Biogeochemistry of Ningaloo Reef

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June 2008

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This dissertation is submitted for partial fulfillment of the Bachelor of Engineering (Environmental) degree at The University of Western Australia.
Acknowledgements

First and foremost, my sincere thanks to Ryan Lowe, Anya Waite and Jim Falter for all their help over the past year. Ryan is a well-respected teacher, proofreader and matlab whiz, and his continual optimism, patience and wit were much appreciated! Jim worked tirelessly to ensure the success of the dissolved oxygen sensors and process the nutrient and oxygen samples as well as acting as an academic supervisor, and Anya provided support throughout the project and academic guidance in the discussion. Thanks also go to Dianne Krikke for all her work in the field and lab, the photographs used in my thesis and for sharing a beer with me on the beach in the Cape Range. Finally, thanks to Alex Wyatt for all his help with the field work and the drifters.

Extra thanks goes to all of the above people for their work ensuring the success of the field trip, without which I would never have found myself snorkeling in Turquoise Bay in the name of environmental engineering!

Cheers to the Ningaloo gang – Di, Ryan, Jim, Marlin, Pascale, Alex, Stuart, Anya and Fraser – for sharing their company, stories and cooking in the bothy each night; to Marlin Atkinson for his impromptu and unsolicited lectures on chemistry and coral reef calcification in the Placka; and to the fish, turtles, reef sharks, sting rays, kangaroos, emus, racehorse goannas, geckos, spiders and “tiger snakes” for providing daily entertainment.

Cheers to my housemates (Anthea, Sal, Jayne, Dani K, Caro and Lisa), friends, and all other CWR/SESE students past and present, all of whom have made four and a half years seem like as many seconds. Special thanks to: Ash, for giving me a desk so that I would stop (literally) stealing the kitchen table: Climbing Kate, for lending me her jumper so many times: Sam for all the “yo face” jokes and Conor for the Malteser muffins. Finally, heartfelt thanks to my family for just about everything else!
Abstract

A coral reef consists of both heterotrophic and autotrophic organisms, which can be considered together as an entire community for the purposes of studying the community metabolism and nutrient cycling. Net production is defined as the difference between photosynthesis and community respiration (due to organism respiration and decomposition), and provides an estimate of excess organic carbon production by the reef community. It is typically close to zero in healthy reef systems, but varies both spatially and temporally.

The link between nutrient uptake and net organic carbon production is one of the least understood processes in coral reef biogeochemistry. Furthermore, the majority of studies conducted on nutrient limitation in coral reef ecosystems have been conducted in the northern hemisphere, and net production has not been studied in any detail on Ningaloo Reef.

The aim of this study was to investigate the link between nutrient uptake and net organic carbon production on the Ningaloo Reef of Western Australia, and to compare Lagrangian (transect sampling) and Eulerian (instrument deployment) methods of estimating net production. Eulerian estimates were calculated based upon the derivation by Falter et al (2008). Finally, it was hoped that the results would yield some understanding of calcification on the Ningaloo Reef. Data was collected during a 10-day field trip to a small (~4 km) reef section at Sandy Bay, Cape Range National Park, in November 2007.

The Eulerian method was found to be an effective method of quantifying net production: and in combination with Lagrangian transects has provided the first estimates of community metabolism on Ningaloo Reef. The reef was found to be just net autotrophic during the study period. Nitrogen was indicated to be the limiting nutrient. Basic stoichiometric calculations suggest production may be dependent upon particulate feeding in combination with dissolved nutrient and POM uptake, and hence that the reef may rely upon outer-reef oceanographic and biological processes for success. Hysteresis was identified in the relationship between production and irradiance on some days of the study, which is suggested to be due to either photoinhibition or heterotrophic behaviour.

Net calcification is believed to have been occurring during the study period, but it is suggested that the balance of calcification to dissolution over an entire year may be close to zero, making the reef sensitive to climate change. However, definitive conclusions about calcification and the sensitivity of the system cannot be made without further research into the seasonal and yearly variation of reef metabolism.
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<th>Definition</th>
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<tr>
<td>Autotrophic</td>
<td>Able to produce oxygen and organic carbon via photo- and chemosynthesis (compare with heterotrophic)</td>
</tr>
<tr>
<td>Benthos</td>
<td>The bottom substrate and associated bottom-dwelling organisms (compare with pelagic)</td>
</tr>
<tr>
<td>Biogeochemistry</td>
<td>Defined here as the study of the metabolism of a coral reef community (can include the biological, chemical, geological and physical fluxes of an ecosystem)</td>
</tr>
<tr>
<td>Calcification</td>
<td>Coral growth: the conversion of calcium and carbonate ions to limestone (the building block of coral skeleton)</td>
</tr>
<tr>
<td>Community Gross Respiration (R)</td>
<td>Total dissolved oxygen uptake by decomposition and the respiration of autotrophic and heterotrophic organisms integrated over 24 hours</td>
</tr>
<tr>
<td>Eulerian</td>
<td>Fixed reference frame for measuring changes in concentration</td>
</tr>
<tr>
<td>Gross Primary Production (GPP)</td>
<td>Total dissolved oxygen released by photosynthetic organisms integrated over 24 hours</td>
</tr>
<tr>
<td>Heterotrophic</td>
<td>Consumes oxygen and organic carbon (compare with autotrophic)</td>
</tr>
<tr>
<td>Hysteresis</td>
<td>Describes an effect where a relationship between two variables depends on its immediate history: for example, the relationship can depend on which “direction” the value has been approached from. See photoinhibition</td>
</tr>
<tr>
<td>Lagrangian</td>
<td>Moving reference frame for measuring changes in concentration</td>
</tr>
<tr>
<td>Pelagic zone</td>
<td>Water column (compare with benthos)</td>
</tr>
<tr>
<td>Photoinhibition</td>
<td>Where a photosynthesizing organism reacts to high light intensity by shutting down its photosynthesizing mechanism: can cause a hysteresis effect</td>
</tr>
<tr>
<td>Photosynthetic quotient</td>
<td>Ratio of moles of carbon fixed during photosynthesis to moles of carbon released by respiration</td>
</tr>
<tr>
<td>Net Autotrophic</td>
<td>A system which is a net producer of oxygen and organic carbon</td>
</tr>
<tr>
<td>Net Community Production (NCP)</td>
<td>Net production integrated over 24 hours</td>
</tr>
<tr>
<td>Net Production (NP)</td>
<td>Excess production of oxygen and organic carbon</td>
</tr>
<tr>
<td>Net Respiration</td>
<td>A system which is a net consumer of oxygen and organic carbon</td>
</tr>
<tr>
<td>Zooxanthellae</td>
<td>Algae living in a symbiotic relationship with a coral host</td>
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**Symbols and Abbreviations**

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Unit</th>
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</thead>
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<tr>
<td>ADCP</td>
<td>Acoustic Doppler Current Profiler</td>
<td>N/A</td>
</tr>
<tr>
<td>CTD</td>
<td>Conductivity-temperature-depth probe</td>
<td>N/A</td>
</tr>
<tr>
<td>DIN</td>
<td>Dissolved inorganic nitrogen</td>
<td>mmol m^{-3}</td>
</tr>
<tr>
<td>DO</td>
<td>Dissolved oxygen</td>
<td>mmol m^{-3}</td>
</tr>
<tr>
<td>G</td>
<td>Calcification</td>
<td>mmol m^{-2} hr^{-1}</td>
</tr>
<tr>
<td>GPP</td>
<td>Gross primary production</td>
<td>mmol m^{-2} d^{-1}</td>
</tr>
<tr>
<td>J</td>
<td>Gas flux</td>
<td>mmol m^{-2} hr^{-1}</td>
</tr>
<tr>
<td>N</td>
<td>Nitrogen</td>
<td>N/A</td>
</tr>
<tr>
<td>NO₃</td>
<td>Nitrate</td>
<td>mmol m^{-3}</td>
</tr>
<tr>
<td>NP</td>
<td>Net production</td>
<td>mmol m^{-2} hr^{-1}</td>
</tr>
<tr>
<td>NCP</td>
<td>Net community production</td>
<td>mmol m^{-2} d^{-1}</td>
</tr>
<tr>
<td>P</td>
<td>Phosphorus</td>
<td>N/A</td>
</tr>
<tr>
<td>PAR</td>
<td>Photosynthetically active radiation</td>
<td>mmol quanta m^{-2} s^{-1}</td>
</tr>
<tr>
<td>PON</td>
<td>Particulate organic nitrogen</td>
<td>mmol m^{-3}</td>
</tr>
<tr>
<td>R</td>
<td>Gross community respiration</td>
<td>mmol m^{-2} d^{-1}</td>
</tr>
<tr>
<td>SRP</td>
<td>Soluble reactive phosphorus</td>
<td>mmol m^{-3}</td>
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1 Introduction

Coral reefs are renowned worldwide for their incredible beauty and ecological diversity, yet they face many threats from anthropogenic activities, especially global climate change. The survival of coral reef communities is vitally important to future generations: they serve as centres of marine biodiversity, sources of new drugs and biochemicals, and a fundamental source of income for many coastal communities (Hoegh-Guldberg 1999). Ningaloo Reef in Western Australia has considerable intrinsic ecological and social value to the community of Western Australia, as well as attracting international research interest.

Biogeochemistry is broadly defined as a field of study into biological, geological, physical and chemical fluxes and reactions. The present study considers specifically the community metabolism and nutrient fluxes of the Ningaloo Reef. The guiding objective behind the study of coral reef biogeochemistry is to determine rates at which carbon is imported, exported, recycled and incorporated by the reef community and the surrounding ecosystem (Kinsey 1985). A coral reef can be examined from the perspective of the entire coral community or even ecosystem, where carbon fluxes are considered to be the direct “currency” of the system (Kinsey 1985).

The first major study of coral reef productivity by Odum and Odum (1955) hypothesized that coral reefs were relatively isolated, closed systems of high productivity in a largely oligotrophic environment, existing in an almost “steady state balance of growth and decay”. Later theories have suggested that the mutualistic symbiosis between zooxanthellae and coral has created an ecosystem where nutrients are continually recycled through the community or retained within the biota (Atkinson & Falter 2003).

More recent literature has now accepted Odum and Odum’s (1955) “steady state” hypothesis as an oversimplification (e.g. Delesalle et al. 1998). A more recent theory states that coral reefs produce low quality organic and inorganic carbon, requiring relatively little nutrient input, and that nutrients which are removed from the water column are exported as particulate material and recycled over spatial scales of hundreds of metres (Atkinson & Falter 2003). However, the connecting processes between nutrient uptake and net carbon production are not yet well understood (Atkinson & Falter 2003).

Net carbon production can be estimated indirectly from oxygen fluxes using Eulerian (fixed reference frame) or Lagrangian (moving reference frame) approaches. Most previous studies
have used a Lagrangian approach where a parcel of water is followed across the reef and manually sampled at intervals. The resulting concentration gradients and known current speeds allow for the calculation of net production across the reef transect during the time of sampling. In contrast, the Eulerian approach uses the fixed deployment of logging instruments to continuously record dissolved oxygen concentrations, as well as current speed and direction in a control volume on the reef. From these measurements the local, advective and gas fluxes are calculated and combined to provide time-series estimates of net production.

The aim of this study was to consider the carbon, oxygen and nutrient fluxes of the Ningaloo Reef community. Both Lagrangian and Eulerian approaches are taken to estimate net production and nutrient uptake rates based upon the recent methodology developed by Falter et al. (2008). There are no previous studies on net production at Ningaloo Reef. The study also aims examines the link between nutrient uptake and net carbon production, which is one of the least understood processes in coral reef biogeochemistry. Finally, the results are used to suggest implications for calcification on the Ningaloo Reef.
2 Literature Review

2.1 Biogeochemistry: community scale metabolism processes

The dominant metabolic processes considered in this study are photosynthesis, calcification and integrated community respiration, all of which are aerobic and occur primarily in the benthos (Atkinson & Falter 2003). The production and respiration of organic carbon are fundamental processes to the movement of mass and energy through a coral reef ecosystem, and the rate of primary production indicates the ability of a reef ecosystem to produce new biomass or biogeochemical energy from inorganic carbon (Falter et al. 2008). Net production (the balance of gross production and respiration) is typically close to zero in reef systems, although it varies spatially and temporally (Atkinson & Falter 2003).

2.1.1 Primary production and respiration

During primary production, coral and coralline algae remove carbon dioxide from the water column, and produce particulate organic matter and oxygen (Figure 1) via photosynthesis or (to a much lesser extent) chemosynthesis (Falter et al. 2008).

Photosynthesis is the conversion of inorganic carbon and water to organic carbon and oxygen, using light as an energy source:

\[
6CO_2(g) + 12H_2O(l) + \text{photons} \rightarrow C_6H_{12}O_6 + 6O_2(g) + 6H_2O(l)
\]

Quantification of the oxygen budget can also reveal information about the carbon budget if it is assumed that the photosynthetic quotient (ratio of moles of oxygen fixed to moles of carbon consumed) is 1.0 (Falter et al. 2008).

Gross primary production (GPP), also referred to in the literature as community gross photosynthesis, is an estimate of carbon dioxide fixed by photosynthetic organisms in the reef community (Crossland, Hatcher & Smith 1991).

Respiration can be roughly defined as the converse process to production, consisting of carbon release and oxygen uptake (Harrison & Booth 2007). Respiration occurs over the entire 24-hour cycle but dominates at night, when light is not available for photosynthesis (Atkinson & Falter 2003). Community gross respiration (R) is an estimate of all carbon dioxide released by decomposition and the respiration of autotrophic and heterotrophic organisms.
Net community production (NCP), the difference between community gross production and respiration, is an estimate of excess production of organic matter by the reef community over 24 hours or longer, and is defined by the following equation (Crossland, Hatcher & Smith 1991):

$$NCP = \int_0^{24} GPP - \int_0^{24} R$$  \hspace{1cm} \text{Equation 1}

Gross primary production rates are typically balanced by respiration rates of a similar magnitude (Crossland, Hatcher & Smith 1991). The roughly equal magnitudes of GPP and R mean that net production is usually close to zero in a reef system (Silverman, Lazar & Erez 2007), but varies locally on both spatial and temporal scales. Typical rates of production and respiration summarized from the literature by Atkinson and Falter (2003) are presented in Table 1 below.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>GPP (mmol m(^{-2}) d(^{-1}))</th>
<th>R (mmol m(^{-2}) d(^{-1}))</th>
<th>NCP (mmol m(^{-2}) d(^{-1}))</th>
<th>G (mmol m(^{-2}) d(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reef-flat</td>
<td>640 (330-1580)</td>
<td>600 (290-1250)</td>
<td>-220 - 310</td>
<td>130 (20-250)</td>
</tr>
<tr>
<td>Algal pavement</td>
<td>460 (170-580)</td>
<td>300 (40-560)</td>
<td>0 - 130</td>
<td>90 (70-110)</td>
</tr>
<tr>
<td>High coverage</td>
<td>1200 (660-1920)</td>
<td>1300 (500-2000)</td>
<td>-830 - 250</td>
<td>240 (110-320)</td>
</tr>
<tr>
<td>Sandy areas</td>
<td>130 (80-230)</td>
<td>130 (90-200)</td>
<td>-40 - 30</td>
<td>35 (10-70)</td>
</tr>
<tr>
<td>Shallow lagoon</td>
<td>450 (210-1080)</td>
<td>430 (180-790)</td>
<td>-200 - 280</td>
<td>40 (20-55)</td>
</tr>
<tr>
<td>Entire Reef</td>
<td>390 (190-640)</td>
<td>370 (190-570)</td>
<td>0 - 70</td>
<td>45 (3-135)</td>
</tr>
</tbody>
</table>

**2.1.2 Autotrophy vs. heterotrophy and coral reef zonation**

The dependence of a coral reef upon external sources of organic carbon, or the extent to which it can produce organic carbon via photo- or chemosynthesis, will be revealed by the difference between rates of production and respiration. The ratio GPP:R > 1 indicates that the reef is autotrophic (dominated by photosynthesis); conversely, GPP:R < 1 indicates heterotrophy (respiration dominates).

Autotrophic reefs are thought to require an external supply of dissolved nutrients (nitrate, phosphate and silicate) for success (Silverman, Lazar & Erez 2007). Conversely, a
heterotrophic reef requires an increased supply of particulate organic matter from the open sea to support growth (Silverman, Lazar & Erez 2007), which may consist of zooplankton as discussed in section 2.1, or dissolved organic matter as suggested by Yahel et al. (2003).

Reef morphology is determined by both underlying geological structures and by net growth, accretion and dissolution of the carbonate structures produced during calcification (below) by living coral (Grigg et al. 2002). Different biogeochemical reactions are related to different morphology zones (Stoddart 1969).

Figure 1: Generalised sketch of a fore-reef and reef flat (Atkinson & Falter 2003).

The fore-reef (Figure 1) is the transition zone between the open ocean and reef itself, the slope of which varies in steepness depending upon the underlying geology and upward growth rates and is usually comprised of spurs and grooves created by the erosive action of breaking waves and currents (Atkinson & Falter 2003). The reef crest is the shallowest part of the reef and can be exposed at high tide, while the reef flat is a flat and shallow area which can include stands of coralline algae, small coral, crustose coral, pure macro-algae and pure soft corals and zooanthids (Atkinson & Falter 2003). Wave energy is usually the primary determinant of a reef community structure (Grigg et al. 2002). The back-reef includes sand deposits, rubble and coral bommies. The lagoon is further toward shore, and usually includes a collection of patch reefs varying in size (Atkinson & Falter 2003).

Traditional views state that net oxygen production (NCP>0) occurs along the primarily autotrophic fore-reef and algal reef crest, where the reef interacts with the open ocean: detritus and dissolved organic carbon are then exported to the reef flat for use by heterotrophic organisms, where net respiration (NCP<0) occurs (Kinsey 1985). However, high net
production has also been identified on back reef areas with significant rubble (Atkinson & Grigg 1984). Atkinson and Falter (2003) suggest that zonation is dependent upon the nature of the substrate: sands and muds tend to be heterotrophic, while areas of hard substrate and algae tend to be autotrophic and coral areas tend to have a GPP:R ratio of 1.0.

