Primary production in the tropical continental shelf seas bordering northern Australia

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Abstract:

Pelagic primary production (^{14}C uptake) was measured 81 times between 1990 and 2013 at sites spanning the broad, shallow Northern Australian Shelf (NAS; 120 - 145°E) which borders the Australian continent. The mean of all areal production measurements was $1,048 \pm 109 \text{ mg C m}^{-2} \text{ d}^{-1}$ (mean $\pm$ 95% CI). Estimates of areal primary production were correlated with integral upper-euphotic zone chlorophyll stocks (above the 50 and 20 percent light penetration depths) accessible to ocean colour remote sensing and total water column chlorophyll standing crop, but not surface (0-2 m) chlorophyll concentrations. While the NAS is subject to a well characterized monsoonal climate regime (austral summer-NW monsoon -wet: austral winter- SE monsoon -dry), most seasonal differences in means of regional-scale chlorophyll standing crop ($11\text{-}33 \text{ mg Chl m}^{-2}$ for 12 of 15 season-region combinations) and areal primary production ($700\text{-}1,850 \text{ mg C m}^{-2} \text{ day}^{-1}$ for 12 of 15 season-region combinations) fell within a 3-fold range. Apart from the shallow waters of the Torres Strait and northern Great Barrier Reef, picoplankton ($< 2 \mu\text{m}$ size fraction) dominated chlorophyll standing crop and primary production with regional means of picoplankton contributions ranging from 45 to >80 percent. While the range of our post-1990 areal production estimates overlaps the range of production estimates made in NAS waters during 1960-62, the mean of post-1990 estimates is over 2-fold greater. We regard the difference to be due to improvements in production measurement techniques, particularly regarding the reduction of potential metal toxicity and incubations in more realistic light regimes.

Keywords: Australia, tropical, shelf, primary production, phytoplankton, chlorophyll

1. Introduction:

The northern margin of the Australian continent is bordered by a broad, shallow (<200 m), continental shelf that connects it to the island of New Guinea and spans much of the distance between the Australian coast and the Indonesian archipelago (Figure 1). The Northern Australian Shelf (NAS) forms part of the greater Australasian-Sunda shelf system, the largest low-latitude continental shelf system (Longhurst, 2007), with a hydrodynamically diverse and productive pelagic ecosystem. While long used by indigenous, artisanal and industrial fishers (e.g. Cane, 2103; Davis, 1989; Edwards, 1983; Fry and Milton, 2009), the underlying pelagic ecology, biogeochemistry and broad-scale primary productivity of the Northern Australian Shelf has been less studied (e.g. CSIRO, 1963a,b; CSIRO, 1964a,b; Alongi et al., 2013; McKinnon et al., 2011; Burford and Rothlisberg, 1999; Rothlisberg et al., 1994; Condie, 2011) than other large global shelf systems. General statistical characteristics of NAS water masses, including seasonally averaged nutrient levels, chlorophyll concentrations and mixed layer depths, have been summarized from archival hydrographic data by Rothlisberg et al. (2005) and Condie and Dunn (2006).

Water masses of the NAS to the west of the shallow Torres Strait (142°E) are primarily derived from the Indonesian Throughflow (ITF), while those to the east are part of the northern Coral Sea gyre. The NAS is characterized by high water temperatures (23° to 32°C) and high levels of insolation (35 to 60+ mol Q m⁻² d⁻¹; Furnas, unpubl. data) throughout the year. The region has a monsoonal climate (e.g. Du et al., 2005; Kawamura et al., 2002), alternating between a generally cloudy and rainy austral 'summer' (NW monsoon; Dec-Mar) and a less-cloudy, drier austral 'winter' (SE monsoon; Jun-Aug). Episodic cyclonic disturbances can occur between December and April in all parts of the NAS save the far-northern Great Barrier Reef and the Gulf of Papua.

The islands of archipelagic Indonesia and New Guinea to the north of the NAS are characterized by steep emergent terrains and volcanic tectonics which, in combination with high rainfall and freshwater runoff, supports high levels of erosion and mineral exports into the ITF, Arafura Sea and

1 Gulf of Papua (Milliman et al., 1999; Milliman and Farnsworth, 2011). The northern margin of the
2 Australian continent to the south also experiences heavy summer rainfall and runoff, but is relatively
3 low-relief and highly weathered (Wasson et al., 1996; Alongi et al., 2013). Surface waters in all parts
4 of the NAS, and particularly those inshore, are subject to local in situ modification by high
5 evaporation rates and direct monsoonal rainfall. The SE monsoon drives seasonal upwelling in the
6 adjacent Banda Sea (Kinkade et al., 1997) that has a significant effect on local primary production.
7 Dissolved nutrient concentrations and phytoplankton biomass (median surface chlorophyll = 0.11 μg
8 L^{-1} ; Furnas, unpubl. data) are generally very low in surface waters throughout the NAS (e.g. Condie
9 and Dunn, 2006; McKinnon et al., 2011), but regional increases may occur during periods of strong
10 vertical mixing or in coastal areas directly influenced by land runoff (e.g. McKinnon et al., 2007;
11 Condie, 2011). Extensive surface and near-surface blooms of *Trichodesmium* and other N-fixing
12 bacteria occur seasonally throughout the NAS, particularly the Arafura Sea (Montoya et al., 2004)
13 and Gulf of Carpentaria (Burford et al, 2009).

14 In addition to its dynamic climate and weather forcing, the NAS is characterized by continuous high
15 levels of tidal energy dissipation (Egbert and Ray, 2001; Condie, 2011) forced by surface and internal
16 tides. The largest surface tides occur along the northwestern margin of the continent (e.g. > 10 m
17 spring tides on the southern Kimberley coast, > 8 m in the southern Joseph Bonaparte Gulf). These
18 tides generate energetic internal waves and tides on the Kimberley Shelf and shelf margin
19 (Katsumata et al., 2010; Rayson et al., 2011). While surface tidal amplitudes in the eastern NAS are
20 not quite as large (to ca. 4 m), tidal height differences across the shallow (35 m) Torres Strait
21 generate strong currents through the Strait (> 1 m sec^{-1} ; e.g. Wolanski et al., 1988; Harris, 1991) and
22 in the adjoining reef matrices of the far-northern Great Barrier Reef and western Gulf of Papua (e.g.
23 Wolanski and Thomson, 1984).

24 Despite the relatively small number of biological oceanographic studies of the NAS, a fairly large
25 number of primary production measurements have been made in NAS waters since the early 1960's.

Most were made by CSIRO oceanographers during 1960-62 (CSIRO, 1963a,b; 1964a,b) as part of a wide-ranging oceanographic campaign in the eastern Indian Ocean. These early results have been broadly summarized in historical reviews of primary production in the wider Indian Ocean (e.g. Kabanova, 1967; Cushing 1973; Krey, 1973). Motoda (1978) and Rothlisberg et al. (1994) presented smaller sets of ^{14}C -based surface productivity measurements from the Gulf of Carpentaria and eastern Arafura Sea. Most recently, McKinnon et al. (2007, 2011, 2013) reported oxygen-based estimates of pelagic photosynthesis and respiration at stations in the Gulf of Papua, on the Sahul Shelf and in the northern Great Barrier Reef.

