Secondary production as a tool for better understanding of aquatic ecosystems

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Abstract: A major challenge for ecologists is understanding ecosystem dynamics and function under environmental and anthropogenic stresses. An approach for addressing this challenge is the analysis of the different components contributing to secondary production, i.e. consumer incorporation of organic matter or energy per time unit, and how this production is influenced by external factors. Production studies have been recognized as a powerful tool in aquatic ecology, with applications in energy/biomass flow studies, trophic ecology, management of biological resources, as well as assessment of environmental stress. In this paper, we summarise ideas and techniques related to the estimation of secondary production and discuss how this approach may be used to evaluate ecological change in aquatic ecosystems. We include a critical review of classical methods and empirical models to estimate secondary production and provide several applications of production studies to current stresses affecting aquatic ecosystems, such as climate change, pollution and the introduction of non-indigenous invasive species. Our goal is to illustrate the advantages of using secondary production as a more integrative tool for the assessment of the ecosystem function, in particular when subjected to strong anthropogenic and climatic stress.

Keywords: secondary production, benthic invertebrates, aquatic ecosystems, functional ecology, global changes**.**

Introduction

Among major present-day concerns for ecologists and policymakers is the assessment of the status and integrity of ecosystems subject to environmental and anthropogenic stressors. Biodiversity, natural productivity and stability are considered as three critical aspects of ecosystems (Worm and Duffy 2003) and, as such, they have been the focus of several studies attempting to evaluate their ecological integrity (Naeem et al. 2009). Approaches combining structure and function have been highly recommended as a mean for assessing ecosystems (following biodiversity-ecosystem functioning debate, Naeem et al. 2009) and one possible approach is through analysis of secondary production that implies measures of structure and functioning. Secondary production represents a measure of population fitness as it integrates both individual growth and population mortality (Rigler and Downing 1984, see a glossary of production related terms in Table 1) and therefore reflects other population properties or processes (e.g. body mass, reproduction, recruitment, growth rate, survivorship rate, development time, life span, trophic status), biotic interactions (e.g. predation, competition, facilitation) as well as the environmental conditions in which populations evolve. Therefore, secondary production estimates may represent an interesting proxy with regard to the functional responses of populations or communities subjected to various environmental stressors.

There has been a long-term interest in evaluating secondary production in aquatic systems, initially driven by the need to determine their carrying capacity for commercial fish and shellfish (Waters and Crawford 1973), as well as a basic component of energy flow and budget studies (Crisp 1984; Benke 2010). Methods for estimating secondary production in aquatic systems evolved (e.g. Winberg 1971; Benke 1984; see complete list of classical methods in Cusson 2004) as evolved the use of production studies, beyond those used for estimating fishery yields and energy flow (Downing 1984; Benke 1993). General reviews on secondary production in aquatic ecosystems may be found in Winberg (1971), Crisp (1984), Downing (1984), Benke (1993), Huryn and Wallace (2000), Cusson and Bourget (2005a) and Benke (2010). Currently, most studies with secondary production of aquatic ecosystems are done with benthic invertebrates, and some with meiofauna, zooplankton and vertebrates (Benke 2010).

The rationale for using secondary production depends on the purpose of the study and resources available, which may influence the selection of the method. The secondary production expresses the quantity of the population/community success through time and it is directly related to the ecosystem functioning. Several ecological questions can be unravelled with production assessment, such as energy flow and contaminant burden. Moreover, many other studies would get greater insight when supported by production analysis (see examples of the applicability and advantages of production studies in Table 2, and also Benke and Hyrun 2010). In this review, we illustrate how secondary production can be a powerful tool for evaluating ecosystem state and assessing impacts from environmental change or human activities (e.g. eutrophication, pollution, climate change, introduction of invasive species) with examples from benthic invertebrate production taken from recent studies on aquatic ecosystems.

The choice of a method affects the accuracy and precision of production estimates, but also the time/cost for the production evaluation. For this reason, we divide our review into two major sections: 1) estimation of secondary production, including methods for estimating actual and potential production of aquatic invertebrates and common estimation errors; 2) use of secondary production for understanding aquatic ecosystem dynamics, with an emphasis on examples from estuarine and marine systems.

Secondary production estimates

Accurate estimates of secondary production require knowledge related to population growth and mortality, necessitating a frequent and intense sampling design to properly assess growth and mortality events for each population (Morin et al. 1987; Cusson et al. 2006). A low sampling effort may still, however, provide relevant information and insight on the functional importance of a species in the ecosystem. In addition, empirical models for evaluating potential production (Table 1, discussed below) have been and continue to be developed (e.g. Brey 2001; Cusson and Bourget 2005a) that, under certain circumstances, provide relatively accurate estimates without an intensive sampling scheme.

Although secondary production cannot be used to directly evaluate the environmental quality of a system, it does provide more information than that derived from other static measures such as density or biomass presented alone. Density and/or biomass estimates of a species or community, which are common in monitoring studies, may differ markedly from production that combines a number of parameters of ecological performance of species into a single estimate. Using estimates from a 10-year period marked by several disturbance events (measured biomass and production from Dolbeth et al. 2007 and density data from Dolbeth et al. 2003 and M. Dolbeth unpublished data), the variation trend of density had the highest differences, followed by biomass and production (Fig. 1a-j). Differences in trends were species-dependent and related to life-history characteristics: e.g. differences were higher for *Scrobcularia plana*, a bivalve with higher body mass (Fig. 1a,f) and for *Cyathura carinata*, an univoltine isopod (Fig. 1h). Differences were also specific in response to environmental changes occurring at each site and in each year: e.g. lower differences for the opportunist gastropod *Hydrobia ulvae* in a sandflat, subsidised by additional resources from macroalgae bloom (Fig. 1g). And finally, differences were also related to estimating production method: lower differences for production estimated with an empirical model (Fig. 1c,d,i), which uses mean biomass as one of the predictor. Exclusive reliance on density or biomass as indicators of the impact of disturbance may therefore be inaccurate: for some species, years having a maximum density were marked by considerably low production (e.g. Fig. 1a), whereas years having a maximum biomass were not necessarily years having the highest production (e.g. Fig. 1b,h,j).

Methods for estimating production may be divided into classical methods (following cohort and/or size classes) and empirical models, which production or P/$\overline{B}$ ratio (Table 1) models follow metabolic rate principles and regression models with empirical data. These empirical models are considered "short-cut" approaches. The estimation of production as the product of a known population P/$\overline{B}$ ratio and biomass has also been used (e.g. Elliott and Taylor 1989), however will not be discussed in this review. If no previous information on the species dynamics is available (e.g. growth, reproduction), some effort should be put into gathering data to apply classical methods, which imply multiple sampling dates and samples per date (accomplishing both accuracy and precision). Once the species dynamics are known accurately, and using good estimates of density and biomass, short-cut approaches may be a useful option, which require less data and resources. In the following sections, we briefly illustrate some of the common methods of production estimation as well as highlight their difficulties and potential sources of error.

Classical methods

Classical approaches are broadly classified as cohort-based (Allen curve, increment summation, removal summation, instantaneous-growth) and size-based (size frequency, mass-specific mortality rate, mass-specific growth rate - also called instantaneous-growth method for non-cohort populations) methods (Table 3) (Crisp 1984; Benke 1993). Although the related mathematical equations appear complex (Table 3), “the final calculation of production is the simplest job that the production biologist has to do; all of the real difficulties are associated with the collection of the data that go into calculation” (Rigler and Downing 1984). The cohort-based methods, applied to populations with synchronic development, are classified according to the way the area under the survivorship curve of each cohort is quantified (Fig. 2a-d, Table 3), as such their estimates are analytically equivalent. The production of the population is the sum of each cohort production along the study period. Cohorts must be recognized and followed to define a survivorship curve (density against individual body mass) (Fig. 2a), which can be done using various techniques (length frequency and modal analyses, growth marks, among others). Hence, repeated sampling of density over the entire development cycle of the target population is required.

Whenever cohorts are not recognized or age determination is not possible (e.g. population with continuous reproduction), size-based methods may be applied or through use of the instantaneous growth method (= mass growth method), as long as the maximum size, the life span and the form of the growth curve are known (Benke 1993, Table 3). These methods require population size-structure with data that express changes in size-structure densities over the whole population cycle.

In summary, the application of the general calculation principle must be adapted to the specific properties of the species population of interest (Winberg 1971). These calculation techniques can be used for all heterotrophic organism (e.g. zooplankton, fish), with the sampling schedule adjusted to the life cycle and life span of the species and to the purpose of the study depending whether the aim is to evaluate processes occurring over shorter or longer time scales.

Sources of bias in classical methods

The accuracy and precision of estimates by classical methods are sensitive to growth and mortality curves (e.g. linear, exponential, logistic) as well as the sampling schemes (Morin et al. 1987; Plante and Downing 1990; Iversen and Dall 1995). In fact, the sampling schedule and effort becomes quite important, since they contribute more to bias of production estimates than the adopted calculation method (Cusson et al. 2006). Of these, the most important element is to cover the complete growth period (Morin et al. 1987; Cusson et al. 2006) as all methods tend to underestimate production when the sampling interval does not cover periods of intense production. However, except for some dominant species, *a priori* knowledge of all species' life cycles (including growth and mortality functions) is rare, and a balance between accurate production estimates and the time taken for its evaluation are also important to consider (Benke 1984). Similarly, sampling should cover periods of high mortality that may not occur at the same time of growth (e.g. winter mortality, Cusson et al. 2006). For instance, using simulated populations Cusson (2004) showed that the mass-specific mortality rate methods become less precise when using an optimized sampling design only in the growth season.

Several studies have provided comparisons and performances of classical production methods, using natural populations (e.g. Wildish and Peer 1981, Benke 1984, Plante and Downing 1990) and computer simulations of hypothetical populations (Morin et al. 1987; Iversen and Dall 1995; Cusson et al. 2006). Generally, cohort methods provide more accurate estimates, although slightly biased estimates from instantaneous growth method have been observed (Cushman et al. 1978, Morin et al. 1987), whereas size frequency methods could overestimate production (Waters and Crawford 1973; Benke 1984; Plante and Downing 1990). The inclusion of the cohort production interval (CPI) in the equation (Benke et al. 1979) could improve the estimates (Plante and Downing 1990; Cusson et al. 2006), however the main source of error arises from growth and mortality curves (Morin et al. 1987) as the method assumes linear growth

(Iversen and Dall 1985).

