EVALUATION OF GROSS PRIMARY PRODUCTION ESTIMATES BASED ON BUOY DATA AND MECHANISTIC MODELLING IN ROSKILDE FJORD

Technical Report from DCE - Danish Centre for Environment and Energy No. 208

2021



EVALUATION OF GROSS PRIMARY PRODUCTION ESTIMATES BASED ON BUOY DATA AND MECHANISTIC MODELLING IN ROSKILDE FJORD

Technical Report from DCE - Danish Centre for Environment and Energy No. 208

2021

Nikolaj Reducha Andersen¹ Christian Lønborg¹ Peter Anton Stæhr¹ Anders Chr. Erichsen² Jacob Carstensen¹

¹Aarhus University, Department of Bioscience ²DHI



Data sheet

Series title and no.:	Technical Report from DCE - Danish Centre for Environment and Energy No. 208		
Category:	Scientific advisory report		
Title:	Evaluation of gross primary production estimates based on buoy data and mechanistic modelling in Roskilde Fjord		
Authors:	Nikolaj Reducha Andersen ¹ , Christian Lønborg ¹ , Peter Anton Stæhr ¹ , Anders Chr. Erichsen ² , Jacob Carstensen ¹		
Institutions:	¹ Aarhus University, Department of Bioscience, ² DHI		
Publisher: URL:	Aarhus University, DCE – Danish Centre for Environment and Energy © http://dce.au.dk/en		
Year of publication: Editing completed:	June 2021 June2021		
Referee: Quality assurance, DCE: Linguistic QA:	Jesper Philip Aagaard Christensen Anja Skjoldborg Hansen Anne Mette Poulsen		
Financial support:	SeaStatus is financed by the Innovation Foundation Denmark as part of the program. Grand Solution		
Please cite as:	Andersen, N.R., Lønborg, C., Stæhr, P.A., Erichsen, A.C. & Carstensen, J. 2021. Evaluation of gross primary production estimates based on buoy data and mechanistic modelling in Roskilde Fjord. Aarhus University, DCE – Danish Centre for Environment and Energy, 20 pp. Technical Report No. 208. <u>http://dce2.au.dk/pub/TR208.pdf</u>		
	Reproduction permitted provided the source is explicitly acknowledged		
Layout:	Graphic Group, AU Silkeborg		
Front page photo:	Colourbox		
ISBN: ISSN (electronic):	978-87-7156-599-7 2245-019X		
Number of pages:	20		
Internet version:	The report is available in electronic format (pdf) at http://dce2.au.dk/pub/TR208.pdf		

Contents

Pre	face		5
Sui	mmar	y	6
Sai	mmer	Ifatning	7
1	Intro	duction	8
2	Methods		9
	2.1	Study site	9
	2.2	Modelling of metabolic rates	9
3	Resu	llts	12
4	Disc	ussion	14
	4.1	The contribution by adjacent areas to metabolic rates	14
	4.2	Benthic contribution to metabolic rates	15
5	Con	clusion	16
6	Refe	rences	17

Preface

This report is the outcome of work package (WP) 6: *Modelling synthesis*, which is part of the project "SeaStatus". In this report, we compare the model estimates of gross primary production (GPP) using two different modelling approaches; a mechanistic model from DHI and a model based on buoy data from Aarhus University. The estimates are based on Station 60 in Roskilde Fjord during the period April-November 2015. The modelling approaches are described and discrepancies in estimates discussed.

Financial support to the report was provided by the Innovation Foundation Denmark as part of the project "SeaStatus – Innovative Technologies for Quantification of Sea Status".

Summary

Accurate models allowing assessment and prediction of metabolic processes in coastal areas are valuable tools that potentially can improve our knowledge of how current and future challenges of, for instance, climate change, eutrophication and ocean acidification impact the functioning of marine coastal ecosystems. Few attempts have been made to compare the outputs of marine ecological models. The evaluation of the mechanistic and buoy models presented in this report shows discrepancies in the estimated gross primary production in Roskilde Fjord. We suggest that oxygen produced elsewhere in the fjord, either benthically or from adjacent eelgrass beds, is the reason for the observed discrepancy since this production is only considered by the buoy model and not the mechanistic model.