### 2.2 Limiting factors to primary production

The limiting factors upon primary production are nutrients, light and temperature. All biogeochemical reactions which occur in pelagic systems also occur in coral reef systems (D’Elia & Wiebe 1990): however the rates, stoichiometry, spatial arrangements and governing mechanisms of these reactions vary between the benthic and pelagic zones (Atkinson & Falter 2003). These processes are summarized in Figure 2 and discussed further in the review below.

![Diagram of biogeochemical reactions in coral reef systems](image)

**Figure 2**: Fundamental biogeochemical reactions in coral reef systems (Atkinson & Falter 2003). POM stands for particulate organic matter. Different types of POM are denoted by the subscripts Allo (allochthonous), Mixed (autochthonous), All (autochthonous + allochthonous), and Auto (solely autotrophic).

#### 2.2.1 Dependence upon external sources of nutrients

The ability of a marine ecosystem to uptake dissolved nutrients is often a limiting factor upon net primary production (Falter & Atkinson 2004). Nutrient uptake across coral reefs has typically been difficult to measure in situ, leading to the hypothesis that reefs remove nutrients from the water column very slowly (Steven & Atkinson 2003).
Reef systems, like pelagic ecosystems, undergo nitrogen uptake and assimilation, reduction, nitrification and nitrogen fixation. Specifically, autotrophs uptake ammonium, nitrate and nitrite from the pelagic zone, reduce these species to organic nitrogen species and then absorb this into their biomass (Atkinson & Falter 2003).

Autotrophic and heterotrophic organisms have been found to have nutrient uptake rates of similar magnitudes (Ribes & Atkinson 2007). Fabricius and Dommasse (2000) found that a zooxanthellate-soft coral dominated reef in a highly turbid environment extracted large quantities of chlorophyll $a$, particulate organic carbon and particulate phosphorus from the water column, but did not uptake particulate nitrogen or phaeophytin, and that rates of depletion were independent of upstream particle concentration. However, a study by Webb and Wiebe (1978) found that nitrification by a reef community on the Great Barrier Reef elevated the nitrate concentration over the reef flat compared to the open ocean water; and that reef corals took up nitrate from seawater enriched with the nutrient. Recent research on the Ningaloo reef appears to indicate that net production of nitrate and ammonium is occurring across the reef crest (Waite & Lowe, unpublished data).

Nutrient uptake in shallow reef communities has been shown to be limited by the physical transfer of nutrients across concentration boundary layers, otherwise known as mass transfer (Atkinson & Bilger 1992). A derivation by Hearn, Atkinson and Falter (2001) shows that in wave-dominated reef communities, first-order nutrient uptake rates are a function of the energy dissipation of waves and currents due to benthic roughness, bottom shear stress and current speed. They argue that a causal relationship between nutrient uptake and the dissipation of energy by breaking waves on reef flats explains “Darwin’s Paradox” of high productivity in oligotrophic waters (Hearn, Atkinson & Falter 2001).

### 2.2.2 Coral – zooxanthellae symbiosis and limits to production

Understanding the interaction between zooxanthellae and reef organisms, especially hermatypic (reef-building) corals, is vital to understanding the carbon cycle in a coral reef community. Zooxanthellae is the collective term for a diverse group of dinoflagellates with a free-living stage involving sexual reproduction, and a non-motile form in which they live in the host tissues of coral and produce by mitosis (Hoegh-Guldberg 2004). The latter stage is the mutualistic symbiotic relationship of importance to reef building.

Zooxanthellae in healthy coral reefs perform intensive photosynthesis which produces larger quantities of organic carbon than can be utilized in their own cell formation (Dubinsky &
Berman-Frank 2001). The excess carbon can be used in calcification or respiration, or exported as DOC (Atkinson & Falter 2003).

Photosynthesis increases with light until a point of saturation. Production can be sustained as light increases even further, but eventually there is a decrease in photosynthesis known as photoinhibition (Neale & Richerson 1987). High levels of irradiance, elevated seawater temperature or UV radiation can lead to an increase in reactive (harmful) oxygen species within zooxanthellae and coral (Levy et al. 2006). However, the exact relationship between photosynthesis and light typically varies between reefs (Falkowski, Jokiel & Kinzie 1990), because zooxanthellae can adjust to changes in irradiance on scales varying between minutes and thousands of years (Levy et al. 2006). For example, polyp expansion and contraction occur within minutes, while changes in the density and species of zooxanthellae can occur within days (Levy et al. 2006).

Zooxanthellae population growth is also limited by their ability to sequester nitrogen and phosphorus either from the surrounding water or from the digestion of prey zooplankton and the excretion of metabolic waste products from the host coral (Dubinsky & Berman-Frank 2001). The algae are able to obtain inorganic carbon, ammonia and phosphate nutrients from the coral tissue via this method (Harrison & Booth 2007). Researchers have hypothesised that the ability to recycle nutrients via this close symbiosis is the reason coral reefs can thrive in oligotrophic waters (Atkinson & Falter 2003).

The C:N:P ratio for balanced growth in coral reef systems is 550:30:1 (Atkinson & Smith 1983), which varies from the typical Redfield ratio (Redfield, Ketchum & Richards 1963) describing phytoplankton growth. Nitrogen is described as the limiting nutrient for zooxanthellae mitosis according to studies performed in the northern hemisphere (e.g. Dubinsky & Berman-Frank 2001).

In a low-nutrient environment, which is typical in shallow water zones with high light availability, the majority of excess carbon is released to the coral host supporting coral metabolism and calcification (Figure 3). However, although the transfer of organic carbon from zooxanthellae to coral can supply the host’s entire carbon needs (Muscatine, Falkowski & Dubinsky 1983), the transfer must be supplemented by the active capture of nitrogen rich zooplankton prey (Muscatine et al. 1989).

In deeper water, where irradiance is between 0.5 and 5 percent of subsurface levels and light rather than nutrient availability limits photosynthesis, zooxanthellae retain most of their
organic carbon rather than releasing it to their coral host; and hence zooplankton predation is the primary source of coral nutrition (Dubinsky & Jokiel 1994).

Figure 3: Scheme describing the effect of eutrophication on the flow of carbon in the mutualistic symbiosis between zooxanthellae and corals under “normal” oligotrophic conditions (Dubinsky & Berman-Frank 2001). Note the heavy favouring of calcification and growth processes.

Figure 4: Scheme describing the effect of eutrophication on the flow of carbon in the mutualistic symbiosis between zooxanthellae and corals when exposed to eutrophication (Dubinsky & Berman-Frank 2001).
Note the decrease in carbon flow to calcification and reproductive processes, and the increase in respiration.

2.2.3 Benthic-pelagic coupling

A study on the Great Barrier Reef (Furnas et al. 2005) found that in a coral reef ecosystem, 90% of the organic materials used by reef organisms are first cycled through pelagic organisms with rapid growth rates and short turnover timescales. Atkinson and Falter (2003) report that the standing stocks of carbon, nitrogen and phosphorus in the pelagic zone are orders of magnitude below those in the benthos: and in Australia, the oligotrophic nature of coastal waters has lead to a traditional focus on the benthic zone in marine ecology studies (Waite & Suthers 2007).

Benthic-pelagic coupling could prove an important factor in understanding biogeochemical cycling. Studies have shown that even in shallow waters with a high benthic biomass, pelagic production can exceed that of the benthos by three-to-five fold (e.g. Segal, Waite & Hamilton 2006). Further, the organic flux contribution of plankton and detritus throughputs to reef systems has historically been underestimated (Kinsey 1985).

In Western Australian coastal waters, production in the reef-enclosed lagoons is thought to be dependent upon local fluxes of ammonium, varying on a diel timescale, while nitrate is the limiting nutrient on the continental shelf (Suthers & Waite 2007).

2.3 Calcification

During calcification, calcium and carbonate ions are sourced from seawater and converted to limestone crystals by symbiotic zooxanthellae in the polyp epithelium (Langdon & Atkinson 2005), i.e.:

\[ \text{Ca}^{2+}_{(aq)} + \text{CO}_3^{2-}_{(aq)} \rightarrow \text{CaCO}_3(s) \]

Calcification rates are vital to the ecological fitness of coral reefs, as they drive growth rates (and therefore the time taken for coral to reach sexual maturity). Low growth rates correspond to a lesser ability to compete for space and light and repair structural damage (Langdon & Atkinson 2005), and leave coral more susceptible to disease, coral bleaching, over-fishing, contaminants and sea level rise (Langdon et al. 2003; Langdon & Atkinson 2005). Large coral colonies also have a greater reproductive output than small colonies (Langdon & Atkinson 2005).
Calcification rates are affected by the changing environmental conditions of light, temperature and nutrients (Langdon & Atkinson 2005). Calcification is positively correlated to photosynthesis and increases with light until a threshold of photoinhibition (Gattuso, Allemand & Frankignoulle 1999), unless nutrient or carbon dioxide enrichment can cause a decoupling of the two processes (Langdon & Atkinson 2005).

Various models have been proposed to explain the complex relationship between calcification, light and photosynthesis. Although corals are capable of calcification in darkness, proving that the process is not entirely dependent upon photosynthesis by zooxanthellae, light-enhanced calcification is 3-5 times faster on average than dark calcification (Barnes & Chalker 1990). A strong correlation has been identified between photosynthesis and calcification at both the organism and community level (Gattuso, Allemand & Frankignoulle 1999), and it is understood that calcification increases with both light and temperature until a threshold where it saturates (photoinhibition) or, in the case of temperature, declines steeply with further increases.

Nutrient enrichment can cause a decrease in calcification, possibly because the photosynthetic activity of zooxanthellae is enhanced, thus decreasing the available pool of dissolved inorganic carbon and limiting the supply of carbonate ions available for calcification (Langdon & Atkinson 2005). Dubinsky and Berman-Frank (2001) argue that net production cannot be directly equated to population growth where nutrients are in high concentrations, since the two become uncoupled: cell division stops and excess carbon is stored, excreted or direction to secondary functions (Figure 3, Figure 4). However, Langdon and Atkinson (2005) argue that except changes in carbonate ion concentrations affect calcification far more than nitrogen concentrations.

Global changes in atmospheric carbon dioxide concentrations have created two major threats to coral reefs: thermal stress (coral bleaching) and the acidification of ocean waters. In the latter process, carbon dioxide which is taken up by the ocean forms carbonic acid, causing a drop in pH and removing carbonate ions vital to calcification from the pelagic zone (Atkinson & Falter 2003; Harrison & Booth 2007). Langdon et al (2003) concluded that a doubling of atmospheric carbon dioxide levels, as predicted over the next century, would result in an 11-40% decline in calcification of corals and coralline algae.
2.4 Ningaloo Reef

Ningaloo Reef is unique as one of the few substantial fringing coral reef systems to be found on the western coast of a continent. The reef is crossed by the Indian Ocean whale shark migratory path, and attracts a number of megafauna including sharks, whales and manta rays. Dense schools of zooplankton are seasonally common to the region, and the surrounding waters can be highly productive, potentially creating high secondary productivity (C. E. Hanson, C. B. Pattiaratchi & A. M. Waite 2005). The reef is the focus of a number of tourism operations and has considerable intrinsic ecological and social value to the community of Western Australia, as well as attracting the interest of researchers worldwide.

2.4.1 Leeuwin and Ningaloo Currents

Interactions between the Leeuwin and Ningaloo Currents are a major driving force for the ecology and physical dynamics of the Gascoyne shelf. The Leeuwin Current is an unusual boundary current to find in the southern hemisphere, because it flows southwards along the Western Australian coast (Figure 5).

The current transports warm tropical water from the Pacific Ocean through the Indonesian Archipelago, down the coast to Cape Leeuwin and then eastwards into the Great Australian Bight as far as Tasmania (Woo, Pattiaratchi & Schroeder 2006; CSIRO Marine Research 2001). It is characterized in satellite imagery as a stream of warm water flowing along the edge of the continental shelf at approximately the 200 meter isobath (Figure 5). The current generates large eddies and loops which occasionally separate from the larger current, carrying warm tropical water over 200 kilometers from the coast (CSIRO Marine Research 2001).

The surface waters of the Leeuwin Current are oligotrophic, and are associated with low phytoplankton biomass and low primary production in the pelagic zone (C. E. Hanson, C. B. Pattiaratchi & A. M. Waite 2005). There is a strong nutricline at the base of the mixed layer, 70-200m from the surface, below which cooler, nutrient-rich water is suppressed by the warmer surface waters. The Leeuwin Current’s warm temperatures and low salinity act to suppress upwelling for most of the year (Furnas 2007).
Figure 5: Satellite imagery showing the Leeuwin Current as a warm southward flow along the West Australian coast (CSIRO Marine Research 2001).

The presence of strong southerly winds and the associated Ningaloo Current during summer (Figure 6) weakens the poleward flow of the Leeuwin Current and can cause sporadic small-scale upwelling from the nutrient-rich waters below the nutricline (Pearce 1991; C. E. Hanson, C. B. Pattiaratchi & A. M. Waite 2005). These small-scale upwelling events have been shown to source nitrate levels of > 1 μM from the nutricline and cause an increase in pelagic production in the Capes Current (C. E. Hanson, C.B. Pattiaratchi & A. M. Waite 2005). The nutricline was found to be shallower and episodic upwelling appeared to occur in El Niño conditions, supplying nutrient-rich waters and the sub-surface chlorophyll maximum to the continental shelf and causing a 2-4 fold increase in phytoplankton primary production (Furnas 2007).
2.5 Study motivation

The link between nutrient uptake and net carbon production is one of the least understood processes in coral reef biogeochemistry. Furthermore, the majority of studies conducted on nutrient limitation in coral reef ecosystems have been conducted in the northern hemisphere, and no studies have considered net production on the unique Ningaloo reef. The aim of this study is to investigate the link between nutrient uptake and net carbon production on the Ningaloo Reef of Western Australia, and to compare Lagrangian and Eulerian methods of estimating net production. Finally, it is hoped that the results will yield some understanding of calcification on the Ningaloo Reef.
3 Methods

The following chapter presents a description of the techniques used in field work, and the analyses used in interpreting the data. Data used in this thesis originates from a field trip to the study site in November 2007, which aimed to build upon the findings of a separate field trip in May 2007. The findings of the May field trip have been reported thus far in Kapeli and Waite (2007), Philp and Waite (2007) and Waite et al (2007).

3.1 Study site

The study site was a section of the Ningaloo Reef bordering the Exmouth Peninsula along the northwest coast of Western Australia (Figure 7). Specifically this work focuses on a small (~4 km) section of reef at Sandy Bay, roughly 45km south-west of Exmouth in the Cape Range National Park.

![Map of Sandy Bay study site](image)

*Figure 7: Sandy Bay study site (Waite et al. 2007).*

The Sandy Bay lagoon has an average depth of 2-3 m, while depths offshore rapidly drop with a ~1:30 forereef slope. The reef itself is approximately 1 km wide and consists of a series of alongshore reef sections 5-10 km long. The deep channels between reef sections are of the order of 10 m deep. Hydrographic data collected during May suggested that the water column was well mixed both inside and outside the reef (Kapeli & Waite 2007). In May, the
temperature ranged from 25.5 to 27.4 °C and average salinity was 37.5 psu (Kapeli & Waite 2007). Surface drifters deployed on the reef flat in May showed a consistent flow regime over the reef crest of the focus reef segment, across the reef flat and exiting from the channel to the south of the segment (Figure 8) in a ‘conveyor belt’ flow pattern (Kapeli & Waite 2007).

Figure 8: Sampling stations (yellow) and drifter tracks (red) at Sandy Bay in May 2007 (Waite et al. 2007). Drifter data courtesy Graham Symonds, CSIRO Floreat, May 2006.

Six sampling stations were defined in May along the ‘conveyor belt’ flow (Figure 8), and some samples were taken at sites RO5 and RO4 in November to provide a seasonal comparison. However, strong winds and associated safety considerations rendered the two outer-reef stations (RO6 and RO7) inaccessible in November, and therefore measurements over this period focused on processes operating on the reef flat and inside the lagoon.
3.2 Field work and laboratory analysis

The field work component of this study consisted of two major components. Firstly, continually logging sensors were used in a fixed deployment on the reef flat to provide Eulerian estimates of net production by reef organisms. Secondly, a series of drifter tracks were combined with manual measurements of oxygen and nutrients to obtain Lagrangian net production estimates and nutrient fluxes.

3.2.1 Eulerian reference frame: continuously logging sensors

Sensors were deployed on the reef flat to allow the calculation of dissolved oxygen (DO) fluxes in the water passing over the coral-dominated reef flat. DO sensors formed a triangle of approximately 200 m length on the reef flat, with the apex closest to the reef crest (Figure 9). An Acoustic Doppler Current Profiler (ADCP) and a Conductivity-Temperature-Depth (CTD) probe were deployed in the centre of the triangle to measure directional currents, water depth and photosynthetically active radiation (PAR). The experimental design followed the procedures designed by Falter et al (2008).

Figure 9: Distribution of sensors on the reef flat.
All sensors were synchronized to the same time, and deployed before midday on the 3rd of November and removed on the morning of the 9th of November. Precise locations of the sensors are shown in Table 2.

Table 2: GPS locations of the continuously logging sensors. The first three locations each contained a DO sensor while the ADCP location contained ADCP and CTD probes.