Secondary production may be summed within trophic groups and guilds, however it must be stressed that community production (as sum of each species production) should be analysed with care when including more than one trophic level (e.g. summing predators and preys) as secondary production is not additive among trophic levels (Waters 1977), especially if dealing with trophic transfer efficiency.

Other authors have erroneously considered the elimination estimate (E, see Table 3, Fig. 2c) as the production estimated by the removal summation method, which is the sum of the elimination plus the cohort change in biomass over a given period (residual biomass - ΔB) (Table 3, Fig. 2c). In a literature review of papers on benthic production from 1970-1999, Cusson (2004) found that 26% (23/87) of elimination estimates were considered as production estimates without consideration of the residual biomass. This can lead to a strong bias as production is not equal to elimination, especially when growth, mortality and recruitment are not constant over time (or in unsteady state, which happens most of the time, Rigler and Downing 1984). Indeed, the larger the residual biomass, the greater the differences between elimination and increment summation estimates (Bachelet 1982). Cusson and Bourget (2005b) computed production estimates from the increment summation and removal summation methods, elimination, as well as potential production from four marine intertidal populations of mussels. They found several negative annual production estimates that indicated major differences between growth and mortality periods with areas of the mussel bed being dismantled. For positive values, differences reach over 550% among methods (assuming that the bias of the potential production is close to zero). Yet, comparisons between elimination and production estimates may be useful for understanding population dynamics and state of the population: if production < elimination = loss of biomass in the population; and inversely, if production > elimination = increase in the population biomass

(Bachelet 1982; Cusson and Bourget 2005b).

Dealing with unsteady and non-synchronous populations may lead to difficulties in estimating production and productivity (Morin et al. 1987). Steady state and perfectly synchronous populations are, in fact, rare in nature (Rigler and Downing 1984; Morin et al. 1987), translating into a bias in the production estimation especially for species having unknown life histories (Benke 1984). This leads to the question of whether or not negative production should be considered, as it may be interpreted as a clear sign of imbalance or unsteady-state conditions. Negative production between sampling dates have been discarded on some production studies (e.g. Wildish and Peer 1981), which may lead to overestimation and decreased accuracy (Cusson et al. 2006). The negative "increment" in calculations results from decreasing average body mass. This happens when an individual burns their fat reserves during harsh conditions. Unless negative production comes from sampling artefacts, they should be kept in all calculations, as they provide important insights about the population condition (e.g. Cusson and Bourget 2005b). The frequency of negative production between successive sampling dates may be influenced by the proximity of the dates, combined with small sample sizes, associated to inadequate sampling of the population (producing lower body mass values in the subsequent sampling date, which in theory should not occur) or to the body mass metrics used. Weight-weight and length-weight conversions tables are also available (e.g. Brey 2001). Even so, the replacement of many negative terms by zeros may produce overestimated values (Downing and Rigler 1984) and decrease strongly both the accuracy and precision of estimates (Cusson et al 2006).

Empirical models

What if the data do not allow the use of classical methods? In order to find an easier way to estimate production, several authors have established models based on empirical relationships between secondary production or P/$\overline{B}$ ratio to the population and/or environmental parameters (Table 4). Empirical models allow to estimate potential production: a) when classical methods cannot be used (e.g. population development cannot be followed because of inconvenient sampling or species with incomplete size or age structure) or there are time constraints for data processing; b) community production assessment, which have rare species or with unknown dynamics (e.g. Sprung 1994; Dolbeth et al. 2003); c) determine spatial and/or temporal comparisons of community production from different habitats in similar ecosystems (e.g. Heck et al. 1995; Pranovi et al. 2008); and finally d) generate of new hypotheses based on production trends (e.g. Ponti et al. 2007; Coelho et al. 2008).

Several empirical models were proposed for aquatic invertebrates (full list in Table 4). There are essentially two kinds of empirical models:

1) Those who relate P/$\overline{B}$ with body mass following metabolic rate principles (e.g. Schwinghamer et al. 1986, Sprung 1993, Table 4). In these models, the P/$\overline{B}$ ratio depends on body mass in a characteristic way: i) due to an intraspecific or physiological effect (P/$\overline{B}$ ratio represents a time-integrated estimate of the growth rate, depending on the body mass in a similar way as other physiological rates with an exponent close to -0.25); and ii) to an interspecific or ecological effect (at given body mass and identical environment, some species may grow faster than others) (Sprung 1993);

2) Those obtained by multiple regression equations between the production or P/$\overline{B}$ ratio and population characteristics (e.g. life span, maximum body mass, mean biomass, among others) and environment characteristics (e.g. temperature, depth) (e.g. Tumbiolo and Downing 1994; Brey 2001, Table 4).

At least 35 empirical models have been published in the literature; of these, 7 were designed exclusively for freshwater ecosystems and 10 exclusively for brackish and marine ecosystems (Table 4). Recent regression models proposed different parameters coefficients depending on the taxa or habitat (e.g. Brey 2001; Cusson and Bourget 2005a, Table 4), but most models used population biomass as a predictor (about 90% of the models, Table 4). Other common predictors were body mass or length, temperature and life span (respectively about 50%, 40% and 20% of the models, Table 4). Several authors found that production was highly correlated with biomass (Brey 1990; Benke 1993; Cusson and Bourget 2005a), which might have induced some authors to use biomass as proxy for production (e.g. O'Gorman et al. 2008). However, as discussed before, biomass and production trends may be quite different (Fig. 1, see also Benke 2010), with general trends in production and $P/\overline{B}$ ratios strongly related to the species life histories (life span, mean body mass) (Benke 1993; Cusson & Bourget 2005a). Comparisons of $P/\overline{B}$ ratios computed for the same species in different habitats (e.g. Dolbeth et al. 2007 seagrass and sandflat areas) also provides evidence for this difference, clarifying that biomass alone is not always a good proxy for production.

Although empirical models are easier to compute, results have to be interpreted with caution as they provide mean estimates and may mislead in several cases (Medernach and Grémare 1999; Brey 2001; Cusson and Bourget 2005a). High deviations between population production estimated with classical techniques (cohort or size-based methods) and with empirical models may be observed (e.g. in Mistri et al. 2001; Cartes et al. 2002; Dolbeth et al. 2005) and when body mass and the standing stock (Table 1) are not correctly evaluated. Production computed by empirical models can give an idea of the potential production level, however, does not guarantee gaining vital information on the actual population condition, such as imbalance or no steady-state conditions that lead to negative annual production values (Cusson and Bourget 2005b).

Calculation techniques for other heterotrophic organisms have also been proposed, mainly to estimate zooplankton production (e.g. review for copepods in Runge and Roff 2000), including empirical models based on temperature dependent weight-specific growth (Stockwell and Johannsson 1997), RNA/DNA quantification as measure of growth/production (Gorokhova 2003) and chitobiase activity (Sastri and Dower 2006), among others.

Ecological importance of secondary production for environmental impact assessments

Global ecological changes are occurring at a very rapid rate and over a large scale due to multiple stressors affecting aquatic ecosystems (e.g. eutrophication, pollution, habitat loss, climate change, invasive species introductions, Kennish 2002; Paerl 2006). Detection of these changes may occur using various static and dynamic biological variables, yet “an organism’s success in an environment might be a function of its ability to fix or retain energy” (the trophic-dynamic concept by Lindeman (1942). As such, secondary production may provide insight into ecosystem dynamics as it combines both static and dynamic components of a population’s ecological performance. Furthermore, secondary production estimates may be employed in a number of ways (Table 2, and more examples in Benke and Huryn 2010), thereby shedding the misconception that it is only useful for trophic flow and efficiency studies (Benke 2010). Besides detecting a given impact, potential consequences related to the bioenergetics and the overall functioning of an ecosystem following the impact, may be evaluated. Assessing ecological processes and resources in terms of the goods and services that they provide is attractive and well understood by policy makers and non-scientists (Costanza et al. 1997; Pinto et al. 2010). Secondary production estimates often represent a direct measure of food provision delivered by an ecosystem and as such have clear socio-economic relevance, particularly when a monetary value is attached to this estimate (Costanza et al. 1997; Pinto et al. 2010). However, secondary production increases do not necessarily represent a healthier ecosystem. Some impacts may induce increases in the overall benthic production, due to compositional changes that benefit highly productive opportunist species but with consequent reduction in faunal complexity (species loss and lower evenness, e.g. Dolbeth et al. 2007; Sousa et al. 2011). The source of the secondary production to the whole community production needs to be understood and weighted in the ecological interpretation of mechanisms. Accordingly, the following section explores some of the main large scale impacts, often driven from human activities, and how secondary production may help in the understanding of their impact within aquatic ecosystems.

Eutrophication

Eutrophication, via nutrient enrichment (N and P) of aquatic environments, represents a major problem affecting global freshwater, transitional (e.g. estuaries, lagoons) and coastal ecosystems (Cloern 2001; Cross et al. 2007). The integrating effect of the physical and biological characteristics of the ecosystem and climate combined with the nutrient loading itself results in variable impacts on these systems (Cloern 2001). Several impacts on the biota have been studied, most of them addressing eutrophication impacts on assemblage structure (Raffaelli et al. 1998; Kennish 2002), and, on a lesser extent, secondary production (e.g. macrofauna, Dolbeth et al. 2003) and stability of recipient food webs (Cross et al. 2007).

The link between secondary production and nutrient loading in aquatic ecosystems may be complicated by the interference of other environmental factors, such as climate change, hydrological manipulations, among others (Cloern 2001; Nixon and Buckley 2002). Eutrophication may lead to compositional and production changes at the autotrophic level (primary production, e.g. Prins et al. 1999; Flindt et al. 1999), in turn affecting the dependent heterotrophic organisms (Raffaelli et al. 1998; Prins et al. 1999), resulting in a different trophic organization (e.g. Dolbeth et al. 2003).

Intermediate levels of nutrient loading may increase primary production and subsequent secondary production (zooplankton, benthos and fish) within impoverished systems (Fig. 3, examples in Prins et al. 1999; Nixon and Buckley 2002; Cross et al. 2006). Nevertheless, anthropogenic nutrient loading rates often exceed those needed to sustain production inputs that may be beneficial to the system (threshold in Fig. 3, Paerl 2006; Singer and Battin 2007) leading to excessive organic matter, algal blooms, oxygen depletion, loss of seagrass or coral, fish mortality, among other effects (Fig. 3, Cloern 2001; Nixon and Buckley 2002; Paerl 2006).