Here, we present a new regional estimate of pelagic primary production across the full extent of the NAS between the far northwestern Australian continental margin (120°E) and the Gulf of Papua (145°E) using consistent ^{14}C uptake methods. These production estimates are considered in relation to the general hydrography of NAS waters, the size structure of primary producers and phytoplankton biomass at depths accessible to current optical remote sensing technologies.

2. Methods;

The primary production measurements presented herein are based on experiments carried out during thirteen (13) cruises to various parts of the NAS between 1990 and 2013 using the same or very similar experimental methods. Twelve sets of measurements were made by one group from the Australian Institute of Marine Science (AIMS: MF, AM) and one set by a group from the San Francisco State University (SFSU: EC, PH). Individual cruises lasted between 7 and 30 days and were usually within a consistent seasonal and weather setting. We have therefore combined the results from multiple cruises to build a composite picture of regional and seasonal productivity.

For convenience, we have divided the NAS into eight geographic regions (Figure 1) with similar bathymetric, hydrographic, circulation and mixing characteristics. Hydrographic properties in all of these regions fluctuate on a seasonal basis in response to changes in insolation, monsoonal wind

1 stress, rainfall and freshwater runoff; however, all experience very similar temperature and
2 insolation conditions. Accordingly, measurements are seasonally assigned to one of the two
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4 dominant seasonal modes of northern Australia: the austral 'summer' NW Monsoon (Dec-Apr: wet
5 season) when the Inter-tropical Convergence (ITC) is located over or just north of the Australian
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7 continent causing widespread overcast, rainy conditions, and the austral 'winter' SE Monsoon (Jun-
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9 Aug: dry season) when clearer, drier conditions are the norm over northern Australia. The relatively
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11 dry inter-monsoonal periods (May-Jun, Sep-Nov) have been included within our 'dry' seasonal
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20 **2.1 AIMS Production Experiments (SHL, TOR, TIM, NWA, NWF, SCT, WES, KIM)**

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22 Briefly, an initial CTD cast was made at most production stations at ca. 0800 local time. Seawater for
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24 production measurements was then collected with Niskin bottles from 4 to 8 depths in the water
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26 column corresponding to nominal mid-day in situ light levels simulated in deck incubators. The
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28 Niskin bottles, with aged rubber closures, were acid-cleaned and rinsed before cruises and were
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30 well-soaked from ongoing usage. The rubber in Niskin bottle closures can be toxic to oceanic
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32 phytoplankton (Price et al., 1986) over time periods of days. To minimize toxic effects, we
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34 endeavoured to draw all water samples for incubations into clean bottles within 30 minutes of
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36 collection. It is possible the Niskin bottles were still subject to contamination (e.g. Marra and
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38 Heinemann, 1987), so our production estimates should be viewed as conservative. The number of
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40 water samples taken varied with water column depth and transparency. Sampling depths were
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42 chosen based on prior mid-day casts near the measurement site with an underwater PAR sensor or
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44 Secchi disk, or in a regional water mass with similar apparent optical characteristics. Secchi depths
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46 were used to estimate the vertical diffuse attenuation coefficient ($1.7/S_d$), from which light
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48 penetration depths ($\%I_0$) were calculated. Simulated light levels of 100/50/30/20/8/4/1.6/0.6
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50 percent of surface PAR ($\%I_0$) were used in deck incubators between 1990 and 1995 and
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52 100/60/25/15/8/4/1.6/0.6 percent of surface PAR from 1997 to 2013.
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1 Sets of 125 or 250 ml clear polycarbonate bottles (3 to 9 depending on what size fractionation was
2 done) were gently filled with water from each depth sampled under subdued light. Filled bottles
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4 were kept in the dark. The bottles were thoroughly cleaned and acid-soaked before each cruise
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6 (Fitzwater et al., 1982) and thoroughly rinsed between experiments. The filled bottles were spiked
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8 with 5 μCi (185 MBq) of ^{14}C bicarbonate (Amersham or NEN) prepared according to Fitzwater et al.
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10 (1982). One third of the bottles from each depth were then wrapped in aluminium foil to serve as
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12 dark bottles. All bottles were incubated for four hours (nominally 1000-1400 local time) in acrylic
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14 deck tanks filled with running surface seawater. In situ light levels (see above) were simulated in
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16 individual tanks using covers made from one to several layers of black shade cloth. Approximately
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18 half of the total daily insolation impinges during the four hour mid-day period. Except for the
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20 deeper samples at the shelf-edge stations, incubator water temperatures remained within a few
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22 degrees of in situ temperatures.
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29 After the incubation period, all bottles were retrieved from the incubators and vacuum-filtered (< 10
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31 KPa) under subdued light. Size-fractionations were carried out by filtering sets of two light bottles
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33 and one dark bottle onto 25 mm filters with appropriate pore sizes. The total autotrophic
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35 population was collected using Whatman GF/F glass-fibre filters. In northern Australian shelf waters,
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37 these filters collect chlorophyll with filtration characteristics very close to cellulose membrane filters
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39 with a pore size of 0.45 μm (Furnas unpubl. data). The > 10 μm and > 2 μm size fractions were
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41 collected on polycarbonate membrane filters (Nuclepore™ or equivalent). After filtration, the wet
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43 filters were placed in scintillation vials, acidified with 100 μl of 10% HCl to remove inorganic C,
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45 allowed to ventilate and stored for later scintillation counting.
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51 Hourly carbon uptake rates were calculated according to Parsons et al. (1984). Areal production
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53 rates were calculated by trapezoidal integration of hourly production rates calculated for the
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55 individual light depths. Daily production was estimated by dividing the total areal C uptake during
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57 the four-hour incubation period by the fraction of total daily PAR (normally close to 50 percent)
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1 impinging during that period. Dawn to dusk surface irradiance was logged at 1-minute intervals
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8 In all cases, discrete water samples were taken in parallel from the sampling bottles for chlorophyll
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10 and dissolved nutrient analyses. The filtration and size-fractionation procedures for chlorophyll
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12 samples were the same as used for primary production measurements. Filtered chlorophyll samples
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14 were frozen (-15°C) in foil envelopes for later analysis ashore. Chlorophyll concentrations were
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16 measured by fluorometry following grinding and extraction in 90% acetone (Parsons et al., 1984).
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18 Areal estimates of chlorophyll standing crop were calculated from the discrete samples by
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20 trapezoidal integration. Water samples for dissolved nutrient (NO_3^- , PO_4^{3-} , Si) analyses were filtered
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22 and frozen for later analysis using standard wet chemical methods implemented on a segmented
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24 flow analyser. When measured, ambient ammonium (NH_4^+) concentrations were determined in
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26 fresh, unfiltered, water samples by manual low-background methods (Dudek et al., 1986; Holmes et
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28 al, 1999).
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34 **2.2 SFSU Experiments (EWG).**