<table>
<thead>
<tr>
<th>Location</th>
<th>Comment</th>
<th>Easting (m)</th>
<th>Northing (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oxy-1 (Apex)</td>
<td>Intertidal Zone</td>
<td>792007</td>
<td>7539559</td>
</tr>
<tr>
<td>Oxy-2 (South)</td>
<td>5.0 m max depth</td>
<td>792222</td>
<td>7539348</td>
</tr>
<tr>
<td>Oxy-3 (North)</td>
<td>5.0 m max depth</td>
<td>792299</td>
<td>7539532</td>
</tr>
<tr>
<td>ADCP</td>
<td>5.0 m max depth</td>
<td>792144</td>
<td>7539489</td>
</tr>
</tbody>
</table>

3.2.1 Dissolved oxygen (DO) sensors

Three TROLL 9000E LTS sensors with Aanderaa RDO optodes (provided by the Hawai‘i Institute of Marine Biology) were deployed on the coral-dominated reef flat to measure dissolved oxygen concentrations in the water column. The first sensor was placed at RO5 station closest to the reef crest (Figure 8). To allow for variation in the dominant current direction, the second and third sensors were placed approximately 200m downstream and 100m to the north and south (Figure 9), in accordance with the methods described by Falter et al. (2008) and discussed further in section 3.3.1. The instruments sampled at 1 minute intervals, and these measurements were averaged over 5 minute intervals during analysis for use in Eularian calculations (section 3.3.1).

The DO sensors required no calibration prior to deployment. However, to adjust for drift in the baseline, Winkler titrations (section 3.2.2.4) were performed to measure DO using water samples taken daily within approximately one metre of each sensor. These measurements were taken at various times of the day including early morning and dusk, to ensure the maximum and minimum values of production were considered in calibration. The optodes were cleaned daily to prevent biofouling.
3.2.1.2 Acoustic Doppler Current Profiler (ADCP)

An ADCP was deployed between the oxygen sensors (Figure 10) and was set to record vertical current profiles. The ADCP was placed in approximately 2m depth and set to a bin height of 10cm prior to deployment, with a blanking distance of 10cm immediately above the sensor. Samples were taken at a rate of 5Hz and were averaged over five minutes. The instrument sampled current vectors to the East and North, as well as vertically upward in the water column.

3.2.1.3 Conductivity-Temperature-Depth (CTD) probe

The CTD probe was moored in association with the ADCP (Figure 9) and recorded photosynthetically active radiation (PAR), temperature and salinity every 2 minutes during the period of deployment. These measurements were averaged over 5 minute intervals during analysis for use in Eulerian calculations. PAR data was compared with measurements taken at Milyering weather station (Australian Institute of Marine Science 2008).
3.2.2 Lagrangian transect sampling regime

The Lagrangian sampling regime relied upon a moving reference frame, where a water mass was tracked by drifters and followed by boat, manually sampling from the reef crest to the channel. Seven transects were performed in total (Table 3). GPS coordinates and times were recorded for each sampling site. Drifters were deployed at the RO5 station close to the reef flat and followed for periods of between 0.5-3 hours.

Exact sampling sites varied depending upon the drifter track, but in general water samples were taken once from the start of the drifter track, at least once during their path over the coral-dominated reef flat, and at least once further toward the reef lagoon. Exceptions were on the 3rd and 4th of November, when the drifters were left for several hours and allowed to continue their path toward the channel. These tracks are referred to as ‘long’ transects.

Table 3: Lagrangian sampling regime

<table>
<thead>
<tr>
<th>Transect</th>
<th>Date</th>
<th>Time</th>
<th>GPS Location</th>
<th>Sampling</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>3/11/2007</td>
<td>10:30</td>
<td>22.13302, 113.49579</td>
<td>Chlorophyll a</td>
</tr>
<tr>
<td>3</td>
<td>5/11/2007</td>
<td>17:33</td>
<td>22.22487, 113.83272</td>
<td>Chlorophyll a</td>
</tr>
<tr>
<td></td>
<td>5/11/2007</td>
<td>18:00</td>
<td>22.22563, 113.83561</td>
<td>Chlorophyll a</td>
</tr>
<tr>
<td></td>
<td>6/11/2007</td>
<td>14:00</td>
<td>22.22499, 113.83545</td>
<td>Chlorophyll a, nutrients, DO</td>
</tr>
<tr>
<td>5</td>
<td>8/11/2007</td>
<td>10:46</td>
<td>22.22484, 113.83266</td>
<td>Chlorophyll a, nutrients, DO</td>
</tr>
</tbody>
</table>
3.2.2.1 Drifters

Drifters approximately 50 cm deep and 1 m wide were used to characterize the flow regime across the reef flat (Figure 11). These were deployed on most days of the field work in association with Lagrangian transect sampling. The drifters each contained a handheld global positioning system (GPS) instrument in a dry casing which recorded their direction and speed. Duplicates were deployed in pairs within one metre of one another in order to verify the consistency of the flow path, with the exception of the 8th of November when equipment failure resulted in the use of only one drifter.

Figure 11: Drifters deployed on a Lagrangian transect (Krikke 2007).

3.2.2.2 Chlorophyll $a$

Chlorophyll samples were taken at various points along the Lagrangian transects. To provide a seasonal comparison with the May data, an additional sample of RO5 was taken on the 2nd of November, and RO4 was also sampled on the 2nd and 5th of November. Sample collection followed the procedures outlined in the JGOFS Protocols (Intergovernmental Oceanographic Commission 1994).
Water samples were collected in 20-litre capacity black carboys to prevent photodegradation and returned to the laboratory for filtering within three hours of collection. The carboys were inverted twice before drawing water to ensure a homogenous sample.

Two replicates were filtered for each sample using a Millipore vacuum pump set to 10-20 psi, a pressure chosen to reduce the likelihood of damage to the cells. Firstly, the total chlorophyll samples were filtered using one replicate of 1 L and one replicate of 500 mL on GF/F 25mm Whatman filters with a 0.7μm pore size. The smaller fraction size was filtered using two replicates of 2 litres each on Nitex mesh filters with a 5μm pore size. Filter papers were removed using tweezers to prevent contamination, wrapped in aluminum foil to prevent photodegradation and stored in the freezer until analysis, which was undertaken within three weeks of collection.

Frozen filter papers were removed from the aluminum paper and covered with 8 mL of 90% acetone to aid extraction, and left to steep for 24 hours in the freezer at 1-2 °C. Samples were allowed to return to room temperature before placing in the fluorometer to record the before-acid reading (Rb). Three drops of 1 M hydrochloric acid were then added and the after-acid reading (Ra) was taken. Chlorophyll a was calculated using Equation 2:

\[
\text{Chlorophyll } a \ (\mu g/L) = \frac{r}{r - 1} \times \left( \frac{R_b - R_a}{V} \right)
\]

Where:

\( r = \frac{R_b}{R_a} \) of a pure chlorophyll a solution (\( r = 2.28 \));

\( v = \) the volume (mL) of the extract; and,

\( V = \) the volume (mL) of the filtered sample.

### 3.2.2.3 Nutrients

Nutrient samples were filtered on the boat using 40cc syringes and GF/F 25mm Whatman filters, following procedures set out in the JGOFS Protocols (Intergovernmental Oceanographic Commission 1994). All samples were analysed at the Hawai’i Institute of Marine Biology.
3.2.2.4 Winkler titrations for dissolved oxygen

Dissolved oxygen concentration in the water column was measured using Winkler titrations following procedures described in the JGOFS Protocols (Intergovernmental Oceanographic Commission 1994). Samples were collected in completely airtight van Dorn bottles, for which the volume was known to a factor of 0.1 mL to give a precision of 0.1 - 0.2%. Water was run through the bottle and overflowed such that it was rinsed with two full volumes before the final sample was collected. Manganese chloride, sodium hydroxide and sodium iodide were added to fix the sample.

The samples were analysed at the temporary onshore laboratory on the same day of collection, using the manual titration method with a visual indicator. The 775 Dosimat Brinkmann Metrohm and IEC Magnetic Stirrer were used to assist with the titration (Figure 12).

![Figure 12: Stirring the sample ready for Winkler titration.](image)

3.3 Estimating primary production

Estimates of primary production made in this study followed the methodology proposed by Falter et al. (2008). The following section gives an overview of that methodology as well as addressing specific areas where the methodology was adapted for the study site.
Measurement of DO fluxes allow the indirect estimation of net organic carbon fluxes based upon stoichiometry of carbon fixation and release, through photosynthesis and respiration respectively (Falter et al. 2008). It is assumed that photosynthesis and respiration follow the same stoichiometry, and thus net oxygen flux is equal to the product of net production and photosynthetic quotient, i.e. (Equation 3):

\[ NP = \frac{J_{O_2}}{PQ} \]  

Where:

\( J_{O_2} \) = net oxygen flux (mmol m\(^{-2}\) hr\(^{-1}\)); and

\( PQ \) = photosynthetic quotient.

The photosynthetic quotient \( PQ \) is equal to the ratio of the number of moles of \( O_2 \) produced by photosynthesis to the number of moles of \( CO_2 \) fixed by photosynthesis. It is assumed to be equal to 1.0 (Falter et al. 2008).

3.3.1 Eulerian method of estimating primary production

3.3.1.1 Guiding principles: a one-dimensional example

The basic principle of calculating net production via the Eularian method is to consider the changes in DO due to respiration and production by coral and other reef organisms within the control volume (local flux), differences in fluxes of DO into and out of the control volume by movements of the currents (advective flux) and the transfer of oxygen between the atmosphere and the ocean (gas flux). Equation 4 provides a summary:

\[ J_{O_2} = J_{local} + J_{advective} - J_{gas} \]  

In an ideal situation where the currents form a series of parallel streamlines in one direction with varying speed (e.g. Figure 13), the problem is one-dimensional.
Figure 13: Ideal situation where the direction of current \( q \) consistently follows the cross-reef axis (\( x \)). \( C_1 \) and \( C_2 \) are dissolved oxygen concentration at two points along a streamline, separated by length \( L \).

The advective term would be a product of the depth-integrated transport term \( Q \) (m\(^2\) hr\(^{-1}\)) and the dissolved oxygen gradient (mmol m\(^{-2}\) hr\(^{-1}\)) along a streamline (Figure 13), e.g. (Equation 5):

\[
J_{\text{advective}} = Q \left( \frac{\Delta C_2 - \Delta C_1}{\Delta t} \right)
\]

Equation 5

Similarly, the local flux would be a depth-integrated average of dissolved oxygen concentration at two points along the streamline (Equations 6, 6):

\[
J_{\text{local}} = h \frac{\partial \bar{C}}{\partial t}
\]

Equation 6

Where \( \bar{C} = \frac{C_1 + C_2}{2} \)

Equation 7

Thus the equation governing net production within the sampling region would be (Equation 8):

\[
NP = h \frac{\partial \bar{C}}{\partial t} + Q (C_2 - C_1) - J_{\text{gas}}
\]

Equation 8

Where:

\( h \) = water depth (m);

\( \frac{\partial \bar{C}}{\partial t} \) = change in dissolved oxygen concentration per hour (mmol m\(^{-3}\) hr\(^{-1}\));

\( Q \) = depth-integrated transport term (m\(^2\) hr\(^{-1}\));

\( C \) = dissolved oxygen concentration (mmol m\(^{-2}\) hr\(^{-1}\)); and
J_{gas} = \text{flux of DO across the air-sea interface (mmol m}^{-2}\text{ hr}^{-1}).

3.3.1.2 Applying the Eulerian method in two dimensions

The theoretical situation proposed above fails in many practical settings because the currents vary in direction between the x (cross-reef) and y (along-reef) directions. An experimental design with only two dissolved oxygen probes would fail to capture the local and advective fluxes in any situation where the streamline varied slightly away from the cross-reef axis.

To capture this variation, a control volume was established which formed a triangle around the cross-reef axis (Figure 14). An ADCP was deployed in the centre of the triangle to capture current speed and direction, which were assumed to be spatially constant within the control volume. See Appendix A for the Matlab code used to calculate net production.

Figure 14: Experimental design of the control volume, showing the DO sensor locations and resultant control volume, the cross-reef axis (x) and the along-reef axis (y). The ADCP was deployed in the centre of the control volume.

The advective flux in the two-dimensional situation hence includes a term for the two-dimensional horizontal gradient in dissolved oxygen, and the local flux is averaged over the control volume. Falter et al. (2008) provides a thorough derivation for estimating this flux...
from the concentrations at the vertex of the triangles. In summary, the governing equation in two-dimensions becomes Equation 9 (Falter et al. 2008):

$$NP = h \frac{\partial C}{\partial t} + \tilde{Q} \cdot \tilde{V}_h C - J_{gas}$$  \hspace{1cm} \text{Equation 9}$$

Where:

- $h =$ average water depth for time $t$ (m);
- $\frac{\partial C}{\partial t} =$ change in dissolved oxygen concentration per time $t$ (mmol m$^{-3}$ s$^{-1}$);
- $Q =$ depth-integrated transport term (m$^2$ s$^{-1}$);
- $\tilde{V}_h C =$ 2-D horizontal gradient in dissolved oxygen;
- $J_{gas} =$ flux of oxygen across the air-sea interface (mmol m$^{-2}$ hr$^{-1}$).

### 3.3.1.3 Gas flux

Gas flux can be considered to be a linear term characterized by Equation 10 (Falter et al. 2008):

$$J_{gas} = k_{O2}(C_{eq} - C)$$  \hspace{1cm} \text{Equation 10}$$

Where:

- $k_{O2} =$ gas exchange constant; and
- $C_{eq} =$ equilibrium concentration of dissolved oxygen at a given temperature and salinity, calculated using formulas from Garcia and Gordon (1992).

The gas exchange constant can be estimated as follows (Equation 11):

$$k_{O2} = \frac{(600/ScO2)^n.k_{600}}{}$$  \hspace{1cm} \text{Equation 11}$$

Where:

- $k_{600} =$ the exchange coefficient;
- $ScO2 =$ the ratio of kinematic viscosity to the diffusivity of dissolved oxygen (a function of temperature and salinity); and
- $n = 0.5$ for wavy surfaces.

The Schmidt number ($Sc$) was assumed to be 600, and the exchange coefficient $k_{600}$ was assumed to be 0.266 (Falter et al. 2008) multiplied by wind speed. Wind speed data was
obtained on 30-minute intervals from the Mylering Research Station in Exmouth, run by the Australian Institute of Marine Science (AIMS). Falter et al (2008) found that gas flux was not a major term in calculating net production.

### 3.3.2 Community metabolism rates

Community rates of reef metabolism were estimated by integrating the net production curve generated by the Eulerian approach. All relationships presented below were obtained from Falter et al (2008). See Appendix D for the Matlab code used to calculate these terms.

Community respiration during dark hours was calculated as in Equation 12:

$$ R_{dark} = -\frac{1}{\tau_{dark}} \int_{sunrise}^{sunset} NP(t)dt $$

Equation 12

Where $\tau_{dark}$ is the time between sunset and sunrise. Daily integrated community respiration (R) was then calculated for each day as in Equation 13:

$$ R^{i} = 24 \left( \frac{R_{dark}^{i} + R_{dark}^{i-1}}{2} \right) $$

Equation 13

NCP was calculated from midnight to midnight the following day (Equation 14):

$$ R_{dark} = \int_{0}^{24} NP(t)dt $$

Equation 14

Finally, GPP was derived from the sum of R and NCP as defined in Equation 1 (section 2.1.1).

### 3.3.3 Lagrangian method of estimating primary production

Net production was also calculated using a Lagrangian reference frame where a water parcel was followed over the reef and repeatedly sampled (section 3.2.2). Firstly, the depth-integrated material derivative is calculated by considering the change in concentration along the streamline: see Equation 15 (Falter et al. 2008);

$$ \frac{DC}{Dt}_{material} = hL \frac{C_{2} - C_{1}}{\Delta t} $$

Equation 15

Where $\Delta t$ is the total time for the water parcel to move from point 1 to point 2 (Figure 13). Net production is then taken as the sum of the depth-integrated material derivative and the Lagrangian gas flux (Equation 16):
\[ NP_L = h \frac{DC}{Dt} - J_{gas} \]  

Equation 16

Note that the drifters only sample the top 30-50cm of the water column (Figure 11). The speed they record does not reflect the depth-averaged velocity, since the roughness of the coral benthos creates drag and causes the velocity profile to move more slowly at the base of the water column. For example, Falter et al (2008) found that drifter speeds were 30-100% faster than depth-averaged velocity. Therefore the ADCP velocity profiles were evaluated to correct this discrepancy (this correction will be presented in more detail in the results). Water depth was estimated using bathymetry data derived from hyperspectral imagery with ~4m horizontal resolution and ~10% uncertainty in the vertical (data from W. Klonowski of Curtin University: subsequently tide-corrected, mosaicked, and gridded by R. Lowe of UWA).

### 3.4 Lagrangian method of estimating nitrogen, phosphorus and chlorophyll uptake

Nitrogen, phosphorus and chlorophyll measurements made in association with drifter tracks were also examined in a Lagrangian reference frame, where the associated nutrient or chlorophyll concentration was substituted for dissolved oxygen concentration in Equations 15 and 16 (however gas flux was obviously neglected). For example, nitrogen uptake was measured as in Equation 17:

\[ N_L = h \frac{DC}{Dt} \]  

Equation 17

### 3.5 Light attenuation coefficient

A light attenuation coefficient was estimated on the reef flat using measurements of photosynthetically active radiation at the benthos (using CTD data) and in the air, using data from the Milyering weather station at the Learmouth airport (Australian Institute of Marine Science 2008). The light attenuation can be calculated by rearranging the equation for light intensity (CSIRO Marine Research 2002) as in Equation 18:

\[ K_d = \frac{\log(I_o) - \log(I_z)}{z} \]  

Equation 18

Where \( Kd \) = light attenuation coefficient; \( z \) = depth (m), given by the tidal depth measured by the ADCP; \( Iz \) = light intensity at depth \( z \), given by the PAR measured at the benthos by the
CTD: and \( I_0 \) = light intensity at the surface, given by the PAR measured at Milyering weather station. See Appendix C for the Matlab code used to calculate the light attenuation coefficient.
4 Results and Analysis

4.1 Eulerian reference frame

4.1.1 Current speed and direction

4.1.1.1 Adjusting for compass failure

Unpublished data collected in May 2007 by Dr. Ryan Lowe showed the currents across the reef flat to flow in the cross-reef direction with little variation to the along-reef direction.