Sammenfatning

Præcise modeller, der tillader bestemmelse og forudsigelse af metaboliske processer i kystområder er værdifulde værktøjer, der potentielt kan forbedre vores viden om, hvordan nuværende og fremtidige udfordringer med f.eks. klimaændringer, eutrofiering og forsuring af havet påvirker de marine kystøkosystemers funktion. Evaluering af en mekanistisk og en bøjedata-model i denne rapport, viser uoverensstemmelser i den estimerede primærproduktion i Roskilde Fjord. Ilt, der produceres andre steder i fjorden end bøjens lokation, vurderer vi til at være medvirkende til denne uoverensstemmelse i primærproduktionen. Det kunne f.eks. være bentisk produktion eller produktion fra tilstødende ålegræsbede, da produktion fra disse steder kun medregnes af bøjemodellen og ikke af den mekanistiske model.

1 Introduction

Accurate models allowing assessment and prediction of metabolic processes in coastal areas are valuable tools that potentially can improve our knowledge of how current and future challenges of, for instance, climate change, eutrophication and ocean acidification impact the functioning of marine coastal ecosystems. Reliable and rapid analysis and modelling of data such as temperature, light, oxygen, current and wind speed are becoming increasingly necessary, especially with the present advancement within the area of, for example, remote sensing and in-situ sensors that generate large amounts of data. But, how well ecosystem models predict different parameters is not only of scientific interest, it also helps to address policy and management questions. In the present report, we compare estimates of primary production obtained from an ecosystem model and a sensor-driven analysis to evaluate the pros and cons of the two methods as well as the degree to which these approaches supplement each other.

Coastal waters are among the most productive areas in the world and are responsible for 18-33% of the oceans' primary production (Wollast, 1998). In shallow parts of coastal waters, both pelagic primary production (PPP) and benthic primary production (BPP) contribute to the total system primary production (PP) (Borum & Sand-Jensen, 1996; Krause-Jensen et al., 2012). The two main parameters affecting the relative importance of BPP relative to total PP are the light reaching the bottom and the suitability of the benthic substrate. Depending on the combination of these two factors, an estuarine system can be dominated by either BPP or PPP (Krause-Jensen et al., 2012).

Primary production in coastal waters is often limited by nutrients, but light availability is the ultimate controller of photosynthesis (Mallin & Paerl, 1992). Therefore, changes in nutrient concentrations and the depth of the euphotic zone will influence ecosystem productivity (Staehr et al., 2012). Food web structure, for instance that of phytoplankton and zooplankton communities, and sizes have been shown to impact PP (Ikeda et al., 2007; Marañón, 2015).

Shallow coastal waters are expected to be dominated by BPP when light conditions enable a dense cover of benthic vegetation by macroalgae and seagrasses. Roskilde Fjord is an example of such a shallow system where light conditions favour primary production by benthic vegetation in most parts of the fjord (Staehr & Borum, 2011). It is therefore expected that a substantial part of the measured PP derives from the benthic habitat.

Although ecological models are commonly applied to assess and understand ecosystem conditions and responses, the parameterisation of the underlying processes driving the changes in state variables is seldom assessed and compared with actual measurements since parameter data are rarely available. Photosynthesis, which is the most fundamental metabolic process and used to describe marine ecosystems worldwide, can be estimated from, for instance, the oxygen production in the water. However, as mentioned above, oxygen can be produced at different locations in the system, which may cause mismatches when comparing results derived from models with different setups. With this study, we aim to compare model estimates of GPP using two different modelling approaches – a mechanistic model developed by DHI and a model based on buoy data from Aarhus University and, on the basis of this, describe if and where such a comparison is reasonable.

2 Methods

2.1 Study site

Roskilde Fjord is a 30 km long eutrophic and shallow (mean depth 3 m; surface area 123 km²; volume 0.362 km³) estuary, which to the north is connected to Kattegat (Kamp-Nielsen, 1992). In the fjord, a sill restricts the water exchange between the northern and the inner southern part. This restricted exchange together with a relatively small freshwater input result in a long freshwater residence time in the inner region of the fjord (about 1 year; Flindt et al., 1997) and a shorter residence time in the outer region (about 3–4 weeks; Flindt et al., 1997). Generally, the water column is well mixed, but stratification due to a high inflow of saline water from the Kattegat can occur in the northern deeper parts of the fjord. The total catchment area of Roskilde Fjord is about 1127 km² and the annual discharge is around 360×10^6 m³ y⁻¹, resulting in a yearly external nutrient loading of about 1000 ton N y⁻¹ and 50 ton P y⁻¹ (Staehr et al., 2017). The catchment area is dominated by agriculture (6%), while urban areas account for 15%. The remaining catchment is covered by forests, wetlands and lakes (Flindt et al., 1997).