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37 For the November 1999 primary productivity measurements, water samples were collected near
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39 0700 local time with a CTD-rosette sampler at six depths corresponding to nominal mid-day in situ
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41 light levels of 100/50/25/10/1/0.1 percent of surface PAR (% I_0). Sampling depths were calculated
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43 using vertical PAR extinction coefficients previously determined near the station using a Satlantic
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45 SPMR free-falling spectroradiometer.
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50 Water for production measurements was pre-screened through 184 μm mesh nylon netting to
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52 remove colonies of *Trichodesmium* and larger zooplankton and then poured into sets of three 500
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54 ml clear polycarbonate bottles, pre-cleaned as recommended in Fitzwater et al. (1982). The bottles
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56 were spiked with 20 μCi of ^{14}C (Amersham). Two bottles from each depth were incubated from 0800
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1 to 1200 local time in open acrylic deck tanks cooled with running surface seawater. In situ light
2 levels were simulated using multi-layer bags of plastic window screen. Time zero samples were
3 filtered to correct for activity adsorbed abiotically to the filters. At the end of the four-hour
4 incubation period, the contents of each bottle were filtered through 25 mm cellulose nitrate filters
5 (0.22 µm pore size) and rinsed with 3 ml of GF/F filtered seawater. All filters were exposed to
6 fuming HCl for 20 min to remove any inorganic C remaining. The filters were stored in scintillation
7 vials for later counting.
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10 Water samples (1000 ml) for chlorophyll analysis were taken from all water samples and filtered
11 onto 25 mm Whatman GF/F glass-fibre filters. Individual filters were placed in cold (-5°C) methanol
12 and extracted overnight in a freezer (-10°C). Chlorophyll fluorescence in the extract was determined
13 by fluorometry (Porra et al., 1989).
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19 Additional hydrographic stations with CTD profiles and discrete water sampling were occupied
20 during all NAS cruises. At most of these stations, water samples were collected for nutrient and
21 chlorophyll analyses, though usually without size fractionation of the chlorophyll. Sampling and
22 analytical procedures were the same as described above. All integrations of areal production and
23 chlorophyll standing crop are based upon discrete samples as profiling fluorometers and sub-surface
24 light sensors were not available on all cruises, particularly the early ones.
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31 **2.3 Statistical tests:**

32 Statistical tests for seasonal and regional differences or zonal trends were carried out using R
33 (Development Core Team R, 2014). Linear models (R library functions - lm, glm) were used to test
34 the significance of slopes of linear trends. ANOVA models (R library function - anova) were used to
35 test for differences and interactions among means of data grouped by categorical variables (e.g.
36 season, region). Individual variables were scaled (longitude) or transformed as appropriate.
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3. Results:

The results presented herein are primarily based on 81 measurements of chlorophyll standing crop and daily primary production made in open waters of the NAS between 1990 and 2013. Within this data set, sixty-three (63) measurements were made by AIMS researchers (MF, AM) and eighteen (18) by SFSU researchers (EC, PH). Half of the measurements (40) were made during the summer wet season (Dec-Apr) when the NW monsoon is dominant over northern Australia and half (41) during the winter-spring dry season (Jun-Nov) when the dry SE monsoon or dry inter-monsoonal conditions generally prevail. For consistency, we will refer to standing crop and production estimates from the December-April period as being 'wet' season or austral 'summer' results and estimates from the May-November period as being 'dry' season or austral 'winter' results.

Northern Australian shelf waters are characterized by a diversity of hydrographic conditions, both regionally and seasonally, which are reflected in individual vertical profiles of density, light penetration, phytoplankton biomass (chlorophyll) and photosynthesis. Vertical profiles which are most generally representative of seasonal or regional conditions are presented in Figures 2-5. The observed diversity of profile structures is caused by a number of recurrent, seasonal and episodic processes influencing water column stratification and vertical mixing; chiefly seasonal cycles of solar heating of the surface layer (e.g. Kawamura et al., 2002), freshwater inputs (rain and runoff; e.g. Qu et al., 1994; Wasson et al., 1996), lateral transport or intrusions of external water masses (e.g. Qu et al., 1994), monsoonal and episodic wind stress (Kawamura et al., 2002; Qu et al., 2005) and tidally generated bottom stress (Condie, 2011; Egbert and Ray, 2001).

At the western end of the NAS, in deeper waters along the Kimberley Shelf margin and on the adjoining shelf, the euphotic zone ($I_z > 0.1\%I_0$) is persistently temperature and density-stratified (Fig. 2A-B). The thickness of the surface mixed layer varies seasonally, particularly due to intense solar heating of the surface layer (0-100 m) during the summer (Fig. 2A), and varying lateral inputs of low-salinity, low-density water from the ITF and equatorial current systems of the Indian Ocean. Over

the course of the austral summer (late inter-monsoon and NW Monsoon), the isothermal surface mixed layer may be reduced to < 10 m in thickness in calm conditions, overlying an often multi-layered, but broadly stable, temperature and density gradient which, in turn, overlies the deep, permanent thermocline (Fig. 2A). Strong winds during the austral winter (SE Monsoon) break down this stratification, creating a thicker isothermal or near-isothermal layer (Fig. 2B) which sometimes extends to depths exceeding 100 m. Vertical chlorophyll distributions in both seasons are usually characterized by low surface concentrations (overall median = $0.11 \mu\text{g L}^{-1}$; range = <0.01 to 0.60, n=153 stations) and a persistent sub-surface maximum dominated by picoplankton-sized (< 2 μm) cyanobacteria. In summer, the sub-surface chlorophyll maximum layer (or layers) can be relatively thin and are embedded within layers of the laminated, but vertically stable density gradient. During the winter SE Monsoon, subsurface chlorophyll is more evenly distributed through the lower part of the thicker surface isothermal layer and extending into the stratified upper thermocline immediately below. The highest near-surface chlorophyll stocks occur during the winter SE monsoon period ($p < 0.05$). Outer-shelf waters are often very clear (Secchi depths to > 40 m) with a deep euphotic zone ($1\% I_0 > 100 \text{ m}$). Seasonal differences in light penetration at open-water sites near the shelf margin reflect the small increase in upper water column phytoplankton biomass (chlorophyll) supported by enhanced vertical mixing within the deeper surface isothermal layer (e.g. Fig. 2B). Despite very low near-surface chlorophyll concentrations and a persistent, well-developed deep chlorophyll maximum, maximum mid-day primary production rates in individual experiments at deep, open water sites were most frequently measured in both winter and summer seasons at relatively high simulated in situ light levels (maximum production in 10 of 24 experiments at $\geq 30\% I_0$ and 16 of 24 experiments at $\geq 20\% I_0$). Production maxima associated with the deep chlorophyll maximum (< 15% I_0) were observed in 8 of 24 offshore production experiments.

