Climate variability drives plankton community composition changes: the 2010−2011 El Niño to La Niña transition around Australia

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The strong La Niña of 2010−2011 provided an opportunity to investigate the ecological impacts of El Niño-Southern Oscillation on coastal plankton communities using the nine national reference stations around Australia. Based on remote sensing and across the entire Australian region 2011 (La Niña) was only modestly different from 2010 (El Niño) with the average temperature declining 0.2%, surface chlorophyll *a* up 3% and modelled primary production down 14%. Other changes included a poleward shift in *Prochlorococcus* and *Synechococcus*. Along the east coast, there was a reduction in salinity, increase in nutrients, Chlorophytes and Prasinophytes (taxa with chlorophyll *b*, neoxanthin and prasinoxanthin). The southwest region had a rise in the proportion of 19-hexoyloxyfucoxanthin; possibly cocco-lithophorids in eddies of the Leeuwin Current and along the sub-tropical front. Pennate diatoms increased, *Ceratium* spp. decreased and *Scrippsiella* spp. increased in 2011. Zooplankton biomass declined significantly in 2011. There was a reduction in the abundance *of Calocalanus pavo* and *Temora turbinata* and increases in *Clausocalanus farrani*, *Oncaea scottodi-carloi* and *Macrosetella gracilis* in 2011. The changes in the plankton community during the strong La Niña of 2011 suggest that this climatic oscillation exacerbates the tropicalization of Australia.

KEYWORDS: nutrients; phytoplankton; zooplankton; ENSO; climate

INTRODUCTION

The impacts of climate change on marine ecosystems are difficult to predict (e.g. Taucher and Oschlies, 2011) yet greater understanding is required to minimize any negative effects on resource users (Sumaila *et al.*, 2011). The responses of oceanic plankton to climate variability are poorly understood in part due to the paucity of long-term, time-series data. There is evidence of changes in the phenology of phytoplankton (Edwards and Richardson, 2004) and speculation on the expected impacts of increased stratification to favour dinoflagellates (Edwards and Richardson, 2004) and acidification to favour *Trichodesmium* (Doney, 2006) but the few oceanic time series [Hawaii Ocean Time Series (HOTS) or Bermuda Atlantic Time Series (BATS)] show little evidence of any trends in phytoplankton biomass or composition. The El Niño Southern Oscillation (ENSO) is a form of climate variability with an irregular oscillation of 3–7 years (Trenberth and Hoar, 1997). La Niña events increase the warm water pool in the western Pacific creating increased precipitation and higher water temperatures around Australia (Philander, 1990) providing an excellent opportunity to observe ecosystem responses to some of the primary, longer term climatic drivers. The shift from El Niño to La Niña results in a global 0.5 GtC year^{-1} increase in oceanic primary production (Jones *et al.*, 2001) and changes the phytoplankton community that drive this carbon flux (Chavez *et al.*, 1998; Behrenfeld *et al.*, 2006). The La Niña shift in phytoplankton community from *Synechococcus* to diatoms has been estimated from remotely sensed ocean colour (Masotti *et al.*, 2011). Both the carbon flux and phytoplankton community changes are poorly validated, and we lack detailed knowledge or understanding of either the direct impacts of this climatic perturbation on marine ecology or its possible feedback (Jochum *et al.*, 2010). The ecological impacts of ENSO on zooplankton are known for only a few locations (e.g. Chelton *et al.*, 1982) or for a single season (e.g. McKinnon *et al.*, 2008) and there is a need to assess these impacts more comprehensively.

Australia has the world's third largest exclusive economic zone of maritime jurisdiction over at least 8 million km^2 of ocean and greater range of climatic variability than other continents (Alexander *et al.*, 2007) that are associated with ENSO events. Periods of more than 3 months of a negative difference in atmospheric pressure at sea level between Darwin and Tahiti (= the Southern Oscillation Index or SOI) coincide with El Niño episodes whereas prolonged periods of positive SOI values coincide with La Niña episodes (Ropelewski and Halpert, 1987). Based on SOI data from the Australian Bureau of Meteorology the La Niña event of 2010–2011 was one

of the strongest in >100 years. The SOI values for October 2010 and December 2010 were each the highest positive values on record for those months, as was the 3-month average October–December 2010. The strong La Niña of 2010–2011 commenced just prior to austral winter and persisted some 13 months (Fig. 1). Across Australia, 2011 was the second wettest year since high-quality records began in 1900 (Australian Bureau of Meteorology Annual Report 2011). The second largest cyclone ever to make landfall in Australia (cyclone Yasi) arrived on the north east coast of Australia in the summer of 2011. Such a strong La Niña event provided an excellent natural experiment to compare with the environmental conditions during the previous and persistent El Niño. The ecological responses of lower trophic levels such as phytoplankton and zooplankton, with their short generation times, should provide insights into possible longer term trends in climate.

Shelf waters along both Australian coasts show relatively rapid and significant, long-term (~60 years) surface warming (Feng *et al.*, 2003, Ridgway, 2007) associated with climate and the strengthening of the poleward boundary currents. At 32°S on Australia's west coast the Leeuwin Current (LC) transports 2–3 Sverdrups (1 Sv = 10^6 m^3 s^{-1}) southward in summer rising to 5 Sv in winter (Feng *et al.*, 2003). The LC flows along the shelf break, suppressing coastal upwelling and creating an oligotrophic marine environment off Western Australia (WA). The El Niño condition results in a weaker LC (Weller *et al.*, 2011) and lower than normal phytoplankton biomass along the WA coast (Thompson *et al.*, 2009). The La Niña event of 2010–2011 was associated with much warmer than normal surface waters off WA (Feng *et al.*, 2013).

The East Australian Current (EAC) is the western boundary current of the south Pacific gyre transporting
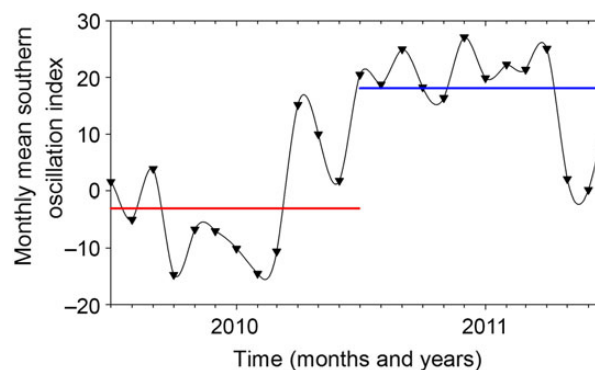
Fig. 1. Mean monthly southern oscillation index for 1 July 2009 to 30 June 2011. Mean SOI values for Austral year 1 July 2009 to 30 June 2010 (2010) was −3.00 (lower horizontal line) significantly different (*P* < 0.001) from mean SOI for 1 July 2010 to 30 June 2011 (2011) which was 18.09 (higher horizontal line).

warm tropical waters to higher southern latitudes along the east coast of Australia. The EAC's flow ranges from 7 Sv in winter to 16 Sv in summer (Ridgway and Godfrey, 1997). The current separates at ~32°S and mostly forms the eastward flowing Tasman Front (~34°S). A portion of the EAC continues southward past Tasmania primarily in the form of a large eddy field. Small-scale upwelling is common along the east coast of Australia ~31°S (Oke and Middleton, 2000) and linked with coastal phytoplankton blooms (Hallegraeff and Jeffrey, 1993, Pritchard *et al.*, 2003). During El Niño events (SOI < 0), there has been a decrease in the sea surface temperature (SST) around eastern Australia (Hsieh and Hamon, 1991), decreased onshore transport, greater downwelling and a deepening of the pynocline (Gibb *et al.*, 1998).

Here we assessed changes in the nutrients, phytoplankton and zooplankton on the continental shelf between July 2009 and June 2011. The Australian continental shelf seas span from tropical (~10°S) to high temperate (~44°S) and have nine national reference stations (NRSs). At three NRSs, there are physical and chemical observations dating back some ~70 years. We considered the biological implications of the long-term physical and chemical trends (Thompson *et al.*, 2009) while the biological sampling at the expanded number of NRSs commenced only in 2008 (Lynch *et al.*, 2014). The expanded NRS system has been assessed for its capacity to observe physical and biological variation. In general, the NRS system captures seasonal variation in temperature and chlorophyll *a* for the vast majority of the shelf (Oke and Sakov, 2012; Jones *et al.*, 2015). For the majority of the nine NRSs, there was a complete year of monthly samples during the El Niño of 2009–2010 and another year of sampling during the strong La Niña of 2010–2011. It is a significant observational challenge to detect the ecological effects of a long-term, and relatively small, trend in temperature in a world with much larger but shorter cycles such as seasonality and ENSO. Fortunately, for short-lived organisms, like plankton, the variability in temperature over shorter temporal scales may provide useful insights into the ecology of a warmer future. The results presented here indicate clear regional patterns in nutrients, phytoplankton and zooplankton as well as differences between years apparently in association with ENSO variation.

METHOD

In situ sample data were collected from the three long running (~70 year) coastal stations and from the more recent expansion to nine NRSs from around Australia (Fig. 2A and Table I). The NRSs are identified by name

and location; for example Yongala-E_{19} is the Yongala NRS on the east coast at 19°S (Fig. 2A). Biological samples were first collected at Maria-E_{43} in 2008 and Darwin-N_{12} was the last station to commence biological sampling in 2011. Of the nine NRSs, seven were sampled at approximately monthly intervals, and two stations (Ningaloo-W_{22} and Esperance-W_{34}) sampled seasonally. A full description of the NRSs can be found in Lynch *et al.* (Lynch *et al.* 2014). All NRS data are available at the Australian Ocean Data Network portal http://portal.aodn.org.au/aodn/ hosted by the Australian Integrated Marine Observing System (IMOS).

