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Analysis of southeast Australian zooplankton observations of 1938–42 using synoptic oceanographic conditions

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ABSTRACT

The research vessel *Warreen* obtained 1742 planktonic samples along the continental shelf and slope of southeast Australia from 1938–42, representing the earliest spatially and temporally resolved zooplankton data from Australian marine waters. In this paper, *Warreen* observations along the southeast Australian seaboard from 28°S to 38°S are interpreted based on synoptic meteorological and oceanographic conditions and ocean climatologies. Meteorological conditions are based on the NOAA-CIRES 20th Century Reanalysis Project; oceanographic conditions use *Warreen* hydrological observations, and the ocean climatology is the CSIRO Atlas of Regional Seas. The *Warreen* observations were undertaken in waters on average 0.45 °C cooler than the climatological average, and included the longest duration El Niño of the 20th century. In northern New South Wales (NSW), week time-scale events dominate zooplankton response. In August 1940 an unusual winter upwelling event occurred in northern NSW driven by a stronger than average East Australian Current (EAC) and anomalous northerly winds that resulted in high salp and larvacean abundance. In January 1941 a strong upwelling event between 28° and 33°S resulted in a filament of upwelled water being advected south and alongshore, which was low in zooplankton biovolume. In southern NSW a seasonal cycle in physical and planktonic characteristics is observed. In January 1941 the poleward extension of the EAC was strong, advecting more tropical tunicate species southward. Zooplankton abundance and distribution on the continental shelf and slope are more dependent on weekly to monthly timescales on local oceanographic and meteorological conditions than continental-scale interannual trends. The interpretation of historical zooplankton observations of the waters off southeast Australia for the purpose of quantifying anthropogenic impacts will be improved with the use of regional hindcasts of synoptic ocean and atmospheric weather that can explain some of the physically forced natural variability.

1. Introduction

The first recorded observations of zooplankton off southeast Australia came from a 'dipping net' deployed from a small boat 1–2 leagues (1 league = 5.556 km) offshore of Murramarang Beach (35°31′S, 150° 24′E, 30 km north of present day Bateman's Bay) on the 23 April 1770 by Joseph Banks (Beaglehole, 1963). Banks found the colonial and solitary form of the ubiquitous salp *Thalia democratica* (originally designated *Dagysa gemma* and *cornuta*, respectively), the larger salp *Thetys vagina* (originally designated *Dagysa strumosa*), a bluebottle (*Physalia physalis*), a jellyfish (*Aequorea forskalea*), a nudibranch (*Glaucus atlanticus*) and a hydrozoan (*Velella velella*). Later, on the 25 April off Bulli (34°20′S, 150°55′E) close to sunset, 'myriads' of *T. democratica* were observed in 'several brown patches'.

After Bank's observations there was a large number of intermittent identifications of planktonic species in the waters off southeast Australia, the history of which is detailed by Dakin and Colefax (1940). The first quantification of plankton as part of a sampling program was undertaken off Sydney Heads in 1931–32 (Dakin and Colefax, 1933), although quantification is described as comparative only.

The earliest comprehensive set of quantitative zooplankton observations off southeast Australia were undertaken between May 1938 and July 1942 (Fig. 1) from the Council for Scientific and Industrial Research (CSIR) research vessel *Warreen* (Thompson and Kesteven, 1942; CSIRO, 1951a, b). The M.V. *Warreen* represented a significant advance over the sail vessels used in earlier plankton studies (Dakin and Colefax, 1940). The cruises also included extensive physical oceanographic measurements that are archived in the World Ocean Database and hundreds of unpublished fisheries observations.

From 1945 to the present day there have been a number of zooplankton sampling programs that have quantified a greater

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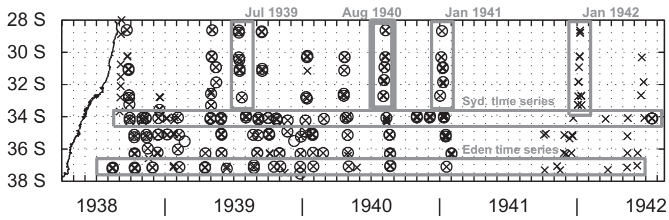

Fig. 1. Spatial and temporal coverage of the *Warreen* sampling on the NSW coast. × —physical observations; ○ —plankton observations using a vertical haul from 50 m to the surface of the N70 net. Multiple stations on a zonal (constant latitude) transect cannot be distinguished and appear as bolder markers. Minor ticks on the *x*-axis delineate months. The grouped observations for which regional oceanographic processes are considered are indicated by a grey box.