Production stations in the shallower Joseph Bonaparte Gulf and Arafura Sea were also characterized by stratified water columns (Fig. 3A-B) with evidence of lateral intrusion of both higher and lower-salinity water masses in individual profiles (e.g. Fig. 3B). The thickness of the surface mixed layer

1 varied seasonally with the degree of solar heating, and episodically over shorter time scales in
2 response to wind stress. In general, temperature had a larger effect on vertical profile density
3 structure than salinity gradients. At Arafura Sea stations, vertical temperature differences were
4 responsible for twice the surface-bottom density difference ($\Delta\sigma_t = 0.53 \pm 0.10$; mean $\pm$ 95% CI)
5 attributable to salinity ($\Delta\sigma_t = 0.25 \pm 0.14$). In the Joseph Bonaparte Gulf, virtually all of the vertical
6 density differences were due to temperature ($\Delta\sigma_t = 1.28$ vs. -0.12). Most (40 of 51) stations in both
7 the Joseph Bonaparte Gulf and Arafura Sea were characterized by a well-defined, near-homogenous
8 benthic boundary layer produced by tidal bottom stress (e.g. Fig. 3B). While the full water column
9 was, or potentially could be, in the euphotic zone, sub-surface light profiles were characterized by
10 enhanced turbidity in the near-bottom layer (e.g. Fig 3A) due to resuspension of benthic particulate
11 matter and higher absorption by phytoplankton. Vertical profiles of chlorophyll in the Joseph
12 Bonaparte Gulf and Arafura Sea were also usually characterized by sub-surface maxima (48 of 51
13 stations), located either at the pycnocline between surface and bottom layers, or within the near-
14 bottom boundary layer (25 of 51 stations). However, during periods of enhanced vertical mixing
15 caused by strong monsoonal winds, sub-surface chlorophyll maxima in the water column became
16 less-well defined. The highest ^{14}C uptake rates at individual production stations within Joseph
17 Bonaparte Gulf and Arafura Sea most frequently occurred within the sub-surface chlorophyll
18 maximum (Fig. 3B).

19 The deeper waters of the northern and central Gulf of Carpentaria exhibited seasonal changes in
20 water column stability, vertical chlorophyll distributions and carbon uptake rates similar to the
21 Arafura Sea. At stations occupied during periods of strong winds (e.g. Fig. 4A, winds $\geq 9 \text{ m s}^{-1}$), Gulf
22 waters were vertically well mixed. In these cases, vertical gradients of density ($\Delta\sigma_t = 0.02$),
23 phytoplankton biomass ($\Delta\text{Chl } a = 0.13 \mu\text{g L}^{-1}$) and nutrient concentrations ($\Delta\text{NO}_x = 0.01 \mu\text{M}$) were
24 small. Picoplankton were the dominant size fraction in Gulf of Carpentaria chlorophyll standing crop
25 (55 ± 9 percent, mean $\pm$ 95% CI, $n=6$) and production measurements (58 ± 6 percent), although
26 extensive near-surface blooms of colonial *Trichodesmium* also occur in the Gulf (M. Furnas, pers.

obs; Burford et al., 2009). In experiments carried out under strong wind conditions (e.g. Fig. 4A), individual production profiles were characterized by a broad sub-surface maximum across a range of in situ light levels. Under conditions of low-wind and strong summer solar heating, or when there were large seasonal freshwater inputs, the Gulf becomes stratified. During these periods (e.g. Fig. 4B), the highest chlorophyll concentrations were usually recorded in the lower water column, below the pycnocline (10 of 10 stations); however, the highest primary production rates in individual profiles were usually still in the near-surface layer (50-20 % I_0 , 5 of 6 production profiles).

During a single set of four experiments in the Gulf of Papua during April 1992 (Fig. 5A), the water column was found to be well-mixed, dominated by picoplankton and characterized by near-uniform production rates through much of the water column. This may not be representative, however, as others (e.g. McKinnon et al., 2007) have observed southward extensions of the Fly River plume into the northern Coral Sea with strong influences on vertical density, chlorophyll and production profiles.

The shallow waters of the Torres Strait (Fig. 5B) and far-northern Great Barrier Reef (Fig. 5C) were usually characterized by well-mixed, or weakly stratified water columns due to wind stress and especially, strong tidal currents through the dense matrix of islands, submerged banks and coral reefs in this region (e.g. Wolanski and Thomson, 1984; Wolanski et al., 1988; Harris, 1991). Torres Strait waters were consistently more turbid (mean $\pm$ 95% CI for the 20% I_0 depth – 10.5 ± 4.3 m, $n=10$) than in the adjoining Gulf of Carpentaria (mean 20% I_0 depth – 18.3 ± 2.7 m, $n=6$), northern Great Barrier Reef (mean 20% I_0 depth – 16.8 ± 8.4 m, $n=5$) and Gulf of Papua (mean 20% I_0 depth – 22.0 ± 8.5 m, $n=4$). Phytoplankton in the $> 10 \mu\text{m}$ size fraction made the largest relative contribution (57 ± 15 percent) to chlorophyll standing crop in the Torres Strait during all times sampled as compared to the Gulf of Carpentaria (32 ± 6 percent), Great Barrier Reef (42 ± 14 percent) and Gulf of Papua (10 ± 1 percent). In contrast, the contribution of larger phytoplankton ($> 10 \mu\text{m}$) to primary production in Torres Strait production measurements (28 ± 10 percent) was not greatly different

1 from that in the Gulf of Carpentaria (32 ± 6 percent) and far-northern GBR (21 ± 8 percent), but
2 much higher than the three size-fractionated measurements in the Gulf of Papua (8 ± 2 percent).
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5 Table 2 summarizes regional and seasonal means and ranges of chlorophyll standing crop and daily
6 primary production rates measured in NAS waters between 1990 and 2013. Both the highest ($2,436$
7 $\text{mg C m}^{-2} \text{ d}^{-1}$) and lowest ($246 \text{ mg C m}^{-2} \text{ d}^{-1}$) daily production rates measured under non-cyclonic
8 conditions were recorded in the Arafura Sea region ($130\text{-}137^\circ\text{E}$). Where at least three
9 measurements are available for a particular region-season combination, means of estimated daily
10 production rates fell between 700 and $1,500 \text{ mg C m}^{-2} \text{ d}^{-1}$. The overall mean of measured daily
11 production rates at NAS stations was $1,048 \pm 109$ (mean $\pm$ 95% CI) mg C m^{-2} . While there was no
12 correlation between daily primary production and surface chlorophyll concentrations (Fig. 6A),
13 estimates of daily primary production were strongly correlated with total chlorophyll standing crop
14 ($p < 0.001$, Fig. 6B) and chlorophyll standing crop above the 50 ($p = 0.003$, Fig. 6C) and 20 ($p < 0.001$,
15 Fig. 6D) percent light penetration depths. Volume-specific daily production within these upper
16 water column light penetration ranges were also correlated with volume-weighted mean chlorophyll
17 concentrations in those ranges (Fig. 6E, F).
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37 NAS production stations were characterized by a clear west to east increase in volume-weighted
38 mean water column or euphotic zone ($I_z \geq 0.6\% I_0$) chlorophyll concentration (Fig. 7A). Predicted
39 mean chlorophyll concentrations increased over 2-fold from 0.21 mg m^{-3} in oceanic waters over the
40 Kimberley Shelf margin (122°E) to 0.49 mg m^{-3} in the shallow waters of Torres Strait and the far-
41 northern Great Barrier Reef (144°E). Over this broad longitudinal range, however, the mean depth of
42 the euphotic zone or water column decreased almost 3-fold from 94 m at 122°E to ca. 33 m at 144°E ,
43 with a number of Torres Strait production stations shallower than 15 m (Fig. 7B). Estimates of areal
44 chlorophyll standing crop exhibited a small, but significant ($p < 0.033$), west-to-east decreasing trend
45 between the Kimberley Shelf margin and Great Barrier Reef (Fig. 7 C). Areal primary production
46 rates (Fig. 7D), in contrast, exhibited no significant west-east trend. As a consequence, mean daily
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areal production to biomass ratios (P/B; Fig. 7E) increased significantly from west ($52 \text{ g C g chl}^{-1} \text{ day}^{-1}$) to east ($70 \text{ g C g chl}^{-1} \text{ day}^{-1}$, $p < 0.001$). Seasonal differences in means of chlorophyll, areal production and P/B ratios (Figure 7 histograms) varied between parameters. In aggregate, the mean of chlorophyll standing crops during the summer wet season ($21.0 \pm 3.1 \text{ mg m}^{-2}$, mean $\pm$ 95% CI) was significantly higher ($p < 0.001$) than in the dry season ($16.6 \pm 2.4 \text{ mg m}^{-2}$) while the wet ($1,159 \pm 127 \text{ mg C m}^{-2} \text{ day}^{-1}$) and dry ($939 \pm 170 \text{ mg C m}^{-2} \text{ day}^{-1}$) seasonal means of areal production rates were not significantly different. Because of this, the aggregate dry season P/B ratio was also higher than in the wet season mean ratio ($p = 0.047$). Median P/B ratios in both the wet ($61 \text{ g C g chl}^{-1} \text{ d}^{-1}$) and dry ($67 \text{ g C g chl}^{-1} \text{ d}^{-1}$) seasons were close to or slightly above the canonical C/Chl ratio (50-60) for actively growing marine phytoplankton (e.g. Goldman, 1980), indicating approximately one daily doubling of water column phytoplankton carbon biomass.