Remotely sensed data

Temperature, chlorophyll *a* and primary production (PP) were assessed at the same regional scale; from 11 to 44°S by 112 to 156°E. The regional scale spatial and temporal distribution of near surface phytoplankton was assessed using ocean colour (chlorophyll *a*) data from the Moderate Resolution Imaging Spectroradiometer (MODIS) downloaded May 2014. Temperature data were also from MODIS (11 μm, night). Both chlorophyll *a* and temperature were obtained from GES-DISC Interactive Online Visualization ANd aNalysis Infrastructure (GIOVANNI) as part of the NASA's Goddard Earth Sciences (GES) Data and Information Services Center (DISC). Total and group-specific primary production was obtained from the NASA Ocean Biogeochemical Model (NOBM). The NOBM is a 3D representation of circulation/biogeochemical/radiative processes at a 1.25° resolution in water deeper than 200 m. NOBM is coupled with the Poseidon ocean general circulation model, which is driven by wind stress, SST and shortwave radiation (Gregg and Casey, 2007). Irradiance data to drive phytoplankton growth are taken from the Ocean-Atmosphere Spectral Irradiance Model (Gregg and Casey, 2009). Satellite ocean chlorophyll (MODIS-Aqua) is assimilated into NOBM following Gregg (Gregg, 2008) using a multi-variate assimilation (Rousseaux and Gregg, 2012). Primary production is computed in the model as a function of growth rate multiplied by the carbon:chlorophyll ratio:

$$PP = \int \sum \mu_i C_i \Phi d\mathrm{z}$$

where μ_i is the growth rate of phytoplankton component *i*, C_i is the chlorophyll concentration of component *i*, Φ is the carbon:chlorophyll ratio and the product is the integrated over depth. It is a diagnostic variable in the model, representing the integral of net carbon uptake in the water column. Photo-adaptation is simulated low, medium and high classes of light adaptation (Gregg and Casey, 2007) with Φ of 25, 50 and 80 g·g^{-1}, respectively.
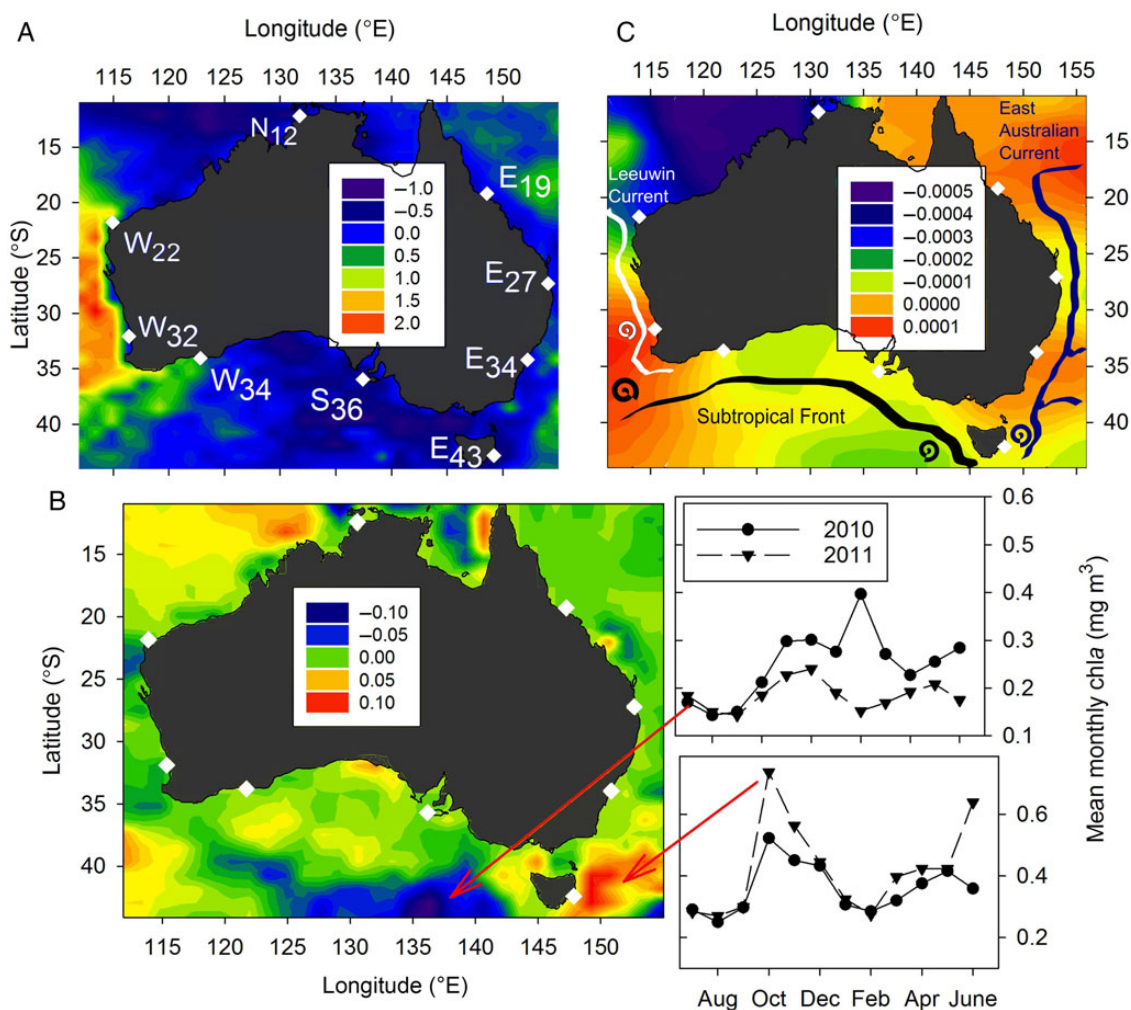
Fig. 2. Inter-annual differences between an El Niño year (July 2009 to June 2010) and a La Niña year (July 2010-June 2011). National Reference Station locations (diamond symbol) identified by location around the continent (N = north, S = south, E = east, W = west) and latitude as subscript: N_{12} = Darwin, E_{19} = Yongala, E_{27} = North Stradbroke Island, E_{34} = Port Hacking, E_{43} = Maria Island, S_{36} = Kangaroo Island, W_{34} = Esperance, W_{32} = Rottnest Island, W_{22} = Ningaloo. (**A**) Inter-annual mean differences in temperature (°C), 11 μm night temperatures from MODIS. (**B**) Inter-annual mean differences in chlorophyll a (μg L^{-1}) from MODIS plus the seasonal progression of chlorophyll *a* concentrations in 2010 versus 2011 in the two regions of strongest inter-annual differences: the southern extreme of the Great Australian Bight (GAB, 42−49°S by 125−142°E) and the south Tasman Sea (39−44°S by 148.5−154°E). (**C**) Inter-annual difference in Total Primary Production (PgC year^{-1}) estimated from the NASA Ocean Biogeochemical Model with schematic representations of the East Australian Current, the Leeuwin Current and the Subtropical Front (after Ridgway and Dunn, 2003).

Nutrients and salinity

Water samples were collected in Niskin type bottles typically at 0, 10, 20, 30, 40 and 50 m although the Yongala-E_{22} station is relatively shallow with samples to 30 m only whereas Kangaroo-S_{36} had some deeper samples (75, 90, 100 m) that were also included in the statistical analysis where sufficient data were available. Samples for salinity were stored in 250-mL amber bottles and analysed on a Guildline Autosal salinometer. For nutrients, triplicate samples were collected into rinsed 10-mL polyethylene tubes and stored at −20°C until analysed. Samples were analysed for nitrate + nitrite,

silicate, ammonium and phosphate using colorimetric methods (Parsons *et al.*, 1984) but automated and refined for flow injection analysis on a Lachat™ system. Nutrient and salinity data are available from the Australian Ocean Data Network portal (http://portal.aodn.org.au/aodn/).

Phytoplankton

The spatial and temporal sampling of phytoplankton is consistent with the recommendations for continental shelf ecosystems (Margalef, 1978) although it was relatively sparse and may not have detected small or short-lived

Table I: *Mean conditions for temperature, salinity, silicate, nitrate, phosphate and ammonium in the 2010 El Niño year (July 2009 to June 2010) and the 2011 a La Niña year (July 2010 to June 2011) and the differences (2011−2010) in absolute terms and as a percentage with statistical analysis based on three-way ANOVA for year, season and depth*

