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Tune in on 11.57 μHz and listen to primary production

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Abstract. In this manuscript we present an an elegant approach to reconstruct slowly varying GPP as a function of time, based on O_2 time series. The approach, called complex demodulation, is based on on a direct analogy with amplitude modulated (AM) radio signals. The O_2 concentrations oscillating at the diel frequency (or 11.57 μHz) can be seen as a 'carrier wave', while the time variation in the amplitude of this carrier wave is related to the time varying GPP. The relation follows from an analysis in the frequency domain of the governing equation of O_2 dynamics. After the theoretical derivation, we assess the performance of the approach by applying it to 3 artificial O_2 time series, generated with models representative for a well mixed vertical water column, a river and an estuary. These models are forced with hourly observed incident irradiance, resulting in a variblity of GPP on scales from hours to months. The dynamic build-up of algal biomass further increases the seasonality. Complex demodulation allows to reconstruct with great precision time varying GPP of the vertical water column and the river model. Surprisingly, it is possible to derive daily averaged GPP - complex demodulation thus reconstructs the amplitude of every single diel cycle. Also in estuaries time varying GPP can be reconstructed to a great extent. But there, the influence of the tides prevent achieving the same temporal resolution. In particular, the combination of horizontal O_2 gradients with the O1 and Q1 harmonics in the tides, interferes with the complex demodulation procedure, and introduces spurious amplitude variation that can not be attributed to GPP. But also other tidal harmonics, in casu K1 and P1, introduce diel fluctuations that can not be distinguished from GPP. We demonstrate that these spurious effects also occur in real-world time series (Hörnum Tief, De). The spurious fluctuations introduced by O1 and Q1 can be removed to a large extent by increasing the averaging time to 15 days. As such, we demonstrate that a good estimate of the running 15 day average of GPP can be obtained in tidal systems. Apart from the direct merits to estimating GPP from O_2 time series, the analysis in the frequency domain enhances our insights in O_2 dynamics in tidal systems in general, and in the performance of O_2 methods to estimate GPP in particular.

1 Introduction

Accurate rate estimates of whole ecosystem metabolism are crucial for our understanding of food web dynamics and biogeochemical cycling in aquatic ecosystems. Starting with the seminal work of Odum (1956), time series of in-situ oxygen concentrations have been used to infer rates of gross primary production (GPP) and community respiration (CR) in natural waters (Staehr et al., 2010, 2012). This so-called diel oxygen method (also often referred to as the Odum method) tracks the oxygen concentration at a specific water depth over a 24 hour cycle, and calculates GPP from the rate of change of oxygen during daylight hours, while adding the rate of community respiration determined at night (Howarth and Michaels, 2000). The diel oxygen method has major advantages over methods that rely on the ex-situ incubation of water samples. First, 'bottle effects' are avoided: GPP and CR rates are obtained at ambient light fields, and natural levels of turbulence, nutrients and grazing; such conditions are hard to mimic in bottle incubation experiments. Second, upscaling bottle incubation GPP rates to depth integrated production depends on a range of assumptions about the in-situ light field, and mixing of the water body. There is, however, a major challenge associated with the in-situ diel oxygen method: oxygen concentrations are not only affected by primary production and respiration, but also by turbulent mixing, advective transport, and air-water exchange. Consequently, the effect of these transport processes on the rate of change of oxygen needs to be properly constrained, before one can confidently estimate GPP and CR. In open systems with substantial gas exchange, estimates of ecosystem metabolism critically depend on the rate of reaeration, and the resulting GPP and CR values are highly sensitive to reaeration parameterizations (Tobias et al. 2009). Similarly, the diel oxygen method runs into trouble when advection and dispersion processes strongly influence the oxygen concentration, as small errors in the parameterization of these transport processes can lead to order-of-magnitude errors in resulting metabolic rates (Kemp and Boynton, 1980).

Recently we examined a novel strategy to apply the diel oxygen method to aquatic systems that have a strong imprint of transport processes (Cox et al., 2015). Based on an analysis in the frequency domain of the governing equation of oxygen dynamics in aquatic systems, we derived a relation between time averaged GPP and the amplitude of the diel harmonic in an oxygen time series. The central idea behind the analysis is that primary production is the dominant process that induces a 24h periodicity in the oxygen concentration while other processes have their imprint at other frequencies. We demonstrated that this assumption is valid in systems with a range of rates of mixing, air–water exchange and primary production. However, the method we outlined allowed only a single average GPP estimate representative for average GPP over the period of the O_2 time series was collected. This means that the slow variability of GPP, on time scales ranging from days to years, could not be resolved. This slow variability is expected due to seasonal and weather related variation of light availability, build-up of algal biomass, reduction of algal biomass by grazing, variable discharges and upstream inputs of nutrients and algal biomass. This GPP-variability will show up in O_2-recordings as slow variations in the amplitude of diurnal O_2 oscillations. Moreover, based on simulations we concluded that the performance of the method in estuarine systems is less, due to the tidal movement of an O_2 gradient along the sensor, but we could not explain exactly how this influences the estimate.