2.2 Modelling of metabolic rates

2.2.1 Buoy model

Rates of GPP were modelled from changes in the concentration of dissolved oxygen (DO) that was measured every 10 min at Station 60 (55°71'3.0"N, 12°06'6.7"E) in Roskilde Fjord. Simultaneously, the amount of photosynthetic active radiation (PAR) was measured on site. Both the oxygen and the PAR logger were located 1 m below the water surface and were active from April to December 2015. Besides DO and PAR, temperature was measured. The technique for GPP estimation, called the "diel oxygen technique", was originally described by Odum (1956). The technique can also be used to estimate NEP (Net Ecosystem Production) and respiration (R), and although they are not part of the overall comparison, these components are also described in this report. A number of relationships are assumed in the modelling approach using the equation:

$$NEP = GPP - R \tag{1}$$

where NEP is the net ecosystem production, GPP is the gross primary production and R is the respiration.

Thus, at a given time, the change in dissolved oxygen provides information about the state of the system using the equation:

$$DO_{t+1} = DO_t + GPP_t - R_t + F_t \tag{2}$$

where DO_{t+1} and DO_t are the dissolved oxygen concentrations in mg l⁻¹ at discrete time *t*+1 and *t* with 10 min resolution, GPP_t is the gross primary production at time *t*, R_t is the ecosystem respiration at time *t*, and F_t is the net exchange of O_2 between the water and the atmosphere at time *t*. The net exchange of O_2 between the water and the atmosphere is calculated by the equation:

$$F_t = \left[K_t \left(DO_t - DO_{sat[t]} \right) / Z \right] / 2 \tag{3}$$

where DO is the measured concentration of dissolved oxygen in the water, $DO_{sat[t]}$ is the measured concentration of dissolved oxygen in the water in equilibrium with the atmosphere at ambient temperature and pressure at time *t*, *k*_t is the coefficient of gas exchange for DO at time *t*, and *Z* is the total depth of the water column at the measurement site.

The GPP component of equation 4 $(P_{max} \times \tanh(\alpha \times I_t/P_{max}))$ was considered according to Platt et al. (1980) and the R component $(R_{20} \times 1.07^{T_w-20})$ was considered according to Jørgensen (1979).

Combined, the overall model to calculate NEP is formulated by the equation:

$$\Delta DO_{t+1} = NEP_{hr} = P_{max} \times \tanh(\alpha \times I_t / P_{max}) - R_{20} \times 1.07^{T_w - 20}$$
(4)

where P_{max} is the light saturation point, α is the initial linear slope of the photosynthesis vs. light relationship describing the average rate of photosynthesis per unit of PAR, I_t is the surface PAR (µmol photons m⁻²s⁻¹) measured at time t, and R_{20} is respiration as a function of the rate of R at 20°C, water temperature (T_w) and a temperature sensitivity constant equal to 1.07.

The three parameters in Eq. (4) (Pmax, α and Rmax) were estimated using a conjugate-gradient optimisation algorithm, and the parameters were subsequently used to calculate hourly rates of NEP, GPP and R, inserting 10 min interval recordings of the mean available light in the water column and water temperature over a 24 h period (Brighenti et al., 2015; Staehr et al., 2018). The GPP model results were transformed to area-specific numbers by multiplication with the depth at Station 60 in Roskilde Fjord, which is 4.6 m.

2.2.2 Mechanistic model

The model developed and applied by DHI is a fully mechanistic biogeochemical model. The chemical and biological pelagic components of the models include one phytoplankton group at the time (diatoms at first followed by flagellates), one zooplankton group, inorganic nutrients (nitrogen and phosphorus), particulate organic matter, two fractions of dissolved organic matter, inorganic materials and dissolved oxygen. The benthic compartment includes a two-layer sediment pool of organic matter (carbon, nitrogen and phosphorus) and inorganic matter (carbon, nitrogen and phosphorus) and, where relevant, benthic vegetation (perennial macroalgae, opportunistic macroalgae, eelgrass biomass, eelgrass shoot density and benthic microalgae).

