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Short communication

Assessment of a field incubation method estimating primary productivity in rockpool communities

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ABSTRACT

An open incubation method has been used in many studies to directly estimate primary productivity and ecosystem functioning by measuring photosynthetic and respiratory rates in intertidal rockpool communities. The method measures changes in dissolved oxygen concentrations recorded in situ during an artificial dark period (respiration) and a natural light period (net primary productivity). Although this method has yielded interesting results, its advantages and limitations have yet to be thoroughly tested. The accuracy of the method was investigated in a controlled laboratory environment and compared with field incubations. Atmospheric oxygen diffusion across the air–water interface did not affect incubation measurements under low wind speed (<2 m s^{-1}). Temperature increases during incubations were not greater than in natural rockpools and did not affect primary productivity. The major problem was the oxygen supersaturation which inhibited photosynthesis, thus leading to an underestimation of primary production. To allow comparable measurements, net primary productivity needs to be recorded during the linear phase of the photosynthetic process (<30 min of light) before water reaches supersaturation (<160%). This method gives rapid and reliable estimates of primary productivity thereby allowing biodiversity and ecosystem functioning relationships to be tested using rockpools as natural mesocosms.

1. Introduction

Macroalgae are the major primary producers of temperate rocky shores (Mann, 2000) and may be important global carbon sinks (Smith, 1981). More importantly, they contribute to the functioning of coastal ecosystems by providing food, dissolved organic matter, habitats and nurseries for many invertebrates and fishes of commercial importance (Mann et al., 1980; Mann, 2000). Climate change and anthropogenic impacts threaten the goods and services macroalgae provide by precipitating the rate of biodiversity loss and habitat degradation (Pimm et al., 1995; Vitousek et al., 1997; Airoldi and Beck, 2007). Precise assessments of ecosystem functioning are necessary to understand the consequences of these changes and preserve the benefits supplied (Naeem, 2002; Hooper et al., 2005; Levin and Lubchenco, 2008). The functioning of rocky shore ecosystems can be evaluated by measuring primary productivity at the community level as a response variable. In general, primary productivity is assessed using proxies such as percentage algal cover and biomass accumulation (e.g. O'Connor and Crowe, 2005), or more directly by determination of photosynthetic and respiratory rates both on emergent rock and in rockpools (e.g. Nielsen, 2001; Martins et al., 2007; Golléty et al., 2008) as well as in mesocosms (Kraufvelin et al., 2010).

Measures of macroalgal photosynthetic and respiratory rates have been extensively studied by monitoring changes in dissolved oxygen concentrations during closed incubations in light and dark bottles in the laboratory or in the field (e.g. Littler and Murray, 1974). However, incubator size limits measurements to pieces of macroalgal tissue or single individuals. Biotic interactions (e.g. self-shading, competition, facilitation) are not taken into account and environmental factors occurring in the field are excluded for laboratory measurements (Duarte and Ferreira, 1993). Similar limitations also apply to other methods measuring photosynthetic activity at the plant level such as the PAM (pulse amplitude modulated) fluorescence method or ^{14}C pulse. Thus, it is difficult to

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extrapolate to the community level from results obtained and such methods are of limited value in assessing ecosystem functioning (Binzer and Middelboe, 2005).

Recent adaptations of incubation methods to the rocky intertidal allow evaluation of community productivity and respiration under natural conditions. On emergent rock, community carbon dioxide flux has been estimated at low tide under light and dark conditions in closed air incubation chambers previously used on soft bottoms (Golléty et al., 2008). In rockpools, adaptation of incubations performed in natural open flow environments (Kinsey, 1985) has been used to monitor photosynthetic rates of communities during low water (e.g. Nielsen, 2001; Martins et al., 2007; Altieri et al., 2009). Community productivity and respiration can be either estimated in the pool water by measuring pH and alkalinity to calculate changes in carbon dioxide or by directly measuring dissolved oxygen concentrations (but see Kraufvelin et al., 2010 for discussion on the similarity of these two methods).

Although monitoring dissolved oxygen has been successfully used in intertidal rockpools to measure primary productivity, there are a number of potential problems and artefacts whose effects on productivity estimates have not yet been assessed. One major concern when working with an open system such as rockpools is the gas exchange occurring at the air–sea interface. Rockpools often reach supersaturation in oxygen during low tide owing to biotic metabolic processes (e.g. Morris and Taylor, 1983) and diffusion to the atmosphere can occur. Excessive diffusion can lead to an underestimation of production measurements. It can be corrected for, but parameterisation of the gas transfer velocity is complex, still not completely understood and large discrepancies remain once applied (see Frost and Upstill-Goddard, 1999 for review). A correction used by Kinsey (1985) has been applied in some rockpool studies (Nielsen, 2001; Martins et al., 2007) but the diffusion magnitude and the accuracy of its correction remain unknown. Wind action can enhance diffusive loss (e.g. Morris and Taylor, 1983) by creating capillary waves at the pool surface (Broecker and Siems, 1984). Such effect of the wind on production measurements has not been assessed in rockpools. The use of black polythene sheets to cover the pools during the dark period can furthermore increase water temperature. Such an increase could affect community metabolism and estimation of primary productivity. It is also important to obtain measurement within the linear period of gas exchange to allow comparison among treatments. The timing of this linear response needs to be determined.