range of organisms (Kott, 1957; Tranter, 1962) for a longer period (Kott, 1957) or been part of more intensive process studies (Tranter et al., 1983; Griffiths and Wadley, 1986; Dela-Cruz et al., 2002) than the *Warreen* cruises. Nonetheless, the zooplankton observations on the *Warreen* cruises provide a unique data set because of (1) the detailed physical observations undertaken at each biological sampling location, (2) the total number of stations was large relative to more recent programs, and (3) the focus, almost 70 years ago, on gelatinous zooplankton whose abundance appears to be increasing globally as a result of human-induced stresses such as fishing, eutrophication, and climate change (Hay, 2006; Richardson et al., 2008).

The 1938–42 *Warreen* cruises sampled stations along the southeast coast of Australia, extending from the southern Great Barrier Reef, along the New South Wales (NSW) and Victorian coasts to the Spencer Gulf, and a few stations on the northern and eastern coasts of Tasmania (CSIRO, 1951a, b). In total 444 stations were sampled. The *Warreen* plankton observations have provided important taxonomic (Thomson, 1947; Thompson, 1948; Zeidler, 1998) and ecological (Thompson and Kesteven, 1942; Sheard, 1953; Wood, 1954) insights for the waters off southeast Australia. The observations also provide snapshots of the zooplankton community under a range of environmental conditions before the acceleration of warming in the second half of the 20th century.

The works of Thomson (1947), Thompson (1948) and Sheard (1964) considered the interaction of physical processes and planktonic observations. Given limited knowledge of the oceanic conditions of the waters off southeast Australia they analysed physical–biological interactions on yearly and continental time-scales. However, it is mesoscale variability that dominates the southeast Australian continental shelf. Ridgway et al. (2008) found the EAC cumulative transport off Sydney from the coast to 153°E varied between −20 and 20 Sv on time-scales of 10 days, but only between −2 and 10 Sv (Fig. 16 of Ridgway et al., 2008) on interannual (2-year) timescales. The waters off northern NSW, southern NSW, Tasmania and in Bass Strait and Spencer Gulf are also now recognised to have different origins and forcing processes (for example Schiller et al., 2008). The emphasis of early studies on yearly and continental time-scales misses the primary physical forcing of the zooplankton communities.

The emphasis of this paper is the consideration of physical forcing of planktonic populations at the regional scales of tens to hundreds of kilometres and days to weeks that early scientists did not have the opportunity to investigate. In particular, the regional perspective distinguishes between the northern New South Wales (NSW) coast (28°−32°30′S) and the southern NSW coast (32°30′−38°S). The northern NSW coast is strongly influenced by the EAC and the location of its separation from the coast (Roughan and Middleton, 2002). The southern NSW coast is most strongly affected by the mesoscale eddy field that is spawned after EAC separation (Tranter et al., 1986). The eddy field can produce a strong poleward extension of the EAC along the southern NSW coast, or, alternatively, direct the EAC eastward forming the Tasman Front Jet (Baird et al., 2008). A strong Tasman Front Jet is often associated with northward flow of cooler Tasman Sea water along the continental shelf. The regional perspective must necessarily also consider the time of year and the wind field, particularly as they affect coastal upwelling processes.

In this paper, synoptic regional oceanography is used to interpret zooplankton observations from the NSW coast in 1938–42. These analyses provide an improved understanding of the physical forcing of the pelagic ecosystem at the time of the *Warreen* cruises, and introduces the possibility of comparing observations in different years, but under similar synoptic conditions, as a means of investigating for long term changes in zooplankton populations.

2. Methods

The physical data collected during the *Warreen* cruises have been included in the National Oceanic Data Center's World Ocean Database 2005 (WOD05) and the CSIRO Atlas of Regional Seas (CARS). Station details such as latitude, longitude, day of sampling, and the temperature, salinity and depth of each measurement have been extracted from the WOD database (443 stations), which themselves are based on the CSIRO Oceanographic Station Lists 1 & 2 (CSIRO, 1951a, b). The time of day of each cast was not recorded in the technical reports of the cruise, and has been obtained from the original shipboard technical logs of the *Warreen* held in the National Archives of Australia. The zooplankton biovolume, dominant organism and taxonomic counts were obtained from the CSIRO Oceanographic Station Lists 1 & 2.