In the model, the following processes are described: phytoplankton assimilation; phytoplankton mortality; nitrogen fixation; zooplankton grazing; zooplankton excretion of detritus; dissolved inorganic nitrogen and phosphorus; oxygen- and temperature-dependent mineralisation of detritus and dissolved organic matter; sediment mineralisation and uptake/release from benthic vegetation and sediment fluxes; and oxygen- and temperature-dependent nitrification and denitrification. The sediment module also includes descriptions for permanent burial of organic matter and includes hydrogen sulphide in the sediment and water phase. More details are provided by DHI on the biogeochemical model (DHI, 2019b) and on the model setup for Roskilde Fjord (DHI, 2019a; DHI, 2020).

 Table 2.1. Biogeochemical model description of GPP processes.

	Processes included
GPP	Pelagic primary production + pelagic planktonic respiration (respiration of detri-
	tus, phytoplankton and zooplankton, mineralisation of labile and refractory car-
	bon, death of phytoplankton and oxygen demand of resuspended sediment) +
	benthic primary production (eelgrass, opportunistic macroalgae, perennial macro
	algae and benthic microalgae) + benthic respiration (sediment oxygen demand,
	mussel respiration, respiration of ephemeral and perennial macroalgae, respira-
	tion of benthic diatoms, respiration of eelgrass)

All the above processes are in g C $m^{-2} d^{-1}$; to convert to g $O_2 m^{-2} d^{-1}$, we use a factor of 3.5, which in the model is considered the ratio of O_2 production/consumption relative to carbon.

3 Results

Gross Primary Production (GPP) output estimates from the buoy data and the mechanistic model are compared for the period April to November 2015.

The GPP model estimates are presented as daily depth-integrated values and as monthly median values in, respectively, Fig. 3.1 and Fig. 3.2, and a table is included, showing the difference between the two model estimates (Table 3.1).



Figure 3.1. Model output of gross primary production from the buoy model and the mechanistic model for the year 2015 at station 60 in Roskilde Fjord. Dots are daily depth-integrated values and the line represents a running mean of the seven previous observations.

Results are not available from December–March; however, the running mean value stills shows a seasonal trend (Fig. 3.1). From the beginning of May until the end of August, the differences in estimated GPP are higher than from September to November. This is especially noticeable in the estimates from the buoy model. The mechanistic model shows more constant estimates from April to October, and only mid-October to mid-November estimates displays a drop in GPP.

There is also a difference in the variance of the two model estimates (Fig. 3.2). The IQR (Inter Quartile Range) showing the estimates between the 25th and the 75th percentile ranged between 1 and 2 g $O_2 m^{-2} d^{-1}$ for the mechanistic model, whereas the buoy model IQR ranged between 3 and 5 g $O_2 m^{-2} d^{-1}$ for the majority of the months. The minimum daily estimates are close for both models – 0.13 g $O_2 m^{-2} d^{-1}$ for the mechanistic and 0.61 g $O_2 m^{-2} d^{-1}$ for the buoy model (both measurements are from November).

The mechanistic model has been validated and compared to pelagic primary production measurements from the national monitoring program on the aquatic environment (NOVANA) in the period 2002-2016, and the model and measured pelagic primary production data exhibit similar seasonality and similar levels. However, in the present study we discuss the differences between the buoy data approach and mechanistic modelling and do not validate either of the two methods. **Figure 3.2.** Model output of gross primary production (GPP) from the buoy model and the mechanistic model for the year 2015 at station 60 in Roskilde Fjord. The boxplot shows the median and the 25th and 75th percentiles for each month and the dots are daily depth-integrated values.



Table 3.1. Median monthly gross primary production (g $O_2 m^{-2} d^{-1}$) in year 2015.

Month	GPP (buoy model)	GPP DHI	Difference
April	3.7	2.6	1.1
Мау	5.5	2	3.5
June	4.8	2.1	2.7
July	6.7	2.2	4.5
August	7.3	2.3	5.0
September	3	1.9	1.1
October	1.3	0.9	0.4
November	0.8	0.3	0.5

4 Discussion

In this report, we compared output estimates of gross primary production (GPP) between a model based on buoy data and a mechanistic model. Our hypothesis was that there would be no differences between the two models since they provide estimates for the same station from the same year. However, our results demonstrate an up to 3-4 times difference in the GPP estimates between the two models. The magnitude of the difference is highly seasonal, with higher differences in the spring-summer months (April–September) and more comparable results in the colder months (October–November). Unfortunately, buoy data are not available for December-March, preventing comparison of GPP estimates for this period.