Initial attempts at data analysis thus revealed that the ADCP was measuring an inaccurate compass bearing, most likely due to technical failure of the compass in the field. Ranges in the ADCP-measured directions were obtained by calculating the value for the given time period and again for a three-hour period inclusive of the period stated. The comparison in Table 4 reveals that there is an average discrepancy of 52 degrees between the surface current direction recorded by the ADCP and the drifters. The surface currents were assumed to be a better indication of the drifter tracks than depth-averaged velocity, since the drifters only sampled the top of the water column.

<table>
<thead>
<tr>
<th>Date</th>
<th>Time Period</th>
<th>ADCP-measured direction of depth-averaged velocity (degrees from “ADCP North”)</th>
<th>ADCP-measured direction of surface velocity (degrees from “ADCP North”)</th>
<th>Drifter-measured direction of surface velocity (degrees from North)</th>
<th>Average discrepancy between ADCP surface currents and drifters (degrees)</th>
</tr>
</thead>
<tbody>
<tr>
<td>3rd Nov</td>
<td>10:00 – 11.00</td>
<td>177-179</td>
<td>183-185</td>
<td>126</td>
<td>58</td>
</tr>
<tr>
<td>5th Nov</td>
<td>17:00 – 18:00</td>
<td>172.8-172.8</td>
<td>164</td>
<td>108</td>
<td>56</td>
</tr>
<tr>
<td>8th Nov</td>
<td>10:30 – 11:30</td>
<td>152.8-153.2</td>
<td>140-142</td>
<td>100</td>
<td>41</td>
</tr>
</tbody>
</table>

4.1.1.2 Defining the cross-reef and along-reef axes

The cross-reef and along-reef axes were defined using the mean direction of current flow for the entire study period, found to be on bearings of 112 degrees and 202 degrees respectively (see Appendix E).
The Eulerian control volume is defined by the slopes on the outer edges of the CV, from the apex to the northern and southern sites (Figure 9). These angles were on bearings of 95 and 135 degrees respectively: therefore the control volume effectively captured the mean cross-reef flow.

The control volume boundaries are shown in red in Figure 15. Most of the variation was captured by the control volume in the first part of the study period, but the changing direction of the surface currents caused discrepancy at some times on the 5th, 6th, 7th, 8th and 9th of November. Overall, the control volume captured the streamline for 60 percent of the data collected.

![Threshold for streamlines inside the control volume](image)

**Figure 15:** Current flow direction with respect to the cross-reef axis (defined at zero degrees) over the study period. Red lines represent the outer boundaries of the control volume. Values outside the boundaries indicate times for which the control volume failed to capture the streamline.

### 4.1.2 Wind speed and direction

Figure 16 and Figure 17 show wind direction and speed respectively for the study period. Raw wind data was obtained in half-hourly intervals from the Milyering weather station at the Learmouth airport. There was no data available between 4pm on the 8th of November and 6am on the 9th of November 2007.
Wind direction was highly variable on the 3rd and 4th of November. However, data for the later part of the study period indicates that the wind strength increased (Figure 17) and was blowing exclusively from the south to south-west (Figure 16). A diurnal pattern is also visible from the 5th to the 8th of November. Wind originates from the southeast in the late morning to early afternoon, tending southerly in the evening and very early morning. The southerly winds from the 5th to the 8th are typical of the wind system which tends to dominate during summer on the Ningaloo coast.

![Wind Direction from Milyering Weather Station](image)

Figure 16: Wind direction from the Milyering weather station at the Learmouth airport. Note that there is missing data from 4pm on the 8th of November to 6am on the 9th of November. Data is courtesy of the Australian Institute of Marine Science (2008).

Wind speed (Figure 17) also varied in a diurnal pattern for most days of the study period, where wind speed peaked around midday. The minimum total wind speed was 0.028 ms⁻¹, recorded on the 5th of November at 3:30am, while a maximum of 10.8 ms⁻¹ was recorded on the 7th of November at 1:00 pm. The diurnal variation in both wind speed and direction is very likely due to the sea breeze system, where temperature differences over the ocean drive a pressure system which causes increased winds from the south-west during the late morning to early afternoon.
4.1.2.1 Current velocity in the cross- and along-reef directions

The depth-integrated velocity data is presented in the cross-reef and along-reef directions (Figure 18).

The along-reef velocity (where the positive direction is a bearing of 202 degrees) is initially centered on zero, but becomes more negative (north-northeasterly) around the 6th of November, corresponding with increased southerly winds (Figure 16). Cross-reef velocity ranged from a minimum of -0.029 m s\(^{-1}\) to a maximum of 0.13 m s\(^{-1}\), and along-reef velocity ranged from -0.11 m s\(^{-1}\) to 0.063 m s\(^{-1}\).

The average velocities over the study period were 0.060 m s\(^{-1}\) in the cross-reef direction and -0.0072 m s\(^{-1}\) in the along-reef direction. The maximum total velocity (a vector sum of both components) was 0.15 m s\(^{-1}\) on the 7th of November at 5:45 am, and the minimum was 0.0027 m s\(^{-1}\) on the 7th of November at 11:35 pm.
Figure 18: Cross-reef (a bearing of 115 degrees, or ESE) and along-reef (a bearing of 205 degrees, or SSW) depth-averaged velocity components for the study period. Note that along-reef velocity becomes more negative on average during the course of the study period.

4.1.3 Temperature

Figure 19: Temperature recorded by the moored CTD instrument in the centre of the control volume. Note that average temperature decreases toward the end of the study period.
4.1.4 Light

Measurements of photosynthetically active radiation (PAR) were recorded by the moored CTD probe. Figure 20 shows the measurements of PAR at the base of the water column, compared to PAR data obtained from the Milyering weather station and plotted over the time of the study period. Note the daily peak in irradiance (solar noon). The Milyering PAR data was adjusted for a discrepancy of approximately 25 minutes between solar noon recorded at Milyering and solar noon recorded by the CTD. A maximum irradiance of 1693 mmol quanta m$^{-2}$ s$^{-1}$ was recorded by the CTD at 1:12 pm on the 3$^{rd}$ of November.

![Comparison of PAR in the air and water](image)

Figure 20: Light available for photosynthesis at the base of the water column (Iz) measured by the CTD meter in the centre of the control volume, and PAR measurements from the Milyering weather station (Io), plotted against time for the study period.

4.1.4.1 Light attenuation coefficient

The light attenuation coefficient (Kd, in m$^{-1}$) is plotted over the period of the day in Figure 21. Only data where PAR > 500 mmol quanta m$^{-2}$ s$^{-1}$ and Io > Iz was included in the calculation. The majority of the scatter in the data was recorded on the 5$^{th}$ of November (shown in red), a day on which sand was captured in surface chlorophyll $a$ samples.

The non-linear relationship of the data to time of day is most likely due to the changing angle of sunlight causing different quantities of light to be reflected from the surface of the water,
since the values of “Io” are measured several metres in the air rather than directly at the top of the water column. Values at solar noon are likely to be the most reliable, since the angle is smallest and hence diffuse scattering will be at a minimum. At solar noon (PAR > 2100 mmol quanta m$^{-2}$ s$^{-1}$), Kd ranged from 0.17-0.35 m$^{-1}$, and the average was 0.22 ± 0.07 m$^{-1}$.

![Light Attenuation over 24 hours](image)

Figure 21: Light attenuation coefficient (Kd) calculated using data at the base of the water column (CTD data) and in the air (Milyering weather data), as well as water depth (below). Values in red were taken on the 5th of November when sand was present in chlorophyll a samples.

### 4.1.5 Tidal fluctuation

Water depth was measured continuously by the ADCP in the centre of the control volume (Figure 22). Average depth was 1.52 m. The maximum depth was 2.08 m, recorded on the 8th of November at 9:45 pm, and the minimum of 0.903 m was recorded on the 9th of November at 5:15 am. These values correspond to the maximum tidal variation observed (1.18 m). Tidal fluctuation would be expected to have a significant impact upon volume flux calculations, since water depth more than doubles at high tide.
Figure 22: Water depth measured over time by the ADCP in the centre of the Eulerian control volume. The semidiurnal tidal signal can be clearly discerned.

4.1.6 Volume flux components in the cross- and along-reef directions

Volume flux results are plotted in Figure 23. The maximum total volume flux (magnitude calculated using both components) was 0.16 m$^2$ s$^{-1}$ recorded on the 8$^{th}$ of November at 8:55 am, while the minimum was 0.0084 m$^2$ s$^{-1}$ on the 7$^{th}$ of November at 11:05 pm. The average volume flux in the cross-reef direction was 0.090 m$^2$ s$^{-1}$, while the average in the along-reef direction was -0.0099 m$^2$ s$^{-1}$ over the study period.

The volume flux in the cross-reef direction was consistently positive with the two exceptions. Cross-reef flux was negative for more than an hour on the 5$^{th}$ of November (from 8:00pm to 9:25pm), during the peak of high tide (average depth 1.81 m). During this time, the velocity magnitude ranged from 0.047 - 0.073 m$^2$ s$^{-1}$ and average wind speed was 6.06 m s$^{-1}$ from a bearing of 200 degrees (SSE). The cross-reef flux was also close to zero on the 7$^{th}$ of November at 11 pm, roughly coinciding with the minimum total velocity (above) and also coinciding with the greatest high tide peak during the study period. The average wind speed for the two hour period around this time was 3.3 m s$^{-1}$ from a bearing of 280 degrees (ENE).
Figure 23: Volume flux components in the cross-reef and along-reef directions, calculated from depth-averaged velocity and the average water depth.
4.1.7 Dissolved oxygen concentration

Dissolved oxygen concentration at each of the three sensors on the reef flat is plotted in Figure 24. The graph clearly shows a diurnal pattern in dissolved oxygen concentration, with a daily peak at midday dropping to a minimum during dark hours. Note that for the first three days the southern site recorded the highest concentration of dissolved oxygen, indicating the streamline was flowing in the positive cross-reef direction toward the south-west. However, the northern site records the highest concentrations on the 6th, 7th and 8th of November, coinciding with the trend to southerly winds plotted in Figure 16. The sensor at the apex (closer to the reef crest) always shows the smallest range in concentration.

A maximum concentration of 331 mmol m$^{-3}$ was recorded at the southern site at 12:40pm on the 4th of November, and a minimum of 126 mmol m$^{-3}$ was recorded at the northern site at 7:00 am on the 9th of November. The concentration at the apex ranged from 170 – 263 mmol m$^{-3}$.

![Figure 24: DO concentration on the reef flat after adjustment for baseline drift using manual Winkler titrations. Data in this graph is courtesy of Dr. Jim Falter from the Hawaii Institute of Marine Biology.](image)

The dissolved oxygen concentrations were then differentiated with respect to time for each sensor (Figure 25). Positive values indicate that dissolved oxygen concentrations are
increasing, while negative values indicate a decrease in concentration for that time. The greatest rate of increase occurs around solar noon, while the greatest rate of decrease occurs after sunset. Note the hysteresis present in the graph: dissolved oxygen concentration increases at a maximum rate of 888 mmol m$^{-3}$ day$^{-1}$ (and reaches at least 600 mmol m$^{-3}$ day$^{-1}$ on four of the five days studied), but decreases occur at a lesser rate. Concentration decreased at a maximum rate of only -677 mmol m$^{-3}$ day$^{-1}$, and reached a rate of decrease of -600 mmol m$^{-3}$ day$^{-1}$ on only two of the five days studied.

![Graph showing dissolved oxygen concentration time-derivatives](image)

Figure 25: The time derivative of dissolved oxygen concentration at each sensor. Positive values indicate an increasing concentration of dissolved oxygen, while negative values indicate a decreasing concentration.

### 4.1.8 Eulerian calculations of net production

The figures below present the results of Eulerian estimates of net production. Positive fluxes (above the x-axis) indicate that net production of dissolved oxygen is occurring, while net oxygen uptake is indicated by a negative flux. The root-mean squared values of the local, advective and gas fluxes at Sandy Bay were 15.5, 28.3 and 2.0 mmol m$^{-2}$ hr$^{-1}$ respectively, indicating that the advective term dominated net production.
4.1.8.1 Local flux

The local flux of dissolved oxygen (i.e., the change in dissolved oxygen within the control volume) is a function of the local time derivatives of dissolved oxygen concentration at each sensor (Figure 25), averaged over the control volume for each time step. It was also a function of average water depth (Figure 22). The results are plotted in Figure 26.

The maximum rate of increase in local DO concentration was 42 mmol m$^{-2}$ hr$^{-1}$, recorded on the 4$^{th}$ of November at 8:47 am, and the maximum rate of decrease was -39 mmol m$^{-2}$ hr$^{-1}$ on the 5$^{th}$ of November at 7:52 pm.

The local flux only considers processes occurring within the control volume: hence the diurnal cycle of dissolved oxygen production and uptake visible in Figure 26 can only be attributed to processes occurring directly on the coral-dominated reef flat. If we can assume benthic processes dominate over pelagic production, the diurnal cycle shown below represents a direct measure of the coral reef metabolism on the reef flat.

![Figure 26: Local flux of dissolved oxygen within the Eulerian control volume, taken as a depth-integrated average of the time derivatives of dissolved oxygen concentration at each DO sensor for each time step.](image)
4.1.8.2 Advective flux

The advective flux of dissolved oxygen (i.e., the dissolved oxygen input or output to the control volume via advection) is plotted in Figure 27 in the cross-reef and along-reef directions. Note that the cross-reef component was generally an order of magnitude higher than the along-reef component, except in the final days of the study period where it is suggested that southerly winds increased the influence of the along-reef current.

The maximum increase in DO concentration due to the cross-reef advective flux was 103 mmol m\(^{-2}\) hr\(^{-1}\), recorded on the 4\(^{th}\) of November at 12:52 pm, and the maximum rate of decrease was -47 mmol m\(^{-2}\) hr\(^{-1}\) recorded on the 9\(^{th}\) of November at 6:57 am. In the along-reef direction, fluxes ranged from -31 mmol m\(^{-2}\) hr\(^{-1}\) at 11:52 am on November 5\(^{th}\) to 19 mmol m\(^{-2}\) hr\(^{-1}\) at 6:32 am on November 8\(^{th}\).

![Figure 27: The advective fluxes of dissolved oxygen in the cross-reef and along-reef directions. A positive value refers to a net input of dissolved oxygen into the control volume due to the volume transfer driven by depth-averaged currents.](image)

Note that in the later part of the week, when the increased southerly winds are suggested to be driving the advective flux in a manner typical of summer weather conditions, the advective fluxes are of the same order of magnitude as the local flux. In the early part of the study...
period, however, where winds were more variable, the cross-reef advective flux (Figure 27) is twice the local flux (Figure 26).

### 4.1.8.3 Gas flux

Figure 28 presents the gas flux term plotted over the study period, which is a function of wind speed, temperature and salinity. Temperature and salinity data were obtained from the CTD. Average wind speed for the entire study period was used to replace missing wind data between 4pm on the 8th of November to 6am on the 9th of November. Note that the scale on the y-axis is an order of magnitude less than the local and advective fluxes, and that the gas flux term is between +1 and -1 mmol m⁻² hr⁻¹ (two orders of magnitude less than the local and advective fluxes) for 69% of the times in the study period. Average gas flux is -0.85 m⁻² hr⁻¹.

Gas flux is defined in Figure 28 such that a positive value refers to an input of oxygen to the ocean from the atmosphere. The greatest dissolved oxygen removal to the atmosphere (-8.7 mmol m⁻² hr⁻¹) occurred on the 7th of November at 1:02 pm, while the greatest positive dissolved oxygen transfer (2.9 mmol m⁻² hr⁻¹) occurred on the 9th of November at 6:57 am.

![Gas Flux](image)

**Figure 28:** The gas flux term (a function of wind speed, temperature and salinity) plotted over time. Average wind speed was used for the period between 4pm on the 8th of November to 6am on the 9th of November. Gas flux is defined here such that a positive value indicates the net transfer of dissolved oxygen from the atmosphere into the ocean.

### 4.1.8.4 Net Production

Figure 29 presents the total production of dissolved oxygen by the reef flat within the control volume, including: production directly within the CV, advective fluxes into and out of the CV and the transfer of oxygen gas between the ocean surface and the atmosphere.
Note the clear diurnal variation in production: a peak in production occurs around midday, and the trough representing oxygen uptake occurs during the dark hours. The maximum value of net production recorded across the entire study period was 83.8 mmol m\(^{-2}\) hr\(^{-1}\) at 3:02 pm on the 4\(^{th}\) of November, while the minimum of -55.7 mmol m\(^{-2}\) hr\(^{-1}\) was observed at 8:57 pm on the 3\(^{rd}\) of November.

Figure 29: Net production for the Eulerian control volume (calculated as the sum of the local and advective fluxes, subtracting gas flux) plotted against time for the study period. A positive value refers to the net production of dissolved oxygen due to processes occurring within the control volume, and/or due to fluxes into or out of the control volume.
4.1.9 Gross production, respiration and net community production

The integrated rates of GPP, R and NCP on the reef flat at Sandy Bay are presented in Table 5 below, along with the resulting GPP:R ratio. Note that all rates are higher on the 4th and 5th of November. The reef was net autotrophic (GPP:R>1) for all days of the study period.

Table 5: Community metabolism rates (in mmol C m\(^{-2}\) d\(^{-1}\)) for each full day of the study period.