A subset of the *Warreen* data has been digitised and archived at the CSIRO Marine and Atmospheric Research Data Centre (http://www.marine.csiro.au/datacentre/). The database contains plankton counts, dominant organism, and biovolume obtained with the N70 net for the 50 m to surface vertical hauls and the surface horizontal tows. Tow duration is also stored for the horizontal tows. Additionally, the database contains surface temperature and salinity observations at the locations of the plankton observations, as well as time-of-day, cloud free surface irradiance, climatological temperature and salinity for the time-of-year and location, and the surface wind velocity estimated from the NOAA-CIRES 20th Century Reanalysis Project version 1.

It is worth considering the accuracy of the position, depth, temperature and salinity of the *Warreen* observations that were taken before the advent of GPS and CTDs. The *Warreen* observations were undertaken using similar equipment and methods to that employed at the time at Woods Hole Oceanographic Institution (WHOI). Measurement errors using these techniques at WHOI have been assessed (Warren, 2008) and are used below to supplement the accuracy estimated by the *Warreen* scientists.

Many of the *Warreen* stations were within sight of land, so position estimates are likely to be accurate within a few hundred metres. For stations beyond sight of land, location would have been determined by a combination of dead reckoning and celestial fixes. In strong currents such as the EAC dead reckoning calculations quickly accumulate errors. Celestial fixes, which rely on cloud free conditions at night, have an accuracy of 0.9–1.8 km (Warren, 2008). In any case, at the time of sampling position was recorded only to the nearest minute. One minute of longitude at 38°S is 1.46 km, which probably represents a reasonable error in station position.

The physical sampling was undertaken using Nansen bottles (CSIRO, 1951a, b). The depth of the measurement was determined using wire out, unless the surface stray angle exceeded 20° (10° from 1940 onwards), in which case a correction was made. A constant stray angle of 20° to the depth of the bottle would represent an overestimation of depth by 6.4%.

CSIRO Oceanographic Station List 2 (CSIRO, 1951b) claims an accuracy of temperature readings of $\pm 0.015\,^{\circ}$C, which is half the estimated maximum error of $0.03\,^{\circ}$C at WHOI at the time (Warren, 2008). The salinity was determined from chlorinity using the Knudsen formula, $S = 1.805\ [Cl^-] + 0.03$. At the time WHOI estimated this method to have an accuracy of at best ± 0.02 and reported salinity to two decimal places.

Ocean climatology: To quantify the synoptic oceanographic conditions at the time of the *Warreen* observations, temperature, salinity and nitrate are compared with the CSIRO Atlas of Regional Seas climatology (CARS, version 2006a). CARS is a four-dimensional interpolation of temperature, salinity and macronutrients based on observations from the 1930s to 2006 (Ridgway et al., 2002). Version 2006a contains data from the Argo float deployments of the last decade. The CARS database interpolates observations in time and space in a least-squares sense, producing a Fourier series description with a mean state, annual and semi-annual cycle on a 1/2° horizontal grid with 10-m resolution in the vertical to 300 m. For a *Warreen* station, the nearest CARS grid location is determined, and the Fourier series used to determine the climatology ocean state for the particular day of the year. The climatological annual cycles of surface temperature and salinity for six locations along the NSW coast are given in Fig. 2.

When comparing *Warreen* observations with the climatology it is should be noted that the error in calculating salinity of ± 0.02 is 7% of the full range of climatological salinities, while the error for temperature is 0.13% of the full range. Errors in salinity are the most significant when comparing *Warreen* observations with climatological values.

The comparison between individual *Warreen* stations and the CARS climatology is shown using anomaly scatter plots (Fig. 3).