	W_{32} (Rottnest Island[a])	S_{36} (Kangaroo Island)	E_{19} (Yongala)	E_{27} (North Stradbroke Island)	E_{34} (Port Hacking)	E_{43} (Maria Island)	W_{34} (Esperance)	W_{22} (Ningaloo)	N_{12} (Darwin)
Latitude °S + decimal minutes	32.00	35.83	19.31	27.34	34.08	42.60	33.93	21.87	12.40
Longitude °E + decimal minutes	115.41	136.44	147.62	153.56	151.25	148.23	121.85	113.95	130.77
Temperature (°C)									
2010	20.45	17.00	25.93	23.86	20.21	15.08	17.94	24.64	28.63
2011	21.82	16.69	25.68	23.98	20.18	14.04	18.63	26.28	27.54
2011−2010	1.36[b]	−0.32[b]	−0.24	0.12	0.03	−1.04[b]	0.69[b]	1.65[b]	−1.08
Salinity									
2010	35.713	35.733	34.917	35.436	35.445	35.273			
2011	35.488	35.912	34.163	35.389	35.460	35.154			
2011−2010	−0.225[c]	0.188[b]	−0.754[b]	−0.047[c]	0.015[c]	−0.119[b]			
Si (μM)									
2010	1.69	0.48	1.25	0.86	1.65	0.83			
2011	1.84	0.23	3.74	1.12	1.52	0.80			
2011−2010	0.150[b] (9%)	−0.247[b] (−52%)	2.486[b] (199%)	0.254[b] (30%)	−0.133[c] (−8%)	−0.031[c] (−4%)			
NO$_3$ (μM)									
2010	0.12	0.32	0.03	1.44	3.63	2.39			
2011	0.27	1.00	0.12	1.83	3.09	2.83			
2011−2010	0.148 (121%)	0.685 (217%)	0.093[b] (340%)	0.392 (27%)	−0.536[b] (−15%)	0.440 (18%)			
PO$_4$ (μM)									
2010	0.13	0.18	0.04	0.16	0.31	0.29			
2011	0.09	0.18	0.12	0.20	0.36	0.49			
2011−2010	−0.040 (−31%)	−0.006 (−3%)	0.076[b] (179%)	0.045[b] (29%)	0.047[b] (15%)	0.205[c] (71%)			
NH$_4$ (μM)									
2010	0.11	0.38	0.08	0.21	0.21	0.12			
2011	0.09	0.29	0.03	0.17	0.23	0.17			
2011−2010	−0.026 (−23%)	−0.098 (−26%)	−0.052[b] (−61%)	−0.046 (−21%)	0.018[c] (8%)	0.057 (49%)			
Pigment (# samples)	54	36	56	44	47	71	30	12	6
Microplankton (# samples)	28	13	19	27	32	27	10	4	2
Microplankton: probability of a difference 2010 versus 2011 (MANOVA)	$P = 0.006$	$P = 0.115$	$P = 0.011$	$P = 0.001$	$P = 0.028$	$P = 0.097$	$P = 0.477$		
Zooplankton (# of samples)	16	6	18	27	24	20	7	3	1
Zooplankton biomass (μg dry weight L^{-1})[d]									
2010	22.3	5.5	28.6	29.4	34.7	12.2	8.65		
2011	8.51	1.86	15.74	14.03	21.96	8.62	7.3	35.91	5.57
2011−2010	(−62%)	(−66%)	(−45%)[b]	(−52%)[b]	(−37%)	(−29%)	(−16%)		
Regression of log Chl *a* versus log zooplankton									
Intercept	0.79	−3.4[b]	0.97	0.39	0.62	2.54[b]			
Slope	0.80	−0.88	0.97	0.05	0.90[b]	1.12[b]			

Number of phytoplankton and zooplankton samples at each station summed over 2010 and 2011. Temperature data are from satellite (NASA MODIS aqua 11 μm night), all other data are from *in situ* samples.
[a]Only sufficient data for comparison across three seasons: spring, summer and autumn in 2010 versus 2011.
[b]Significant annual difference ($P < 0.05$).
[c]Significant different in at least one season in 2010 relative to same season in 2011 ($P < 0.05$).
[d]Analysis by bootstrap, linear regression and general additive model were all consistent, presented results are from the bootstrap analysis.

blooms. A single depth-integrated picoplankton, phytoplankton and pigment sample was created from up to six equal volume subsamples from 0, 10, 20, 30, 40, 50 m. In addition, two fixed depth pigment samples (typically 20 and 40 m but some variation with station) were also collected at most stations. Biomass, as total chlorophyll *a*, at each station was calculated as the average from all available samples. The larger phytoplankton (>20 μm = microplankton) were analysed using conventional methods (Lund *et al.*, 1958; Hötzel and Croome, 1999); samples were preserved in acid Lugol's solution, settled, identified and enumerated using an inverted light microscope (Olympus IX71). The total number of pigment samples analysed was 356 but this ranged from 6 at Darwin-N_{12} to 71 at Maria-E_{43} (Table I). The smaller plankton (<2 μm) were classified and enumerated by flow cytometry. Triplicate samples of 1 mL were fixed in high grade glutaraldehyde (0.25% final concentration) for 15 min and quick frozen in liquid nitrogen until analysis (Marie *et al.*, 1999). Samples were thawed at $37°$C and 1-μm fluorescent beads (Molecular Probes) were added as an internal standard. The flow cytometer was also calibrated against cultured strains of both *Prochlorococcus* and *Synechococcus*. Samples were analysed using a FACSCANTO II (Becton Dickinson) flow cytometer fitted with a 488-nm laser on high throughput mode at a flow rate of 60 μL min^{-1} for 2 min (Patten *et al.*, 2011). *Prochlorococcus*, *Synechococ*cus and picoeukaryotes were discriminated in scatter plots of red and orange autofluorescence of chlorophyll and the accessory pigment phycoerythrin (Marie *et al.*, 1999).

Pigment processing

Water samples were obtained as above, kept dark and cool (on ice) for up to several hours until filtered. Sample volumes were variable but typically ranged from 1 to 5 L. Pigments were concentrated by filtering onto a glass fibre filter (Whatman GFF, retains particles >0.7 μm), folded into a cryovial and stored in liquid N_2 for ≤ 3 months until extracted. Extraction was into 3 mL of 100% acetone during 15 min of sonication at 40 KHz and 100 Watts at $0°$C, followed by filtration and centrifugation. Concentrations of all pigments were determined from standards (Sigma^{TM} or DHI Denmark). The method used (Van Heukelem and Thomas, 2001) gave partial resolution to chlorophylls c_1 and c_2, and full resolution of monovinyl and divinyl (DV) chlorophylls *a* and *b*, lutein and zeaxanthin. Pigments were assigned to phytoplankton taxa following Jeffrey *et al.* (Jeffrey *et al.*, 1997). The pigment alloxanthin is assigned to cryptophytes as they are considered the source although following ingestion the plastids may be present in a range of other taxa such as *Mesodinium rubrum* and *Dinophysis* species (Raho

et al., 2014; Rial *et al.*, 2013). The *Prochlorococcus* abundance determined by flow cytometry was correlated with the concentration of DV chlorophyll *a* across all samples ($r^2 = 0.57$, $P < 0.0001$) as was *Synechococcus* correlated with zeaxanthin ($r^2 = 0.50$, $P < 0.0001$). Marker pigments were assigned to taxonomic groups following Jeffrey *et al.* (Jeffrey *et al.*, 1997) and normalized against chlorophyll *a*.

Zooplankton

Zooplankton were sampled approximately monthly using a weighted drop net with 100-μm mesh (Heron, 1982). One tow was preserved in formalin and then in the laboratory dried for 24 h at $\sim 60°$C and weighed. A second sample was initially preserved in formalin and subsequently transferred to proponal phenoxitol prior to counting under a dissecting microscope. The spatial and temporal variation in total zooplankton biomass (dry weight) was assessed using a three-way ANOVA with year, station and season as factors. There were sufficient monthly, depth-integrated samples (total 125) from Yongala-E_{19}, Stradbroke-E_{27}, Hacking-E_{34}, Maria-E_{43}, Kangaroo-S_{36}, Esperance-W_{34} and Rottnest-W_{32} for statistical analysis of the seasonal variability and interannual difference between 2010 and 2011. For each of these NRSs, the mean abundance of each zooplankton taxonomic group was calculated for the El Niño period, for the La Niño period and for both periods combined. The statistical significance of the percentage change in average abundance of zooplankton groups from the El Niño period to the La Niña period were estimated using bootstrap analysis, linear regression and a general additive model. The results were consistent but only the bootstrap results are presented.

Statistics (temporal and spatial treatment)

In the southern hemisphere, the winter solstice occurs in late June and, for the purpose of assessing inter-annual variability, the austral year is assumed to commence in July. Therefore, to capture a typical annual cycle of phytoplankton biomass and composition, the 2010 year was defined from 1 July 2009 to 30 June 2010 (hereafter = 2010). The 2011 year was defined from 1 July 2010 to 30 June 2011 (hereafter = 2011). The average monthly Southern Oscillation Index (SOI, from the Australian Bureau of Meteorology http://www.bom.gov.au/climate/current/soihtm1.shtml accessed December 2013) for 2010 was -3.0 ± 9.6 (standard deviation) and significantly different ($P < 0.001$) from average monthly SOI in 2011 of 18.1 ± 8.5. Seasons were defined as conventional austral: June, July August = winter, September, October, November = spring, December, January,

February = summer and March, April, May = autumn. For most stations and parameters, there were at least three samples at approximately monthly intervals in each season. At most NRSs, there were sufficient nutrient, salinity and pigment data available to undertake a two-way (season, year) or three-way (depth, season, year) ANOVA. Graphical representation of remotely sensed data was contoured using running average for temperature and running median for chlorophyll *a* and PP.

Microplankton and zooplankton data were transformed with the fourth-root transformation of the species community matrix followed by the Hellinger transformation (Legendre and Gallagher, 2001) and used in principal component (t-PCA) and redundancy analysis (t-RDA). The relationships between species composition and ENSO were examined with the RDA conditioned on station and constrained by the categorical ENSO variable. The statistical significance of the relationship between species composition and ENSO was tested with permutational multivariate analysis of variance (MANOVA). The community matrix was transformed as for the t-PCA. The analyses performed were a one-way MANOVA on ENSO and a two-way MANOVA on ENSO and station.