Most examples of coastal eutrophication impacts on secondary production have shown the effect of phytoplankton or macroalgal blooms on invertebrate population production (Verdelhos et al. 2005; Cardoso et al. 2008) and community production (Prins et al. 1999; Dolbeth et al. 2007). In general, macroalgal blooms temporarily enhance macrofauna production and turnover rates (Dolbeth et al. 2003; Pranovi et al. 2008) presumably through increased food supply, habitat heterogeneity and shelter (Raffaelli et al. 1998; Norkko et al. 2000). Taking in to account a 10-year study of estuarine production in a sandflat area, the highest macrofauna density and production were recorded during a macroalgal bloom (1993, Fig. 1j). Analysis of biomass alone results in a very different trend (considerably lower in 1993 at the sandflat, Fig. 1j), suggesting that this latter approach underestimates the importance of macroalgal blooms. However, a relatively elevated $P/\overline{B}$ ratio (Table 1) revealed additional information. The generally elevated $P/\overline{B}$ ratios observed on the algal substratum relative to other habitats (Tumbiolo and Downing 1994; Cusson and Bourget 2005a) stem from low juvenile mortality and high growth rates (mainly from opportunistic species) as well as temporary benefits (protection, structural complexity and organic food) supplied by the macroalgae (Raffaelli et al. 1998; Norkko et al. 2000). This example highlights that higher production and $P/\overline{B}$ ratios do not necessarily represent better conditions, because of the associated changes in species composition that most contributed to production. Further, higher oxygen production may not compensate oxygen demand resulting in system collapse, hypoxic-anoxic conditions, production of large amounts of detritus (Flindt et al. 1999) and a decline in community production (Dolbeth et al. 2003; Pranovi et al. 2008), which can remain considerably low in the months and years following the bloom (Dolbeth et al. 2003, 2011).

Eutrophication and the subsequent changes in primary producers and blooms have resulted in the decline of macrophyte beds (such as *Zostera* spp., *Ruppia* spp., *Posidonia* spp.) in several coastal areas worldwide (Flindt et al. 1999; Duarte et al. 2002). In general, higher benthic production is observed in seagrass areas compared to bare sand or mudflat areas (e.g. Sprung 1994; Heck et al. 1995). As such, the replacement of seagrass by opportunists tends to result in an overall decrease in whole ecosystem production, with the consequent carrying capacity decrease (Fig. 3, Dolbeth et al. 2007; McArthur and Boland 2006).

Freshwater, transitional and marine systems have different patterns of nutrient cycling, due to differences in the relative importance of N and P as limiting elements (Cloern 2001). The effects of nutrient enrichment on primary and secondary production are better understood for freshwater ecosystems. Changes in the macroinvertebrate structure and production due to the bottom-up effects of eutrophication have been described for lakes (e.g. Specziár and Bíró 1998) and streams (Cross et al. 2006, 2007). Increases in whole invertebrate community production result from an increased nutritional quality of the basal resource (e.g. detritus-associated microbes, leaf litter, diatoms (Cross et al. 2006, 2007; Singer and Battin 2007). In these habitats, invertebrate production increases with nutrient enrichment (highest community production value in Fig. 4 is from a eutrophic stream), mainly due to opportunistic species (Specziár and Bíró 1998; Singer and Battin 2007) and high $P/\overline{B}$ ratios. Freshwater food chains may also shorten (Cross et al. 2007; Singer and Battin 2007). Nutrient enrichment may eventually lead to reductions in total community secondary production via loss of carbon, with potential shifts in community structure, such as reduced diversity and evenness (Cross et al. 2007; Singer and Battin 2007).

Chemical pollutants

Aquatic ecosystems are increasingly exposed to diverse sources of environmental contamination including heavy metals, petrochemical products, pesticides, butyltin compounds and the so-called "emergent pollutants of concern" (e.g. pharmaceutical compounds, polychlorinated dibenzo-p-dioxins, brominated flame retardants (de Boer et al. 1998; Eljarrat and Barceló 2003). Contaminants pose a great risk to water quality, biological communities and ultimately to human health. Monitoring of contaminated aquatic environments has focused on the collection of potential contaminants, ecotoxicological tests or mesocosms experiments (Grubaugh and Wallace 1995). However, new monitoring approaches have emerged based on biological assessment techniques, including secondary production.

Biological assessment through use of secondary production for the evaluation of the biological integrity of an ecosystem subject to contamination may be performed through spatial and/or temporal comparisons between reference and impacted sites (e.g. Méndez et al. 1997). For instance, Whiles and Wallace (1995) compared temporal changes in macroinvertebrate production within a river, in the years before, during and after contamination. Comparisons were also made with an adjacent non-polluted reference river. Production estimates provide an improved understanding of contaminant effects on populations and ecosystems, through the exploration of overall production and $P/\overline{B}$ ratios of dominant species and/or of species particularly sensitive to the contaminants. Assessment of specific species production provides precise information regarding the state of impacted sites and allows for the comparison of production among habitats along a gradient of contamination. These approaches have been applied to a wide range of contaminants and habitats (pesticides in streams: Lugthart and Wallace 1992; Whiles and Wallace 1995; heavy metals in streams and estuaries: Woodcock and Huryn 2007; Runck 2007; Coelho et al. 2008).

Although an indirect method for evaluating the aquatic environment condition, secondary production nonetheless enables an assessment of the cumulative impacts of contaminants throughout the food web and ultimately provides clues for understanding whole ecosystem impacts. For example, in a study of headwater streams treated with insecticide, Lugthart and Wallace (1992) and Whiles and Wallace (1995) showed that abundance data of the macroinvertebrate community failed to accurately depict production changes and that biomass data underestimated the importance of small-sized functional groups. In contrast, the studies showed that decreasing production during contamination and subsequent post-disturbance recovery in production provide an enhanced picture of community dynamics, including the role of specific taxa or functional groups and changes in activities such as leaf litter processing. Moreover, calculating the production of benthic organisms within a contaminated habitat and knowing concentration of contaminants in their tissues, allows for estimating the heavy metal pool eligible for trophic transfer, detecting bioaccumulation or bioamplification along the trophic chain (e.g. Coelho et al. 2008), as well as providing insight into the contaminant biogeochemical cycle, and the critical role of benthic species in the mobilization of heavy metals from the sediments or periphyton (Runck 2007; Coelho et al. 2008).

Climate change

Understanding how climate change will affect the health of natural ecosystems and their functioning represents a major research focus (Ottersen et al. 2004; Emmerson et al. 2005). Interacting effects of multiple stressors directly or indirectly related with climate (e.g. rising temperatures, altered precipitation patterns, nutrient cycling changes, sea level rise, increasing storminess, ocean acidification, species distribution and biodiversity changes) will greatly affect the structure and functioning of ecosystems, inducing changes in the productivity and stability of aquatic food webs (Emmerson et al. 2005). For instance, temperature directly affects metabolism, controlling growth and generation times, therefore with great potential impacts on population and community secondary production (Benke 1984; Tumbiolo and Downing 1994; Huryn 1998).

Extreme weather events, such as floods, droughts and heatwaves, have clear effects in the secondary production of aquatic ecosystems (e.g. in Whiles and Wallace 1995; Huryn and Wallace 2000; Dolbeth et al. 2011). These events may affect the components of the ecosystem differently and therefore their impacts on the secondary production may be direct or indirect. Fluctuations in temperature and salinity will have direct effects on species range tolerances (Freitas et al. 2007) and cause higher mortality due to lower metabolic efficiencies and diverted energy into other tissues (e.g. negative impacts on calcifying organisms following ocean acidification, Doney et al. 2009). There seems to be a tendency for higher growth rates and shorter lifespan, for the same taxa group, with increases in temperature, leading to higher turnover ratios (Cusson and Bourget 2005a). If temperature regimes change, we would also expect changes in production levels, but as stressed above, several indirect effects may interfere. Low seasonal temperatures, nutrient or food limitation, or other climate constrains such as ice scouring in cold-temperate and arctic freshwater and marine areas often result in low production estimates (Huryn and Wallace 2000; Aitken et al. 2008; Winterbourn et al. 2008). An increase in temperature in these cold-temperature areas, however, would not necessarily lead to increased productivity, mainly due to the expected habitat loss or disturbance from high rate of shore erosion, or fragmentation (Winterbourn et al. 2008). The impact of climate change within carbon cycling of these marine benthic communities is difficult to predict. Nevertheless, factors affecting the community composition and primary production have been suggested to have significant impacts on the carbon processing and storage in the bottom sediments (Aitken et al. 2008), therefore influencing the benthic production.

Other indirect effects from climate changes on secondary production include changes in coastal marine primary production as result of reduced or higher water runoff from organically enriched allochthonous waters (Salen-Picard et al. 2002), or as result of differences in the occurrence of upwelling events (Ottersen et al. 2004) or El Niño events (Daneri et al. 2000), which also influence predator-prey interactions (e.g. Freitas et al. 2007). The array of climate impacts is definitely complex because of their interacting effects. For example, Cardoso et al. (2008) found that floods in the Mondego estuary had a direct impact on the development and production on the Gastropod *Hydrobia ulvae*, a key species of the system, but not on the abundance of its main habitat, the eelgrass beds of *Zostera noltii*. However, heat waves and drought events, through their effects on temperature and salinity, directly affected the biomass of *Z. noltii*, which had indirect effects on the dynamics of *H. ulvae* leading to decreases in production (50% to 70% decrease, Cardoso et al. 2008).

Climate change impacts are difficult to dissociate from the already ongoing human interference in several aquatic ecosystems (e.g. Pranovi et al. 2008; Dolbeth et al. 2011) and may ultimately increase the vulnerability of certain ecosystems, leading to an aggravation of other impacts, such as eutrophication (Lloret et al. 2008). Studies of aquatic ecosystems must integrate the impacts from several stressors highlighting the importance of implementing long-term monitoring schemes in sensitive sites and at an appropriate scale. Combining secondary production with the long-term datasets will upgrade the level of understanding of ecosystem functioning (see for instance Dolbeth et al. 2007, 2011; Pranovi et al. 2008), for which use of density or biomass alone fails to provide a broader overview of potential impacts. Another important issue is that more effort should be undertaken into documenting aquatic habitats before the projected environmental changes intensify (e.g. in the arctic environment, Aitken 2008).