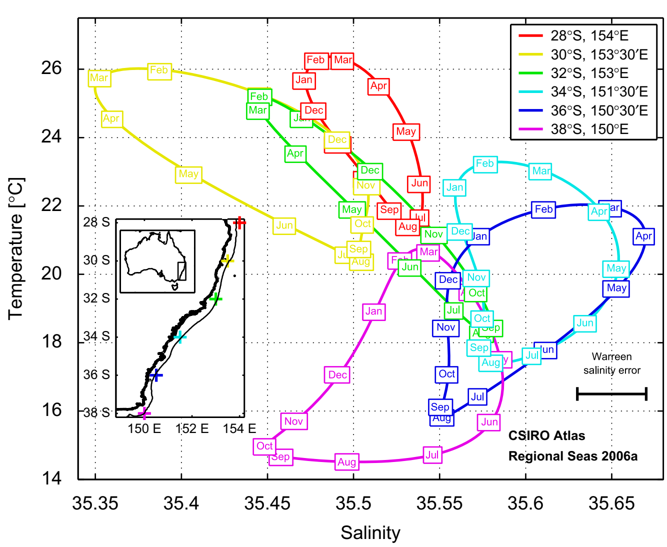

Fig. 2. Climatological temperature–salinity properties of the southeast Australian continental shelf. The main panel shows the annual cycle of surface T–S properties in the CSIRO Atlas of Regional Seas version 2006a for the points closest to the 200 m isobath at 28°S, 30°S, 32°S, 34°S, 36°S and 38°S. Month labels are centred on the 15th of each month. The insert shows the location of the CARS sites along the southeast Australian seaboard with the 200 m isobath drawn as a thin line. The size of the uncertainty in salinity estimates (± 0.02) during the *Warreen* observation is shown in the bottom left hand corner. Temperature errors are less than the thickness of the horizontal line.

The difference between the station surface temperature and salinity, and that for the nearest CARS station interpolated to the day of the sampling, is quantified by symbol colour. Increasing redness indicates *Warreen* stations with a higher temperature or salinity, while bluer indicates colder or fresher. Grey indicates the station is within $1.0\,^{\circ}$C or within a salinity of 0.05 of the climatology.

Warreen cruise design: During the 1938–39 cruises, physical measurements of temperature and salinity were taken at depths of 0, 10, 20, 30, 40, 50, 100, 150, 200, 300, 400 and 600 m, depth permitting. For the 1940–42 cruises, hydrographic measurements were enhanced to include pH, NO_3 and PO_4, and were generally undertaken in cross-shelf transects, with three stations on the shelf, and three off the shelf.

At more than half of the stations nets were towed in horizontal, vertical and oblique patterns. The plankton observations included counts of Nyctiphanes (later corrected by K. Sheard to adult Euphausiacea in general, Sheard, 1953, p. 33), Thaliacea, Larvacea and Chaetognatha. Despite copepods being the dominant organism in 62.5% of the nets (Thompson and Kesteven, 1942), their abundance was not quantified. Abundance was measured from emptying the first tenth of a shaken column vessel (Thompson and Kesteven, 1942).

In this paper the plankton samples from the deployment of a N70 net are analysed. The N70 net was originally described in the Discovery Reports (Kemp et al., 1929; Wiebe and Benfield, 2003). The N70 is designed for the capture of small to medium sized macroplankton. The net has a 70-cm diameter circular opening. The filtering component of the net is made in sections. The front section is 3 ft 2 in long with 40 meshes to the inch ($\sim$430 μm opening) while the back section is 4 ft 5 in long with 74 threads to the inch ($\sim$222 μm opening).

The volume of water sampled for the horizontal and oblique tows is difficult to estimate. The nets were deployed at 0.89 m s^{-1} (based on an estimate on p. 52 of Thompson and Kesteven, 1942, of covering 1600 m in 30 min). No estimate of local current is available. In shelf regions off southeast Australia currents can exceed 1 m s^{-1}. On average (excluding Euphausiacea), a factor of 6.2 ± 2.1 greater concentration of biovolume and zooplankton abundance was found in the vertical hauls assuming a 0.9 m s^{-1} towing speed than the surface horizontal tows (Table 1). Consequently, the horizontal and oblique tows cannot be quantitatively compared directly with the vertical hauls, which are taken to be the best measure of *in situ* concentration.

Thompson and Kesteven (1942) visually inspected the *Warreen* tows to identify the dominant animal group. The categories considered were Crustacea, Copepoda, Chaetognatha, Coelenterata (both Ctenophora and Cnidaria), fish eggs and larvae and Tunicata (Thaliacea and Larvacea).

3. Results

3.1. Climatological context of the plankton observations

In this paper synoptic ocean conditions are quantified by reference to anomalies from the climatological mean temperature and salinity values (Fig. 2). A brief description of the mean state is required to interpret the anomalies. The greatest influence on water mass properties off NSW is the EAC. The EAC is sourced from tropical Coral Sea waters, which are warmer and fresher than the Tasman Sea waters off central NSW. When the EAC is strongest in summer, the TS properties off northern NSW (30°S) are most distinct from further south. In southern NSW, the influence of Bass Strait waters are seen. These waters are also fresher than central NSW, and have the greatest influence along