In this paper we investigate an elegant approach to reconstruct the slowly varying GPP as a function of time, thereby improving the temporal resolution of the Fourier method. The approach also enhances our theoretical understanding of the how the tidal movement of an O_2 gradient results in spurious diel O_2 patterns that can not be attributed to GPP. This insight is also relevant for classic diel O_2 methods. The approach is based on on a direct analogy with amplitude modulated (AM) radio signals. AM-radio transmits sound (0 - 15 kHz) by modulating the amplitude of an electromagnetic carrier wave (a single frequency from the 150 kHz - 30 MHz band). The sound that we want to hear from our radio is translated to the time varying amplitude of the carrier wave. This is conceptually similar to a time varying GPP, that will cause a time variation in the diel

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amplitude of oxygen concentrations: the 'carrier wave' then are the O_2 concentrations oscillating at the diel frequency, or 11.57 μHz.

2 Material and methods

2.1 Theory

In (Cox et al., 2015), we demonstrated that the time averaged GPP can be estimated from high frequency in-situ O_2 series as

$$\overline{GPP(t)} \approx 4\pi A_{O_2} \frac{\sin\theta - \theta\cos\theta}{\theta - \frac{1}{2}\sin 2\theta} \quad \text{with} \quad \theta = \pi \mathrm{fDL} \tag{1}$$

where fDL is the relative fraction of light hours during the day, and A_{O_2} is the amplitude of the diurnal fluctuations in the O_2 series, derived from the Fourier transform as $A_{O_2} = |\mathcal{F}(O_2)(2\pi)|$. We derived this relation by analysing the Fourier transformed differential equations describing oxygen dynamics. It is valid when 4 assumptions are satisfied. First, biochemical processes consuming oxygen have negligible diurnal periodicity, an assumption underlying all diel oxygen methods. Second, the measurement domain is perfectly mixed. This assumption is necessary when one wants to estimate depth averaged GPP from single depth O_2 measurements with any diel oxygen method. Third, diurnal fluctuations of horizontal or vertical fluxes into the measurement domain are negligible. Finally, the evolution of GPP over a day is approximated by a truncated sinusoid. In Cox et al. (2015) we assessed these assumptions and concluded that they are valid in a wide range of systems. In tidal systems the performance of the Fourier method was least, although also there relation 2 holds to a large extent.

When GPP varies slowly with time, so will A_{O_2}. The mathematical procudure to extract the slowly varying amplitude of a signal is called *complex demodulation* (Bloomfield, 2000). Assume we are interested in the slowly varying amplitude of a cosine function

$$x(t) = A(t)\cos(\omega t + \phi) \tag{2}$$

$$= \frac{A(t)}{2}\left(\exp i(\omega t + \phi) + \exp -i(\omega t + \phi)\right) \tag{3}$$

where we used Euler's relation to write the cosine function as a sum of complex exponentials, and with i the imaginary unit. The amplitude $A(t)$ is assumed to vary slowly when compared to the periodic oscillation in the cosine functions. Multiplying with $\exp -i\omega t$ gives

$$y(t) = \frac{A(t)}{2}\exp i\phi + \frac{A(t)}{2}\exp\left(-i(2\omega t + \phi)\right) \tag{4}$$

As A(t) is assumed to vary slowly, we can low-pass filter y(t) to get

$$y'(t) = \frac{A(t)}{2}\exp i\phi \tag{5}$$

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Discussion started: 13 March 2017

where the prime denotes low-pass filtering. After noting that for fixed amplitude sinusoid $|\mathcal{F}(A\cos\omega t)(\omega)| = A/2$, we have

$$GPP'(t) \approx 4\pi|y'(t)|\frac{\sin\theta - \theta\cos\theta}{\theta - \frac{1}{2}\sin 2\theta} \quad \text{with} \quad y(t) = O_2(t)\exp 2\pi i t \tag{6}$$

This relation allows to estimate slowly varying GPP based on high frequency O_2 time series. It is the central result of this paper.