Non-indigenous invasive species

The introduction of non-indigenous invasive species (NIS) is one of the leading topics in ecology with profound implications in research areas such as biogeography, evolution and genetics (Sax et al. 2007). High rates of NIS introductions can be found in several aquatic ecosystems, with some of these species causing remarkable ecological and economic losses (Cox 2004). Knowledge on the population biology of NIS will be necessary to develop effective management procedures and policies (Townsend 2003), with proxies that may provide insights on potential impacts for the ecosystem functioning (Sousa et al. 2011). Secondary production has great advantages over other approaches due to the incorporation of bioenergetics performance of a population that integrate biotic interactions with others members of the community (Huryn and Wallace 2000; Hall et al. 2006; Kimmerer 2006).

Studies estimating the secondary production of NIS are scarce. The few existing studies highlight the importance of production as a measure of NIS functional importance in the food web and for the understanding of the species strategies towards the environment (resource allocation, among others, Hall et al. 2006, Kimmerer 2006; Sousa et al. 2008b). Townsend (2003) showed that most of annual invertebrate production was consumed by non-indigenous trout

(*Salmo truta*) introduced in New Zealand streams. Subsequent decrease in herbivory enhanced up to a six-time increase in algal productivity compared with non-invaded sites, leading to important changes in ecosystem functioning (e.g. increased nutrient flux).

Studies of various non-indigenous invasive molluscs species (*Potamopyrgus antipodarum*, Hall et al. 2006; *Crassostrea gigas* and *Ruditapes philippinarum*, Ruesink et al. 2006; *Dreissena polymorpha*, Chase 1999; Czarnoleski et al. 2003; and *Corbicula fluminea*, Sousa et al. 2008b) showed that these taxa can reach production values 7 to 40 times higher than any other taxa within the same community (example for *C. fluminea* in Fig. 4), highlighting the importance of production measures in order to assess the degree to which NIS dominate the whole community. This increase in secondary production does not necessarily represent a gain for the ecosystem, due to the impact that single species such as NIS may have for the functioning of the ecosystem. Studies with NIS production and incorporating data at other levels of the food chain are important to determine single-species impacts on predation and/or competition with indigenous species and changes in the food web (Hall et al. 2003; Kimmerer 2006). NIS may provide a new prey source for native predators, though a great portion may enter directly to the detritus food-web (Sousa et al. 2008*b*), altering the structure of ecological interactions in the community. On the contrary, an invasive species having a high abundance may lead to the depletion of primary production, inducing changes in the food web (Kimmerer 2006).

One of the most striking conclusions of the NIS production studies is that gains in NIS (as much as the indigenous species losses) can markedly influence ecosystem processes and that associated changes in ecosystem functioning are often directly attributable to a few high-impact species, which play entirely new roles in the ecosystem (Ruesink et al. 2006). Sometimes, these changes may be considered beneficial in an economic context (Ruesink et al. 2006; Pranovi et al. 2008). For instance, Ruesink et al. (2006) showed primary production increases over 50% due to introduced tracheophyte plants (*Spartina alterniflora* and *Zostera japonica*), although causing management problems difficult to reverse in the Willapa Bay, USA. In the same bay, secondary production increased over 250%, due to introduced bivalves (*C. gigas* and *R. philippinarum*) resulting in an important economic resource for humans, despite the decline of the indigenous oyster abundance. However, these temporarily beneficial increased productions may be negative in the long-term, especially as NIS dominance generally implies an increasing loss of valuable native or rare species (e.g. Sousa et al. 2008a).

Food web quantification/ecological modelling

An important aspect of production estimation is its integration with food web studies (Crisp 1984; Downing 1984). In this approach, population-level production is part of a larger scheme tracing material or energy flux through the ecosystem and enables understanding of fundamental aspects of ecosystem structure, function and management (Downing 1984). The assessment of biomass/energy flow and the rational management of resources require knowledge of the complete food web. Secondary production analysis in isolation is limited in being able to discern the importance of predatory interactions, as it is an end product of organic matter processing (Benke et al. 2001; Huryn and Wallace 2000). These food-web analyses help to reveal top-down or bottom-up controls in the system (e.g. Hyrun 1998; Nyström et al. 2003), by exploring the trophic position of a species, its production and how the energy/biomass circulates within the food web (Benke and Huryn 2006, see other examples in Benke and Huryn 2010). This approach also reveals species/resource carrying capacities in an ecosystem having well-defined boundaries as production at a given trophic level sets the limit for production within higher trophic levels, while simultaneously affecting rates of resources removed from lower levels (Huryn 1998; Huryn and Wallace 2000). As such, negative or positive cascade effects caused by either anthropogenic and/or climate impacts in the ecosystem may be predicted (e.g. Huryn 1998; Patrício and Marques 2006; Baeta et al. 2011).

Some invertebrate species within a community have high production levels, or may attain large production values following certain events (e.g. opportunist species after disturbance events, NIS production). But is this production actually consumed by other trophic levels? Few studies have explored this question as the definition of trophic relations and food web is already an extremely difficult task (Raffaelli 2000). However, several studies have combined production values to quantify energy (or material) flowing from producers to consumers or within consumers (into energy flow webs), which are successful in revealing much about aquatic systems' functioning and the identification of key species in the system (Raffaelli 2000; Benke et al. 2001; Kimmerer 2006). Other developments have been achieved by combining ecosystem processes estimates with modelling approaches (e.g. ECOPATH), where production or the $P/\overline{B}$ ratio is an essential component of the models (Patrício and Marques 2006). Secondary production studies may also be used to evaluate how much production would be necessary to sustain aquaculture in ponds (Arias and Drake 1994; Ponti et al. 2007).

Conclusions

The present paper highlighted several examples where the evaluation of secondary production served as a powerful tool for improving our understanding of aquatic ecosystem structure and functioning. Ecosystem functioning may be regarded as the sum of all processes involved in the transfer and cycling of energy and materials, therefore including biological production. In this regard, the evaluation of secondary production has several advantages over other static variables such as biodiversity, density and biomass. The benefits of production estimates are 1) the characterization of the functional role of a population or community in an ecosystem, 2) the assessment of disturbance impacts on ecosystem processes, including variation of energy/biomass/compounds flow and their availability within the system, and 3) the evaluation of the carrying capacity of a system for a given resource (as also discussed in Gray and Elliott 2009). The evaluation of secondary production may be time-consuming using classical methods however empirical models represent a possible alternative when reliable estimates of population biomass, mean individual body mass and, even better, a life-span are available.

Secondary production is now being applied to broader questions in marine and freshwater benthic ecology (Benke and Huryn 2010). Ecological studies should integrate multiple stressors and attempt to disentangle their impacts on communities, which may be done using various biotic proxies. The use of secondary production provides a more integrative approach for the evaluation of population and ecosystem functions and resistance/resilience following a disturbance. Production may not be used for detecting a disturbance as we cannot predict the subsequent production changes. However, it may reveal other aspects that cannot be detected through static measures such as significant declines of production levels (even negative production) or higher turnover rates and their potential consequences for other trophic levels, including humans. The accurate characterization of natural energy/biomass flux and an improved evaluation of potential impacts of disturbances on communities are indispensable from both an environmental and socio-economic perspective for the understanding of how ecosystems respond to these impacts and how multiple stressors affect ecosystem goods and services.

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Table 1. Secondary production related terms glossary. References for terms from Winberg (1971), Benke (1984, 1993), Crisp (1984) and Rigler and Downing (1984).

Term	**Definition**
Body mass or individual weight	The amount of living tissue of one individual; If estimated as population biomass divided by density it will correspond to average amount per individual
Biomass	The amount of living tissue of the individuals being studied per area (apply to population or community); is the product of average body mass and density. It is often called as standing stock
Density	Number of individuals per unit area (apply to population or community)
Steady-state populations	Population where averaged biomass and size-structure of the population are constant from a year to another; rarely occur in nature
Production or "actual production"	Organic matter or energy incorporation in a given area per time unit; it is considered a flow, generally expressed as biomass per area and per time (e.g. g m^{-2} yr^{-1}), but energy units are also used (e.g. KJ m^{-2} yr^{-1})
Productivity	Production rate, i.e., the velocity/rate at which energy or biomass is produced per unit area (efficiency of the production); Some authors link productivity and $P/\bar{B}$ ratio
Potential production	Production under theoretical steady-state conditions, with no changes in overall biomass and age/size frequency from year to year
Primary production	Production by autotrophic organisms
Secondary production	Production by heterotrophic organisms
$P/\bar{B}$ ratio	Annual production divided by the annual mean biomass, and is a measure of a species biomass turnover rate, which is the inverse form of the species average lifespan under a set of conditions

Table 2. Literature examples of the different applications of secondary production studies in aquatic ecosystems.

Applicability of secondary production studies	Some study examples (literature)
Gain information on a species population dynamics	Bachelet 1992, Cardoso et al. 2005, 2008, Cusson and Bourget 2005*a*, Grilo et al. 2009
Assessment of anthropogenic impacts on the ecosystem (e.g.):	
– *Eutrophication (nutrient enrichment)*	Macroalgal blooms and long-term eutrophication impacts in estuaries (Dolbeth et al. 2003, 2007, Pranovi et al. 2008) Impact of nutrient enrichment in a detritus-based freshwater ecosystem (Cross et al. 2006, 2007)
– *Pollution (heavy metals, sewage)*	Pollution impacts in community production (Lugthart and Wallace 1992, Whiles and Wallace 1995, Woodcock et al. 2005), Estimate heavy metal impact thorough food web (Runck 2007, Singer and Battin 2007) Eligible mercury pool from an contaminated estuary (Coelho et al. 2008)
Effects of catchment land use change	Examples in Benke and Huryn (2010)
Assessment of climate impacts on the ecosystem (e.g.):	
– *Precipitation variations*	Flood impacts (Lugthart and Wallace 1992, Dolbeth et al. 2007); Altered cycles of floods and droughts (Cardoso et al. 2008, Grilo et al. 2009, Dolbeth et al. 2011)