Several factors may affect the GPP model estimates; for example, large daily variability in ecosystem production has been associated with variations in cloud cover and consequent changes in sunlight levels (Fisher et al., 2003) as well as wind-induced changes in mixing and resuspension impacting the light climate and transport (Staehr & Sand-Jensen, 2007). Depending on water depth, sediment characteristics and macrophyte density, such external forcing will interact with the hydrodynamics, eventually influencing the metabolic processes and oxygen transport in the nearshore shallow habitats (Hume et al., 2011). In the present report, we have not evaluated all the factors that may contribute to the discrepancies in results from the two models. Instead, we have identified those that we consider to be the primary causes of the relatively pronounced differences observed. The models exhibit the largest deviation in the productive season, which we suggest is related to production of oxygen by nearby macrophyte beds and benthic microalgae. This oxygen is subsequently transported to Station 60 and thus influences the buoy estimates. Below, we describe the two high-productive habitats and discuss how they may lead to the observed discrepancies in modelled rates.

4.1 The contribution by adjacent areas to metabolic rates

The buoy model estimates metabolic rates by the open-water diel oxygen technique (Staehr et al., 2018), which is based on measurements of changes in O_2 in the pelagic zone. However, oxygen is potentially not produced solely in the pelagic zone, it may be influx from other adjacent high-productive areas such as nearby beds of eelgrass (*Zostera marina*). Eelgrass covers about 8% of the seabed in Roskilde Fjord and the eelgrass beds are mainly located along the shallow coastline where they may contribute substantially to the system GPP (Duarte & Chiscano, 1999; McGlathery et al., 2001; Öberg, 2006).

Reductions in water clarity of shallow coastal waters, mostly due to eutrophication, have caused global losses and reduced depth colonisation of seagrass meadows (Orth et al., 2006; Short & Wyllie-Eciieverria, 1996; Waycott et al., 2009). With decreasing nutrient level and increasing water clarity in the coming years, the oxygen produced by eelgrass and other macrophyte beds will expectedly increase even further. As the mechanistic model does not consider primary producers outside Station 60, oxygen produced in adjacent areas is only evident in the buoy model.

4.2 Benthic contribution to metabolic rates

Currently, the benthic vegetation in Roskilde Fjord is restricted to depths shallower than 3 m. This is mainly a consequence of the organic-rich sediments that are unsuitable for rooted plants (Staehr et al., 2019). Benthic microalgae living at the surface of the soft sediments in the relatively deeper parts of the inner fjord (3 to 4.5 m depth) can establish very dense covers with visible production of oxygen (Peter Staehr, pers. obs.). So, although the prevailing light conditions suggest a substantial benthic production by submerged vegetation, it is more likely that the BPP in the central fjord surrounding station 60 originates from a dense benthic film of microalgae on the muddy sediments. A few measurements of BPP around station 60 indicate rates below 1 g O_2 m² d⁻¹ or less than 5% of the total areal GPP, suggesting that most of the GPP in the central station 60 area is pelagic (Staehr et al., 2018), which is confirmed by the mechanistic model.

A few studies exist that have attempted to measure the BPP from microalgae in estuarine systems in the Baltic Sea, which is comparable to that of Roskilde Fjord (reviewed in Ask et al., 2016). Ask et al. (2016) studied the contribution of BPP from microalgae in an estuary in the Bothnian Bay and concluded that the contribution corresponded to 17% of the total system PP (31% when upscaled to the whole Bothnian Bay). The authors argue that benthic microalgae are more adapted to low light than pelagic microalgae, and BPP is therefore often underestimated due to the earlier assumption that PP does not take place below the photic zone. The benthic conditions at Station 60 in Roskilde Fjord are a soft bottom consisting of mud/silt without any major vegetation and a water depth of around 4.6 m. Under these conditions, the GPP from benthic microalgae has been calculated to range between 200 and 300 mg C m⁻² d⁻¹ (as in other comparable shallow estuary systems reviewed in Ask et al., 2016). Benthic primary production is not based on explicit measurements in either the buoy model or the mechanistic model. The relative importance of BPP from microalgae could therefore be a factor explaining the differences in GPP output between the models.