Picoplankton ($< 2 \mu\text{m}$) assemblages, primarily composed of cyanobacteria (Furnas, in prep.), were the dominant size class of primary producers across the NAS west of Torres Strait (Fig. 8) and in the Gulf of Papua. Apart from stations in the shallow Torres Strait (27 ± 10 percent; mean $\pm$ 95% CI) and far-northern Great Barrier Reef (21 ± 8 percent) regions, the picoplankton contribution to chlorophyll at production stations averaged 57 to 80 percent of the total standing crop (Fig. 9). Regional means of picoplankton contributions to areal primary production ranged between 57 ± 10 percent (Torres Strait) and 83 ± 2 percent (Gulf of Papua). Larger phytoplankton cells and colonies retained on $10 \mu\text{m}$ filters made their largest contributions to chlorophyll standing crop in the Arafura Sea (29 ± 13 percent; mean $\pm$ 95% CI), Gulf of Carpentaria (31 ± 7 percent), Torres Strait (57 ± 15 percent) and Far-northern Great Barrier Reef (43 ± 14 percent). The mean contributions of phytoplankton chlorophyll $> 10 \mu\text{m}$ to standing crop were less than 20 percent in the other regions. In contrast, regional means of the $> 10 \mu\text{m}$ size fraction contributions to daily production varied within a narrower range (Gulf of Papua, 8 ± 2 percent; Gulf of Carpentaria, 32 ± 6 percent), with the remaining six regional means falling between 17 and 27 percent.

1 In parallel to the west - east increasing trend of volume weighted average euphotic zone chlorophyll
2 concentration, both surface (0 – 2 m) chlorophyll concentrations ($p < 0.001$, Fig. 10A) and near-
3 surface (above 50% I_0) chlorophyll standing crop (Fig. 10B) increased significantly ($p < 0.001$) toward
4 the east. A parallel increasing west - east trend of near-surface (above 50% I_0) primary production
5 (Fig. 10C) was also observed. The west - east increase was also observed in surface chlorophyll data
6 (not shown) from all AIMS NAS stations ($n = 153$) occupied between 1990 and 2013. Neither
7 maximum volumetric ^{14}C uptake rates ($4.6 \pm 0.7 \text{ mg C m}^{-3} \text{ hr}^{-1}$, mean $\pm$ 95% CI) in vertical profiles or
8 chlorophyll-specific carbon uptake ($P_B : 13.0 \pm 1.1 \text{ mg C mg chl}^{-1} \text{ hr}^{-1}$) exhibited significant seasonal
9 differences or longitudinal trends across the NAS. While means of maximum C uptake and P_B in
10 profile data differed between regions, these differences were not significant.

23 4. Discussion:

24 Australia is often (self-) described as an island continent surrounded by an unproductive ocean
25 environment. This description is primarily focused on fisheries yield (e.g. Molony et al., 2011) as
26 Australian waters do not support the large-tonnage pelagic or demersal fisheries associated with
27 highly productive eastern boundary current upwelling systems (e.g. Peru, Namibia, etc.), shallow
28 high latitude shelf seas with seasonal nutrient renewal (e.g. Grand Banks, Bering Sea) or estuarine-
29 coastal-shelf systems coupled to large productive catchments (e.g. Gulf of Mexico, equatorial west
30 Africa). Because of the broad link between primary production and fisheries yield (e.g. Pauly and
31 Christiansen, 1995; Chassot et al., 2010), this is taken to imply that the primary productivity of
32 Australian waters is also generally low. However, our ^{14}C measurements, and those of others (e.g.
33 CSIRO, 1963a,b, 1964a,b; Rothlisberg et al, 1994; Furnas, 2007; Furnas and Mitchell 1989; 1999a,b)
34 clearly show that the continental shelves of tropical Australian shelf are not un-productive. Modal
35 ^{14}C -based daily carbon fixation rates are on the order of $800\text{-}1,000 \text{ mg C m}^{-2} \text{ day}^{-1}$ ($290\text{-}365 \text{ g C m}^{-2}$
36 yr^{-1}), with production during episodic events reaching $8,000 \text{ mg C m}^{-2} \text{ day}^{-1}$ (e.g. CSIRO, 1963b;
37 Furnas, 2007). The mean of pelagic net primary production rates (gross photosynthesis –

community respiration; McKinnon et al, 2007, 2011, 2013) measured in three regions of the NAS during the same period using O_2 fluxes was $685 \text{ mg C m}^{-2} \text{ d}^{-1}$ (range = -500 to +5,700 $\text{mg C m}^{-2} \text{ d}^{-1}$), with almost all stations having a positive metabolic status (P/R ratio = 1.6 ± 0.2 ; mean $\pm$ 95%CI, $n=46$). The regional ranges and mean values for daily production rates were of similar magnitude to those previously measured in eastern Indonesian waters (Gieskes et al., 1990; Kinkade et al., 1997). The NAS and Indonesian waters experience similar monsoonal forcing regimes. Seasonal differences in chlorophyll standing crop in Indonesian waters were on the order of 2.5 to 4-fold (Kinkade et al., 1997), primarily due to upwelling of nutrient-enriched deep waters in deeper channels and basins (e.g. Banda Sea, Makassar Strait). As on the NAS, however, as reported herein ($1,159$ vs $939 \text{ mg C m}^{-2} \text{ d}^{-1}$ ~ ca. 20 percent) seasonal differences in mean daily production rates were small (NW monsoon - $1,180 \pm 90 \text{ mg C m}^{-2} \text{ d}^{-1}$ vs. SE monsoon - $1,150 \pm 840 \text{ mg C m}^{-2} \text{ d}^{-1}$; Kinkade et al., 1997).