– *Temperature variations*	Heat wave impacts (Grilo et al. 2009, Dolbeth et al. 2011)
Management of biological resources (e.g.):	
– *Rational management of biological resources in natural ecosystems*	Downing 1984, Rainer 1985
– *Assessment of carrying capacity for natural fish and shellfish resources*	Costa et al. 2002
– *Evaluation of aquaculture yields*	Evaluate benthic production exploitable for fish aquaculture (Arias and Drake 1994, Ponti et al. 2007)
Energy or materials flow (e.g.):	
- *Food web quantification*	Food web quantification combining gut analysis with production (Benke et al. 2001); Analyses of top-down or bottom-up controls of the system (e.g. Hyrun 1998, Nyström et al. 2003); Ecopath models (Patrício and Marques 2006)
- *Quantification of the role of animals in ecosystem chemical flows*	Mercury transfer from sediments to the estuarine trophic web (Coelho et al. 2008); N cycled through earthworms (Whalen and Parmelee 2000); How stoichiometry properties (ratio C:N:P) affect stream production and quantitative food webs (Cross et al. 2007, Singer and Battin 2007)
Biotic interactions (competition and predator–prey relationships)	Cross and Benke 2002

Evaluation of the functional importance of non-indigenous invasive animals, including abiotic (e.g. changes in nutrient fluxes) and biotic interactions (e.g. competition with indigenous species)	Single-species impacts on ecosystem processes and functions, such as nutrient cycles (Hall et al. 2006, Kimmerer 2006, Sousa et al. 2008*b)*, including economic impacts (Ruesink et al. 2006)
Evaluate food provisioning services from an ecosystem (goods & services)	Secondary production as a direct measure of food provision delivered by an ecosystem; Economic contribution of seagrass habitats to fish production (McArthur and Boland, 2006); Economic impact of NIS commercial species – sustainable harvests (Ruesink et al. 2006)

Table 3. Classical production methods for the computation of the secondary production. Units are in mass or energy per area per time. **Legend:** P, total production; P_{ci}, cohort i production; N, density; $\overline{w}$, average body mass or individual weight; E, elimination; E_{ci}, cohort i elimination; $\overline{B}$, mean biomass; t and t+1, successive sampling dates (t = 1, 2, …, n); ΔB_{ci}, residual biomass from cohort i; $B_{\delta i}$, final biomass from cohort i, $B_{\iota i}$, initial biomass from cohort i, T, total sampling time; CPI, cohort production interval; a, number of size classes; j and j+1, successive size classes (j = 1, 2, …, n); i and i + 1, successive sampling dates. See other variants in Cusson et al. 2006.

Methods	Equation	Reference
Cohort methods		
Increment summation	$P=\sum_{i=1}^{i=n} P_{ci}$ $P_{ci}=\sum_{t=0}^{T-1}\left(\frac{N_t+N_{t+1}}{2}\right)\times\left(\overline{w}_{t+1}-\overline{w}_t\right)$	Winberg 1971, Crisp 1984, Cusson 2004, Cusson et al. 2006
Increment removal	$P=\sum_{i=1}^{i=n}\left(\Delta B_i+E_i\right)$ $\Delta B_i=B_{\delta i}+B_{\ell i}$ $E_i=\sum_{t=0}^{T-1}\left(\frac{\overline{w}_t+\overline{w}_{t+1}}{2}\right)\times\left(N_{t+1}-N_t\right)$	
Instantaneous growth	$P=\sum_{i=1}^{i=n} P_{ci}$ $P_{ci}=\sum_{t=0}^{T-1}\left(\ln\frac{w_{t+1}}{w_t}\right)\times\left(\frac{\overline{B}_t+\overline{B}_{t+1}}{2}\right)$	
Allen's curve		

	$P=B_i+\int_{w_i}^{w_a} f(w)dw$	
Size-based methods		
Size–frequency modified by Benke (1979)	$P=a\left[\sum_{j=1}^{a-1}\left(\overline{N}_j-\overline{N}_{j+1}\right)\times\sqrt{\left(\overline{w}_j\times\overline{w}_{j+1}\right)}\right]\times\frac{365}{CPI}$	Benke et al. 1979
Size–frequency modified by Grémare et al. (1989)	$P=\sum 0.5\times\left(\left(Y_{ij}+Y_{i+1j}\right)-\left(Y_{i,j+1}+Y_{i+1,j+1}\right)\right)\times\left(w_j\times w_{j+1}\right)^{0.5}$	Grémare et al. 1989
Mass–specific growth or instantaneous growth for non–cohort populations	Growth rates (g) determined independently of field sampling $g=\frac{\ln w_{t+\Delta t}/w_t}{\Delta t}$ $P=\sum_{j=1}^{a-1} g_j\times\overline{B}_j$	Benke et al. 1993

Explanation box: classical methods to compute secondary production are generally classified as cohort- and size-based methods. For cohort methods, cohorts must be recognized initially and the production will be the area within the survivorship curve of each cohort (body mass against population density, see Fig. 1). Different cohort-based methods consist in different ways in computing that area. When population development is not synchronous and cohort cannot be identified, size-based methods can be used, including the instantaneous growth method, as long as an independent growth rate is determined. Size-frequency method requires the evaluation of population size-structure, so estimates of density must be repeatedly obtained for each size class.

Table 4 Chronologic list of empirical methods found in the literature, with indication of the models (equation, n and R^2) and units and habitat, when provided by the author

Method	**Equation**	**Symbols and units**	**Habitat**
McNeill and Lawton (1970)	Poikilothermic individuals model: $P = -0.2367 + 0.8233 \log R$ Homoeothermic individuals model: $P = -1.7761 + 1.0137 \log R$	P: production (Kcal/m^2/time unit), R: respiration (Kcal/m^2/time unit)	
Allen (1971)	Z = P/B if: 1) steady state population, 2) growth is described by von Bertalanffy model (VBGF), and 3) mortality is described by the single negative exponential mortality model Linear growth (weight): $A^{-1} = P/B$	P: production, B: biomass, Z: exponential mortality constant	

	$G = P/B$		
Johnson and Brinkhurt (1971)	$P = B\frac{\bar{T}^2}{10}$ according to the estimates from Bay of Quinte and Lake Ontario	P: production ($Kcal/m^2/yr$), $\bar{B}$: mean biomass ($Kcal/m^2$), T: mean bottom temperature (ºC)	Freshwater
Hughes (1971*a*, *b*)	Several Patellidea species models (only 2 examples below): *Fissurella barabarensis* model: $\log P = 67.8155L - 96.5294L^2 + 61.7353L^3 - 14.6648L^4 - 15.6538$ *Nerita tessellata* model: $L \leq 14 : \text{Log}P = 0.6239x + 1.7815$ $L > 14 : \text{Log}P = 6408.27l - 7715.28l^2 + 4128.83l^3 - 828.68l^4 - 1993.59$	L: shell length (mm), $l = \log L$	Marine
Lévêque (1973)	Poikilothermic individuals model:	P: production ($Kcal/m^2$/time unit),	

<table>
<tr><th></th><th></th><th></th><th></th></tr>
<tr><td></td><td>$\log P = -0.28 + 0.83 \log R$
(derived from McNeill and Lawton 1970)</td><td>R: respiration (Kcal/m^2/time unit)</td><td></td></tr>
<tr><td>Neveu (1977), Lapchin and Neveu (1980) in Carrasco and Arcos (1984)</td><td>$P = 4GN \times \bar{B} \times \left(12/m_j\right)$</td><td>GN: number of generations per year,
$\bar{B}$: mean biomass,
m_j: cohort duration (equivalent to CPI from size frequency method)</td><td></td></tr>
<tr><td>Humphreys (1979)</td><td>Models for different <i>taxa</i>:
$P = bR + a$
<table>
<tr><th>Models</th><th>a</th><th>b</th><th>n</th><th>R^2</th></tr>
<tr><td>Mollusca</td><td>– 0.717</td><td>1.033</td><td>45</td><td>0.86</td></tr>
<tr><td>Crustacea</td><td>– 0.213</td><td>0.946</td><td>9</td><td>0.959</td></tr>
<tr><td>Other invertebrates</td><td>– 0.483</td><td>1.018</td><td>19</td><td>0.911</td></tr>
<tr><td>Carnivore invertebrates</td><td>– 0.407</td><td>0.979</td><td>11</td><td>0.902</td></tr>
</table></td><td>P: production (cal/m^2/yr),
R: observed respiration rate (cal/m^2/yr)</td><td>Aquatic and terrestrial invertebrates (Insecta excluded)</td></tr>
</table>

Detritivore invertebrates	– 0.601	1.069	22	0.907
Herbivore invertebrates	– 0.5	0.971	16	0.943

Robertson (1979)	General model: $\log_{10} P/\bar{B} = 0.66 - 0.726 \log_{10} L$ n = 49; $R^2 = 0.69$ Bivalvia model: $\log_{10} P/\bar{B} = 0.6207 - 0.78261 \log_{10} L$ n = 19; $R^2 = 0.835$	P: production ($gDW/m^2/yr$), $\bar{B}$: mean biomass (gDW/m^2), L: life span (yr)	Marine and brackish water
Waters (1979)	$P/\bar{B} = 5GN$	P: production, B: biomass, GN: number of generations per year	Freshwaters brooks
Banse and Mosher (1980)	$P/\bar{B} = 0.65 w_{Mat}^{-0.37}$ n = 41	P: production ($Kcal/m^2/yr$), $\bar{B}$: mean biomass ($Kcal/m^2$), w_{Mat}: weight at maturity (Kcal)	Freshwater (Boreal)

Humphreys (1980)	$\log(P/\bar{B}) = -0.758 - 0.677\log(B/w_{Max})$ n = 34, R^2= 0.4096	P: production ($cal/m^2/yr$) $\bar{B}$: mean biomass (cal/m^2), w_{max}: maximum individual weight ($(mg)^{0.75}$)	Aquatic and terrestrial invertebrates (Insecta excluded)
Warwick (1980)	$P/\bar{B} = 0.538 - 0.112L$ n = 80, R^2=0.57	P: production, $\bar{B}$: mean biomass, L: life span (yr)	
Parsons et al. (1984)	$\log_{10}(P/\bar{B}) = 0.69 - 0.14L$ n = 55, R^2 = 0.60	P: production, B: biomass, L: life span (yr)	
Wildish (1984)	$\log_{10}(P/\bar{B}) = 0.660 - (1.10\log_{10} L)$	P: production, B: biomass, L: life span (yr)	