<table>
<thead>
<tr>
<th>Date</th>
<th>GPP (mmol C m(^{-2}) d(^{-1}))</th>
<th>R (mmol C m(^{-2}) d(^{-1}))</th>
<th>NCP (mmol C m(^{-2}) d(^{-1}))</th>
<th>GPP:R Ratio</th>
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</thead>
<tbody>
<tr>
<td>4/11/2007</td>
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<td>140</td>
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<td>8/11/2007</td>
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<td>Average (all)</td>
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<td>559</td>
<td>76</td>
<td>1.14</td>
</tr>
</tbody>
</table>
4.1.10 Net production vs. irradiance

A scatter graph of net production vs. light on the Ningaloo reef is presented in Figure 30. The comparison of net production to light was undertaken using only those times for which a water particle passing the apex would be captured by the control volume. The times used in analysis were only those for which the streamline was within the CV (59.4 percent of the data).

Net respiration is occurring for points below the x-axis, while net production is occurring for points above the x-axis. Note that for most times of low light (PAR ranging from 0 to around 300) respiration is occurring, but that there is considerable scatter in the data. The expected increase of production with light is present: however there is also a second slope of decreasing production in periods of high light intensity for some days (Figure 30).

![P-I Curve](image)

Figure 30: Scatter graph comparing net production with the availability of photosynthetically active radiation, after applying a threshold to remove values where the streamline is not fully captured by the control volume. Each colour represents a different date of the study period.

Further analysis of this curve is presented below. The Matlab code used to analyse the data and generate the graphs is contained in Appendix F.
The effect of excluding the streamlines not captured by the control volume is examined in Figure 31, where both the raw (a) and filtered (b) data are presented. Note that there is more obvious scatter in the unfiltered data, but that the basic shape of the curve remains unchanged.

![Figure 31: Comparison of a) raw data, and b) data filtered by applying a threshold which excludes times when the streamline was not captured by the control volume. Each colour represents a different date of the study period.](image)

4.1.10.1 Hysteresis

Figure 32 shows the relationship between net production and photosynthetically active radiation (irradiance) for the time between sunrise and solar noon (before peak irradiance). Production reached a maximum of 81.2 mmol m\(^{-2}\) hr\(^{-1}\) on the 4\(^{th}\) of November. Note that while PAR is very low (before sunrise) the reef was net respiring or at zero, but that it quickly reached net production after PAR reached more than 200 mmol quanta m\(^{-2}\) s\(^{-1}\). The slope of the curve suggests photoinhibition occurred at between 600-800 mmol quanta m\(^{-2}\) s\(^{-1}\). Although there is scatter in the data, the curve is consistent for different days of the study period.
Figure 32: Net Production vs. light before peak irradiance (between midnight and solar noon), after applying a threshold to remove values where the streamline is not fully captured by the control volume.

The afternoon P-I curve is shown in Figure 33, showing a different response to decreasing light. On the 3rd, 4th and 5th of November, the reef was net producing until irradiance dropped to around 400 mmol quanta m\(^{-2}\) s\(^{-1}\) (note that this is twice the irradiance level at which the reef was always net producing in the morning). At values of light between 200 and 400 mmol quanta m\(^{-2}\) s\(^{-1}\), there is considerable scatter: but below 200 mmol quanta m\(^{-2}\) s\(^{-1}\) the reef was net respiring on all days studied. Production reached a maximum of 84.2 mmol m\(^{-2}\) hr\(^{-1}\) (slightly more than before solar noon), and there are a number of values on the 4th of November for which production was above the range of 40-60 mmol m\(^{-2}\) hr\(^{-1}\) observed before solar noon (Figure 32).

There was a separate afternoon response on the 6th, 7th and 8th of November. On these days, net production quickly dropped after solar noon and the reef switched to net respiration in very high light (around 1100 mmol quanta m\(^{-2}\) s\(^{-1}\)).
4.2 Lagrangian reference frame

4.2.1 Drifter tracks
Drifters were deployed from the start of the Eulerian control volume (the Apex) on five days of the study period, with three deployments on the 4th of November (Figure 34). Drifters followed the expected flow regime through the Eulerian control volume on most days of deployment, with the exception of the 4th of November. Data plotted in Figure 34 is from one drifter only. The two drifters were observed to remain in close proximity during all transects.
Figure 34: Drifter tracks plotted using GPS coordinates for five days of the study period, showing the flow regime over the reef flat and into the lagoon. The Eulerian control volume (CV) is shown in black. Drifter data courtesy of Alex Wyatt, UWA.

Note that the drifter tracks on the 3rd and 4th of November curve to the south, while the remainder appear to have a more directly cross-reef or northerly trajectory.

4.3 Transect sampling for trends across the reef flat

The following section presents the results of manual sampling during Lagrangian transects across the reef flat. The data is plotted against the time of each sample. The aerial photograph (Figure 35) shows sampling locations. Transects sampled areas of the densely coral-
dominated zone on the reef flat (dark areas of the photograph) and the sparsely coral-dominated zone, as well as the lagoon (light green).

Figure 35: Lagrangian transect sampling locations for chlorophyll $a$, nitrate, SRP and dissolved oxygen on the 6th and 8th of November, plotted over the Eulerian control volume.
4.3.1 Chlorophyll $a$ transect sampling

Figure 36: Results of transect sampling for chlorophyll $a$ on the 3rd November 2007. The decreasing trend is significant for $p<0.05$.

Figure 37: Results of transect sampling for total chlorophyll $a$ on the 4th November 2007. An estimate of significance could not be made for only two sampling points.
Figure 38: Results of transect sampling for total chlorophyll $a$ on the 5$^{th}$ November 2007. An estimate of significance could not be made for only two sampling points.

Figure 39: Results of transect sampling for total chlorophyll $a$ on the 6$^{th}$ November 2007. An estimate of significance could not be made for only two sampling points. Both samples were taken over the reef flat.
4.3.2 Nitrate transect sampling

The results of sampling for dissolved nitrate (NO₃⁻) and nitrate (NO₂⁻) species are presented in Figure 41 and Figure 42. Results are reported as nitrate only, since several authors (e.g. Atkinson & Falter 2003) have reported that concentrations of nitrite are typically very low.

![Chlorophyll Transect Results 8/11](image1)

**Figure 40:** Results of transect sampling for total chlorophyll a on the 8th November 2007. The last two points were taken over the lagoon. There is no significant linear relationship with or without the values over the lagoon.

![Nitrate Transect Results 6/11](image2)

**Figure 41:** Results of transect sampling for nitrate on the 6th November 2007. The apparently decreasing trend is not significant.
The first three points shown in Figure 42 represent uptake on the reef flat. The final sample was taken over the lagoon, and the different reef zone is suggested to be the explanation for the increase in concentration.

![Nitrate Transect Results 8/11](image)

Figure 42: Results of transect sampling for nitrate on the 8th November 2007. The apparently decreasing trend is not significant.

4.3.3 Dissolved oxygen transect sampling

![DO Transect Results 6/11](image)

Figure 43: Results of transect sampling for dissolved oxygen on the 6th November 2007. The apparently increasing trend is not significant. All samples were taken over the reef flat.
Figure 44: Results of transect sampling for dissolved oxygen on the 8\textsuperscript{th} November 2007. The increasing trend is significant with $p<0.02$. Samples were taken over the reef flat with the exception of the last point, which was over the lagoon.

4.3.4 SRP transect sampling

Figure 45: Results of transect sampling for soluble reactive phosphorus on the 6\textsuperscript{th} November 2007. There is no apparent or significant trend. All samples were taken over the reef flat.
Figure 46: Results of transect sampling for soluble reactive phosphorus on the 8th November 2007. There is no apparent or significant trend. Samples were taken over the reef flat with the exception of the last point, which was over the lagoon.

4.3.4.1 Correction for surface velocity measured by drifters

Figure 47 below shows the average velocity profile through the water column for the study period, using ADCP data. The slower currents at the bottom of the water column can most likely be attributed to bottom shear effects due to the turbulence around the rough coral reef surface. Note that water depth varied between 90.3 and 208 cm during the study period and that the average depth was 150 cm (Figure 22): however, data above 110 cm was neglected due to contamination from wave action.

Since the drifters only sample the first 50 cm of the water column, they are likely to experience faster currents than the depth-averaged speed. To correct for this anomaly, a linear model was used to convert surface velocity to depth-averaged velocity. Surface velocity at a given time was estimated as the average of the first five 10 cm bins recorded by the ADCP, and depth-averaged velocity was the average of all bins. Both variables were calculated at each time step (every 5 minutes) for the entire time period of the Lagrangian transect, in addition to two hours previous and subsequent to the transect (Table 6).

A linear conversion factor was calculated by determining the slope of the relationship between the two variables when the x-intercept was set to zero. The conversion factors are shown in Table 6. See Appendix B for the Matlab code used to calculate these conversion
factors. Note that the conversion factor was not calculated using the average surface and depth-averaged velocities shown in Table 6: these are provided as a comparison only.

![Average velocity profile](image)

**Figure 47:** The velocity profile (magnitude) over depth, averaged over all times of the study period, showing the effect of bottom shear forces and wind-induced surface currents on the velocity profile.

Without adjusting for the difference between surface and depth-averaged velocity, Lagrangian calculations would be overestimated by between 4 and 11 percent (Table 6).

**Table 6:** Conversion factors between surface and depth-averaged velocity. Surface velocity was estimated using the first five bins (top 50cm of the water column) of ADCP velocity.

<table>
<thead>
<tr>
<th>Transect Date</th>
<th>Time Period</th>
<th>Average Surface Velocity (m/s)</th>
<th>Average Velocity over Depth (m/s)</th>
<th>Conversion Factor (linear)</th>
</tr>
</thead>
<tbody>
<tr>
<td>3(^{rd}) Nov</td>
<td>9:25 - 14:30</td>
<td>8.96</td>
<td>8.40</td>
<td>0.93</td>
</tr>
<tr>
<td>4(^{th}) Nov</td>
<td>8:30 - 14:00</td>
<td>9.61</td>
<td>8.67</td>
<td>0.89</td>
</tr>
<tr>
<td>5(^{th}) Nov</td>
<td>15:30 – 20:00</td>
<td>5.50</td>
<td>5.46</td>
<td>0.96</td>
</tr>
<tr>
<td>6(^{th}) Nov</td>
<td>11:30 – 16:00</td>
<td>7.14</td>
<td>6.80</td>
<td>0.94</td>
</tr>
<tr>
<td>8(^{th}) Nov</td>
<td>9:00 – 14:00</td>
<td>8.27</td>
<td>7.53</td>
<td>0.89</td>
</tr>
</tbody>
</table>
### 4.3.4.2 Net production estimates and uptake rates

The net production estimates and uptake rates of two Lagrangian transects across the reef flat are presented in Table 7 (refer to sample locations in Figure 35).

Table 7: Lagrangian calculations of net production, nutrient uptake and chlorophyll \( a \) uptake (mmol/m\(^3\)/hr) by reef organisms. Conversion factor refers to the multiplying factor used to convert the surface velocities sampled by the drifters into a depth-averaged velocity more representative of the “Dt” term in the net production equation.

<table>
<thead>
<tr>
<th>Date</th>
<th>Reef zone</th>
<th>1st Sample Time</th>
<th>2nd Sample Time</th>
<th>Linear Conversion Factor</th>
<th>Ave. Depth (Bathymetry)</th>
<th>Tide Correction (ADCP data)</th>
<th>h (m)</th>
<th>NP(_L) (+J)</th>
<th>SRP(_L)</th>
<th>NO(_3^-)</th>
<th>Chl ( a )_L</th>
</tr>
</thead>
<tbody>
<tr>
<td>6/11/2007</td>
<td>Coral-dominated reef flat</td>
<td>13:26</td>
<td>13:42</td>
<td>0.94</td>
<td>1.29</td>
<td>-0.17</td>
<td>1.12</td>
<td>124</td>
<td>0.039</td>
<td>-0.51</td>
<td>-0.14*</td>
</tr>
<tr>
<td>6/11/2007</td>
<td>Sparse coral (reef flat)</td>
<td>13:42</td>
<td>14:00</td>
<td>0.94</td>
<td>1.34</td>
<td>-0.18</td>
<td>1.16</td>
<td>29</td>
<td>-0.036</td>
<td>-0.25</td>
<td></td>
</tr>
<tr>
<td>8/11/2007</td>
<td>Coral-dominated reef flat</td>
<td>10:46</td>
<td>11:04</td>
<td>0.89</td>
<td>1.29</td>
<td>0.22</td>
<td>1.51</td>
<td>42</td>
<td>0.045</td>
<td>-0.49</td>
<td>-0.0032</td>
</tr>
<tr>
<td>8/11/2007</td>
<td>Sparse coral (reef flat)</td>
<td>11:04</td>
<td>11:19</td>
<td>0.89</td>
<td>1.49</td>
<td>0.21</td>
<td>1.7</td>
<td>39</td>
<td>-0.18</td>
<td>-1.7</td>
<td>-0.069</td>
</tr>
<tr>
<td>8/11/2007</td>
<td>Lagoon</td>
<td>11:19</td>
<td>12:00</td>
<td>0.89</td>
<td>1.92</td>
<td>0.15</td>
<td>2.07</td>
<td>63</td>
<td>0.054</td>
<td>0.46</td>
<td>-0.013</td>
</tr>
</tbody>
</table>

*The first chlorophyll \( a \) value is the uptake rate from 13:26 to 14:00 on 6/11/2007.
4.4 *Comparison of net production estimates in Lagrangian and Eulerian reference frames*

Figure 48 shows the Lagrangian estimates of net production plotted over the Eulerian time series of net production. One sample from the coral-dominated reef flat and one from the sparsely-populated reef flat are presented for each day, with the average in the centre of the error bar. The sample taken over the lagoon on the 8th of November was neglected here.

![Graph showing comparison of net production estimates](image)

**Figure 48:** Lagrangian estimates of net production plotted over the Eulerian time series. Transects from two separate days are presented.
5 Discussion

This study has provided the first estimates of net production on the Ningaloo Reef. Furthermore, it has provided a comparison of Eulerian and Lagrangian approaches, and demonstrated the effectiveness of the Eulerian approach based upon the methodology developed by Falter et al. (2008). The major results of the study are summarized as follows.

1. Net production results and community metabolic rates calculated by the Eulerian approach generally concur with the findings of Falter et al. (2008) and with ranges reported in the literature. Net production ranged from -56 – 84 mmol m$^{-2}$ hr$^{-1}$, gross primary production from 477-905 mmol m$^{-2}$ d$^{-1}$, community respiration from 412-768 mmol m$^{-2}$ d$^{-1}$ and net community production from 15-140 mmol m$^{-2}$ d$^{-1}$. Lagrangian and Eulerian rates of production generally agreed, although there were too few Lagrangian estimates to form an analysis. Lagrangian net production is thought to have been overestimated on one occasion.

2. Ratios of GPP:R were slightly higher than 1.0 (1.03-1.19), revealing that the reef was only just autotrophic during the early summer study period. The ratio is typically slightly higher in summer than winter, suggesting that net heterotrophy could be observed during winter periods when less light is available for photosynthesis. However this theory would need to be validated by further study.

3. Uptake of both nitrate and chlorophyll $a$ was detected over the reef flat during very short time periods, while phosphate levels appeared relatively constant. Nitrogen or some other nutrient not measured is suggested to be limiting production on the Ningaloo Reef. The system is shown to be benthic-dominated, but suggested to be coupled to the pelagic zone through a nutritional requirement for particulate nitrogen.

4. The P-I curve varied before and after peak irradiance, suggesting the presence of either photoinhibition (hysteresis) or diurnal variation in heterotrophic respiration.

5. Net calcification is believed to have been occurring during the study period. However, the balance of calcification to dissolution over an entire year may be close to zero and therefore the system could be sensitive to changes in atmospheric carbon dioxide concentrations. Definitive conclusions would rely upon further study.
5.1 Evaluation of Eulerian and Lagrangian approaches

The results of this study generally concur with the findings of the methodology derived by Falter et al (2008), on which the Eulerian part of this study was based. Rates of NP, GPP and R were consistent with measurements made on reef flats over the past 35 years (Table 8). Note, however, that NCP was positive for all days of the study period, in contrast to the variation reported in the literature.

Table 8: Community metabolic rates measured and calculated over the reef flat at Sandy Bay compared with those recorded using an identical method at Kaneohe Bay and general literature values for reef flats. Averages are in bold followed by ranges in parentheses. References: 1. Falter et al (2008), and reviews by 2. Atkinson and Falter (2003) and 3. Kinsey et al (1985).

<table>
<thead>
<tr>
<th></th>
<th>Sandy Bay, Ningaloo (summer)</th>
<th>Kaneohe Bay, Hawaii (winter)</th>
<th>Literature values for reef flat algal / coral zones</th>
</tr>
</thead>
<tbody>
<tr>
<td>NP (mmol m⁻² hr⁻¹)</td>
<td>-56 - 84</td>
<td>-40 - 75</td>
<td>-</td>
</tr>
<tr>
<td>GPP (mmol C m⁻² d⁻¹)</td>
<td>634 (477-905)</td>
<td>250-660</td>
<td>640 (330-1580)</td>
</tr>
<tr>
<td>R (mmol C m⁻² d⁻¹)</td>
<td>559 (412–768)</td>
<td>330-650</td>
<td>600 (290-1250)</td>
</tr>
<tr>
<td>NCP (mmol C m⁻² d⁻¹)</td>
<td>15–140</td>
<td>-200 - 190</td>
<td>-220 - 310</td>
</tr>
<tr>
<td>GPP:R ratio</td>
<td>1.04 (1.03 - 1.19)</td>
<td>1.02 (0.69 - 1.43)</td>
<td>1.2 (0.7-2.5)</td>
</tr>
</tbody>
</table>

The advective term was found to dominate net production, while gas flux was a minor term (see section 4.1.8), concurring with the findings of Falter et al (2008). The root-mean squared value of the advective flux term was 6.3 mmol m⁻² hr⁻¹ higher than at Kaneohe Bay, but the other two terms were of a similar magnitude (2008).