The most obvious explanation for the apparent difference between the relatively high measured primary production and low production at higher trophic levels is that much of the newly fixed carbon is rapidly consumed and recycled within the microbial food web before it gets incorporated into larger organisms (e.g. meso-zooplankton) suitably sized for consumption by larger predators. The size-fractionation experiments clearly show that very small ($< 2 \mu\text{m}$) cyanobacteria and eukaryotes are responsible for most (50-80%) of the chlorophyll standing crop and primary production in NAS waters. A similarly large proportion of this production is therefore subject to mortality from viral pathogens (e.g. Suttle, 2007; Weitz et al., 2014) or consumption by nano- or micro-eukaryotic grazers (e.g. Calbet, 2008; Calbet and Landry, 2004). In the case of viral mortality, a significant portion of the host biomass is converted at lysis into DOM and pico-detritus which is consumed by pelagic bacteria ($< 2 \mu\text{m}$) and detritivores ($< 10 \mu\text{m}$) and recycled back into microbial biomass (Weitz et al., 2014). Regions within the NAS where significant proportions of primary production was attributable to larger ($> 10 \mu\text{m}$) phytoplankton which are more directly consumed by larger grazers included the shallower parts of the Kimberley shelf (mean percent primary production $> 10 \mu\text{m} = 25$), the Gulf of Carpentaria (32 percent) and Torres Strait (28 percent).

The range of post-1990 areal production estimates reported herein overlaps the range of areal primary production estimates (Table 1) previously measured in NAS waters during the 1960-62 CSIRO Indian Ocean campaigns (CSIRO, 1963a,b; CSIRO, 1964a,b). The comparison with the 1960's results herein is limited to stations (n=70) within the domain (shelf + continental margin) encompassing our 1990-2013 production experiments as shown in Figure 1. Direct comparisons between old and new measurements of primary production are constrained by significant sampling and methodological differences between the studies. At the time, the CSIRO production measurements were made using state-of-the-art methods. Most of the 1960-62 production stations involved sampling at fixed depths (0m, 25m, 50m, 75m 100m, 150m....) regardless of the (unknown) chlorophyll and light attenuation profiles, storage of isotope stocks in glass and incubations in glass bottles. Given the evolution of production measurement techniques over the last 50 years, particularly through the change to plastic samplers, incubation bottles and labware, the use of low-metal reagents, introduction of rigorous cleaning to reduce metal contamination of samplers, labware and isotope stocks (e.g. Carpenter and Lively, 1980; Fitzwater et al., 1982; Marra and Heinemann, 1987) and sampling with more attention to sub-surface light penetration and phytoplankton biomass profiles, higher modern production estimates would be expected. The CSIRO measurements used three experimental incubation approaches: in-situ incubations, simulated in-situ incubations using filtered and attenuated artificial light, and incubations under constant artificial light. Most of the early production measurements (CSIRO, 1963a,b; 1964a,b; Motoda, 1978) are based on incubations of water samples from fixed sampling depths in continuous artificial light (CSIRO – 1100 fc “cool white” light $\sim 160 \mu\text{mol Q m}^{-2} \text{ s}^{-1}$; Motoda - 1100 fc “cool white” fluorescent). This light intensity is less than half of the low end of the PAR range (50-20% $I_0 \sim 1100$ - $400 \mu\text{mol Q m}^{-2} \text{ s}^{-1}$) at which optimal photosynthesis was observed in many of our simulated in situ incubations. Potential contamination issues aside, the incubation light levels in these early artificially illuminated experiments were sub-optimal for phytoplankton in the upper half of the euphotic zone where the highest photosynthesis rates took place. In particular, phytoplankton in

1 surface (<10 m) and deep (> 50 m) samples would have been exposed to non-representative
2 illumination. The most appropriate comparisons are therefore between experiments using in-situ or
3 simulated in-situ incubations. The CSIRO areal production estimates for NAS experiments based on
4 in-situ and simulated in-situ incubations (n=70) and constant artificial light incubations (n=111)
5 yielded very similar estimates of areal production, with mean values of 414 ± 209 and 396 ± 56 mg C
6 $\text{m}^{-2} \text{d}^{-1}$ (mean $\pm$ 95% CI), respectively. These means are approximately 40 percent of the mean
7 production value ($1,048 \pm 109$ mg C $\text{m}^{-2} \text{d}^{-1}$) calculated from our post-1990 measurements using
8 simulated in-situ incubations based on attenuated natural sunlight. The difference between the
9 overall means is highly significant ($p < 0.015$) as are the differences between regional means, where
10 they can be compared. We believe that these ≥ 2 -fold differences in mean areal production rates
11 are due to a combination of the use of contamination-minimizing sampling and incubation methods
12 in post-1990 experiments and sub-optimal irradiance regimes during incubations in the 1960-62
13 experiments.

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31 Current global and regional estimates of marine primary production are now primarily calculated
32 using empirical and ecophysiological models parameterized from hydrographic climatologies and
33 satellite imagery (e.g. Behrenfeld et al., 1998, 2005; Field et al., 1998). The accuracy of these models
34 depends on the extent to which measurable spatial distributions of near-surface chlorophyll and
35 other optical properties can be used to infer underlying vertical distributions of phytoplankton
36 biomass, light penetration, vertical mixing and primary production. In both clear oligotrophic
37 oceanic waters and turbid coastal systems, only a small portion of total water column chlorophyll
38 may occur within the depth stratum ($1/K_s$; Andre, 1992) accessible to remote sensing. In the clearest
39 oceanic waters, the accessible depth range is on the order of 25-30m. Integrated upper water
40 column production estimates from nominally clear-water, open-shelf NAS sites (n = 39) indicate that
41 approximately half (49 ± 5 percent: mean $\pm$ 95% CI) of areal primary production occurs within this
42 depth range. Empirical studies (e.g. Eppley et al., 1985; Joint and Groom, 2000) show that near-
43 surface chlorophyll concentration is a robust predictor of water column primary production. With
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the exception of a few outliers in our experiments, there were good correlations between estimated areal primary production and measured chlorophyll standing crops above the 50 and 20% light penetration depths, a depth range accessible to satellite observation (Figure 6C-F). Likewise, there were clear correlations between the depth-averaged photosynthesis rates and depth-weighted mean chlorophyll concentrations above both the 50 percent (slope = $7.1 \pm 1.4 \text{ mg C hr}^{-1} \text{ mg Chl}^{-1}$; mean $\pm$ 95% CI, $r^2 = 0.65$) and 20 percent (slope = $7.3 \pm 1.2 \text{ mg C hr}^{-1} \text{ mg Chl}^{-1}$, $r^2 = 0.72$) light penetration depths. These correlations indicate that while there can be a considerable diversity of vertical hydrographic, light penetration, chlorophyll and primary production profiles across the NAS, remote sensing algorithms for estimating upper euphotic zone chlorophyll concentration will provide sufficient information to usefully estimate both near-surface and areal primary production. The primary complication to this is that dense and extensive surface and near-surface aggregations of the highly reflective cyanobacterium, *Trichodesmium* occur at least episodically in the Joseph Bonaparte Gulf, Arafura Sea and Gulf of Carpentaria (Furnas, pers. obs., Burford et al., 2009). Pixels in satellite imagery affected by significant coverage of dense surface aggregations of *Trichodesmium* can be readily detected (e.g. McKinna et al., 2011), but sparse surface aggregations or diffuse near-surface populations of *Trichodesmium* remain difficult to resolve.