5 Conclusion

This study compared model estimates of gross primary production (GPP) from Station 60 in Roskilde Fjord from April to November 2015. Discrepancies between the models occurred, especially in the high productive season from May to August. These discrepancies are most likely explained by the fact that the buoy model is a "system" model for the whole fjord and therefore also measures oxygen produced elsewhere in the fjord. Contrarily, the mechanistic model is based on the "point" of Station 60 and only predicts the primary production at this exact location.

In future works, the mechanistic model could be set up to incorporate other areas of the fjord. However, to be able to compare the two models on a larger scale, the buoy model must estimate water movement to determine the areas from where the measured oxygen originates as well as their size.

6 References

Ask, J., Rowe, O., Brugel, S., Strömgren, M., Byström, P., & Andersson, A. (2016). Importance of coastal primary production in the northern Baltic Sea. *Ambio*, *45*(6), 635–648. https://doi.org/10.1007/s13280-016-0778-5

Borum, J., & Sand-Jensen, K. (1996). Is total primary production in shallow coastal marine waters stimulated by nitrogen loading? *Oikos*, *76*(2), 406. https://doi.org/10.2307/3546213

Brighenti, L. S., Staehr, P. A., Gagliardi, L. M., Brandão, L. P. M., Elias, E. C., de Mello, N. A. S. T., Barbosa, F. A. R., & Bezerra-Neto, J. F. (2015). Seasonal changes in metabolic rates of two tropical lakes in the Atlantic Forest of Brazil. *Ecosystems*, *18*(4), 589–604. https://doi.org/10.1007/s10021-015-9851-3

DHI. (2019a). Development of Mechanistic Models. Mechanistic Model for Roskilde Fjord. Hydrodynamic model documentation. DHI report (project no. 11822245).

DHI. (2019b). Development of Mechanistic Models. Short Technical Description of the Biogeochemical Models Applied for the Mechanistic Model Development. DHI technical report (project no. 11822245).

DHI. (2020). Development of Mechanistic Models. Mechanistic Model for Roskilde Fjord. Technical documentation on biogeochemical model. DHI report (project no. 11822245).

Duarte, C. M., & Chiscano, C. L. (1999). Seagrass biomass and production: A reassessment. *Aquatic Botany*, *65*(1–4), 159–174 https://doi.org/10.1016/S0304-3770(99)00038-8

Fisher, T. R., Gustafson, A. B., Radcliffe, G. M., Sundberg, K. L., & Stevenson, J. C. (2003). A Long-term record of photosynthetically available radiation (PAR) and total solar energy at 38.6°N, 78.2°W. *Estuaries*, *26*(6), 1450–1460. https://doi.org/10.1007/BF02803653

Flindt, M. R., Kamp-Nielsen, L., Marques, J. C., Pardal, M. A., Bocci, M., Bendoricchio, G., Salomonsen, J., Nielsen, S. N., & Jørgensen, S. E. (1997). Description of the three shallow estuaries: Mondego River (Portugal), Roskilde Fjord (Denmark) and the Lagoon of Venice (Italy). *Ecological Modelling*, *102*(1), 17–31. https://doi.org/10.1016/S0304-3800(97)00092-6

Hume, A. C., Berg, P., & McGlathery, K. J. (2011). Dissolved oxygen fluxes and ecosystem metabolism in an eelgrass (*Zostera marina*) meadow measured with the eddy correlation technique. *Limnology and Oceanography*, *56*(1), 86–96. https://doi.org/10.4319/lo.2011.56.1.0086

Ikeda, T., Sano, F., & Yamaguchi, A. (2007). Respiration in marine pelagic copepods: A global-bathymetric model. *Marine Ecology Progress Series, 339*, 215–219. https://doi.org/10.3354/meps339215

Jørgensen SE. (1979). *Handbook of Environmental data and ecological parameters*. National society for Ecological Modelling.