RESULTS

Temperature

Over the broad region ($11-44°$S by $112-156°$E) the average temperature fell from 20.85 to 20.81°C during 2011 (Fig. 2A). During the La Niña of 2011, however, the surface seawater along the west coast of Australia was much warmer than the previous El Niño year with mean annual difference of $\sim 2°$C along most of the coast (Fig. 2A). At the west coast NRS at 22, 32 and 34°S, the increases in surface water temperatures during 2011 were 1.65, 1.36 and 0.69°C, respectively (all $P < 0.05$, Table I). Satellite data showed that oceanic waters off the north east of Australia also warmed by up to 1°C in 2011 (Fig. 2A). Most of the remaining east and south coast continental shelf waters had mean surface temperatures that were similar or slightly cooler in 2011 than 2010 (Fig. 2A). In particular, the NRSs along the south coast (Kangaroo-S_{36}) and in the far southeast (Maria-E_{43}) were -0.32 and $-1.04°$C colder, respectively; during the La Niña of 2011 ($P < 0.05$, Table I).
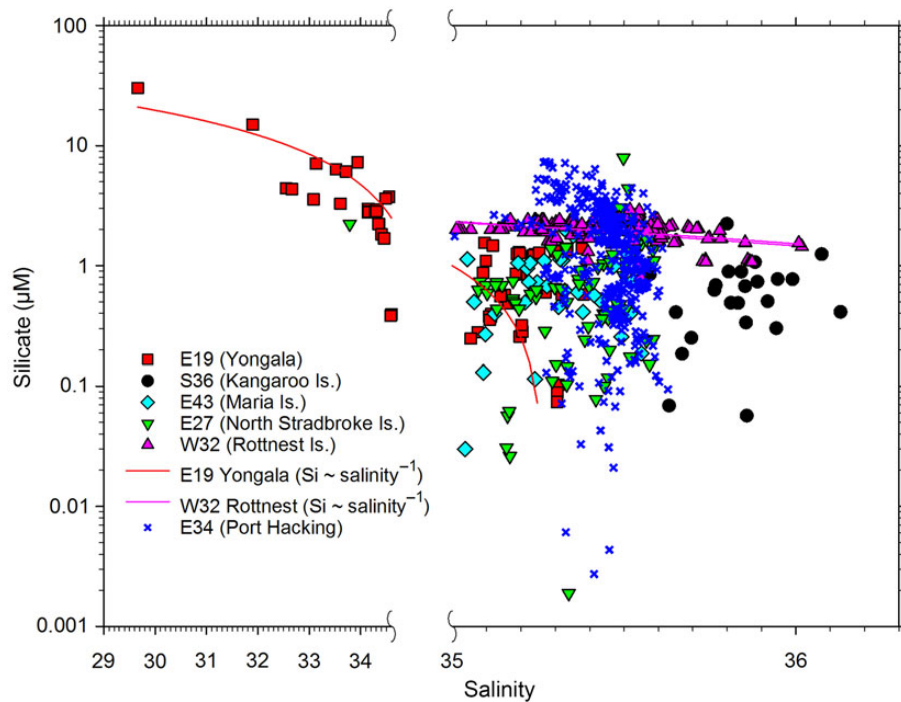
Salinity

There were significant ($P < 0.05$) differences in salinity between 2010 and 2011 at all of the NRSs where there was sufficient data for a three-way ANOVA with year, season and depth (Table I). The average annual decline in salinity across all these coastal stations was -0.157 while the greatest decline was -0.754 on the middle east coast (Yongala-E_{19}) followed by Rottnest-W_{32}>Maria-E_{43}>Stradbroke-E_{27} (Table I). At these four stations, salinities were significantly lower for at least one season in 2011 relative to 2010. The station on the middle south coast (S_{34}) was the only NRS to show a strong increase ($+0.188$, $P < 0.05$) in mean annual salinity in 2011 relative to 2010 (Table I).

Nutrients

There were significant ($P < 0.05$) changes at all stations in the concentrations of silicate between 2010 and 2011 (Table I). Although the relationship between salinity and silicate concentration was not strong across all NRSs, there was a significant negative correlation between the mean annual variation in salinity and the variation in the concentrations of silicate over all stations ($P < 0.005$). The overall relationship was largely determined by the strength of the relationship at Yongala-E_{19} although both Yongala-E_{19} and Rottnest-W_{32} showed significant negative relationships between salinity and silicate concentration ($r^2 = 0.78$, $P < 0.001$, $r^2 = 0.19$, $P < 0.0001$, respectively; Fig. 3). The relatively broad temporal variation in silicate at North Stradbroke-E22, Port Hacking-E_{34} and Kangaroo Island-S_{36} did not have a relationship with salinity and presumably must be determined by changes in water mass rather than nearby riverine inputs. The largest rise in silicate concentrations in 2011 relative to 2010 was at NRS Yongala-E_{19} where the depth averaged annual mean concentration rose ~ 2.5 μM while the surface annual mean in 2011 increased to ~ 7 μM driven by a peak value of 30 μM observed 18 January 2011 and associated with heavy rainfall shortly before the landfall of cyclone Yasi (3 February 2011). Silicate concentrations also rose in 2011 at Rottnest-W_{32}, Yongala-E_{19}, Stradbroke-E_{27} and but fell at Kangaroo-S_{36}, Hacking-E34 and Maria-E_{43} (Table I).

Nitrate concentrations rose in 2011 at five of six stations by an overall mean of 145% and sometimes by considerably more (Table I). Increases were observed on the west coast, south coast and at three of four stations along the east coast. The only station not showing an increase in nitrate in 2011 was Hacking-E_{34}. Further investigation of the Hacking-E_{34} data showed that the surface (0, 10, 20 m) concentrations of nitrate were not significantly different between the long-term ($1953-2005$) mean, 2010 or 2011 (Fig. 4A). It was only at depth that nutrient concentrations in 2011 fell significantly ($P < 0.05$) below those observed in 2010 and the long-term average for this station ($P < 0.05$). On the west coast of Australia at

Fig. 3. Data on silicate and salinity from the National Reference Stations (NRS) with an overall negative relationship between salinity and silicate ($P < 0.005$) and significant individual relationships for E_{19} (Yongala) and W_{32} (Rottnest Island) NRSs.
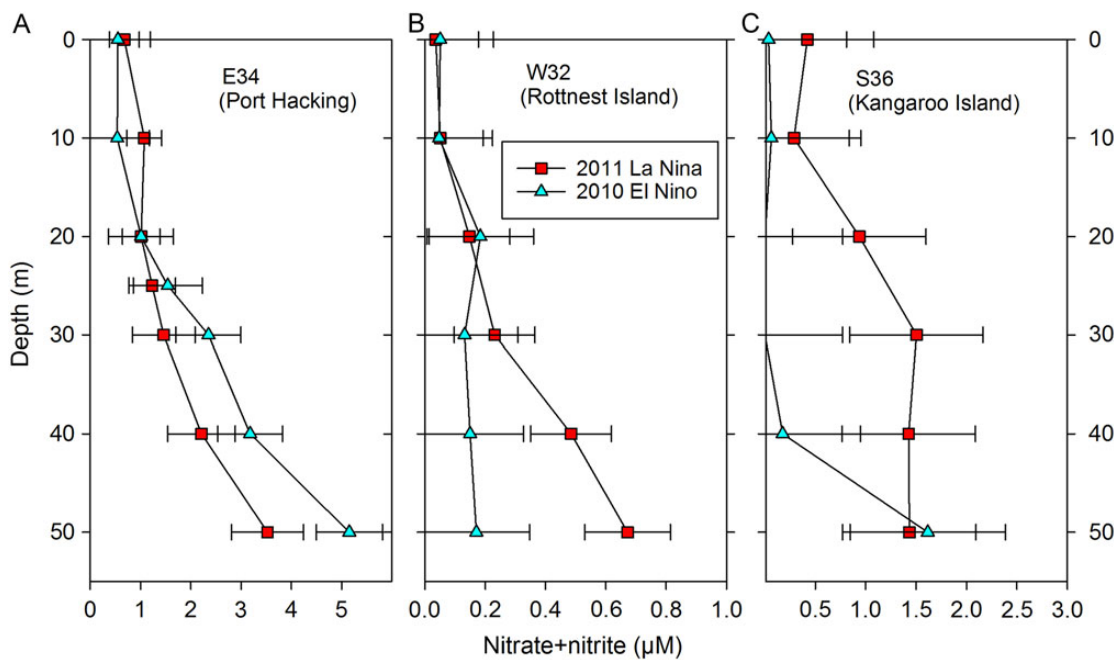
Fig. 4. Relationship between depth and mean annual nitrate concentrations derived from $\sim$ monthly sample in an El Niño year (July 2009 to June 2010) and a La Niña year (July 2010 to June 2011) at three different National Reference Stations [means $\pm$ standard deviation (SD)]. (**A**) E_{34} (Port Hacking NRS at 34.08°S and 151.25°E), (**B**) at W_{32} (Rottnest Island NRS at 32.00°S and 115.41°E), (**C**) at S_{36} (Kangaroo Island NRS at 35.83°S and 136.44°E). The historic means and standard errors are shown for E_{34} (Port Hacking, 1944–2005) and W_{32} (Rottnest Island, 1951–2001).

the Rottnest-W_{32} NRS, the surface concentrations of nitrate also were similar between 2010 and 2011 (Fig. 4B). At depths >30 m; however, there was a marked increase ($P < 0.05$) in nitrate concentrations in 2011 at Rottnest-W_{32} that also exceeded the long-term means for this station at 40 and 50 m. While Rottnest-W_{32} and

Hacking-E_{34} stations are similar in latitude and water depth it seems clear that waters at these two shelf stations had different responses to the 2011 La Niña event in terms of nutrient supply to the euphotic zone; rising on the west coast and falling on the east coast. The largest rise in mean annual nitrate concentration was 0.685 μmol L^{-1} at Kangaroo-S_{36} where nitrate was episodically present much closer to the surface in 2011 than 2010 (Fig. 4C). Unfortunately, the episodic nature of the regional upwelling meant it did not persist through an entire season and this short-term temporal variability (∼monthly) meant it was not statistically significant on a seasonal basis ($P = 0.11$).

Phosphate concentrations rose significantly in 2011 at the four east coast NRSs (Table I). The largest percentage rise was 179% at Yongala-E_{19} but the greatest absolute rise was 0.20 μM was at the most southerly station, Maria-E_{43}, where concentrations during the summer of 2011 were significantly greater ($P < 0.001$) than the summer of 2010.