In summary, modern estimates of water column primary productivity on the Northern Australian Shelf, primarily measured using ^{14}C uptake methods, have an annual mean value close to $1,000 \text{ mg C m}^{-2} \text{ day}^{-1}$. Despite seasonal (monsoonal) differences in environmental forcing, calculated means of austral summer (wet) and austral winter (dry) season areal productivity only differed on the order of 20% and were not significantly different. Likewise, while there were significant differences between means of measured productivities at regional scales, there was no significant west-east trend in areal primary production across the NAS. Picoplankton ($< 2 \mu\text{m}$) dominated phytoplankton community standing crop and primary production in most parts of the NAS, though phytoplankton collected by $10 \mu\text{m}$ filters were more important in the shallow, well-mixed waters of the Torres Strait and far-northern Great Barrier Reef shelf regions. While ranges of measured values overlap, the

1 overall mean of our 1990-2013 production measurements was approximately 2.5 times the mean of
2 areal production estimates made in the early 1960's. The increase is most likely due to
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4 improvements in sampling and incubation procedures, particularly through the adoption of
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6 samplers, labware and procedures for handling seawater samples and isotope stocks to reduce
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8 exposure to toxic metals. Despite a considerable diversity of seasonal and regional water column
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10 stability regimes and vertical phytoplankton biomass profiles on the NAS, most areal primary
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12 production occurred in the upper water column, above the mid-day 20 percent isolume depth.
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14 Upper water column productivity and phytoplankton biomass (chlorophyll) stocks were highly
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16 correlated. This indicates that remote sensing procedures producing reliable estimates of near-
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18 surface or upper euphotic zone chlorophyll concentrations without significant surface
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20 *Trichodesmium* contamination will support useful estimates of regional primary production.
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Figure Legends:

Figure 1. Australia's northern continental shelf and locations of ^{14}C primary production stations occupied in open shelf waters between 1992 and 2013. Major regional zones are identified. The thin blue line shows the 200 m isobath in the study area.

Figure 2. Representative vertical profiles of temperature ($^{\circ}\text{C}$), salinity (‰), density (σ_t) size-fractionated chlorophyll (mg m^{-3}), chlorophyll fluorescence from CTD casts, sub-surface light (PAR) penetration and size-fractionated mid-day primary production ($\text{mg C m}^{-3} \text{ hr}^{-1}$) measured on the outer Kimberley shelf margin during (A) the mid-summer (NWF457; Feb 1995; NW Monsoon) and (B) winter (SCT057; June 2008, SE Monsoon). In situ chlorophyll fluorescence is given in arbitrary instrument units (A) or empirically calibrated estimates of chlorophyll (B), depending on the instrument used. Note differences in scales.

Figure 3. Representative vertical profiles of temperature ($^{\circ}\text{C}$), salinity (‰), density (σ_t) size-fractionated chlorophyll (mg m^{-3}), chlorophyll fluorescence from CTD casts, sub-surface light (PAR) penetration and size-fractionated mid-day primary production ($\text{mg C m}^{-3} \text{ hr}^{-1}$) measured in (A) the northern Joseph Bonaparte Gulf during the late-summer (TIM008: Apr 1992; NW Monsoon) and (B) the Arafura Sea in the early-summer (WES007; Dec 2011, pre-NW Monsoon). Plots, symbols, lines and annotations are as given in Fig. 2A. Note differences in scales.

Figure 4. Representative vertical profiles of temperature ($^{\circ}\text{C}$), salinity (‰), density (σ_t) size-fractionated chlorophyll (mg m^{-3}), chlorophyll fluorescence from CTD casts, sub-surface light (PAR) penetration and size-fractionated mid-day primary production ($\text{mg C m}^{-3} \text{ hr}^{-1}$) measured in the Gulf of Carpentaria during (A) strong ($> 9 \text{ m sec}^{-1}$) wind conditions (NWA166; Nov 1992, pre-NW Monsoon) and (B) late-summer (TIM029; Apr 1992, post-NW Monsoon, low-wind conditions). In situ chlorophyll fluorescence and underwater light

profiles were not measured at NWA166. Plots, symbols, lines and annotations are as given in Fig. 2A. Note differences in scales.

Figure 5. Representative vertical profiles of temperature ($^{\circ}\text{C}$), salinity (‰), density (σ_t) size-fractionated chlorophyll (mg m^{-3}), chlorophyll fluorescence from CTD casts, sub-surface light (PAR) penetration and size-fractionated mid-day primary production ($\text{mg C m}^{-3} \text{ hr}^{-1}$) measured in (A) the Gulf of Papua during the late-summer (TIM040: Apr 1992; post-NW Monsoon), (B) the Torres Strait during mid-summer (TOR073; Feb 1990, NW Monsoon) and (C) the far northern GBR in mid-summer (TOR054; Feb 1990, NW Monsoon) . In situ chlorophyll fluorescence and underwater light profiles were not measured at TOR054 and TOR073. Plots, symbols, lines and annotations are as given in Fig. 2A. Note differences in scales.

Figure 6. Relationships between estimates of daily primary production and (A) surface chlorophyll; (B) total water column chlorophyll standing crop; (C) chlorophyll standing crop above the 50 percent isolume depth; (D) chlorophyll standing crop above the 20 percent isolume depth; (E) volume-averaged daily primary production above the 50 percent isolume depth relative to the volume-averaged chlorophyll concentration above the 50 percent isolume depth, and (F) volume-averaged daily primary production above the 20 percent isolume depth relative to the volume-averaged chlorophyll concentration above the 20 percent isolume depth. Daily production in B ($\text{mg C m}^{-2} \text{ d}^{-1}$) = $29.8 \times \text{Chl Standing Crop} (\text{mg m}^{-2}) + 478$, $r^2 = 0.302$. Where correlations are significant ($p < 0.05$), regression lines and 95 percent confidence intervals about the lines are shown. Open triangle symbols identify outlier data points not used in regression calculations.

Figure 7. Longitudinal trends at 1990-2013 production stations across the NAS in: (A) depth-weighted mean euphotic zone (above 0.6% I_0 for stations with depths > 120 m) or water column chlorophyll concentration; (B) euphotic zone (above 0.6% I_0 with depths > 120 m) or water column depth; (C) areal chlorophyll standing crop; (D) daily primary production, and (E) the daily areal primary production: biomass ratio in the wet (NW monsoon) and dry (SE monsoon) seasons. Regression lines and 95 percent confidence intervals for the regression (shaded areas) are shown. One outlier chlorophyll value (open triangle) was excluded. Adjoining box plots summarize the distribution of measured values by season. Solid bars encompass the 25th-75th percentile range of values, with median shown. Whiskers encompass the 10th-90th percentile range. Solid symbols identify values outside 10th-90th percentile ranges.