Lagrangian estimates of net production at Sandy Bay ranged from 39-124 mmol m⁻² hr⁻¹. With the exception of one value of 124 mmol m⁻² hr⁻¹ recorded on the coral-dominated reef flat, the results of the Lagrangian and Eulerian methods agree (Figure 48). It is possible that this overestimate was due to an inaccurate conversion between surface velocity (drifter speed) and the depth-averaged velocity recorded by the ADCP. Falter et al (2008) reported that this discrepancy overestimate production by 30-100 percent. Alternately the method of estimating the average depth over which the water parcel traversed could be the explanation, since it is inversely proportional to net production and hence the sensitivity of this term is also high.

The Eulerian method of estimating net production is considerably less labour-intensive than the Lagrangian. The DO sensors require daily cleaning and calibration, while the Lagrangian
approach requires following drifters over (in some cases) several hours. A number of these drifter tracks would be required (including some at night) in order to quantify the diurnal NP curve and obtain estimates of community production rates. The temporal information obtained via the Eulerian approach is considerably more extensive for the effort expended. However, the Lagrangian approach can allow for the comparison of different spatial zones and has the advantage of requiring few technical instruments.

5.2 Autotrophy vs. heterotrophy and seasonal variation

Typically, autotrophy is thought to occur on the reef crest while heterotrophy occurs on the back reef (Atkinson & Falter 2003). The control volume in this study included areas of both coral-dominated reef flat close to the reef crest and sparsely coral-dominated back reef, and so it is assumed that the control volume is representative of the reef system as a whole. It should be noted that Lagrangian estimates of net production sampling closer to the reef crest were higher than those closer to the back reef (although this observation relies upon only two transects). However, sampling could not occur to the extent of the reef crest due to safety concerns.

The ratio of GPP:R varied from 1.03 to 1.19 at Sandy Bay (Table 5), indicating that the reef was always slightly biased toward autotrophy during the study period. Falter et al (2008) recorded days of both heterotrophy and autotrophy at Kaneohe Bay, although both reefs had ratios of 1.0 on average. However, the maximum ratio was still quite low in comparison to literature values, and none of the GPP:R ratios measured at Sandy Bay in summer reached the maximum recorded in Kaneohe Bay in winter (Table 8).

The limiting factors upon primary production are nutrients, light and temperature, all of which are subject to seasonal variation. The reef would be expected to be at its most autotrophic during summer, when photosynthesis is most favoured by high irradiance levels and long daylight hours. Literature values reported in Kinsey (1985) for shallow reef-flat areas show that the production to respiration (GPP:R) ratio is typically slightly higher in summer than winter. Thus a study of production on the reef in a winter period might reveal net heterotrophy, which would have significant implications for the dependence of the reef upon nutrient input from ocean waters.
5.3 **Nutrient limits to benthic primary production**

During the study period, the reef was removing nitrate from the water column at a rate of 0.5 mmol m\(^{-2}\) hr\(^{-1}\) over the coral-dominated reef flat, and between 0.3-1.7 mmol m\(^{-2}\) hr\(^{-1}\) over the sparsely covered reef flat. This result disagrees with the theory that nutrient concentrations change little across most fore-reefs and reef flats (see the review by Atkinson and Falter 2003). Furthermore, these uptake rates were measured over very short time periods (approximately 20 minutes between samples), contradicting reports in the literature that concentration changes can only be observed over several hours even on shallow reef flats (e.g. Steven & Atkinson 2003).

Dissolved phosphorus did not appear to be a limiting nutrient, since SRP concentrations remained relatively constant (0.18-0.22 mmol m\(^{-2}\)) across the reef flat. Many studies in the have found phosphorus to be the limiting nutrient for primary production on coral reefs (Larned 1998): however based upon the results of the Lagrangian transects performed at the study site, it appears that dissolved nitrogen could be limiting production on Ningaloo Reef.

Chlorophyll \(a\) uptake also occurred, ranging from 0.04-0.14 μg m\(^{-2}\) hr\(^{-1}\) averaged over the entire reef flat. The trend of chlorophyll \(a\) uptake concurs with the significant decrease in chlorophyll biomass measured by Philp and Waite (2007) from outside to inside the reef. It appears that some kind of predation is occurring by reef flat organisms upon the pico- and nanoplankton over the reef flat: however, this study did not attempt to identify which of the reef organisms were responsible for this predation.

The longest Lagrangian transect (on the 8\(^{th}\) of November) followed the water parcel as it left the coral-dominated reef flat and continued into the lagoon. This transect indicated that relatively high net production (63 mmol m\(^{-2}\) hr\(^{-1}\)) was occurring in the lagoon, along with the net production of nitrate (0.46 mmol m\(^{-2}\) hr\(^{-1}\)) and net uptake of chlorophyll \(a\). However, these estimates are based upon only one transect and should not be considered representative.

### 5.3.1 Benthic-pelagic coupling

Benthic dominance (as opposed to pelagic, or phytoplankton dominance) over nutrient uptake can be demonstrated by calculating pelagic DIN uptake rates using simple assumptions. Ammonium uptake rates, as measured by Kapeli and Waite (2007) range from 2 μmol m\(^{-3}\) hr\(^{-1}\) in the lagoon to 14 μmol m\(^{-3}\) hr\(^{-1}\) on the reef front (Table 9). Ammonium and nitrate uptake is controlled by diffusion through boundary layers between the organism and surrounding water column; and NH\(_4\) uptake rates are proportional to NH\(_4\) concentration (Thomas & Atkinson...
Nitrate uptake rates have not been studied in detail (Atkinson & Falter 2003): however, using the assumption that they are also proportional to concentration, an estimate can be made of total NO$_3$ uptake by pelagic organisms (Table 9). Hence total DIN uptake reaches a maximum of 50-60 μmol m$^{-3}$ hr$^{-1}$ on the reef front, and is around 20-30 μmol m$^{-3}$ hr$^{-1}$ on the reef flat. By comparison, the whole-system (benthic and pelagic) was uptaking nitrate alone at rates of 500 μmol m$^{-2}$ hr$^{-1}$ over the reef flat, and (using an NO$_3$/NH$_4$ ratio of 3:1) DIN at rates of 560 μmol m$^{-2}$ hr$^{-1}$. Therefore pelagic processes, at most, can only account for 5-10 percent of the total DIN uptake and the system must be benthic-dominated. This result concurs with the findings of a literature review by Gattuso, Frankignoulle and Wollast (1998).


<table>
<thead>
<tr>
<th></th>
<th>Pelagic NH$_4$ uptake (μmol m$^{-3}$ hr$^{-1}$)</th>
<th>NO$_3$/NH$_4$ concentration ratio</th>
<th>Pelagic NO$_3$ uptake (μmol m$^{-3}$ hr$^{-1}$)</th>
<th>Total DIN uptake (μmol m$^{-3}$ hr$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reef front</td>
<td>14</td>
<td>3</td>
<td>42</td>
<td>50-60</td>
</tr>
<tr>
<td>Reef flat</td>
<td>3</td>
<td>8</td>
<td>24</td>
<td>20-30</td>
</tr>
<tr>
<td>Lagoon</td>
<td>2</td>
<td>5</td>
<td>10</td>
<td>10-15</td>
</tr>
</tbody>
</table>

The typical C:N ratio for a coral reef benthos is 18.3:1 (Atkinson & Smith 1983). Hence using the assumption that the photosynthetic quotient is 1.0 (Falter et al. 2008), around 4.37 mmol m$^{-3}$ hr$^{-1}$ of nitrogen (as DIN) should be required to drive the maximum net carbon production measured on the reef flat (around 80 mmol m$^{-2}$ hr$^{-1}$). Therefore DIN uptake by zooxanthellae directly from the water column (0.56 mmol m$^{-2}$ hr$^{-1}$) can only account for around 10-15 percent of the total nitrogen requirement for carbon production. However it should be noted that differences in light availability, nutrients, temperature and hydrodynamics can cause the C:N ratio to vary as much as an order of magnitude between reef systems (Atkinson & Smith 1983), and these stoichiometric estimates would be considerably improved by a direct quantification of the C:N ratio at the study site.

Coral have also been shown to obtain nutrients by the capture of detrital POM, small zooplankton prey and pico- and nanoplankton cells (Picciano & Ferrier-Pages 2007). The nutrients obtained by the coral host can then be recycled into the zooxanthellae to drive photosynthesis, as discussed in section 2.2.2. Chlorophyll $a$ decreased at rates up to 0.14 μg m$^{-2}$ hr$^{-1}$ across the reef flat, indicating a decrease in phytoplankton biomass. However, even
assuming this decrease is entirely due to coral predation, chlorophyll \( a \) uptake could only provide up to 0.07 mmol m\(^{-2}\) hr\(^{-1}\) of DIN, or 1-2 percent of the required nitrogen supply. (The results of Yentsch and Vaccaro (1958) were used to assume 7 mg of DIN is available per 1 mg of chlorophyll \( a \).)

Philp and Waite (2007) found a decrease in total zooplankton biomass and a change in taxa structure from outside to inside the reef using measurements during daylight hours at the study reef, suggesting some form of coral predation on zooplankton. This theory is supported by literature findings that coral growth cannot be supported by the transfer of nutrients from zooxanthellae, and must be supplemented by zooplankton predation (Muscatine et al. 1989). It is suggested that a combination of detrital POM, zooplankton prey and dissolved inorganic nitrogen uptake from the water column is required to supply enough nitrogen to support benthic production on the levels measured at Sandy Bay.

Wyatt et al (unpublished) found that chlorophyll \( a \) concentration was highest in the open ocean, dropping sharply across the reef crest and continuing to decrease into the lagoon. Conversely, unpublished data collected by A/Prof A. Waite (UWA) and Dr. R. Lowe (UWA) during May 2007 found that the net production of nitrate and ammonium was occurring across the reef crest, where nitrate peaked at station RO5 (the apex) and uptake occurred across the reef flat. While the present study could not quantify nutrient concentrations outside the reef or on the crest, the trend of net uptake of nitrate across the reef flat was consistent in November.

Note that the stoichiometric estimate of DIN supply calculated using the results of this study (discussed above) is an order of magnitude higher than the estimate of particulate nitrogen supply. It appears that on the reef flat, dissolved nitrogen is a more important source of nitrogen than particulate feeding. However, Wyatt et al (unpublished) argue that particulate feeding is a very significant source of nitrogen based upon a whole-reef study at Sandy Bay in May 2007. It is suggested that heterotrophic organisms on the reef crest are predating upon pico- and nanoplanckton and releasing DIN into the water column, which is then used by autotrophic organisms on the reef flat to support the high levels of organic carbon production recorded in this study.

### 5.4 Hysteresis: photoinhibition vs. heterotrophy

A comparison of P-I curves before and after solar noon revealed that hysteresis was present in the compensation point (where production and respiration are equal and net production is at
zero) on all days of the study. The compensation point occurred at a PAR of between 0-200 mmol quanta m\(^{-2}\) s\(^{-1}\) as light increased after sunrise (Figure 32): however, the reef switched to net respiration at between 200-400 mmol quanta m\(^{-2}\) s\(^{-1}\) as light decreased after peak irradiance (Figure 33). Furthermore, a marked hysteresis effect was observed in the P-I curve on the 6\(^{th}\), 7\(^{th}\) and 8\(^{th}\) of November (Figure 33), when net production rapidly after solar noon and the reef was net respiring at a very high irradiance (around 1100 mmol quanta m\(^{-2}\) s\(^{-1}\)).

5.4.1 Photoinhibition theory

Previous studies have shown that increasing irradiance results in an increase in photosynthesis in many autotrophic organisms up until a point of saturation (Levy et al. 2006). Production can be sustained as light increases even further, but eventually there is a decrease in photosynthesis known as photoinhibition (Neale & Richerson 1987). The reef at Sandy Bay appeared to begin to saturate at around 600-800 mmol quanta m\(^{-2}\) s\(^{-1}\), before which the production increases rapidly with increasing light and after which any increase occurs more slowly (Figure 32).

![Figure 49: Hysteresis response of photosynthesis in phytoplankton over a daily light cycle, showing curves before (upper) and after (lower) exposure to high irradiance. The arrows indicate the direction of the curve as time increases. Deep samples (I\(_I\) deep) are expected to have a more sudden response than surface (I\(_I\) surface) samples (Neale & Richerson 1987).](image)

The hysteresis observed in the field on the later days of the study period (Figure 32) closely resembles the response of phytoplankton photosynthesis to high irradiance (Figure 49), where a sharp decrease in photosynthesis occurs at the point of saturation. Photosynthesis cannot
fully recover after this point of saturation, and therefore photosynthesis levels remain low until sunset. On a community level, then, a decrease in photosynthesis could explain the dominance of net respiration on the reef earlier in the afternoon.

Photoinhibition may have occurred in only part of the system, or to a lesser extent, on the first days of the study. Levy et al (2006) report that the photoinhibition of unshaded zooxanthellae is usually masked in whole-reef studies, because most of the cells are located in branched colonies or deep-seated colonies and these remain light-limited even in peak irradiance.

The study period was in early summer during a time of very high irradiance. Note that Neale and Richerson (1987) recorded photoinhibition at 500 mmol quanta m⁻² s⁻¹, while at Sandy Bay production continued to increase (albeit gradually) until a much higher irradiance (around 1700 mmol quanta m⁻² s⁻¹). Zooxanthellae are capable of acclimatizing to high levels of light by adjusting processes within their cells over timescales ranging from minutes to thousands of years (Levy et al. 2006; Hoogenboom, Anthony & Connolly 2006), and the zooxanthellae at Sandy Bay may have adapted to utilize the high levels of available light to their advantage.

The presence of photoinhibition can indicate either that the photosynthetic apparatus in zooxanthellae have been damaged by high irradiance levels, or that physiological processes in the algae have been triggered to cope with the increased stress (Hoogenboom, Anthony & Connolly 2006). Given that the production-irradiance response appeared to recover by the following morning even when photoinhibition was evident, it is unlikely that there were any permanent effects.

5.4.2 Heterotrophic theory

It could be argued that the photoinhibition theory is discounted by the fact that the reef did not appear to be affected by comparable levels of PAR on the first three days of the study. An alternative explanation is that the reef experienced an increase in respiration due to increased heterotrophic feeding, rather than (or in addition to) a decrease in photosynthesis. Daily variation in light intensity and spectrum, temperature, nutrient and food availability can all cause changes in the respiration of coral (Levy et al. 2006). While light intensity was relatively constant throughout the week (Figure 20), temperature decreased on average (Figure 19), most likely due to upwelling from the Leeuwin undercurrent caused by the increase in southerly winds mid-week (Figure 16).

Upwelling from the Leeuwin undercurrent could have supplied dissolved nutrients to the continental shelf, although it would seem more likely that this would cause an increase in
production (since zooxanthellae are capable of absorbing DIN directly from the water column). All community rates of GPP, R and NCP were considerably lower than average on the last three days (Table 5), but this is most likely because of the decreased cross-reef advective flux (Figure 27), which can be attributed to the forcing of wind direction (Figure 16) onto surface currents.

The photoinhibition mechanism may be the explanation for the low GPP:R ratios recorded in Table 5, particularly later in the study period. If so, levels of community gross photosynthesis may not necessarily be considerably lower in winter (as suggested in section 5.2). However, if increased respiration by heterotrophic organisms is the explanation then the system may be more complicated than previously considered.

5.5 Implications for calcification

Calcification is expected to be only weakly affected by daily or seasonal changes in nutrient concentrations. Nitrate concentrations were between 0.45-0.89 mmol m\(^{-2}\) in November 2007 and from undetectable - 1.64 mmol m\(^{-2}\) in May 2007 (unpublished data, Lowe & Waite 2007). Concentrations of nitrate can range from 0.05-9.8 mmol m\(^{-2}\) over coral reefs (Atkinson & Falter 2003), and decreases in calcification are not expected to occur until concentrations reach levels of 5-20 mmol m\(^{-2}\) (Langdon & Atkinson 2005). Similarly, ammonium levels ranged from undetectable - 0.54 mmol m\(^{-2}\) in May 2007 unpublished data, Lowe & Waite 2007) whereas concentrations recorded in the literature reach up to 2.4 mmol m\(^{-2}\) (Atkinson & Falter 2003). It is not expected that nutrient concentrations on Ningaloo Reef are causing a decoupling of photosynthesis and calcification as suggested in the literature (e.g. Dubinsky & Berman-Frank 2001; Langdon & Atkinson 2005), and therefore it is argued that it is possible to extrapolate some implications for calcification from the results of this study.

The relationship between photosynthesis, respiration, calcification and dissolution on a community level is presented in Figure 50. Carbon dioxide and alkalinity concentrations can be both affected by, and affect, the balance between net calcification and net dissolution of the reef (Suzuki 1998).

Given that the reef at Sandy Bay was autotrophic during the study period, it is expected that net calcification (reef growth) was occurring. Using a relationship between GPP and G (G = -37.1 + 0.22*GPP, significant for P=0.0002) calculated by Gattuso, Allemand and Frankignoulle (1999), calcification rates at Sandy Bay would have ranged from 86-163 mmol C m\(^{-2}\) d\(^{-1}\) and averaged 100 mmol C m\(^{-2}\) d\(^{-1}\) during the study period. These estimates seem
reasonable as they are well within literature ranges of calcification on reef flats (Table 1). However, it should be noted that this relationship was derived using a combination of data from algal-dominated zones, whole reefs, lagoons, sediments, high activity areas, reef flats and algal pavements, and that none of these sites exhibited significant relationships on their own (Gattuso, Allemand & Frankignoule 1999).

Figure 50: Relationship between carbon dioxide concentrations and net production and calcification rates on coral reefs (Suzuki 1998).