Regional temporal and spatial patterns in phytoplankton assessed by remote sensing

Based on the 205,248 9×9 km^2 MODIS pixels in the region, the average chlorophyll a concentration around Australia during 2011 was 0.317 ± 0.67 μg L^{-1} during 2011 and ∼3% greater than the average of 0.308 ± 0.54 μg L^{-1} during 2010 (Fig. 2B). Over the 205 248 pixels in the annual data set, the maximum increase during 2011 was ∼7 μg L^{-1} but contouring across the spatial domain showed areas ∼10 000 km^2 where the mean was elevated by 0.1 μg L^{-1} in 2011. The area with the largest absolute increase was in the southern Tasman Sea between Tasmania and New Zealand (Fig. 2B). The increase in phytoplankton biomass in the south Tasman Sea was largely associated with a much stronger austral spring bloom in October 2011 (Fig. 2B inset). In contrast, the phytoplankton biomass in the southern extreme of the Great Australian Bight (GAB) was much lower in late summer 2011 with no evidence of the bloom that occurred at this time and location in 2010 (Fig. 2B inset).

## Spatial and temporal variation in phytoplankton assessed by pigments at the NRS

In general, the NRS Maria-E_{43} (0.66 ± 0.06 μg L^{-1}) had the highest in $situ$ chlorophyll a followed by the NRS Hacking-E_{34} (0.51 ± 0.06 μg L^{-1}) while the lowest chlorophyll a concentrations were found at Kangaroo-S_{36} (0.24 ± 0.07 μg L^{-1}, Fig. 6). Monthly samples from

Kangaroo-S_{36} showed a significant increase in chlorophyll a in 2011 relative to 2010 (Fig. 6); similar to the result from the remotely sensed ocean colour data. Kangaroo-S_{36} was the only NRS with a statistically significant change in measured, in $situ$ mean annual chlorophyll a concentrations where the concentration rose from 0.078 ± 0.049 to 0.38 ± 0.043 μg L^{-1} or by 487%. No other station had a statistically significant rise in annual chlorophyll a concentration during 2011 although concentrations were greater at Yongala-E_{19} (17%), Hacking-E_{34} (32%), Maria-E_{43} (27%) and Esperance-W_{34} (37%) in 2011 (Fig. 6).

Phytoplankton assessed by pigments at the NRS

Low latitude sites tended to have more zeaxanthin (primarily $Synechococcus$) than higher latitude sites with the greatest relative abundance found at Yongala-E_{19}, followed by Darwin-N_{12}, Ningaloo-W_{22} and Stradbroke-E_{27} (Fig. 5). Similarly, divinyl chlorophyll a ($Prochlorococcus$) was a greater portion of the pigments at Yongala-E_{19} and W_{22} relative to stations further south. Over all sites fucoxanthin was the major accessory pigment with an average ratio of 0.203 (e.g. 0.203:1 fucoxanthin:Chl a) and the lowest relative variability across sites with a coefficient of variation (CV) of 17%. NRS Stradbroke-E_{27} had both the greatest proportion of fucoxanthin (0.27) and 19-butanoyloxyfucoxanthin (0.094) suggesting a phytoplankton community dominated by diatoms and pelagophytes (Fig. 6 and Supplementary data, Table SI). Although 19-hexanoyloxyfucoxanthin (Haptophytes) was relatively most abundant at Rottnest-W_{32} (0.22), it was also quite ubiquitous with an average ratio of 0.15 and a CV of only 35% across all stations. NRS Kangaroo-S_{36} had nearly double the relative amount of peridinin (photosynthetic dinoflagellates, 0.08) compared with the next highest NRS (Esperance-W_{34}, 0.04), while the average for all sites was only 0.02. The NRS Kangaroo-S_{36} was also the only station with four dinoflagellate genera in its top 13 by biovolume ($Noctiluca$ > $Ceratium$ > $Gyrodinium$ ∼ $Protoperidinium$); with pigments and cells counts suggesting this region along the south coast of Australia has more dinoflagellates (Supplementary data, Table SI). Maria-E_{43} had the greatest relative concentrations of chlorophyll b, prasinoxanthin and neoxanthin suggesting more Chlorophytes and Prasinophytes possibly Euglenophytes (all "greens").

Based on pigments, there were significant changes in the phytoplankton community composition between 2010 and 2011 but there were insufficient samples to test for these inter-annual differences at Ningaloo-W_{22} and Darwin-N_{12}. At all five remaining stations between 20 and 40°S, DV chlorophyll a ($Prochlorococcus$) increased in
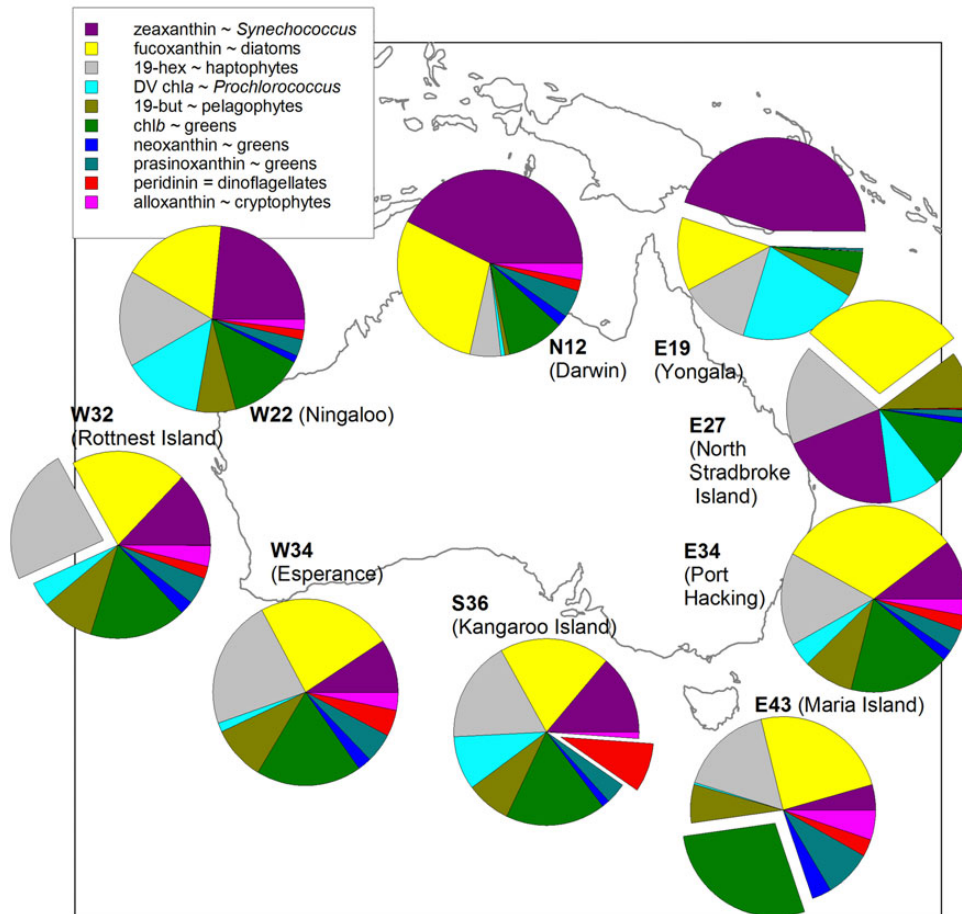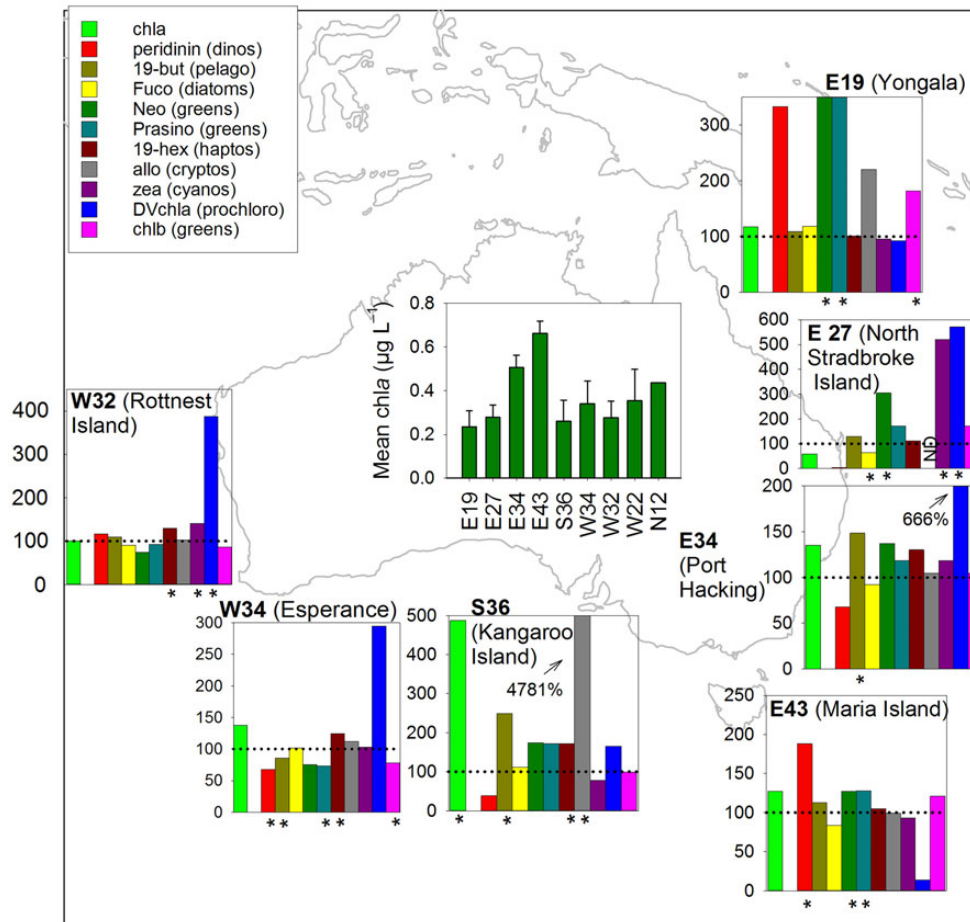
Fig. 5. Phytoplankton marker pigments from approximately monthly samples, normalized to chlorophyll *a* and averaged from July 2009 to June 2011 plotted at the approximate locations of the nine national reference stations around Australia (sections are separated where these were clearly the dominant location for particular pigments). Absolute values for marker pigment:chlorophyll *a* ratios are given in Supplementary data, Table SI.