Diurnal tidal constituents moving back and forth a horizontal oxygen profile will also result in diurnal O_2 fluctuation, but these can not be attributed to GPP. To assess their impact we will analyse the first order order term in the spatial Taylor expansion of simulated oxygen time series (see below for details on simulations). When we denote by $O_2(x,t)$ the horizontal oxygen profile in a reference frame moving with the tides, the time series recorded by a sensor ${O_2}^S(t)$ at a fixed location $x = 0$ is given by

$$ {O_2}^S(t) = O_2(x(t),t) \tag{7}$$

$$ = O_2(0,t) + \left.\frac{\partial O_2(x,t)}{\partial x}\right|_{x=0} x(t) + \mathcal{O}(x^2(t)) \tag{8}$$

where $x(t)$ is the time varying tidal excursion at the sensor location. The second term in the latter equation represents the first order effect of the tides moving back and forth the O_2 gradient. Based on simulation results, we can calculate this first order correction for the impact of the tides on the GPP estimate, by substituting $O_2(t)$ in equation 6 by ${O_2}^S(t) - \left.\frac{\partial O_2(x,t)}{\partial x}\right|_{x=0} x(t)$. Obviously, in real world situation such correction term can not be easily estimated and would require an estimate of time varying horizontal gradients and tidal excursion at the sensor location. But when numerically simulating oxygen concentration, this additional information is readily available. Similarly, it is straightforward to apply the classic Odum method, sensu Cole et al. (2000), to the model output for comparison.

2.2 Application to artificial data

To assess the performance of complex demodulation to estimate time varying GPP, we use artificial data sets generated with two numerical models. The first model describes a water body with no appreciable lateral transport of oxygen, representative for a lake or the surface layer of the ocean, where vertical turbulence and air-water exchange are the dominant transport processes. The second describes a typical riverine or estuarine situation, characterized by substantial horizontal gradients in the O_2 concentration. A full description of these models is found in (Cox et al., 2015).

As the models are forced with observed hourly irradiance data, GPP is a function of time. This causes an overall seasonality in GPP as well as shorter term variability due to changes in cloudiness. As forcing we used incident light recorded in 2009 on the roof of NIOZ-Yerseke (Nl.) using a Licor LI-190 SA cosine sensor. Additionaly, the dynamic build-up and break-down of algal biomass add both to the seasonality and to the short term variability.

We use a single numerical model to simulate typical riverine and estuarine situations. To emulate the occurence of tides, the output of the riverine model is resampled, using simulated velocities generated with a separate 1D tide resolved hydrodynamic

Biogeosciences Discuss., doi:10.5194/bg-2017-81, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 13 March 2017

model. We thus simulate estuarine transport with the riverine model, assuming a reference frame moving with the tides. This allows us to investigate the influence of tides on the GPP estimates (more details in Cox et al. (2015)).

2.3 Application to real world data

To test the performance on real world data, we used a full year of O_2 measurements, recorded at the Hörnum Tief measurement pole near Sylt island in the German Wadden Sea. The O2 time series were quality checked: outliers and other unphysical observations were removed manually (Götz Floeser, personal communication). There were short gaps in the time series ($<$ 4h) that were linearly interpolated to obtain a consistent data set at a fixed sampling rate (Δt=10 min).

3 Results

The results of the simulations with the open water model are shown in figure 1. The top panel shows the simulated depth averaged O_2 concentrations over the course of the year. The bottom panel shows both simulated depth averaged GPP and reconstructed GPP from complex demodulating the O_2 signal. Simulated GPP was filtered using a moving average filter of 1 day width - the values in figure 1 thus represent daily averaged GPP. The correlation between simulated and reconstructed GPP is very strong ($r^2 = 0.995$). It might come as a surprise that it is possible to reconstruct the daily averaged GPP from O_2 series since this means effectively that the amplitude of the diel oxygen fluctuations were resolved up to every single cycle. This is part of the power of complex demodulation.

Very similar results are obtained with the riverine model ($r^2 = 0.997$, model output not shown). These results reaffirm that under the simulated conditions, the impact of diurnal fluctuations in air-water exchange and in horizontal dispersive transport on O_2 is negligible compared to the impact of GPP.

The picture changes in the estuarine situation. The Fourier method nicely captures the seasonality in GPP as well as some of the variability on shorter scales (figure 2). But large mismatches are apparent, particularly during Winter and early Spring when GPP is low. These mismatches are largely explained by the first order effect of the tides. Indeed, including the first order term in the spatial Taylor expansion drastically improves the GPP estimate (figure 4, top panel). Short episodes of overestimation are still present during Winter time, showing that higher order terms of the impact of the tides are important in those periods.

This motivates us to further analyze this term. If the horizontal O_2 gradient is constant or slowly varying, the impact on GPP of the correction term results from the effect of the complex demodulation procedure on the tidal excursion $x(t)$. Thus, the tidal constituents close to the diurnal frequency in the tidal excursion will dominate the correction term. The most dominant harmonics in tidal velocity (and thus in tidal excursion) are the lunar diurnals O1 (T=25.8193 hours, Amplitude=0.0284 m s^{-1}) and K1 (T=23.9344 hours, Amplitude=0.0162 m s^{-1}), the solar diurnal P1 (T=24.0659 hours, Amplitude=0.0134 m s^{-1}) and the large lunar elliptic diurnal Q1 (T=26.868350 hours, Amplitude=0.0098 m s^{-1}) (Figure 3). Although these components are very small compared to the major M2 component (Amplitude=1.18 m s^{-1}) and other components with about semi-diurnal periodicity, they are the ones that interfer with the diurnal fluctuations we want to attribute to primary production.