Shwinghamer et al. (1986)	$P/\bar{B}=0.525\bar{w}^{-0.304}$ or $\log_{10}(P/\bar{B})=-0.2798-0.304\log\bar{w}$ 42 studies, $R^2 = 0.25$	P: production (Kcal/m^2/yr), $\bar{B}$: mean biomass (Kcal/m^2) $\bar{w}$: weight of mean individual length (Kcal)	Marine (Boreal intertidal mudflats)
Dauvin (1989)	$P/\bar{B}=0.17GN+0.21$	P: production, $\bar{B}$: mean biomass, GN= number of generations per year	
Plante and Downing (1989)	$\log_{10}P=0.05+\left(0.79\log_{10}\bar{B}\right)+\left(0.05\bar{T}\right)-\left(0.16\log_{10}w_{Max}\right)$ $n = 138$; $R^2 = 0.79$	P: production (gDW/m^2/yr) $\bar{B}$: mean biomass (gDW/m^2), $\bar{T}$: mean temperature (ºC), w_{max}: maximum individual weight (mgDW)	Freshwater (lentic systems)
Brey (1990a)	General models: $\log_{10}P=-0.473+\left(1.007\log_{10}\bar{B}\right)-\left(0.274\log_{10}\bar{w}\right)$	P: production (gAFDW/m^2/yr), $\bar{B}$: mean biomass (gAFDW/m^2), $\bar{w}$: mean individual weight	Marine

n = 337, $R^2 = 0.851$

(gAFDW)

$$\log_{10}(P/\bar{B}) = -0.473 + (0.007 \log_{10} \bar{B}) - (0.274 \log_{10} \bar{w})$$

N = 337, $R^2 = 0.478$

Models for different *taxa*:

$$\log_{10} P = a + (b_1 \log_{10} \bar{B}) - (b_2 \log_{10} w)$$

Models	**a**	**b1**	**b2**	**n**	**R²**
Crustacea	-0.614	1.022	-0.360	65	0.913
Mollusca	-0.591	1.030	-0.283	182	0.869
Polychaeta	-0.018	1.022	-0.116	72	0.861

Edgar (1990)

Juvéniles : $P_{daily} = 0.063 \times \bar{B}_{day}^{0.86} \times T_{day}^{0.80}$

Adultes : $P_{daily} = 0.0050 \times \bar{B}_{day}^{0.78} \times T_{day}^{0.92}$

Mass or energy per area per day

Ardisson and Bourget (1991)

Mytilus edulis model (age less than 5 months and pelagic)

$P = 0.0135 L_{max}^{2.557}$ or $P = 1.953 B^{1.466}$

Mass or energy per area per time unit

Marine: for Mytilus edulis

<table>
<tr><th></th><th></th><th></th><th></th></tr>
<tr>
<td>Morin and Bourassa (1992)</td>
<td>$\log P = -0.75 + 1.01\log\bar{B} - 0.4\log w + 0.037\bar{T}$
or $P = 0.18\bar{B}^{1.01} \times w^{-0.34} \times 10^{0.037\bar{T}}$
n = 291; $r^2 = 0.87$</td>
<td>P: production ($gDW/m^2/yr$),
$\bar{B}$: mean biomass (gDW/m^2)
$\bar{w}$: mean individual weight (gDW)
$\bar{T}$: mean temperature (ºC)</td>
<td>Freshwater (lotic systems)</td>
</tr>
<tr>
<td>Benke (1993)</td>
<td>General models:
$\log_{10}\left(P/\bar{B}\right) = 0.546 + 0.035\bar{T} - 0.247\log_{10} w_{Max}$
N = 1565; $r^2 = 0.47$
$\log_{10} P = -0.536 + 1.005\log B - 0.035\bar{T} - 0.245\log_{10} w_{Max}$
N = 1565; $r^2 = 0.92$
Models for different *taxa*:
$\log_{10} P/B = a + cT + d\log_{10} w_{Max}$
<table>
<tr><th>Models</th><th>a</th><th>c</th><th>d</th><th>n</th><th>R^2</th></tr>
<tr><td>Chironomidae</td><td>0.557</td><td>0.050</td><td>-0.085</td><td>258</td><td>0.27</td></tr>
</table>
</td>
<td>P: production ($mgDW/m^2/yr$)
$\bar{B}$: mean biomass ($mgDW/m^2$),
w_{Max}: maximum individual weight (mgDW/ind),
$\bar{T}$: mean temperature (ºC)</td>
<td>Freshwater</td>
</tr>
</table>

Simulidae	0.658	0.031	-0.805	84	0.64
Total Diptera	0.443	0.051	-0.186	437	0.49
Ephemeroptera	0.716	0.030	-0.382	345	0.35
Trichoptera	0.447	0.026	-0.025	451	0.20
Plecoptera	0.592	0.015	-0.160	159	0.25
Odonata	-0.220	0.039	0.048	35	0.54
Megaloptera	0.548	0.016	-0.063	25	ns
Amphipoda	-0.221	0.111	-0.058	47	0.24
Isopoda	1.284	0.013	-0.608	30	0.20
Total Crustacea	1.023	-0.111	-0.234	84	0.48
Mollusca	0.760	-0.034	0.168	16	0.47
Annelida	-0.943	1.15	0.035	11	0.90

Sprung (1993)	2-step approach: 1. Obtain the best P/$\bar{B}$ possible for the species (P/$\bar{B}_{spec}$) at an average body weight for the environment (e.g. from literature data of similar environment); 2. Calculate the actual P/$\bar{B}$ (P/$\bar{B}_{Ind}$) for the body weight measured:	Mass or energy per area per time P/$\bar{B}_{spec}$: estimate of the typical P/$\bar{B}$ of the species (yr^{-1})	Marine and brackish water (Non-boreal)

	$P/\bar{B}_{Ind} = \left(\frac{P/\bar{B}_{spec}}{\bar{w}^{-0.25}}\right) \times w_{Ind}^{-0.25}$		
Morin and Dumont (1994)	$P = \sum_{i=1}^{n-1} \frac{\left(B_i g_i + B_{i+1} + g_{i+1}\right)}{2} \Delta t$ for g_i predicted by: $\log_{10} g_i = -2.09 - 0.27 \log_{10} w_i + 0.025 T_i$	P: production, B: biomass, g_i: growth rate at time *i* w_i: individual weight at time *i*	Freshwater
Tumbiolo and Downing (1994)	General models: $\log_{10} P = 0.24 + \left(0.96 \log_{10} \bar{B}\right) - 0.21 \log_{10} w_{Max} + \left(\left(0.03 T_s\right) + \left(-0.16 \log_{10}(D+1)\right)\right)$ $n = 125$, $r^2=0.86$ $\log_{10} P = 0.18 + 0.97 \log_{10} \bar{B} - 0.22 \log_{10} w_{Max} + 0.04 T_b \times \log_{10}(D+1)$ $n = 337$, $r^2 = 0.478$	P: production (gDW/m^2/yr), B: mean biomass (gDW/m^2) w_{max}: maximum individual weight (mgDW), T_b: mean bottom temperature (ºC), T_s: mean surface temperature (ºC)	Marine

		D: depth (m)	
Urban and Campos (1994)	Veneracea and Tellinacea (Bivalvia) model: $\log_{10}(P/\bar{B}) = -0.432 - (0.221\log_{10}\bar{w})$	Mass or energy per area per time	Veneracea, Tellinacea (Bivalvia)
Brey (1999a)	General models: $\log_{10}(P/\bar{B}) = 10.154 - (0.271\log_{10}\bar{w}) - 2824.247(1/T + 273) - 0.063$ n = 933, $r^2 = 0.756$ $\log_{10}(P/\bar{B}) = 8.256 - 2.22\log_{10}w - 2432.055 \times (1/(T + 273)) + 0.239(1/D) + 0.241(DESubT) + 0.203(DLInEpi) + 0.242(DLMEpi) - 0.287(DTM) - 0.203(DTP) - 0.128(DTC) - 0.475(DTE) - 0.116(DHHabitat1)$ $r^2 = 0.77$	P: production (kJ/m^2/yr), $\bar{B}$: mean biomass (kJ/m^2), $\bar{w}$: mean individual weight (kJ), T: mean temperature (ºC), D: depth (m), See legend for qualitative variables	
Brey (1999b)	General models:	P: production (kJ/m^2/yr), $\bar{B}$: mean biomass (kJ/m^2),	

	$P/\bar{B} = 0.036 + 0.997 \times Z$ $P/\bar{B} = 0.193 - 0.269\varphi$ $\log\left(P/\bar{B}\right) = 1.684 + 0.993\log\left(1/A_{Max}\right) - 0.035\log WMax - 303.904 \times \left(1/\left(1+273\right)\right)$ n = 837, $R^2 = 0.87$	Z: instantaneous mortality rate, φ: growth performance index, A_{Max}: maximum observed age (yr), w_{Max}: maximum individual weight (kJ), T: mean annual temperature (ºC), D: depth (m)	
Brey (2001) v 4–04	$\log\left(P/\bar{B}\right) = 7.947 - 2.294\log w - 2409.856 \times \left(1/\left(T+273\right)\right) + 0.168\left(1/D\right)$ $+0.194\left(DESubT\right) + 0.180\left(DLInEpi\right) + 0.277\left(DLMEpi\right) - 0.174\left(DTAC\right)$ $-0.188\left(DTE\right) - 0.33\left(DTI\right) - 0.062\left(DHHabitat1\right) + 582.851\left(\log w \times \left(1/\left(T+273\right)\right)\right)$ n = 1102; $R^2 = 0.77$ Computation worksheet available at: http://www.thomas-brey.de/science/virtualhandbook/	P: production ($kJ/m^2/yr$), $\bar{B}$: mean biomass (kJ/m^2), $\bar{w}$: mean individual weight (kJ); T: mean temperature (ºC), D: depth (m), See legend for qualitative variables	Marine, brackish and freshwater (lakes)

Cartes et al. 2002	Suprabenthic crustaceans models: $\log P = 0.155 + 0.985 \log \bar{B} - 0.269 \log w + 0.028T$ n = 91, $R^2 = 0.965$ $\log(P/\bar{B}) = 0.349 - 0.203 \log w + 0.020T + 0.36S_{cap} - 0.119 \log D$ n = 91, $R^2 = 0.528$ $\log(P/\bar{B}) = 0.103 + 0.036T - 0.186 \log \bar{w}$ n = 91, $R^2 = 0.367$	P: production ($mgDW/m^2/yr$), $\bar{B}$: mean biomass ($mgDW/m^2$), $\bar{w}$: mean individual weight (mgDW), T: mean temperature (ºC), Scap: swimming capacity (qualitative variable: 0,1) D: depth	Marine suprabenthic crustaceans
Cusson and Bourget (2005b)	General models: $\log_{10} P = 0.45 + 1.01 \log_{10} \bar{B} - 0.84 \log_{10} L - 0.09\bar{w}$ n = 348, $R^2 = 0.92$ $\log_{10}(P/\bar{B}) = 0.39 + 0.86 \log_{10} L - 0.08 \log_{10} \bar{w} - 0.007 \log_{10} T$ n = 352, $R^2 = 0.73$	P: production ($kJ/m^2/yr$), $\bar{B}$: mean biomass (kJ/m^2), $\bar{w}$: mean individual weight (kJ/ind), L: life span (yr) D: depth (m) T: temperature (ºC)	Marine and transitional waters