The aim of this study was to (1) examine possible flaws ascribed to the implementation of incubation in rockpools and (2) develop a standardised procedure that includes monitoring of environmental factors influencing and limiting primary productivity. Precise estimates of primary productivity would give useful information on rockpool ecosystem functioning and allow comparison between different communities. Rockpools could therefore be used as model systems where linkage between diversity and ecosystem function (productivity) can be relatively easily made. Potential problems owing to oxygen diffusion, supersaturation, wind, the use of dark covers (i.e. inducing temperature increase) were assessed. Additionally, the linearity of oxygen exchange rates was tested in rockpools to ensure accuracy of the results and avoid potential problems owing to supersaturation.

2. Materials and methods

2.1. Incubation

Rockpool incubation comprises measurements of the change in dissolved oxygen concentration during a dark and light period. Measurements are taken from water samples (in 120 ml plastic beakers) collected after stirring the pool water gently. Stirring allows assessment of the average dissolved oxygen concentration over the whole pool by breaking down any vertical stratification (Morris and Taylor, 1983). Dissolved oxygen concentration (mg O_2 l^{-1}), saturation (%), time, temperature and pH are recorded at each measurement using a portable oxygen/pH meter with an oxygen optical probe and a coupled pH probe (HQ20 Hatch Lange Ltd portable LDO™, Loveland USA). The HQ20 oxygen meter automatically corrects measurements for temperature, and atmospheric pressure while salinity can be entered manually. Dissolved oxygen measurements were not affected when salinity was set either at a constant 35 or varied from 34.5 to 38 (natural rockpool summer salinity recorded in SW England).

Initial measurements are taken just after the pools are uncovered by the tide to allow assessment of initial dissolved oxygen concentration (i.e. natural seawater conditions). Then, the dark period is achieved through placement of optically dark polythene sheets a few centimetres above the pool surface held down at the pools borders with weights. A second set of measurements is taken at the end of the dark period. Then the polythene sheet is removed and the pools are left exposed to daylight (light period) until a third and last set of measurements is taken.

A number of environmental variables are monitored throughout the incubation to document experimental conditions. Wind velocity at the pool water surface is monitored during the incubation with a handheld anemometer (Silva Alba Windwatch). Irradiance (Photosynthetic Active Radiation: PAR) is recorded throughout the incubation (LI-COR Li-250 Light meter). pH is monitored to identify and avoid periods of carbon dioxide depletion (high pH) common after a long isolation from the sea (Dromgoole, 1978b; Morris and Taylor, 1983) which could limit photosynthesis. Rockpool mean depth, surface and bottom areas and volume are recorded to express photosynthetic rate accordingly and allow precise comparison.

2.2. Determination of primary productivity

Respiratory demand (R) by both animals and algae is calculated over the dark period as follows:

$$R = \left|\Delta[O_2]_{dark}/\Delta t_{dark}\right| \quad (1)$$

Where $\Delta[O_2]_{dark}$ is the difference in dissolved oxygen concentration between measurements taken respectively at the beginning and end of the dark period and Δt_{dark} is the time difference between these measurements. Net primary productivity (NPP) is calculated over the light period as follows:

$$NPP = \Delta[O_2]_{light}/\Delta t_{light} \quad (2)$$

Where $\Delta[O_2]_{light}$ is the difference in dissolved oxygen concentration between measurements taken respectively at the end and beginning of the light period and Δt_{light} is the time difference between these measurements. Both R and NPP are expressed as concentration of dissolved oxygen per unit of time (mg O_2 l^{-1} min^{-1}). Gross primary productivity (GPP) corresponds to the photosynthetic rate of the pool macroalgae community and is calculated based on the photosynthesis and respiration equation:

$$GPP = (NPP + R) \times V \quad (3)$$

For standardisation of the results, GPP measured as dissolved oxygen produced per volume and unit of time (mg O_2 l^{-1} min^{-1}) is corrected for rockpool volume (V, in l) to allow direct comparison of photosynthetic rate per pool (mg O_2 min^{-1}) (Martins et al., 2007). GPP can be further determined per unit of substratum area bearing the pool biota (mg O_2 min^{-1} m^{-2}) or per unit of biomass (mg O_2 min^{-1} g^{-1}).