Although net calcification was most likely occurring during the study period, the possibility that the reef could experience a respiration-dominated system during winter (net heterotrophy, as discussed in section 5.2) suggests that the balance of calcification to dissolution over an entire year may be close to zero. Therefore the system could be sensitive to changes in atmospheric carbon dioxide concentrations, where excess carbon dioxide is taken up by the ocean and forms carbonic acid, causing a drop in pH and removing carbonate ions vital to calcification from the pelagic zone (Atkinson & Falter 2003; Harrison & Booth 2007). However, it should be noted that these conclusions are drawn from a study period of only one week, and should not be considered an accurate portrayal of seasonal or yearly variation. The system may be much more resilient than suggested by the results of this short study.
6 Conclusion and Recommendations

Quantifying net production on a coral reef system provides invaluable information about the community metabolism and the ability of a coral reef to utilize inorganic carbon for growth. This study demonstrates the effectiveness of the Eulerian approach designed by Falter et al (2008) for estimating net production on a shallow reef, and provides the first estimates of community metabolism on the Ningaloo Reef.

While the reef was found to be slightly net autotrophic during the study period, dissolved inorganic nutrient uptake alone was shown to be insufficient to support the rates of primary production measured on the reef flat. Particulate organic matter uptake and feeding upon phyto- and zooplankton may also be a source of nutrients, but the importance of these sources could not be definitively quantified based upon the data collected in this study. However, the ratio of gross community production to community respiration was close to 1.0 and it is suggested that net heterotrophy may be observed on the reef flat during winter periods. Furthermore, it is suggested that pico- and nanoplankton feeding is occurring on the reef crest, releasing dissolved nutrients into the water column which are required to support the production observed on the reef flat. These results indicate that interactions with outer-reef oceanographic and biological processes may be required for success.

The results of Eulerian sampling demonstrated the temporal variation expected on a diurnal timescale, but also revealed that community metabolism rates varied over the study period, possibly in response to hydrodynamic forcing. All rates reduced in magnitude toward the end of the study period, which is believed to be due to the reduced advective flux caused by a change in wind direction. There were insufficient Lagrangian transects undertaken to quantify spatial variation between the reef flat and other reef zones, however some conclusions could be drawn by comparing the results of this study to previous studies of nutrient and particulate uptake at Sandy Bay.

The ratio of gross primary production to community respiration also became closer to 1.0 toward the end of the study period, and hysteresis was observed in the P-I curve revealing the dominance of respiration at mid-afternoon on the last three days. Photoinhibition was suggested to be the cause of this phenomenon, although increased heterotrophic activity is an alternative explanation.
Net calcification is believed to have been occurring during the study period, since the reef was net autotrophic and the low nutrient concentrations were not considered likely to cause competition between photosynthesis and calcification for supplies of dissolved inorganic carbon. However, the possibility that the reef is net heterotrophic in winter suggests that the balance of calcification to dissolution over an entire year may be close to zero. Thus, the system may be sensitive to an increase in atmospheric carbon dioxide concentrations caused by climate change. However, definitive conclusions about calcification and the sensitivity of the system cannot be made without further research into the seasonal and annual variability in these processes.

The recommendations for further research resulting from this study are summarized below:

1. The Eulerian approach designed by Falter et al (2008), demonstrated here to be a very effective method of estimating net production and community metabolism rates, should be applied to the same reef section at different times of year in order to evaluate the seasonal and annual variability in reef metabolism, and specifically to identify the autotrophic or heterotrophic status of the reef over longer timescales.

2. Future Lagrangian transects should be combined with ADCP data to correct for the anomaly between depth-integrated currents and surface currents.

3. Further studies should be undertaken to quantify the nitrogen sources for reef nutrition, specifically with regards to the nitrogen budget of DIN uptake, POM uptake and particulate feeding on the Ningaloo reef flat and reef crest. In combination with studies into net production, this information could improve scientific understanding of carbon and nutrient cycling on coral reefs.

4. Further Lagrangian transect sampling should be undertaken to identify whether nitrogen is the limiting nutrient to benthic production on Ningaloo Reef as suggested by this study.

5. Alkalinity sampling should be undertaken to identify the saturation state of Ningaloo Reef, in combination with Eulerian or Lagrangian estimates of net production, to allow further conclusions to be drawn upon the balance of coral calcification and dissolution on the Ningaloo Reef and the status of the reef as a sink or a source of carbon dioxide. Ideally, this sampling should be conducted into the future to quantify the effect of increasing carbon dioxide concentrations upon the health of the reef.
7 References


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Appendix A: Calculating net production

The following text is a summary of the .m files used to calculate net production using the Eulerian method derived by Falter et al (2008).

The Matlab code below was originally written by Dr. Jim Falter (HIMB) and Dr. Ryan Lowe (UWA), and was modified by Rowena Beaton in 2008 for use in this dissertation.

```matlab
%% First load the raw data and define start and stop times.
clear all
load('datafromJim.mat')
load('ADP.mat')
load('wind.mat')
start = 733349.4583333334;
stop = 733355.2916666666;

% turn off warnings for interpolation of NaN-values
warning off

% Synchronise ADCP data to DO data (03-Nov 11:00am to 09-Nov 07:00am)
[st_ind,fn_ind] = findtime(time,start,stop);
time = time(st_ind:fn_ind);
v_e_depth = v_e_depth(st_ind:fn_ind);
v_n_depth = v_n_depth(st_ind:fn_ind);
depth = depth(st_ind:fn_ind);

% Synchronise CTD data to DO data
[st_ind,fn_ind] = findtime(sbe19.data(:,1),start,stop);
PAR = sbe19.data(st_ind:fn_ind,4);
PARtime = sbe19.data(st_ind:fn_ind,1);

%% %%%%%%%%%%%%% % Transform raw ADCP data into volume flux components
% Correct the adcp velocities: they were out by 52 degrees ACW
theta = 52*pi/180; % radians
real_e_depth = v_e_depth.*cos(theta) - v_n_depth.*sin(theta);
real_n_depth = v_e_depth.*sin(theta) + v_n_depth.*cos(theta);

% Project the adcp velocities from N-E vectors into reef x-y directions
% Reef x-axis: ESE, 117 degrees from North
% Reef y-axis: SSW, 207 degrees from North
theta2 = 22*pi/180;
Vx = real_e_depth.*cos(theta2) - real_n_depth.*sin(theta2);  % [cm/s]
Vy = - real_e_depth.*sin(theta2) - real_n_depth.*cos(theta2);  % [cm/s]

% calculate Eulerian + Stokes transport components
% Put a 1-hr moving average on the data
% Assume Stokes all in cross-reef direction
step = 5.0006/60/24; % days
ADP.time = [start:step:stop];
```

2008
ADP.Vx = interp1(time, Vx, ADP.time, 'linear')/100;  % [m/s]
ADP.Vy = interp1(time, Vy, ADP.time, 'linear')/100;  % [m/s]
ADP.depth = interp1(time, depth, ADP.time, 'linear');  % [m]

ADP.Qx = moving_average(ADP.Vx,3).*ADP.depth;  % [m^2/s]
ADP.Qy = moving_average(ADP.Vy,3).*ADP.depth;  % [m^2/s]

%% Reduce DO data and calculate dCdt
adcp_burst_length = 5;  %minutes
adcp_burst_int = 5;       %minutes
dt_oxy = 1;               %minutes

% create a time vector for all data
step = 1;  % minutes
DOadj.time = [start:step/60/24:stop]'

% set data to required time interval
DOadj.cv1 = interp1(oxygen.time, oxygen.cv1(:,2), DOadj.time, 'linear');
DOadj.cv2 = interp1(oxygen.time, oxygen.cv2(:,2), DOadj.time, 'linear');
DOadj.cv3 = interp1(oxygen.time, oxygen.cv3(:,2), DOadj.time, 'linear');

i = find(DOadj.time>=start & DOadj.time<=stop);
i = i(1:end-1);

M_reshape = adcp_burst_int/dt_oxy;
N_reshape = length(DOadj.time(i))/M_reshape;
i_burst = 1:(adcp_burst_length/dt_oxy);

t = DOadj.time(i) - DOadj.time(1);  % [days]
Nwin = 3*60/dt_oxy + 1;
order = 2;
dCdt.cv1 = polysmooth_deriv(t, DOadj.cv1(i,1), Nwin, order);  % mmol/m3/day
dCdt.cv2 = polysmooth_deriv(t, DOadj.cv2(i,1), Nwin, order);
dCdt.cv3 = polysmooth_deriv(t, DOadj.cv3(i,1), Nwin, order);

%% %%%%%%%%%%%%% % temporally average concentrations and time-derivatives

temp = reshape(DOadj.time(i), M_reshape, N_reshape);
hydroxy.time(:,1) = nanmean(temp(i_burst,:))' % [days]

temp = reshape(DOadj.cv1(i,1), M_reshape, N_reshape);
hydroxy.cv1(:,1) = nanmean(temp(i_burst,:))' % [mmol/m^3]

temp = reshape(DOadj.cv2(i,1), M_reshape, N_reshape);
hydroxy.cv2(:,1) = nanmean(temp(i_burst,:))' % [mmol/m^3/day]

temp = reshape(DOadj.cv3(i,1), M_reshape, N_reshape);
hydroxy.cv3(:,1) = nanmean(temp(i_burst,:))' % [mmol/m^3/day]

% coordinates of triangle vertices
cv_xy = [792007,7539559;792222,7539348;792299,7539532];
hydroxy.O2ave = mean_tri_surf(cv_xy(1:3,1), cv_xy(1:3,2), [hydroxy.cv1(:,1), hydroxy.cv2(:,1), hydroxy.cv3(:,1)]); % [mmol/m^3]

% define corresponding time stamps from ADCP/hydro data
hydro.i_np = interp1(time, (1:length(time))', hydroxy.time, 'nearest');

% Calculate equilibrium concentrations
T = interp1(sbe19.data(:,1), sbe19.data(:,2), hydroxy.time, 'linear');
S = interp1(sbe19.data(:,1), sbe19.data(:,3), hydroxy.time, 'linear');
hydroxy.O2sat = oxy_sat(T, S); % [mmol/m^3]

%% %%%%%%%%%%%%%%%%%%%%%%%%% calculate spatial gradients
% transform UTM coordinates to reef x-y coordinates
% UTM = [east,north]
% reef = [ESE, NNE] = [x,y] = [cross-reef, along-reef]

UTM.D12 = [cv_xy(2,1)-cv_xy(1,1), cv_xy(2,2)-cv_xy(1,2)];
reef.D12 = [UTM.D12(1,1)*cos(theta) - UTM.D12(1,2)*sin(theta);  %[m]
            UTM.D12(1,1)*sin(theta) + UTM.D12(1,2)*cos(theta)]';

UTM.D13 = [cv_xy(3,1)-cv_xy(1,1), cv_xy(3,2)-cv_xy(1,2)];
reef.D13 = [UTM.D13(1,1)*cos(theta) - UTM.D12(1,2)*sin(theta);
            UTM.D13(1,1)*sin(theta) + UTM.D13(1,2)*cos(theta)]';

C12vect = [repmat(reef.D12, length(hydroxy.time), 1), hydroxy.cv2(:,1)-hydroxy.cv1(:,1)];
C13vect = [repmat(reef.D13, length(hydroxy.time), 1), hydroxy.cv3(:,1)-hydroxy.cv1(:,1)];

Vcross = cross(C12vect, C13vect);
dCdx = -Vcross(:,1)./Vcross(:,3);  % [mmol/m^4]
dCdy = -Vcross(:,2)./Vcross(:,3);

%% %%%%%%%%%%%%%%%%%%%%%%%%%%%%% calculate NP terms in mmol/m2/hr

%% Local flux
NP.time = hydroxy.time;

Ztri(:,1) = hydroxy.cv1(:,2).*ADP.depth./24;
Ztri(:,2) = hydroxy.cv2(:,2).*ADP.depth./24;
Ztri(:,3) = hydroxy.cv3(:,2).*ADP.depth./24;
NP.local(:,1) = mean_tri Surf(cv_xy(1:3,1), cv_xy(1:3,2), Ztri);

%% Advective flux
NP.Qx(:,1) = ADP.Qx.*dCdx*3600;
NP.Qy(:,1) = ADP.Qy.*dCdy*3600;

%% Gas flux  Jgas = kO2.(Ceq–C)
vex = interp1(wind.time, wind.speed, hydroxy.time, 'linear');
i = find(isnan(vex));
vex(i) = nanmean(vex);  % replace missing wind speed data with ave. speed
k600 = 0.266*vex.^2;
kO2 = k600/100;  % [m/hr]  ASSUME Sc=600
hydroxy.O2ave = mean_tri_surf(cv.xy(1:3,1), cv.xy(1:3,2), [hydroxy.cv1(:,1), hydroxy.cv2(:,1), hydroxy.cv3(:,1)]);
NP.gas(:,1) = kO2.*(hydroxy.O2sat - hydroxy.O2ave)/24; % [mmol/m^2/hr]

%% Total net production
NP.total(:,1) = NP.local(:,1) + NP.Qx(:,1) + NP.Qy(:,1) - NP.gas(:,1);

%% Light
light = interp1(PARtime, PAR, NP.time, 'linear');

%% final steps
warning on
save NP depth light
clear C12vect C13vect DOadj MAT M_reshape N_reshape Nwin PAR PARtime S T
clear UTM Vcross a1 a1_depth a2 a2_depth a3 a3_depth adcp_burst_int
clear adcp_burst_length currs_rot cv.xy hydro i i_burst order oxygen reef
clear sbe19 step t temp theta theta_prin_naut time v_dir_depth v_e v_e_depth
clear v_n v_n_depth v_speed_depth v_up v_up_depth vex

The Matlab function below was created by Dr. Jim Falter and Dr. Ryan Lowe and was used unchanged in this dissertation, with the exception of blocking the function from removing “NaN” values.

```matlab
function dydx = poly_smooth_deriv(x, y, N, order)

% function dydx = poly_smooth_deriv(x, y, N, order)
%
% POLY_SMOOTH takes a time-series with regularly spaced data, some of which
% may not exist and smooths it using a polynomial of ORDER
% N MUST BE ODD to keep data centered

dydx = nan*zeros(size(y));
P = nan*zeros(length(y),order+1);
mult = [order:-1:1];

if rem(N,2)~=1 % check N is odd
    N = N+1;
else
    end;

n = length(y);
half = (N-1)/2;

%set initial points to be first polynomial field
for i = 1
    nlow = 1+i-1;
    nhigh = N+i-1;
    x_sub = x(nlow:nhigh);
    %re-scale x_sub if its value is too big (i.e. a datenum)
    x_sub = x_sub - x_sub(1);
    y_sub = y(nlow:nhigh);

    %remove nans from time-series
    mat = [x_sub, y_sub];
    mat = denan(mat(1,:));
```
% if size(mat,1)>= order+3
    P = polyfit(mat(:,1), mat(:,2), order);
P_deriv = mult.*P(1:order);
dydx(1:i+half) = polyval(P_deriv, x_sub(1:half+1));
else
    end;
end;

% calculate middle points one at a time
for i = 2:(n - 2*half)-1
    nlow = 1+i-1;
nhigh = N+i-1;
x_sub = x(nlow:nhigh);
    % re-scale x_sub if its value is too big (i.e. a datenum)
x_sub = x_sub - x_sub(1);
y_sub = y(nlow:nhigh);
    % remove nans from time-series
    mat = [x_sub, y_sub];
    if size(mat,1)>= order+3
        P = polyfit(mat(:,1), mat(:,2), order);
P_deriv = mult.*P(1:order);
dydx(i+half) = polyval(P_deriv, x_sub(half+1));
else
    end;
end;

% set final points to be last polynomial field
for i = (n - 2*half)
    nlow = 1+i-1;
nhigh = N+i-1;
x_sub = x(nlow:nhigh);
    % re-scale x_sub if its value is too big (i.e. a datenum)
x_sub = x_sub - x_sub(1);
y_sub = y(nlow:nhigh);
    % remove nans from time-series
    mat = [x_sub, y_sub];
    if size(mat,1)>= order+3
        P = polyfit(mat(:,1), mat(:,2), order);
P_deriv = mult.*P(1:order);
dydx(i+half:end) = polyval(P_deriv, x_sub(half+1:end));
else
    end;
end;
The following Matlab function was created by Rowena Beaton to find a specific time period in a matrix of date numbers. It is also used in the code contained in appendices B and C.

```matlab
function [st_ind,fn_ind] = findtime(Tmatrix,start,finish)

st_ind = length(find(Tmatrix<=datenum(start)));  
fn_ind = length(find(Tmatrix<=datenum(finish)));  
return
```
Appendix B: Correcting Lagrangian transect speed

The following Matlab code was used to calculate the linear conversion factors (Table 6) used to correct the drifter speeds of Lagrangian transects for over-estimation due to the discrepancy between surface and depth-averaged speeds (discussed in section 4.3.4.1).