Biogeosciences Discuss., doi:10.5194/bg-2017-81, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 13 March 2017

The spectrum of the correction term is indeed dominated by 3 frequencies related to those dominant harmonics (figure 4, central panel) - a low frequency peak at $|f_{K1} - f_{P1}|/2$ and two peaks at larger freqencies $|f_1 - f_{O1}|$ and $|f_1 - f_{Q1}|$. The low frequency peak is the result of the interaction of the K1 and P1 terms. Indeed, summing two cosine waves with slightly different frequencies f_1 and f_2 results in a signal with frequency $|f1 + f2|/2$ with a slowly varying amplitude, a phenomenon known as "beat". If both waves have equal amplitude, the frequency of this slow amplitude variation is given by $|f1 - f2|/2$ (when the amplitudes are not equal, the frequency becomes a function of time). Thus, approximately the interaction between K1 and P1 results in a signal with very close to diurnal periodicity (T 0.9999985 days). The period of the amplitude variation is 365.1 days.

The two other peaks result from the impact of complex demodulation on the O1 and Q1 components. The multiplication of the time series with $\exp(-i\omega t)$ has the effect of shifting all frequencies in the frequency spectrum of the signal down with ω. As a result, any frequencies close to the modulation frequncy ω_1 will lead to low frequency fluctuations in the demodulated signal. Taking the O1 as an example, $f = |f_1 - f_{O1}|$ corresponds to a period of 14.2 days. If the low pass filter in the second step of complex demodulation is too wide, these low frequencies are not filtered out. Since all results presented so far were obtained by applying a moving average filter of 1 day, this is the case.

But, this also means that it is possible to remove part of spurious GPP simply by decreasing the filter width (i.e. increasing the averaging time). Using a moving average filter of 15 days has almost the same effect as applying the correction term (figure 4, bottom panel). Obviously, this also means that GPP variability on time scales of less than 15 days can not be resolved. But the correspondence between complex demodulated O_2 and the 15d moving average GPP is striking. This is an important finding. In real world situations it would be very hard to measure the correction term, as it would require the time resolved observation of both the O_2 gradient and the tidal excursion at the measurement location. In contrast, increasing the averaging time is straightforward. The difference with the first order correction is still present, but small. The major cause of this difference is the K1, P1 interaction. In contrast to the spurious GPP due to $O1$ and $Q1$, which can be filtered out, the effect of the K1, P1 interaction can not be filtered out. Its frequency is so close to ω_1 that it is not possible to distinguish from GPP.

At this point it is relevant to take a look at the results of the classic Odum method. Applying the Odum method to the tidal O_2 time series to estimate daily GPP results in huge fluctuations (figure 5, top panel). Surprisingly, these fluctuations have exactly the $|f1 - fO1|$ frequency, as can be seen from the spectrum (figure 5, bottom panel). On the same spectrum we see that also the $|f1 - fQ|$ frequency is present. And indeed, 15d averaging the daily GPP estimates removes most of the fluctuations. Still, as expected for tidal systems, the performance of the Odum method is rather poor.

Applying the Fourier method to real world O_2 series shows the same phenomena as shown above. As an example, we analyse an O_2 time series from the Hörnum Tief measurement pole near Sylt island in the German Wadden Sea. At this location, the impact of the O1 component is even larger than in our simulations. This is both obvious from the demodulated time series and from the spectrum of the difference between the 1d and 15d low pass filtered demodulated O_2 series (figure 6). Either the O1 tidal consituent is indeed very large at this station, or the horizontal O_2 gradients are large. Here, however, the impact is much less apparent in winter. This is not surprising as horizontal gradients in O_2 are nearly absent during Winter time, and therefore tidal O_2 oscillations are very small. The smoothed line on the figure is the result of a moving average of 15d width.

Biogeosciences Discuss., doi:10.5194/bg-2017-81, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 13 March 2017

4 Discussion

The analysis in this paper again stresses the power of analyzing O_2 data in de Fourier domain. As demonstrated here, the technique of complex demodulation can give a robust estimate of daily GPP in non-tidal systems. The crucial advantage is that no other process has to be estimated. This is a major advantage compared to classic diel oxygen methods that requires an accurate estimate of air-water exchange and transport, which is often difficult (Tobias et al., 2009; Kemp and Boynton, 1980; Van de Bogert et al., 2012).

It is, however, important to keep in mind that the Fourier method performs well in many, but not all real-world systems. In some systems the method exhibits a systematic upward or downward bias. This bias is determined by the light saturation parameter of photosynthesis, the vertical turbulent mixing rate, light extinction coefficient, the water depth and the piston velocity. In most realistic settings, the bias is less than 10%. In some typical systems the bias will be much larger: this includes shallow systems where air-water exchange is large, deep systems where vertical mixing is not fast enough. When vertical mixing is low, the measurement depth is of crucial importance when only a single sensor is available. A complete analysis can be found in Cox et al. (2015). Those results are also applicable here: in situations where the Fourier method will work, estimating time varying GPP with complex demodulation will also work.