MS: mesh size (mm)

Models for different *taxa*:

$$\log_{10}\left(P/\bar{B}\right) = a + \left(b_1 \log_{10} L\right) + \left(b_2 \log_{10} \bar{w}\right) + \left(b_3\left(D+1\right)\right) + \left(b_4 T\right) + \left(b_5 \log \bar{B}\right)$$

Models	**a**	**b_1**	**b_2**	**b_3**	**b_4**	**b_5**	**n**	**R^2**
Amphipoda	0.52	-1.17	-0.10	-0.003	-	-	57	0.84
Bivalvia	0.47	-0.79	-0.12	-	-	-	116	0.69
Equinodermata	-0.03	-0.94	-0.19	-	0.04	-	26	0.78
Gastropoda	0.36	-0.71	-	-	-	-	43	0.5
Polychaeta	-0.03	-0.95	-	0.002	0.05	-	64	0.55

Models for different depth/substratum:

$$\log_{10}\left(P/\bar{B}\right) = a + \left(b_1 \log_{10} L\right) + \left(b_2 \log_{10} \bar{w}\right) + \left(b_3\left(D+1\right)\right) + \left(b_4 T\right) + \left(b_5 MS\right)$$

Models	**a**	**b_1**	**b_2**	**b_3**	**b_4**	**b_5**	**n**	**R^2**
Intertidal	0.55	-0.89	-0.09	-	-	-	107	0.71
0-20 m depth	0.73	-0.92	-0.1	-0.01	-0.01	-	142	0.8
21-50 m depth	0.7	-0.84	-	-0.01	-	-	48	0.84

51-930 m depth	-0.49	-0.35	-0.2	-	0.08	-	38	0.86
Algae	0.84	-1.06	-	-0.02	-	-	24	0.65
Hard	0.33	-0.062	-0.14	-	-	-	53	0.74
Muddy	0.36	-0.76	-0.11	-	-	0.03	158	0.65
Sandy	0.64	-1.09	-	-	-	-	148	0.69

Legend: Qualitative variables (Brey 1999a, Brey 2001): DE SubT, if subtidal (1) or intertidal (0); DL InEpi, if infauna (1) or epifauna (0); DL Epi, if motile epifauna (1) or not (0); DT M, if Mollusca (1) or not (0); DT P if Polychaeta (1) or not (0); DT C, if Crustacea (1) or not (0); DT AC, Annelida or Crustacea (1) or not (0); DT E, if Echinodermata (1) or not (0); DT I, if Insecta (1) or not (0); DH Habitat1, lake (1) or other habitat (0)

Figure captions

Fig. 1. Scores for the annual production, mean annual density and biomass for four dominant species and the entire macrobenthic intertidal community of Mondego estuary from 1993 to 2002 (9 to 30 species on average), where several disturbance impacts occurred in a seagrass bed (a-e) and sandflat area (f-j). Eutrophication led to a macroalgal bloom in the sandflat in 1993, and a restoration plan was implemented in 1998 to restore the environmental quality (Dolbeth et al. 2007). Scores range between 1 and 0, which represent respectively the highest and lowest values obtained within the 10-year study for each parameter. For the populations of *S. plana* (a, f), *H. ulvae* (b, g) in both areas and *C. carinata* in the sandflat (h), production was estimated using classical techniques; for the remaining species by empirical models (c, d and i), and for the community, production was estimated using both techniques (see Dolbeth et al. 2007 for details). Lines are coincident when production, biomass and density have the same rank trend during the study period.

Explanation box for Fig. 1: to compare annual production, mean annual density and biomass, each parameter value during a 10-year study period (1993-2002, data on biomass and production from Dolbeth et al. 2007, on density from Dolbeth et al. 2003 and unpublished data) was normalized using the equation: $P_{Ni} = \frac{P_i - P_{\min}}{P_{\max} - P_{\min}}$, where P_N is the normalized parameter value (annual mean density, mean biomass or production), P_i is the parameter value for the year i of the 10-year study period. For some species and areas annual values from the 3 parameters were similar, especially when production was estimated by the empirical model (e.g. *H. diversicolor* - c, d and *C. carinata* in sandflat - i). Higher discrepancies in the scores were observed for other species (e.g. *S. plana* – a and *C. carinata* - h) and for the community in the sandflat (j), meaning that density and/or biomass provide different information than production. For example, the highest density but lowest biomass and production of *S. plana* in the seagrass bed was observed in 1994 (a).

Fig. 2. Schematic representation of the surface calculation under the Allen's curve that represents the somatic production from a single cohort. The area under the curve in graph (a) represents the production after 6 hypothetical sampling occasions (t_1 to t_6). This area can be estimated from the increment summation (b), removal summation (c) and from Allen curve methods (d). All mathematical equations and symbols are found in Table 1. Modified from Cusson (2004).

Fig. 3. Conceptual model for possible effects of eutrophication in production levels (↑: production increases; ↓: production decreases). The threshold between positive and negative impacts from nutrient loading will depend on (1) the system attributes acting as filters that modulate the responses to nutrient enrichment, including if it is already an impoverished or nutrient-enriched system; (2) nutrient enrichment as one of many interacting stressors (within climate, hydro-morphological characteristics of ecosystem, invasive species, among other stressors); (3) the complex linkages between responses in production levels; (4) impacts of change in the ecosystem for goods and services among other impacts that influence human exploitation of resources. Arrows between trophic groups compartments: black flow arrows, direct responses (e.g. food provided by phytoplankton, phytobenthos, macroalgae; O_2 depletion due to blooms); gray flow arrows, indirect responses (e.g. habitat heterogeneity, shelter from predators provided by seagrass); dashed flow arrows, possibility of both direct and indirect responses.

Fig. 4. Boxplot of annual secondary production for freshwater benthic communities, brackish water benthic communities and the non-indigenous invasive species *C. fluminea* populations alone. The middle line and extremities of the box are at the 25th, 50th, and 75th percentiles; the maximum length of each whisker represent 5th and 95th percentiles; outliers are shown individually. Data from Benke (1993), Hall et al. (2006), Dolbeth et al. (2003, 2007) and Sousa et al. (2008b).

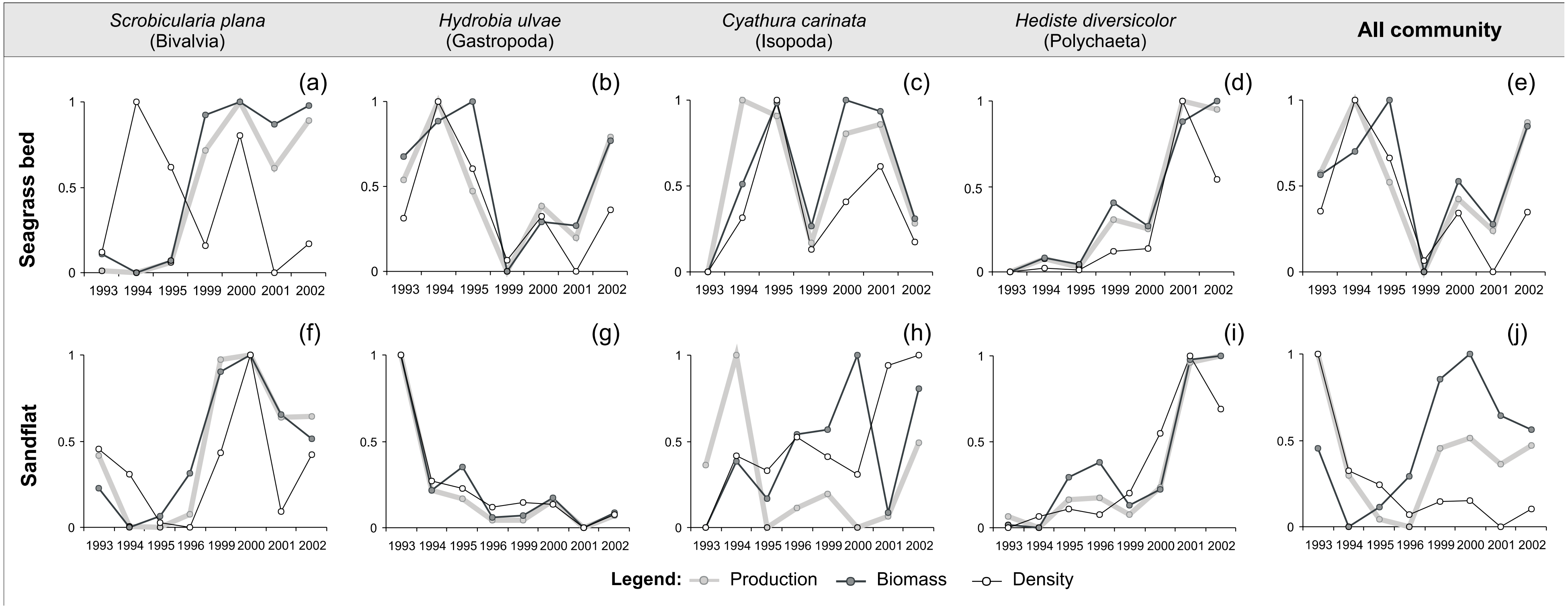
Scrobicularia plana
(Bivalvia)
Hydrobia ulvae
(Gastropoda)
Cyathura carinata
(Isopoda)
Hediste diversicolor
(Polychaeta)
All community
Seagrass bed
Sandflat
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
0
0.5
1
1993 1994 1995 1999 2000 2001 2002
1993 1994 1995 1996 1999 2000 2001 2002
Legend:
Production
Biomass
Density

Fig. 1.