2011 (Fig. 6). The largest increases were at Hacking-E_{34} (666%), Stradbroke-E_{27} (571%), Rottnest-W_{32} (387%) and Esperance-W_{34} (295%). At Esperance-W_{34} and Hacking-E_{34}, the large percentage increases reflect the near absence of this pigment in 2010. This temporal variability also meant only the large increases in DV chlorophyll *a* (>300%) at Rottnest-W_{32} and Stradbroke-E_{27} were statistically significant.

Broad geographic patterns of change between 2010 and 2011 were also seen in two other pigments. The pigment 19-hexanoyloxyfucoxanthin increased at Rottnest-W_{32}, Esperance-W_{34} and Kangaroo-S_{36}, all stations in the south or south west of Australia. The pigment neoxanthin increased significantly at Yongala-E_{19}, Stradbroke-E_{27} and Maria-E_{43} plus Hacking-E_{34} (NS); basically along the entire east coast of Australia. Other pigments that showed significant inter-annual variability at one or more stations included: peridinin, 19-butanoyloxyfucoxanthin,

fucoxanthin, prasinoxanthin, alloxanthin, zeaxanthin and chlorophyll *b*. For these pigments, the temporal change was not very widespread. For example, peridinin (photosynthetic dinoflagellates) increased at Maria-E_{43} and decreased at Esperance-W_{34} (Fig. 6). The pigment 19-butanoyloxyfucoxanthin declined at Esperance-W_{34} and rose at Kangaroo-S_{36} and Hacking-E_{34}. The main marker pigment for diatoms, fucoxanthin, did not show any increase at any station in 2011 with only a significant decline at Stradbroke-E_{27}. Prasinoxanthin responses were very similar to those of neoxanthin with significant increases at Yongala-E_{19} and Maria-E_{43} in 2011. Alloxanthin (cryptophytes or their grazers and predators) had a very large 4781% increase in relative concentration at Kangaroo-S_{36} in 2011. Zeaxanthin increased at the mid-latitude NRS Stradbroke-E_{27} and Rottnest-W_{32} during 2011. Chlorophyll *b* concentrations were greater at Yongala-E_{19} in 2011 and declined at Esperance-W_{34}.

Fig. 6. The percentage change in phytoplankton marker pigments (normalized to chlorophyll *a*) between an El Niño year (July 2009 to June 2010) and a La Niña year (July 2010 to June 2011) at Australia's national reference stations. Pigments with asterisk were statistically different between 2010 and 2011 (ANOVA, *P* < 0.05). Centre panel shows averaged chlorophyll *a* concentration at each national reference station from July 2009 to June 2011.

Microplankton assessed by light microscopy at the NRS

The microplankton species observed at the NRS and counted under the light microscope were dominated by diatoms, (53% of total biovolume) followed by dinoflagellates (40%) and ~7% other taxa (Supplementary data, Table SI). The dinoflagellate *Noctiluca scintillans* was the dominant species observed (37% of total biovolume) followed by *Guinardia* (14%), *Rhizosolenia* (10%), *Proboscia* (5.3%), *Cerataulina* (3.2%), *Leptocylindrus* (2.8%), *Pseudosolenia* (2.4%), *Dactyliosolen* (2.2%) and other taxa at <1% of total biovolume (Supplementary data, Table SI). There were significant effects of location (NRS) and year on the species observed at the NRS (MANOVA, *P* < 0.001) for Rottnest-W_{32}, Hacking-E_{34}, Stradbroke-E_{27} and Yongala-E_{19} (Table I). The three taxa most associated with 2010 were *Ceratium* > *Chaetoceros* (20–30 µm) > *Dactyliosolen fragilissimus*, while the three taxa most associated with 2011 were *Scrippsiella* > *Pseudo-nitzschia* >

Thalassionema (RDA, data not shown). Across all the NRS in 2011, there was an average 40% decline in abundance of *Ceratium* species that was most acute at Hacking-E_{34}. *Scrippsiella* species abundances also declined in 2011 at Hacking-E_{34} (−78%) but rose an average of 230% at the other NRS, particularly Kangaroo-S_{36} (+460%). Generally, centric diatoms were more associated with El Niño, whereas pennate diatoms were more associated with La Niña (RDA, data not shown). Of the four NRS with a significant difference in microplankton between 2010 and 2011, the largest increase in pennate diatoms was at Yongala-E_{27} where they increased 307% (*P* = 0.067).

Picoplankton assessed by flow cytometry at the NRS

Densities of picoplankton determined by flow cytometry indicated that the mean annual concentration of *Prochlorococcus* was significantly greater along the east coast

of Australia in 2011 relative to 2010 at Stradbroke-E_{27} and Hacking-E_{34} (Fig. 7). Similarly, at the mid-latitude station Rottnest-W_{32} along the west coast, *Prochlorococcus* abundances were greater in 2011. Rottnest-W_{32} also saw an increase in *Synechococcus* as did Maria-E_{43} and Yongala-E_{19} in 2011 relative to 2010.

Primary production

For the model domain (Fig. 2C), there was a 14% decrease in the annual PP between 2010 and 2011. This overall decrease in PP was mostly determined by a strong reduction off the northwest of Australia while the majority of the domain was neutral to positive. Along the east

coast rises in PP were estimated for areas containing the NRS Yongala-E_{19}, Hacking-E_{34} and Maria-E_{43}, and these were consistent with *in situ* increases in chlorophyll *a* observed at these stations (Fig. 6). There was a strong positive increase in PP off the west coast between 30 and 35°S that weakened between 35 and 45°S.
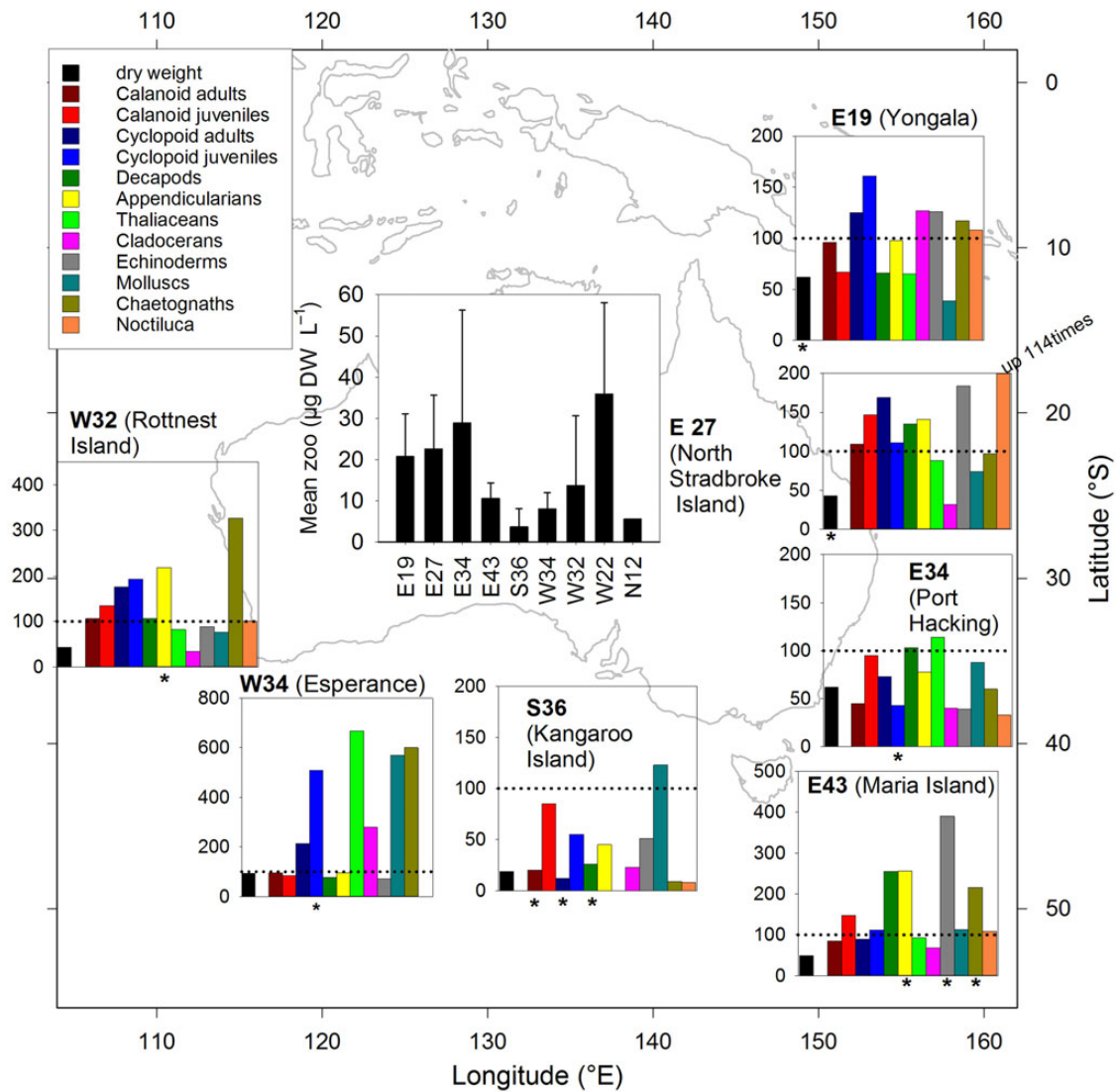
Zooplankton at the NRS