The biggest advantage of Fourier domain analysis lies in tidal systems. Two major reasons make diel oxygen methods difficult to apply in estuarine and coastal systems: 1. the tidal signal dominates O2 time series and 2. gas transfer is high and difficult to correctly estimate. The Fourier method circumvents these problems to a large extent. The M2 component and other semi-diurnals are effectively filtered out by the analysis. As demonstrated above by the analysis of the first order correction term, this does not entirely cancel out the effect of the tides. On the contrary, the diurnals $O1$, $Q1$, $K1$ and $P1$ can induce significant diurnal components in the O_2 signal that can not be attributed to GPP. We have shown that averaging over a sufficient period, resulting in a sufficiently narrow low pass filter, allows to filter out the effect of the $O1$ and $Q1$ components. A minor drawback is that this comes at the expense of the resolution of the GPP estimate: variability on time scales smaller than 15 days can not be resolved.

Resolving variability on time scales smaller than 15 days will be hard, perhaps impossible, in tidal systems with significant diurnals. This boils down to measuring or estimating at least the first order spatial correction term, which consists of two factors: the tidal excursion and the O_2 gradient. It might be possible to estimate the tidal excursion based on hydrodynamic models. Those models are not typically built to correctly reproduce the diurnals, so some care has to be taken. But in principle this is feasible. More difficult is the O_2 gradient. Indeed, the gradient that appears in equation 8 is the horizontal gradient in the reference frame moving with the tides. It is not immediately clear if and how this can be calculated from observed O_2 time series, but it would require a number of O_2 sensors along the horizontal. Moreover, we have to resolve not only the long term trend but also the diurnal fluctuations in this horizontal gradient, since these will contribute to the complex demodulated signal. The same difficulty arises when trying to constrain the higher order term in the Taylor series. The second order term for example is half the product of the second spatial derivative of the oxygen profile (in the moving reference frame) and the square of the tidal excursion.

Biogeosciences Discuss., doi:10.5194/bg-2017-81, 2017
Manuscript under review for journal Biogeosciences
Discussion started: 13 March 2017

5 Conclusions

The analysis in the frequency domain not only lead to a new method to estimate GPP. It results also in non-trivial new insights. In (Cox et al., 2015) we already demonstrated that the theoretically calculated effects of observational and stochastic noise on the GPP esatimate, is very well in agreement with simulation results that assess their impact on diel oxygen methods (Batt and Carpenter, 2012). In our current paper we unraveled how the diurnals $O1$ and $Q1$ affect GPP estimates; the low frequency fluctuations $|f1 - fO1|$ and $|f1 - fQ1|$ that are the result of the demodulation procedure also show up in the GPP estimates with classic Odum method. Our results enhance our theoretical understanding of O_2 dynamics, and how they influence the O_2 based estimates of GPP.

6 Code availability

Scripts will be made available as an R-package on www.rforscience.com

7 Data availability

Data from the Hörnum Tief station is publicly available on the Cosyna data portal http://codm.hzg.de/codm/

Author contributions. Tom J.S. Cox Contributed to theory development, numerical simulations and manuscript writing. Karline Soetaert and Justus van Beusekom contributed to manuscript writing

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Biogeosciences Discuss., doi:10.5194/bg-2017-81, 2017
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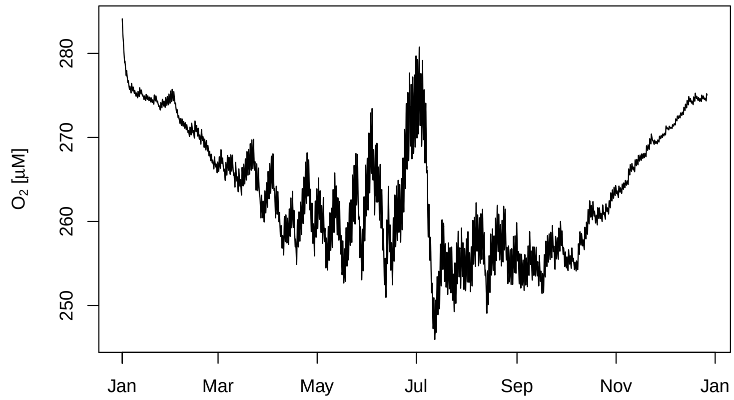