Kamp-Nielsen, L. (1992). Benithic-pelagic coupling of nutrient metabolism along an estuarine eutrophication gradient. *Hydrobiologia*, *235–236*(1), 457–470. https://doi.org/10.1007/BF00026234

Krause-Jensen, D., Markager, S., & Dalsgaard, T. (2012). Benthic and pelagic primary production in different nutrient regimes. *Estuaries and Coasts*, *35*(2), 527–545. https://doi.org/10.1007/s12237-011-9443-1

Mallin, M. A., & Paerl, H. W. (1992). Effects of variable irradiance on phytoplankton productivity in shallow estuaries. *Limnology and Oceanography*, *37*(1), 54–62. https://doi.org/10.4319/lo.1992.37.1.0054

Marañón, E. (2015). Cell size as a key determinant of phytoplankton metabolism and community structure. *Annual Review of Marine Science*, *7*, 241–264. https://doi.org/10.1146/annurev-marine-010814-015955

McGlathery, K., Anderson, I., & Tyler, A. (2001). Magnitude and variability of benthic and pelagic metabolism in a temperate coastal lagoon. *Marine Ecology Progress Series*, *216*, 1–15. https://doi.org/10.3354/meps216001

Öberg, J. (2006). Primary production by macroalgae in Kattegat, estimated from monitoring data, seafloor properties, and model simulations. *Continental Shelf Research*, *26*(19), 2415–2432. https://doi.org/10.1016/j.csr.2006.07.005

Odum, H. T. (1956). Primary production in flowing waters. *Limnology and Oceanography*, 1(2), 102–117. https://doi.org/10.4319/lo.1956.1.2.0102

Orth, R. J., Carruthers, T. J. B., Dennison, W. C., Duarte, C. M., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Olyarnik, S., Short, F. T., Waycott, M., & Williams, S. L. (2006). A global crisis for seagrass ecosystems. In *BioScience* (Vol. 56, Issue 12). Oxford Academic. https://doi.org/10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2

Platt, T., Gallegos, C., & Harrison, W. (1980). Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. *Journal of Marine Research*, *38*, 687–701.

Short, F. T., & Wyllie-Eciieverria, S. (1996). Natural and human-induced disturbance of seagrasses. In *Environmental Conservation* (Vol. 23, Issue 1, pp. 17–27). https://doi.org/10.1017/s0376892900038212

Staehr, P. A., Asmala, E., Carstensen, J., Krause-Jensen, D., & Reader, H. (2018). Ecosystem metabolism of benthic and pelagic zones of a shallow productive estuary: Spatio-temporal variability. *Marine Ecology Progress Series*, *601*, 15–32. https://doi.org/10.3354/meps12697

Staehr, P. A., & Borum, J. (2011). Seasonal acclimation in metabolism reduces light requirements of eelgrass (*Zostera marina*). *Journal of Experimental Marine Biology and Ecology*, 407(2), 139–146 https://doi.org/10.1016/j.jembe.2011.05.031

Staehr, P. A., Göke, C., Holbach, A. M., Krause-Jensen, D., Timmermann, K., Upadhyay, S., & Ørberg, S. B. (2019). Habitat model of eelgrass in Danish coastal waters: Development, validation and management perspectives. *Frontiers in Marine Science*, *6*, 175. https://doi.org/10.3389/fmars.2019.00175

Staehr, P. A., & Sand-Jensen, K. (2007). Temporal dynamics and regulation of lake metabolism. *Limnology and Oceanography*, *52*(1), 108–120. https://doi.org/10.4319/lo.2007.52.1.0108

Staehr, P. A., Testa, J., & Carstensen, J. (2017). Decadal changes in water quality and net productivity of a shallow Danish estuary following significant nutrient reductions. *Estuaries and Coasts*, *40*(1), 63–79. https://doi.org/10.1007/s12237-016-0117-x

Staehr, P. A., Testa, J. M., Kemp, W. M., Cole, J. J., Sand-Jensen, K., & Smith, S. V. (2012). The metabolism of aquatic ecosystems: History, applications, and future challenges. *Aquatic Sciences*, *74*(1), 15–29. https://doi.org/10.1007/s00027-011-0199-2

Waycott, M., Duarte, C. M., Carruthers, T. J. B., Orth, R. J., Dennison, W. C., Olyarnik, S., Calladine, A., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Short, F. T., & Williams, S. L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(30), 12377–12381. https://doi.org/10.1073/pnas.0905620106

Wollast, R. (1998). Evaluation and comparison of the global carbon cycle in the coastal zone and in the open ocean. *The Sea*, *10*, 213–252. https://ci.nii.ac.jp/naid/10012001948

EVALUATION OF GROSS PRIMARY PRODUCTION ESTIMATES BASED ON BUOY DATA AND MECHANISTIC MODELLING IN ROSKILDE FJORD

ISBN: 978-87-7156-599-7 ISSN: 2245-019X