Across all stations and all years (2008–2014, $n = 243$), the $\log_{10}$ dry weight of zooplankton was a significant linear, negative function of latitude ($P < 0.001$) and year ($P < 0.001$) and a positive function of $\log_{10}$ chlorophyll *a* ($P < 0.005$) with an overall $r^2 = 0.235$ ($P < 0.001$). At all
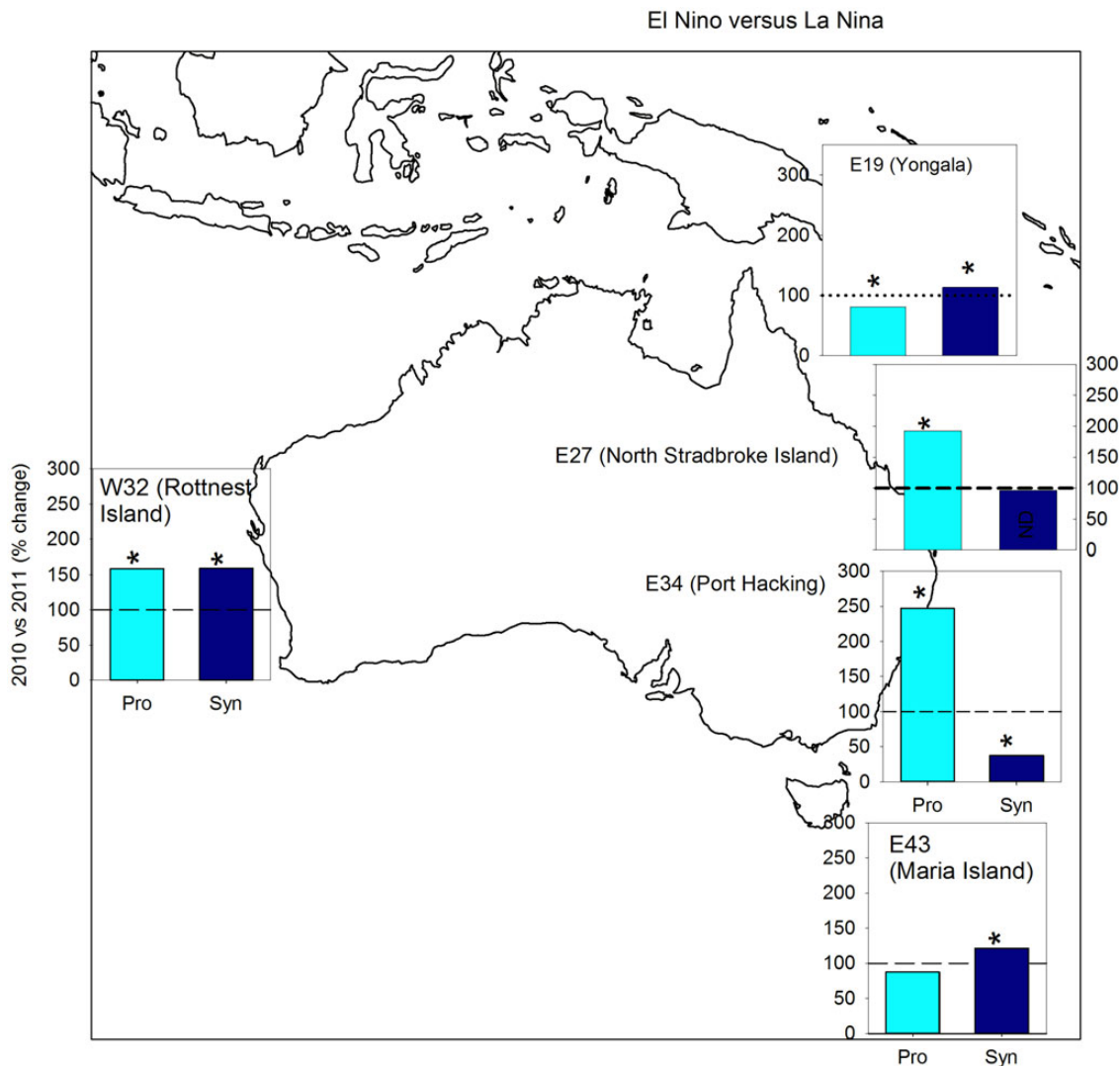
Fig. 7. The percentage change in *Prochlorococcus* and *Synechococcus* between an El Niño year (July 2009 to June 2010) and a La Niña year (July 2010-June 2011) at five national reference stations (determined by flow cytometry from approximately monthly samples). Bars marked with asterisk are significantly different between years.

stations except Kangaroo-S_{36}, the relationship between $\log_{10}$ chlorophyll a and $\log_{10}$ zooplankton biomass was positive (Table I). The biomass for each station, year and season was estimated from a regression model of (log) biomass on station, season and ENSO, with interactions between station and season and between station and ENSO. The average, overall zooplankton biomass declined from 17.5 to 8.2 µg DW L^{-1} (-53%) across these seven stations ($P = 0.0047$). At all of these seven stations, the biomass of zooplankton was greater in the El Niño year than the La Niña year although this was statistically significant only at Yongala-E_{19} and Stradbroke-E_{27} (Table I and Fig. 8).

Across all stations, $\sim 20\%$ of the variation in zooplankton community composition was associated with location (station), while only 2% was identified as inter-annual variation. The species that were more abundant in 2010 (El Niño) included *Calocalanus pavo* and *Temora turbinata*. Species generally associated with 2011 (La Niña) included *Clausocalanus farrani/jobei*, *Mecynocera clausi* and *Canthocalanus pauper* (RDA, data not shown). At the individual NRS, statistically significant changes in the abundance of individual species or the major taxonomic groups during the 2011 La Niña event were relatively rare (Fig. 8 and Supplementary data, Table SII). Of the major taxonomic groups identified and on the west coast

Fig. 8. Zooplankton at Australia's national reference stations. Middle panel: Average biomass 2010 and 2011 at each station. Error bars are standard deviations. Other panels: Inter-annual percent differences in zooplankton biomass between an El Niño year (July 2009 to June 2010) and a La Niña year (July 2010 to June 2011) at the IMOS National Reference Station locations around Australia (see Fig. 2A and Table I for more precise locations).

of Australia only appendicularians (Rottnest-W$_{32}$) and cyclopoid juveniles (Esperance-W$_{34}$) increased (Fig. 8 and Supplementary data, Table SII) in 2011. On the east coast of Australian at Maria-E$_{43}$ appendicularians, echinoderms and chaetognaths also increased (Fig. 8) during 2011. Significant reductions in zooplankton biomass were found at Kangaroo-S$_{36}$ for cyclopoid adults, calanoid adults and decapods in 2011 (Supplementary data, Table SII). The only other NRS to record a decrease was Hacking-E$_{34}$ where cyclopoid adults also declined in 2011. Considerable inter-annual variability in biomass of many taxonomic groups was evident at most stations but the statistical power was low.

DISCUSSION

Based on the 70-year record of warming observed at three NRSs (Thompson *et al.*, 2009), the poleward flowing currents on the east and west coasts of Australia are transporting more heat to higher latitudes, pushing tropical water (Hill *et al.*, 2011) and carrying tropical species southward (Johnson *et al.*, 2011; McLeod *et al.*, 2012). Southward transport by the west coast boundary current (Leeuwin) increases considerably during a La Niña event (Morrow and Birol, 1998; Feng *et al.*, 2003). There is a transport response in the EAC associated with La Niña but it is lagged by 9 months to 3 years (Holbrook *et al.*, 2011). The north east coast of Australia is on the edge of the Pacific warm pool containing some of the warmest ocean water on the planet (Wang and Enfield, 2001). During La Niña, these warm waters move towards Australia and the average surface temperature of the surrounding ocean may rise >1°C as far as 25°S (Kim *et al.*, 2012); as was observed in 2011. In a driver → state → response conceptual model (Rapport and Friend, 1979) where La Niña is the driver, the observed altered states included currents, temperature, salinity, stratification, irradiance and nutrients while the responses were phytoplankton and zooplankton. Observations at the nine national reference stations around Australia showed significant differences in temperature, salinity, nutrients, plus the biomass and composition of phytoplankton and zooplankton communities between 2010 and 2011; ostensibly in response to the shift from El Niño to La Niña. Based on remote sensing and across the entire Australian region, 2011 was only modestly different from 2010 with the average temperature declining 0.2%, surface chlorophyll *a* up 3% and modelled PP down 14%. Other changes included the poleward shift in tropical communities, the east coast decrease in salinity, increase in nutrients and taxa with chlorophyll *b* while the southwest had a rise in the proportion of 19-hexoyloxyfucoxanthin.

These sub-regional changes in environmental conditions and ecology are discussed further below.

WEST COAST

During the La Niña of 2011, the west coast of Australia was broadly warmer than in 2010. Contrary to La Niña events along the west coast of North America (Schwing and Moore, 2000), warming along the west coast of Australia is the normal La Niña response (Feng *et al.*, 2008) although the strength of this warming in 2011 was unprecedented (Feng *et al.*, 2013). La Niña events typically strengthen the southward flow of the LC (Morrow and Birol, 1998; Feng *et al.*, 2003). In the northwest of Australia, a previous La Niña event in 1999 was linked to a phytoplankton biomass and PP decline (Furnas, 2007). A reduction in SST and PP plus localized reductions in chlorophyll *a* were all indicated by remote sensing and model results during the La Niña event of 2011. The reduction in chlorophyll *a* and PP is consistent with a thicker layer of LC water acting to depress the nutricline in this region (Hanson *et al.*, 2005; Furnas, 2007). In 2011, there was a strong increase in *Prochlorococcus* and *Synechococcus* at the mid-latitude Rottnest-W$_{32}$ NRS on the west coast of Australia. For both taxa, this is consistent with the observed warmer, more tropical conditions.