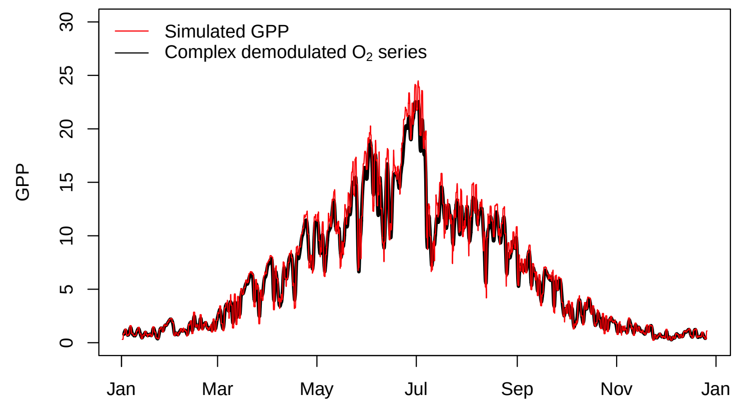

Figure 1. Simulated O_2 concentrations with the open water model (top); Simulated GPP and reconstructed GPP by complex demodulation of the O_2 time series (bottom)

Biogeosciences Discuss., doi:10.5194/bg-2017-81, 2017
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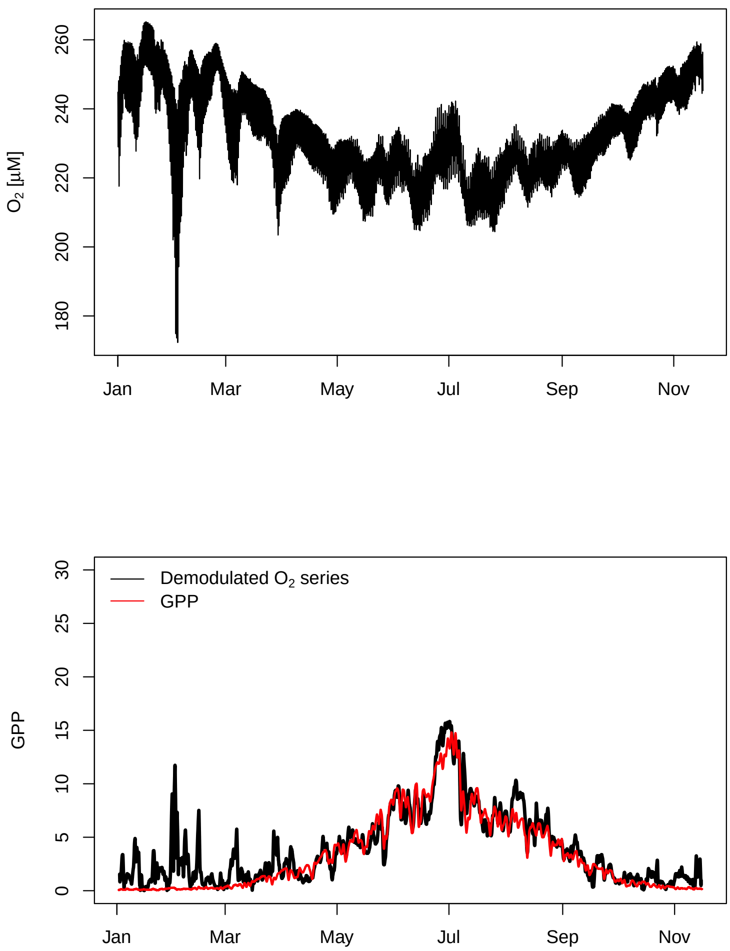

Figure 2. Simulated O_2 concentrations with the estuary model (top); Simulated GPP and reconstructed GPP by complex demodulation of the O_2 time series (bottom)

Biogeosciences Discuss., doi:10.5194/bg-2017-81, 2017
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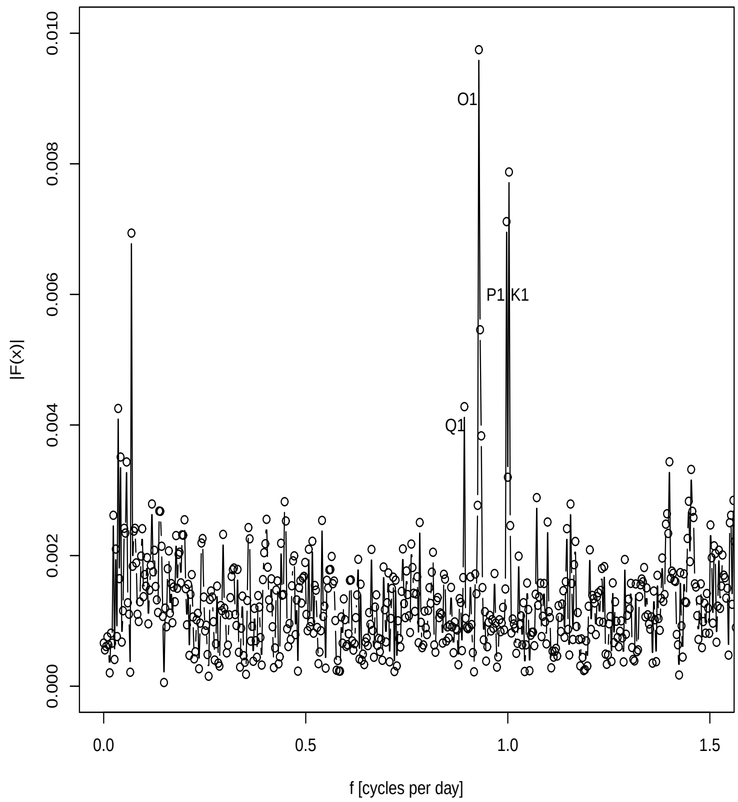