See Appendix A for the “findtime” function called in “correct_lag”.

```matlab
% Run file for the correct_lag function which calculates: 1. average surface speed and 2. average depth-averaged speed, using ADCP data

clear all

[s1,v1] = correct_lag(3,9,25,14,30); % 3rd november
[s2,v2] = correct_lag(4,8,30,14,0); % 4th november
[s3,v3] = correct_lag(5,15,30,20,0); % 5th november
[s4,v4] = correct_lag(6,11,30,16,0); % 3rd november
[s5,v5] = correct_lag(8,9,0,14,0); % 8th november

surf_aves = [nanmean(s1);nanmean(s2);nanmean(s3);nanmean(s4);nanmean(s5)];
depth_aves = [nanmean(v1);nanmean(v2);nanmean(v3);nanmean(v4);nanmean(v5)];

% The correct_lag function calculates:
% 1. s – average surface velocity for each time selected
% 2. v – average velocity profile speed for each time selected
% using the velocity profiles from the ADCP.

function [s,v] = correct_lag(day,st_hr,st_min,fn_hr,fn_min)

%% Load data
load('ADP.mat')
bins=(20:10:260);

%% Set specific time period
start = [2007,11,day,st_hr,st_min,0];
finish = [2007,11,day,fn_hr,fn_min,0];
[st_ind,fn_ind] = findtime(time,start,finish);

%% Calculate velocities and depth-averaged velocities for all time
% Correct the adcp velocities: they were out by 52 degrees ACW
theta = 52*pi/180; % radians
real_e = v_e.*cos(theta) - v_n.*sin(theta);
real_n = v_e.*sin(theta) + v_n.*cos(theta);

% Transform to reef x-y axes
theta = 27*pi/180; %% RADIANS!!!!
Vx = real_e.*cos(theta) - real_n.*sin(theta); % ESE, 127 degrees [cm/s]
Vy = -real_e.*sin(theta) - real_n.*cos(theta); % SSW, 217 degrees
Vmag=sqrt(Vx.^2+Vy.^2);

%% Select times
Vmag_t = Vmag(:,st_ind:fn_ind);

%% Surface velocity (first 5 bins)
```

2008
```matlab
for ii = 1:length(Vmag_t)
    temp_v = Vmag_t(1:12,ii);
    ind = isnan(temp_v);
    if ind == false(12,1);
        J=12-5;
        surf = temp_v(J:12);
    else
        I = find(ind,1,'first');
        J = I-5;
        surf = temp_v(J:I);
    end
    s(ii) = nanmean(surf);
end
s = s';

%% Velocity profiles
v = nanmean(Vmag_t(1:12,:),1);
v = v';
return
```
Appendix C: Calculating light attenuation coefficient

The following Matlab code was used to calculate light attenuation as discussed in section 3.5.

See Appendix A for the code of the “findtime” function.

```matlab
clear all
load('airPAR.mat')
load('datafromJim.mat')
load('ADP.mat')

%% PAR data from the Mylering weather station (30 mins)
half_time(:,1) = airPAR(27:251,1);   % time (half-hourly)
myl_PAR(:,1) = airPAR(27:251,2);   % irradiance at surface (half-hourly)

%% PAR data from the CTD (adjust by 26 minutes so peak light time matches between Mylering and PAR data)
start = datenum([2007,11,4,0,0,0]);
stop = datenum([2007,11,8,16,0,0]);
[s_CTD,f_CTD] = findtime(sbe19.data(:,1),start,stop);
ctd_T = sbe19.data(s_CTD-13:f_CTD-13,1);  % time (2 mins)
ctd_PAR = sbe19.data(s_CTD:f_CTD,4);  % PAR data (2 mins)

%% Define PAR variables (interpolate Mylering data to 2-min intervals)
Io = interp1(half_time,myl_PAR,ctd_T,'linear');
Iz = ctd_PAR;
T = ctd_T;

%% Plot a comparison of PAR data
figure(1)
plot(T,Io,'k-')
hold on
plot(T,Iz,'b-')
title('Comparison of PAR in the air and water')
xlabel('Time [Days]')
ylabel('Photosynthetically Available Radiation')
datetick('x',19)
legend('Io','Iz','location','best')

%% Match ADCP depth data to PAR data
[s_ADCP,f_ADCP] = findtime(time,start,stop);
adcp_T = time(s_ADCP-5:f_ADCP-5);  % time (5 mins)
adcp_D = depth(s_ADCP:f_ADCP);     % time (5 mins)
z = interp1(adcp_T,adcp_D,ctd_T,'linear');

%% Remove data where I>Io and only include peak light periods
for ii = 1:length(T)
    if Io(ii)>Iz(ii)
        Io(ii) = NaN;
        Iz(ii) = NaN;
    end
    if Io(ii)<500
        Io(ii) = NaN;
        Iz(ii) = NaN;
    end
end
```
%% Calculate attenuation coefficient
warning off
Kd = (log(Io)-log(Iz))./z;
ind_inf = isinf(Kd);
Kd(ind_inf) = NaN;
warning on

%% Organise data by time of day
clear Coeff.day
ind=1;
for jj = 1:6
    st = datenum([2007,11,jj+3,0,0,0]);
    [a,b] = findtime(T,st,st);
    if jj==1
        ind(jj)=1;
    elseif jj==6
        ind(jj) = length(T);
    else
        ind(jj) = a;
    end
end
Coeff.day = NaN*ones(800,5);
for kk = 1:5
    temp_i = ind(kk):ind(kk+1);
    co_i = temp_i-temp_i(1)+1;
    temp = Kd(temp_i);
    Coeff.day(co_i,kk) = temp;
    if kk==1
        Coeff.day(co_i,6) = T(temp_i);
    end
end

%% Calculate averages
Coeff.max = nanmax(Kd);
Coeff.min = nanmin(Kd);
Coeff.ave = nanmean(Kd);

a = [Coeff.day(:,1),Coeff.day(:,3:5)];
Coeff.max(2) = nanmax(nanmax(a));
Coeff.min(2) = nanmin(nanmin(a));
Coeff.ave(2) = nanmean(nanmean(a));

%% Plot light attenuation coefficient vs. time of day
hold off
x = (Coeff.day(:,6)-733349.98162)*24;
figure(3)
plot(x,Coeff.day(:,1),'k.',x,Coeff.day(:,2),'r.',x,Coeff.day(:,3),'k.'
    hold on
plot(x,Coeff.day(:,4),'k.',x,Coeff.day(:,5),'k.'
axis([0,24,0,0.7])
xlabel('Time [hrs after midnight]')
ylabel('Light Attenuation Coeff Kd')
title('Light Attenuation over 24 hours')
legend('4th, 6th, 7th and 8th Nov','5th Nov')
hold off

clear a2 a2_depth a3 a3_depth currs_rot temp theta_prin_naut v_dir_depth
clear v_e v_e_depth v_n v_n_depth v_speed_depth v_up v_up_depth al ai_depth
clear s f sbe19 airPAR start stop oxygen t ii tempL tempT a
Appendix D: Calculating community metabolic rates

The following code was used to calculate community metabolic rates (Table 5).

Net community production:

```matlab
% RUN CALCULATE_TERMS BEFORE RUNNING THIS CODE.
% clear areas

% Seperate into each day
for ii = 1:6
    ind = find(NP.time-date2dnum(2007,11,ii+2,0,0,0)<1);
    midnight(ii,1) = ind(length(ind));         % indices of midnights
    midnight(ii,2) = NP.time(ind(length(ind))); % time (days)
    midnight(ii,3) = NP.total(ind(length(ind))); % NP (mmol m^-2 hr^-1)
end

% Calculate areas under curve (numerical integration)
for ii = 1:5
    for jj = midnight(ii,1):midnight(ii+1,1)
        a = NP.time(jj);  % [days]
        b = NP.total(jj)*24; % [mmol m^-2 d^-1]
        c = NP.time(jj+1);
        d = NP.total(jj+1)*24;

        x = [c;c;a;a;c]; y = [d;0;0;b;d];

        if b>0 && d>0 % area above curve
            areas(jj,ii) = polyarea(x,y);
        end

        if b<0 && d<0 % area below curve
            areas(jj,ii) = -1*polyarea(x,y);
        end

        if b*d < 0 % crossing x-axis
            m = (d-b)/(c-a);
            k = d - m*c;
            r = -k/m;

            x1 = [r;a;a;r]; y1 = [0;b;0;0]; area1 = polyarea(x1,y1);
            x2 = [c;c;r;c]; y2 = [d;0;0;d]; area2 = polyarea(x2,y2);

            if b < 0
                areas(jj,ii) = area2 - area1;
            elseif d < 0
                areas(jj,ii) = area1 - area2;
            end
        end
    end
end

% Calculate net community production over 24 hours (mmol m^-2 d^-1)
NCP(ii,1) = sum(areas(:,ii));
```
Net respiration:

```matlab
% RUN CALCULATE_TERMS BEFORE RUNNING THIS CODE.
% clear areas

% Find sunset and sunrise times (using light data, PAR~0)
ind = find(light<0.05);
sun_times = time(ind);
for kk = 1:length(ind)-1
    temp(kk) = ind(kk+1)-ind(kk);
end
I = find(temp>1);
sunrise(1:5,1) = ind(I);
sunrise(1:5,2) = time(ind(I));
sunrise(6,1) = ind(length(ind));
sunrise(6,2) = time(ind(length(ind)));
for mm = 1:length(I)
    J = I+1;
end
sunset(1,1) = ind(1);
sunset(1,2) = time(ind(1));
sunset(2:6,1) = ind(J);
sunset(2:6,2) = time(ind(J));
Tdark = (sunrise(:,2)-sunset(:,2));  %time elapsed (days)

% Calculate areas under curve (numerical integration)
for ii = 1:6
    for jj = sunset(ii,1):sunrise(ii,1)
        a = time(jj);     % days
        b = total(jj); % mmol m-2 hr-1
        c = time(jj+1);
        d = total(jj+1);
        x = [c;c;a;a;c];
y = [0;b;0;0;b;d];
        if b>0 & & d>0 % area above curve
            areas(jj,ii) = polyarea(x,y);
        end
        if b<0 & & d<0 % area below curve
            areas(jj,ii) = -1*polyarea(x,y);
        end
        if b*d < 0 % crossing x-axis
            m = (d-b)/(c-a);
            k = d - m*c;
            r = -k/m;
            x1 = [r;a;a;r];
y1 = [0;b;0;0];
            area1 = polyarea(x1,y1);
            x2 = [c;c;r;c];
y2 = [d;0;0;d];
            area2 = polyarea(x2,y2);
```

if b < 0
    areas(jj,ii) = area2 - area1;
elseif d < 0
    areas(jj,ii) = area1 - area2;
end

% Calculate night-time community respiration rates (mmol m-2 d-1)
Rdark(ii,1) = -(1/Tdark(ii))*sum(areas(:,ii));
end

% Calculate daily integrated community respiration rates
for nn = 2:6
    R(nn-1,1) = 24*(Rdark(nn)+Rdark(nn-1))/2;
end

% finish
clear ind sun_times kk temp I J mm ii jj a b c d x y m k r x1 x2 areas nn
Appendix E: Control volume boundary thresholds

The following Matlab code was used to calculate times for which the streamline was outside the control volume (Figure 15). It also calculates the mean stokes direction, which defined the cross-reef and along-reef axes (section 4.1.1.2).

```matlab
% Corrects the adcp velocities and identifies values where the streamline
% was outside the control volume
% RUN CALCULATE_TERMS BEFORE RUNNING THIS CODE
load('ADP.mat')

% Synchronise ADCP data to DO data (03-Nov 11:00am to 09-Nov 07:00am)
[st_ind,fn_ind] = findtime(time,start,stop);
time = time(st_ind:fn_ind);
v_e_depth = v_e_depth(st_ind:fn_ind);
v_n_depth = v_n_depth(st_ind:fn_ind);
depth = depth(st_ind:fn_ind);

% Correct the adcp velocities: they were out by 52 degrees
theta = 52*pi/180;  % radians
real_n_depth = v_e_depth.*sin(theta) + v_n_depth.*cos(theta);
real_e_depth = v_e_depth.*cos(theta) - v_n_depth.*sin(theta);

% Find cross-reef axis
stokes = -1*nanmean(atan2(real_n_depth,real_e_depth))*180/pi;

% Transform into reef x-y axes
theta2 = stokes*pi/180;
Vx = real_e_depth.*cos(theta2) - real_n_depth.*sin(theta2);  % [cm/s]
Vy = -real_e_depth.*sin(theta2) - real_n_depth.*cos(theta2);  % [cm/s]

% Calculate direction of depth-averaged velocity
phi = atan2(Vy,Vx);       % Direction [radians]
phi = phi*180/pi;                             % Direction [degrees]

% Define angles of control volume
Oxy2 = -22.6;
Oxy3 = 16.6;

OxyLine2 = Oxy2*ones(length(phi));
OxyLine3 = Oxy3*ones(length(phi));

% Identify times when current direction is outside the CV
ind_cw = find(phi>Oxy2);
ind_acw = find(phi>Oxy3);
ind_out = ind_cw;
ind_out(1,length(ind_cw)+1:length(ind_cw)+length(ind_acw)) = ind_acw;
phi_out = NaN*ones(length(phi));
phi_out(ind_out) = phi(ind_out);

% Calculate percentage of streamlines captured by the CV
percent_in = 100-length(ind_out)/length(phi)*100;
return
```
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Appendix F: Matlab code to analyse the P-I curve

The following Matlab code was written to generate the P-I curve and analyse it for changes before and after peak irradiance (section 4.1.10).

```matlab
%% Choose: all data or selected data only
type = 1;
if type == 1    % Remove data where streamline is outside control volume
    light_thres = light_inCV;
elseif type == 0                % Use all data
    light_thres = light;
end

%% Find and index sunset and sunrise times (using light data, PAR~0)
ind = find(light<0.05);
sun_times = NP.time(ind);
for kk = 1:length(ind)-1
    temp(kk) = ind(kk+1)-ind(kk);
end
I = find(temp>1);
sunrise(1:5,1) = ind(I);
sunrise(1:5,2) = NP.time(ind(I));
sunrise(6,1) = ind(length(ind));
sunrise(6,2) = NP.time(ind(length(ind)));
for mm = 1:length(I)
    J = I+1;
sunset(1,1) = ind(1);
sunset(1,2) = NP.time(ind(1));
sunset(2:6,1) = ind(J);
sunset(2:6,2) = NP.time(ind(J));

%% Find and index daily peaks in irradiance
peak(1,2) = max(light(1:sunset(1,1)));
peak(1,1) = find(light==peak(1,2));
for ii = 1:5
    temp = light(sunrise(ii,1):sunset(ii+1,1));
    peak(ii+1,2) = max(temp);
    peak(ii+1,1) = find(light==peak(ii+1,2));
end

%% Separate data into before/after peak irradiance
clear morn_light aft_light
m_ind = 1:peak(1,1);  
a_ind = peak(1,1)+1:sunset(1,1);

morn_light = NaN*ones(250,6);  
morn_NP = NaN*ones(250,6);  
morn_t = NaN*ones(250,6);

aft_light = NaN*ones(250,6);  
aft_NP = NaN*ones(250,6);  
aft_t = NaN*ones(250,6);
```
```matlab
morn_light(1:length(m_ind),1) = light_thres(m_ind);
morn_t(1:length(m_ind),1) = NP.time(m_ind);
morn_NP(1:length(m_ind),1) = NP.total(m_ind);
aft_light(1:length(a_ind),1) = light_thres(a_ind);
aft_t(1:length(a_ind),1) = NP.time(a_ind);
aft_NP(1:length(a_ind),1) = NP.total(a_ind);

m = length(m_ind)+1;
a = length(a_ind)+1;
for jj = 1:5
    mtemp = sunrise(jj,1):peak(jj+1,1);
    atemp = peak(jj+1,1):sunset(jj+1,1);
    m = length(mtemp);
a = length(atemp);

    morn_light(1:m,jj+1) = light_thres(mtemp);
    morn_t(1:m,jj+1) = NP.time(mtemp);
    morn_NP(1:m,jj+1) = NP.total(mtemp);

    aft_light(1:a,jj+1) = light_thres(atemp);
    aft_t(1:a,jj+1) = NP.time(atemp);
    aft_NP(1:a,jj+1) = NP.total(atemp);
end

%% Plot results

%% Plot afternoon P-I curve
figure(1)
hold on
title('Afternoon P-I Curve')
scatter(aft_light(:,1),aft_NP(:,1),3,'c','filled')
scatter(aft_light(:,2),aft_NP(:,2),3,'k','filled')
scatter(aft_light(:,3),aft_NP(:,3),3,'r','filled')
scatter(aft_light(:,4),aft_NP(:,4),3,'g','filled')
scatter(aft_light(:,5),aft_NP(:,5),3,'m','filled')
scatter(aft_light(:,6),aft_NP(:,6),3,'b','filled')
legend('3rd','4th','5th','6th','7th','8th','location','SouthEast')
xlabel('Photosynthetically Available Radiation [mmol photons/m^2/s]')
ylabel('Net Production [mmol/m^2/hr]')
axis([0 1800 -60 100])
hold off

%% Plot morning P-I curve
figure(2)
hold on
title('Morning P-I Curve')
scatter(morn_light(:,1),morn_NP(:,1),3,'k','filled')
scatter(morn_light(:,2),morn_NP(:,2),3,'r','filled')
scatter(morn_light(:,3),morn_NP(:,3),3,'g','filled')
scatter(morn_light(:,4),morn_NP(:,4),3,'m','filled')
scatter(morn_light(:,5),morn_NP(:,5),3,'b','filled')
legend('4th','5th','6th','7th','8th','location','SouthEast')
xlabel('Photosynthetically Available Radiation [mmol photons/m^2/s]')
ylabel('Net Production [mmol/m^2/hr]')
axis([0 1800 -60 100])
hold off

%% Plot daily data
figure(3)
```

hold on

title('P-I Curve')
scatter(aft_light(:,1),aft_NP(:,1),3,'c','filled')
scatter(aft_light(:,2),aft_NP(:,2),3,'k','filled')
scatter(aft_light(:,3),aft_NP(:,3),3,'r','filled')
scatter(aft_light(:,4),aft_NP(:,4),3,'g','filled')
scatter(aft_light(:,5),aft_NP(:,5),3,'m','filled')
scatter(aft_light(:,6),aft_NP(:,6),3,'b','filled')
scatter(morn_light(:,1),morn_NP(:,1),3,'k','filled')
scatter(morn_light(:,2),morn_NP(:,2),3,'r','filled')
scatter(morn_light(:,3),morn_NP(:,3),3,'g','filled')
scatter(morn_light(:,4),morn_NP(:,4),3,'m','filled')
scatter(morn_light(:,5),morn_NP(:,5),3,'b','filled')

legend('3rd','4th','5th','6th','7th','8th','location','SouthEast')

xlabel('Photosynthetically Available Radiation [mmol photons/m^2/s]')
ylabel('Net Production [mmol/m^2/hr]')

hold off

return