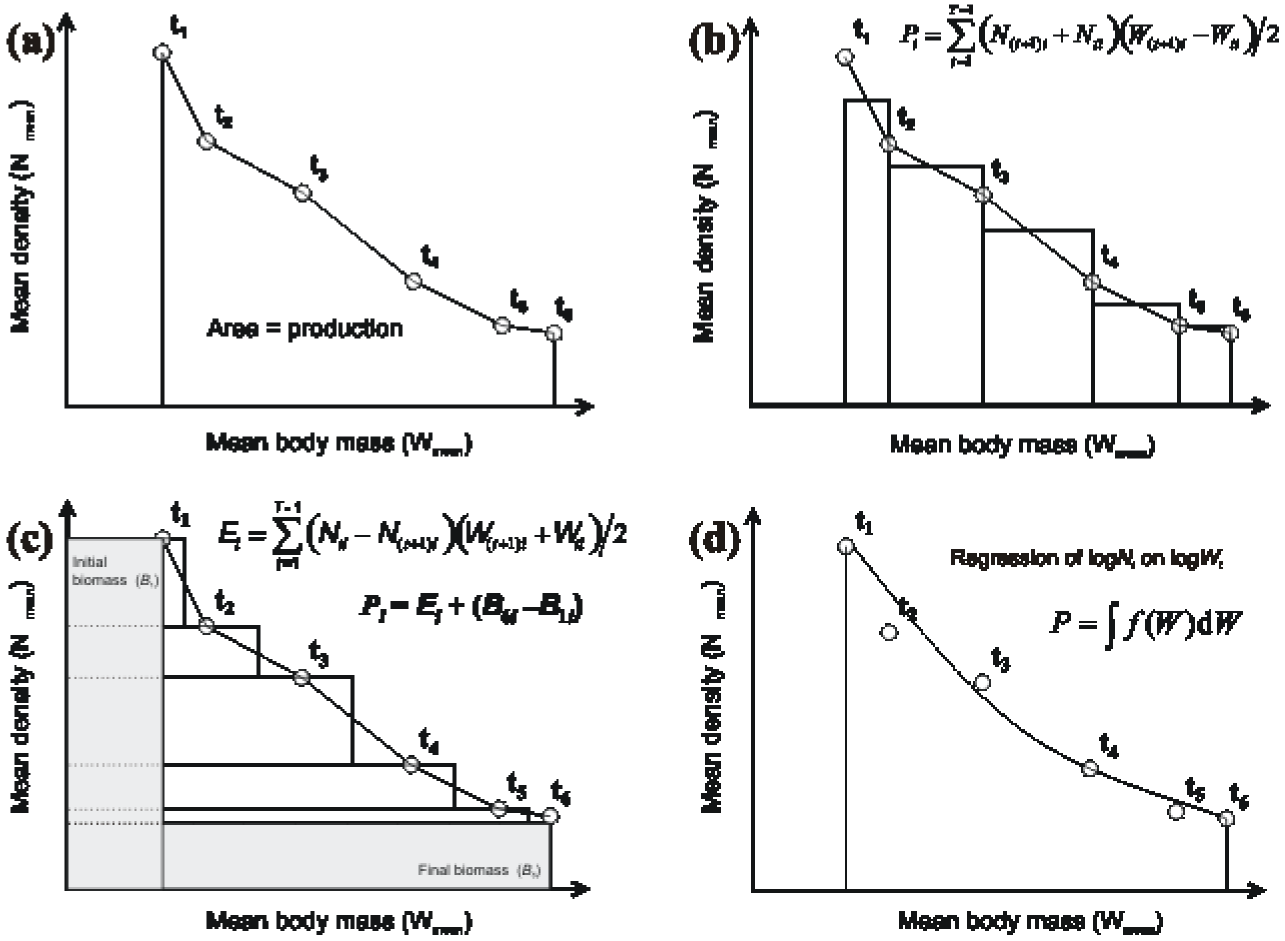
(a)
Mean density (N mean)
t_1
t_2
t_3
t_4
t_5
t_6
Area = production
Mean body mass (W mean)
(b)
$P_i = \sum_{t=1}^{T-1} \left(N_{(t+1)i} + N_{ti}\right)\left(W_{(t+1)i} - W_{ti}\right)/2$
Mean density (N mean)
t_1
t_2
t_3
t_4
t_5
t_6
Mean body mass (W mean)
(c)
$E_i = \sum_{t=1}^{T-1} \left(N_{ti} - N_{(t+1)i}\right)\left(W_{(t+1)i} + W_{ti}\right)/2$
$P_i = E_i + (B_{ti} - B_{1i})$
Initial biomass (B_1)
Final biomass (B_t)
Mean density (N mean)
t_1
t_2
t_3
t_4
t_5
t_6
Mean body mass (W mean)
(d)
Regression of logN_t on logW_t
$P = \int f(W)\,\mathrm{d}W$
Mean density (N mean)
t_1
t_2
t_3
t_4
t_5
t_6
Mean body mass (W mean)

Fig. 2.

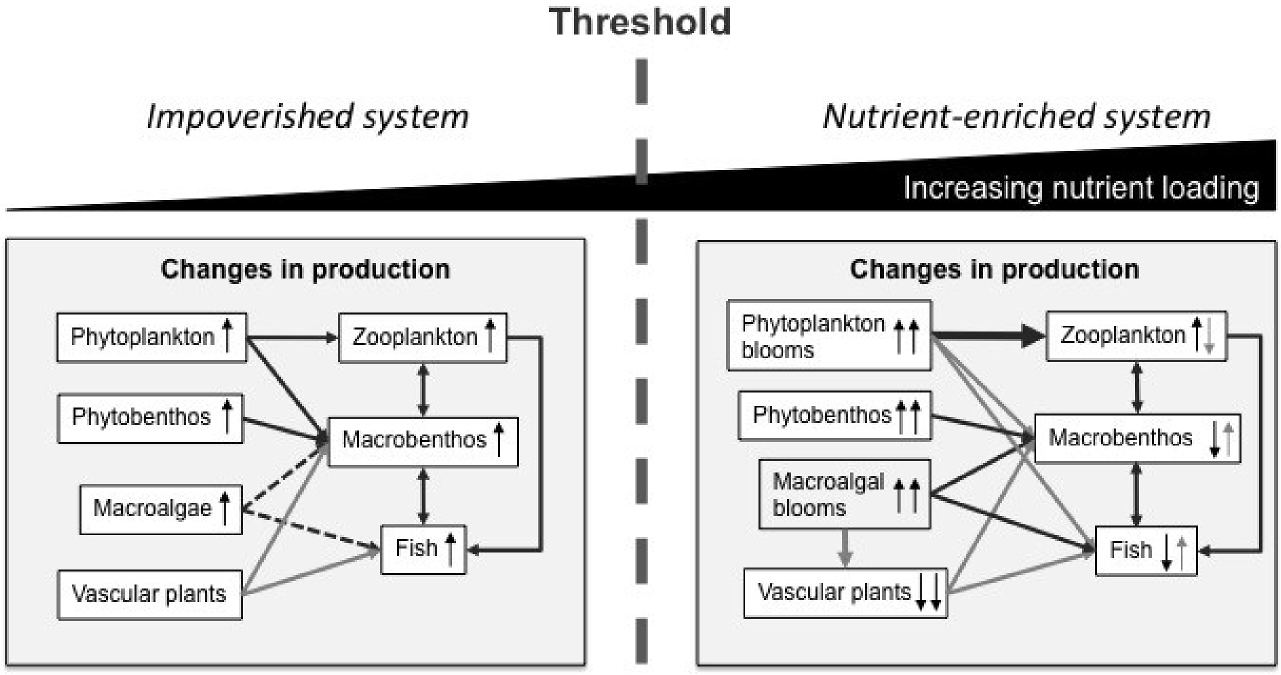
Threshold
Impoverished system
Nutrient-enriched system
Increasing nutrient loading
Changes in production
Phytoplankton ↑
Zooplankton ↑
Phytobenthos ↑
Macrobenthos ↑
Macroalgae ↑
Fish ↑
Vascular plants
Changes in production
Phytoplankton blooms ↑↑
Zooplankton ↑↓
Phytobenthos ↑↑
Macrobenthos ↓↑
Macroalgal blooms ↑↑
Fish ↓↑
Vascular plants ↓↓

Fig. 3.

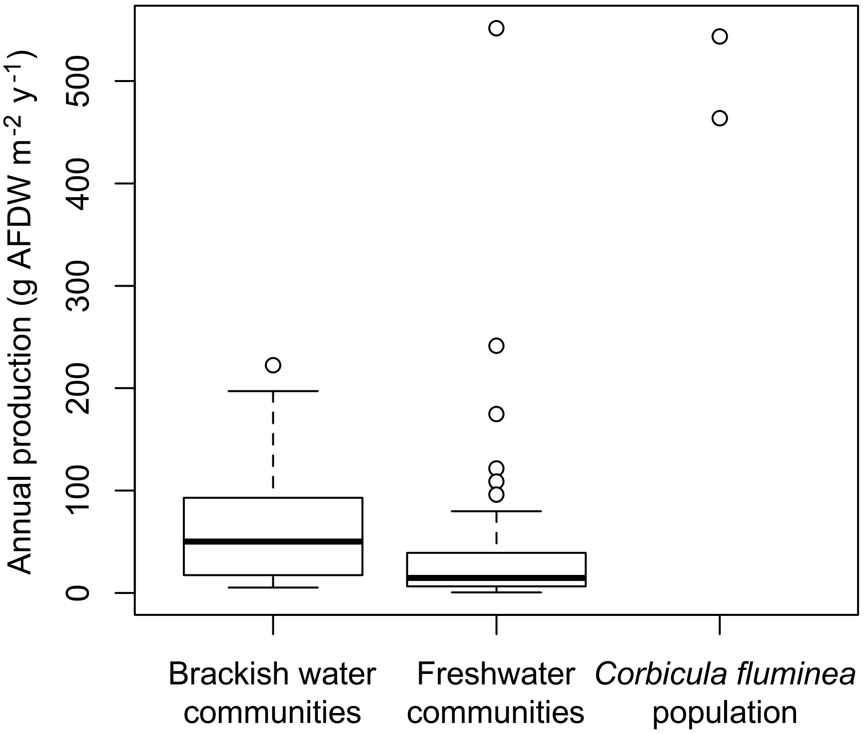
Annual production (g AFDW m-2 y-1)
0
100
200
300
400
500
Brackish water communities
Freshwater communities
Corbicula fluminea population

Fig. 4.