Figure 3. Spectrum of the velocity time series used for estuarine model calculations. Close to diurnal frequencies O1, Q1, P1 and K1 are marked

Biogeosciences Discuss., doi:10.5194/bg-2017-81, 2017
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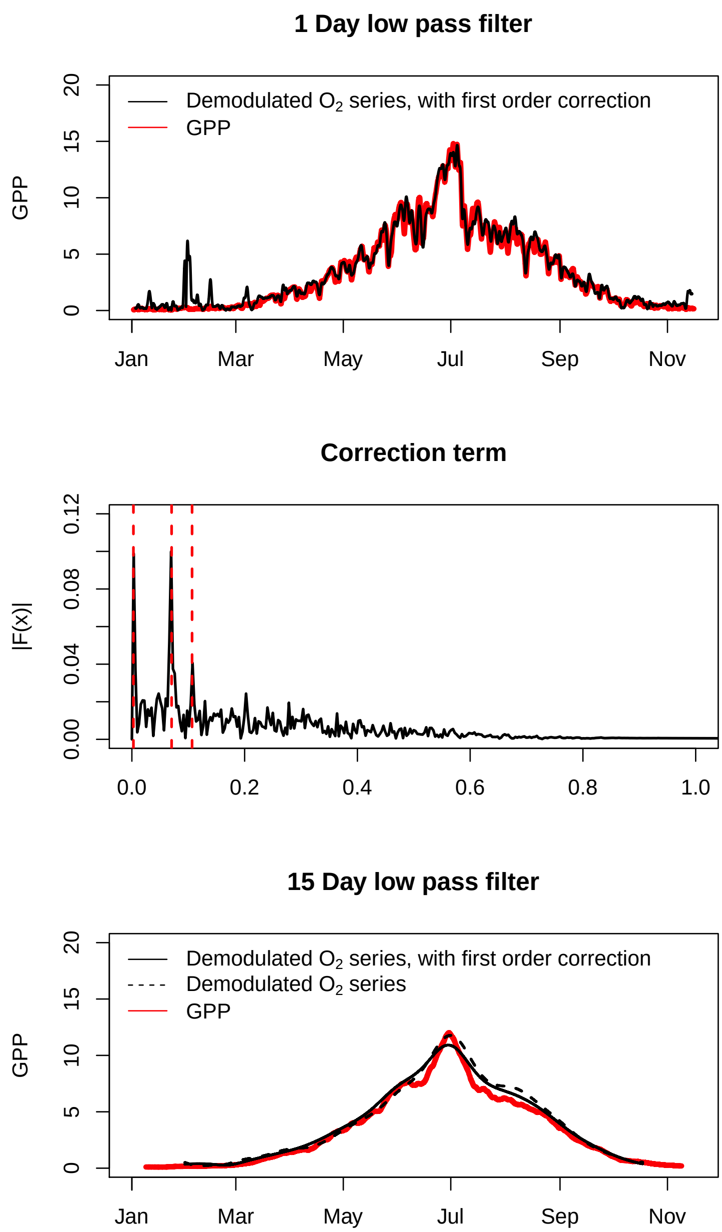

Figure 4. Simulated GPP in the estuarine model and reconstructed GPP by complex demodulating the O_2 series taking into account the first order term in the spatial Taylor expansion (top). Spectrum of the correction term: constituents due to P1, K1 interaction, O1 and Q1 are marked (center). 15 day averages of simulated GPP, complex demodulation with 15d moving average with and without the first order term in the spatial Taylor expansion (bottom)

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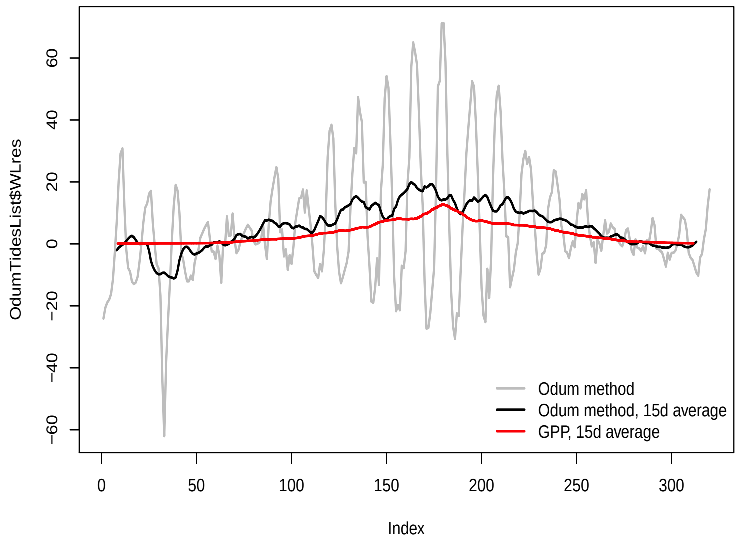

