral community patterns: *Lanice conchilega* (Pallas, 1766) associations studied over six years. J. Sea Res. **46**: 261–272. doi:10.1016/S1385-1101(01)00091-0

Zwarts, L., and J. H. Wanink. 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. Neth. J. Sea Res. **31**: 441–476. doi:10.1016/0077-7579(93)90059-2

Acknowledgments

We acknowledge Electricité de France (EDF) and Elvire Antajan (IFREMER) for providing the data from Gravelines, which were collected in the framework of the research program IGA (Impact des Grands Aménagements) conducted by IFREMER with financial support from EDF. Data from the Bay of Morlaix were collected in the framework of the Programme GDR Manche of the CNRS, supported by IFREMER (Réseau National d'Observation) contracts. We thank the captain and crew of the ship "NO Mysis," the staff of the Marine Biological Station of Roscoff for the field work, and many students for their technical help. We greatly thank Thomas Brey for precious advice on the use of his empirical model, and Verena Trenkel and Etienne Rivot for fruitful discussions on statistical analyses and theoretical considerations. We thank two anonymous reviewers for their helpful comments on an earlier version of the manuscript. A Ph.D. grant from the French Ministry of Higher Education, Research and Innovation to E. Saulnier helped to fund this study. We also thank the French Ministry for the Ecological and Inclusive Transition through the Marine Strategy Framework Directive Agreement and the French Biodiversity Agency (Agence française pour la biodiversité) for financial support of this study as part of the CAPANOUR project.

Conflict of Interest

None declared.

Submitted 23 July 2018
Revised 17 October 2018
Accepted 31 October 2018

Associate editor: Ronnie Glud