Along the west coast of Australia, there is an annual, shelf-scale phytoplankton bloom that coincides with the intensification of the LC (Koslow *et al.*, 2008). There, the phytoplankton biomass is positively associated with La Niña and correlated with the Southern Oscillation Index (Thompson *et al.*, 2009). Contrary to predictions for a warmer world (e.g. Bopp *et al.*, 2005), silicate and nitrate were more concentrated in the euphotic zone during 2011 at depths between 20 and 50 m. The very unusual, positive co-variation of temperature and nutrients is evident in the ~70 year time series from Rottnest-W$_{32}$ on the west coast (Thompson *et al.*, 2009). This co-variation originates with the entrainment and southward flow of nitrate at the base of the warm, relatively fresh and silicate rich LC (Thompson *et al.*, 2011a). The increase in *Synechococcus* at this latitude may reflect the increased nitrate supply deep in the euphotic zone (Campbell *et al.*, 1997; Hickman *et al.*, 2010). A La Niña event also produces a greater number of eddies (Fang and Morrow, 2003) often as pairs; one warm and one cold core eddy. The cold core eddies can be dominated by *Prochlorococcus* (Waite *et al.*, 2007) while the warm core eddies can be dominated by large diatoms, pelagophytes and coccolithophorids (Thompson *et al.*, 2007) that are transported offshore and increase PP in the south eastern

Indian Ocean (Moore *et al.*, 2007) at the latitudes between 30 and 40°S.

EAST COAST

The surface nutrient concentrations along the east coast of Australia are extremely low (Condie and Dunn, 2006) with low silicate previously reported to limit diatom blooms (Grant, 1971). Between the La Niña of 1999 and 2008, during the millennium drought and the long period of prevailing El Niño conditions, diatoms declined significantly along Australia's southeast coast (Ajani *et al.*, 2014). Although the east coast has low surface nutrients, the mean annual nitrate concentration at 50 m on the east coast (Hacking-E_{34}) was 5.15 μmol L^{-1} or $\sim$25 times greater than the west coast (Rottnest-W_{32}). This shallow nutricline along the south east coast has a strong influence on the pelagic ecology of this region with sporadic upwelling induced phytoplankton blooms (Hallegraeff and Reid, 1986, Armbrecht *et al.*, 2014) and a much larger annual spring bloom relative to the west coast (Thompson *et al.*, 2011b). A more productive east coast was observed throughout the 2010 and 2011 ENSO with an average of 83% more chlorophyll *a* and 66% more diatoms at the Hacking-E_{34} than the Rottnest-W_{32} NRS. The shelf station (Yongala-E_{19}) is nearest to the larger monsoonal and tropical rivers in the NE of Australia and recorded the largest decreases in salinity and quite considerable increases in silicate, phosphate and nitrate in 2011. These are consistent with observed impacts of greater precipitation and flow into many receiving water bodies (e.g. Mallin *et al.*, 1993; Paerl *et al.*, 2001; Tréguer and De La Rocha, 2013). All four NRS along the east coast of Australia recorded increases in phosphate in 2011 but changes to nitrate concentrations were spatially more variable.

The normal pattern of proportionally more of the smaller celled taxa such as *Prochlorococcus* and *Synechococcus* at low latitudes is easily visible across the four NRS along the east coast. This latitudinal gradient in phytoplankton is also evident off the continental shelf around Australia (Thompson *et al.*, 2011b) and elsewhere (van de Poll *et al.*, 2013) although few studies of equivalent spatial extent have more than a single snapshot in time. During 2011, as measured by cell counts and pigments, *Prochlorococcus* increased significantly at both east coast, mid-latitude NRS (27 and 34°S). During La Niña periods, the Pacific warm pool significantly expands the tropical nature of the waters offshore of north east Australia (Philander, 1990; Kim *et al.*, 2012 favouring a deeper phytoplankton community including *Prochlorococcus* that is well adapted to low light and a more stable water column (Chisholm *et al.*, 1988).

Chlorophyll *b* containing taxa (greens) showed a strong increase from 19 to 43°S along the east coast of Australia. Chlorophyll *b* has been reported to peak at these mid-latitudes (e.g. Wright *et al.*, 1996; Rousseaux *et al.*, 2013). The La Niña event of 2011 broke the "Millennium Drought" for eastern Australia (Van Dijk *et al.*, 2013) including the landfall of a very large cyclone in the northeast of the continent resulting in lower salinities and higher nutrients in the vicinity. The increase in "greens" along the east coast was associated with a reduction in salinity is a worldwide phenomenon (Thompson *et al.*, 2015). Within water bodies, there is often a tendency for Chlorophytes to be more abundant during oligohaline periods or to increase along a gradient of declining salinity (e.g. Hall *et al.*, 2013). Similarly, a 307% increase in pennate diatoms at the Yongala-E_{19} NRS during 2011 may reflect the local decline in salinity and increase in silicate (Lehman, 2000). A decline in salinity and an increase in nutrient supply are hypothesized to be the primary drivers for an increase in Chlorophytes, Prasinophytes and pennate diatoms during the La Niña of 2011.

Further offshore during 2011, the Tasman Sea was characterized by cooler average temperatures, greater standing stocks of chlorophyll *a* during spring (c.f. Kelly *et al.*, 2015) and greater PP suggesting enhanced vertical mixing throughout the preceding winter; similar to La Niña responses elsewhere (Behrenfeld *et al.*, 2006; Rousseaux and Gregg, 2012). The temporal variability in PP within the southern Tasman Sea has been linked to westerly winds (Harris *et al.*, 1991) and the relative influence of the EAC and the sub-tropical front (STF) (Kelly *et al.*, 2015). The relative contribution of ENSO and the southern annual mode (SAM) to primary production in the Tasman Sea will require a longer time series to resolve.

SOUTHWEST

The third major change in phytoplankton during 2011 was the increase proportion of 19-hexanoyloxyfucoxanthin in the southwest of Australia. Normally, in the austral summer, there is a coccolithophorid bloom along the STF that extends from the east coast of South America, below Africa and Australia and past New Zealand (Balch *et al.*, 2011). This summer bloom is normally found at the southern extent of the GAB but in 2011 this region was much lower in chlorophyll *a* than during 2010. It is hypothesized that, during 2011, the STF was closer to Australia. The location of the STF shows significant inter-annual variability (Kazmin and Rienecker, 1996; Graham and De Boer, 2013) with its position varying by hundreds of kilometres in the GAB (Schodlok *et al.*, 1997; Tomczak *et al.*, 2004). The

reduction in summer phytoplankton biomass in the southern extreme of the GAB at $>40°$S with an increase in 19-hexanoyloxyfucoxanthin at three southwest NRS suggests the "great calcite belt" was closer to Australia during the La Niña event of 2011.

SOUTH

The greatest observed *in situ* increase in phytoplankton biomass was at the NRS Kangaroo-S$_{36}$. This NRS also experienced intermittently increased nutrient concentrations during 2011. The Kangaroo-S$_{36}$ NRS is downstream of the Bonney Upwelling; one of the very few regions in Australia that is known for its wind driven and Ekman transport or conventional upwelling (Kämpf *et al.*, 2004; McClatchie *et al.*, 2006). Enhanced chlorophyll *a* has been reported to lag the end of an El Niño event by ∼6 months (Middleton *et al.*, 2007). The dinoflagellate community changed in 2011 with an increase in peridinin, a 460% increase in *Scrippsiella* spp. and 82% decline in *Ceratium* spp. At this NRS, the zooplankton biomass was also reduced in 2011 with lower abundances of adult forms of copepods and cyclopoids. As the only NRS to show an inverse trend between chlorophyll *a* and zooplankton biomass, we speculate that the young age of this upwelling water had not yet allowed a cohort of copepods or cyclopoids to develop. The shift from *Ceratium* to *Scrippsiella* is also consistent with increased mixing (Smayda and Reynolds, 2001). Thus, the localized increase in chlorophyll *a* during 2011 would seem to be a result of both bottom up forcing (more nutrients) and less grazing.

La Niña events along the west coast of America off Peru (Ayòn *et al.*, 2008) and California (Hayward, 2000; Marinovic *et al.*, 2002) tend to increase upwelling, phytoplankton and zooplankton whereas there was a 54% decline in zooplankton biomass around Australia during the La Niña of 2011. For Australia, the most consistent reductions in zooplankton were observed in the northeast of the continent. This region is influenced by the increasing temperature and size of the western Pacific warm pool during La Niña events (Philander, 1990; Kim *et al.*, 2012). La Niña conditions create more tropical pelagic habitat throughout the tropical western Pacific extending to the north east of Australia. These conditions appear to result in more tropical plankton and reduced the macro-zooplankton community. Around Australia the strong correlation between monthly chlorophyll *a* and zooplankton suggests the timing and magnitude of seasonal blooms are important in the transfer of biomass from phytoplankton to zooplankton. This strong link at short time scales implies a longer time series with multiple events may be necessary to statistically assess the effects of La Niña events. For zooplankton, only a few specific

responses could be conceptually linked to a known La Niña driver. In this case, the decline of the copepod *T. turbinata* during 2011 is consistent with other reports of it being less abundant under lower salinity conditions (Lopes *et al.*, 1998).

We conclude that mean annual temperature is likely to be a poor predictor of planktonic ecology in coastal or temperate ecosystems. The role of changing temperature in determining oceanographic currents, winds, precipitation, mixed layer depth, stratification intensity and nutrient supply will impact more on planktonic ecology. For many other species, it is not yet possible to predict whether they will be winners or losers (e.g. Hallegraeff, 2010). We suggest that observations from ecosystems with strong inter-annual variability in climatic drivers provide the best possible laboratory to study and predict the ecology of the future ocean.

SUPPLEMENTARY DATA

Supplementary data can be found online at http://plankt.oxfordjournals.org

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