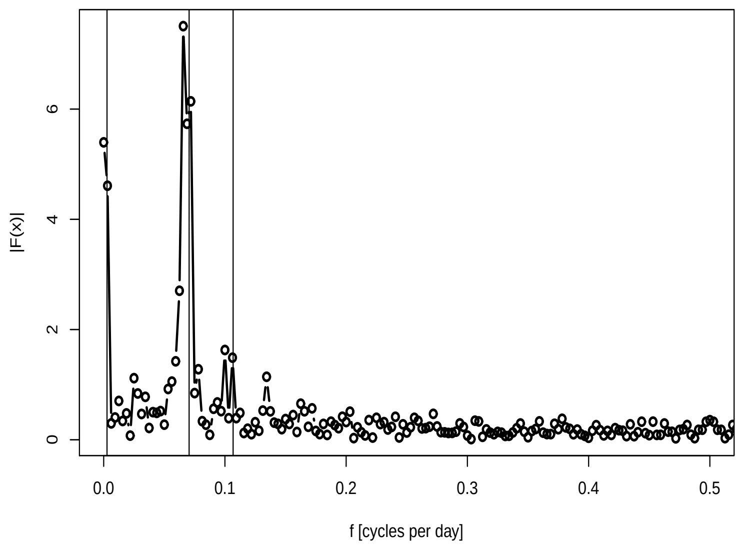

Figure 5. Result of the bookkeeping method applied to the simulated estuarine O_2 time series, and simulated GPP (top). The spectrum of the result of the Odum method shows the same P1, K1 interaction and O1 and Q1 constituents as the the first order Taylor expansion term in figure 4

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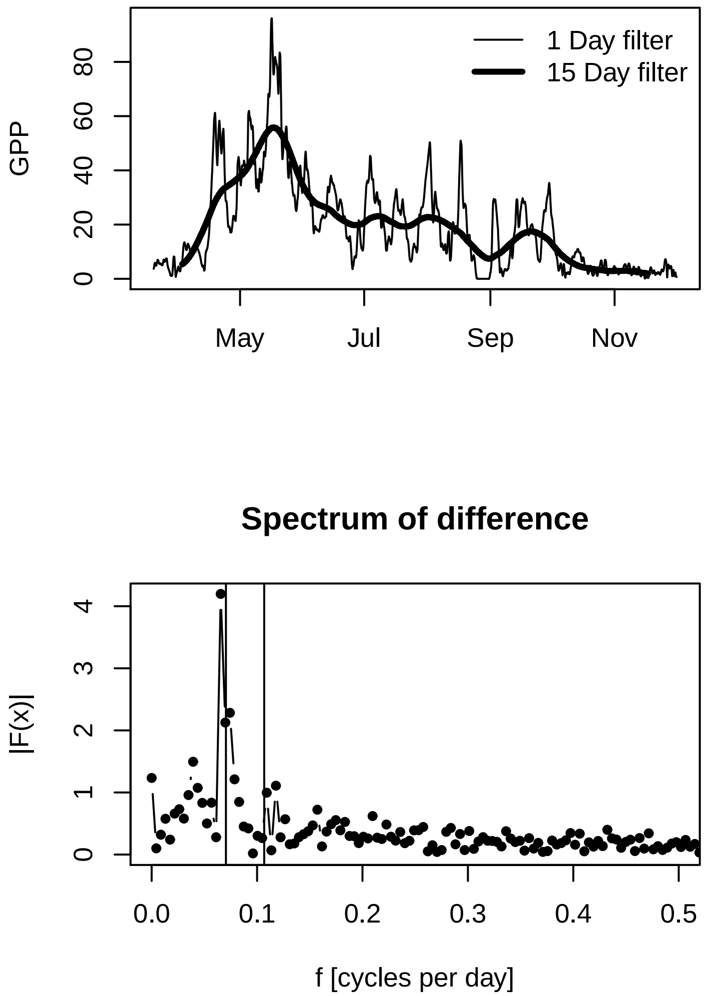

Figure 6. Complex demodulation of O_2 time series recorded in Hoernum Tief (top). The spectrum of the difference of complex demodulation applied to the O_2 series with a 1 day or a 15 day filter shows the Q1 and O1 constituents also predicted by theory and by the simulation results