Figure 8. Relative contributions of phytoplankton size classes to chlorophyll standing crop and daily primary production across the NAS. Station data are grouped by regions shown in Figure 1 and ordered by longitude within regions. KSM = Kimberley Shelf Margin, Kim = Kimberley Shelf, JBG = Joseph Bonaparte Gulf, AS = Arafura Sea, GoC = Gulf of Carpentaria, TS = Torres Strait, GoP = Gulf of Papua, GBR = Far Northern Great Barrier Reef.

Figure 9. Regional contributions of picoplankton (< 2 μ m size fraction) to chlorophyll standing crop and primary production. Station data are grouped by the regions shown in Figure 1. Bars encompass data points between the 25th and 75th percentiles, with median. Whiskers encompass the 10th to 90th percentile range. Solid symbols identify data points outside the 10th to 90th percentile range.

Figure 10. Longitudinal trends across the NAS of: (A) surface chlorophyll concentrations at primary production stations, (B) near-surface chlorophyll standing crop and (C) near-surface primary production. Regressions with significant slopes > 0 ($p < 0.05$) and 95 percent confidence intervals (shaded bands) are shown.

Figure 1

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Table 1. Published estimates of pelagic primary production in eastern Indonesian and northern Australian shelf waters.

Region	Time Frame	Mean ($\pm$ SD) mg C m ⁻² d ⁻¹	Range mg C m ⁻² d ⁻¹	Method	Source
Banda and Arafura Seas	Aug 1984	1850	510-6830	¹⁴ C-SIS**	Geiskes et al., 1990
	Feb 1985	950	310-2130	¹⁴ C-SIS	"
Eastern Indonesian Seas	Aug 1993	1180 $\pm$ 90		¹⁴ C-IS**	Kinkade et al., 1997
	Feb 1994	1230 $\pm$ 220		¹⁴ C-IS	"
Northern Shelf	1960	447 $\pm$ 967	1 - 5960	¹⁴ C-IS**	CSIRO, 1963a
Northern Shelf	1960-62	235 $\pm$ 108	80 - 420	¹⁴ C-SIS**	CSIRO, 1963a,b; 1964a,b
Northern Shelf	1960-62	396 $\pm$ 301	24-1840	¹⁴ C-CAL**	"
Gulf of Carpentaria	Dec 1968	1330 $\pm$ 630	59 - 280	¹⁴ C-CAL ^a	Motoda et al., 1978
Gulf of Carpentaria		914	410 - 2130	¹⁴ C-SIS	Rothlisberg et al. 1994
Sahul Shoals	2004 - 05	509 $\pm$ 766	-190 - 2753	O ₂ -SIS	McKinnon et al., 2011
Joseph Bonaparte Gulf	2004 - 05	1132 $\pm$ 678	267 - 1767	O ₂ -SIS	"
Kimberley Shelf	2005	732 $\pm$ 70	689 - 813	O ₂ -SIS	"
Darwin Harbour	Feb 2004	2165		O ₂ -SIS	Burford et al., 2008
	Oct 2004	979		O ₂ -SIS	"
Gulf of Papua (inshore)	2004	626 $\pm$ 504		O ₂ -SIS	McKinnon et al., 2007
Gulf of Papua (offshore)	2004	157 $\pm$ 450		O ₂ -SIS	"
Gulf of Papua (inshore)	1990	249 $\pm$ 70		¹⁴ C-SIS	Robertson et al., 1998
Central NW Shelf	1994-95	750	450 - 2500	¹⁴ C-SIS	Furnas and Mitchell, 1999
Central and Southern GBR	1983-88	620	129 - 1972	¹⁴ C-SIS	Furnas, 1989

** IS – in situ incubation, SIS – simulated in situ incubations, CAL – Constant artificial light incubation

^a –reported mid-day hourly rate x 10 to estimate daily rate

Table 2. A summary of regional and seasonal estimates of chlorophyll a standing crop, daily primary production and the contribution of picoplankton measured at primary production stations in continental shelf waters across northern Australia (1990-2013).

	Season	Chl Standing Crop (mg m ⁻²)		Daily Production (mg C m ⁻²)	
		Wet	Dry	Wet	Dry
Kimberley Shelf Margin	Mean ± 1 S.D.	24.0 ± 8.8	18.3 ± 5.4	952 ± 171	703 ± 277
	n	5	12	6	12
	Range	16.8 – 36.7	7.1 – 25.3	587 – 1222	440 – 1034
	Mean % < 2µm (n)	80 (5)	71 (12)	77 (6)	86 (12)
Kimberley Shelf	Mean ± 1 S.D.	14.9 ± 8.0	17.9 ± 9.1	1611 ± 183	869 ± 267
	n	2	8	2	8
	Range	9.3 – 20.6	7.4 – 37.8	1482 – 1740	537 – 1408
	Mean % < 2µm (n)		59 (3)		63 (3)
Joseph Bonaparte Gulf	Mean ± 1 S.D.	33.0	23.7 ± 6.8	467	1436 ± 351
	n	1	5	1	6
	Range		17.9 – 35.2		944 – 1803
	Mean % < 2µm (n)	66 (1)	70 (1)	63 (1)	72 (1)
Arafura Sea	Mean ± 1 S.D.	27.6 ± 7.5	12.1 ± 5.7	1853 ± 358	914 ± 539
	n	7	9	7	9
	Range	15.8 – 39.9	4.4 – 18.8	793 – 2436	246 – 1569
	Mean % < 2µm (n)	45 (2)	62 (1)	55 (2)	82 (1)
Gulf of Carpentaria	Mean ± 1 S.D.	34.0 ± 8.4	10.8 ± 6.9	1461 ± 438	1421 ± 340
	n	5	3	5	4
	Range	19.6– 41.3	12.9– 25.1	875 – 1714	935 – 1831
	Mean % < 2µm (n)	55(1)	54 (2)	56 (4)	60 (2)
Torres Strait	Mean ± 1 S.D.	13.3 ± 5.0	3.8 ± 1.7	748 ± 458	411 ± 210
	n	8	2	8	2
	Range	6.8 – 23.0	2.6 – 5.0	331 – 1573	263 – 560
	Mean % < 2µm (n)	23 (8)	58 (2)	55 (8)	66 (2)
Gulf of Papua	Mean ± 1 S.D.	11.1 ± 4.6		708 ± 183	
	n	4		4	
	Range	7.0 – 17.6		471 – 918	
	Mean % < 2µm (n)	80 (3)		82 (3)	
Far-northern Great Barrier Reef	Mean ± 1 S.D.	16.2 ± 5.1	6.8	1153 ± 349	442
	n	6	1	6	1
	Range	7.1 – 21.9		611 – 1640	
	Mean % < 2µm (n)	28 (6)	74 (1)	61 (4)	81 (1)