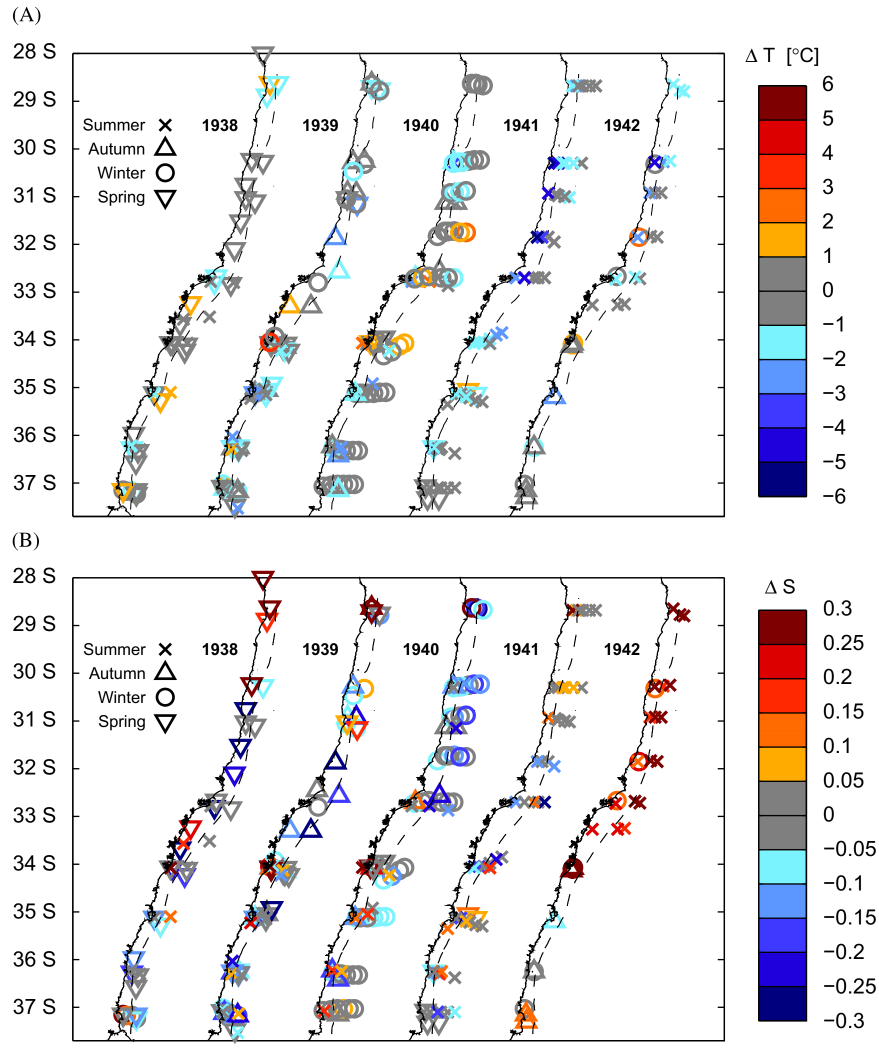

Fig. 3. (A) Temperature [°C] and (B) salinity anomalies of surface *in situ* observations from the *Warreen* cruises relative to the CSIRO Atlas of Regional Seas 2006a version for all stations with physical observations between May 1938 and July 1942. A positive anomaly (red) is warmer or saltier than the climatology, and a negative anomaly (blue) is colder or fresher. Dashed line is the 200 m isobath. Seasons are identified by symbols and are for the months of—Summer: December–February; Autumn: March–May; Winter: June–August; Spring: September–November for location of drawn coastline on Australian seaboard see insert in Fig. 2. For more detail of northern NSW temperature anomalies see Fig. 4. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the southern NSW coast in winter. About these mean annual cycles are anomalies due to long-term trends and mesoscale oceanographic events. The anomalies can be used to understand the component of variability in the plankton observations due to oceanographic processes such as water mass movements and upwelling events.

Along the NSW coast, the *Warreen* observations are on average 0.45 °C cooler and 0.038 saltier than the climatological mean. The observations in individual years (1938–42) were 0.21, 0.51 0.28, 1.10, and −0.05 °C cooler and 0.0074, −0.0028, −0.011, 0.0026 and 0.2820 saltier, respectively, than the climatological mean. The temperature changes are greater than the observational error of 0.03 °C, and are consistent with a strengthening of the EAC and a regional rate of sea surface warming of 1–2 °C per century (Ridgway, 2007; Thompson et al., 2009). The salinity changes are small relative to the observational error (~ 0.02). Only 1942 has an anomaly from the climatological mean greater than the error. Note the anomalies are for the time and place of the *Warreen* observations, and are not necessarily representative of the full year.

The longest duration and 7th strongest El Niño of the 20th century lasted 15 months, centred on July 1941 (Livezey et al., 1997). Unfortunately plankton observations were not sustained through much of this period, so it is hard to judge its importance. In any case, the strong upwelling event in January 1941 was during the early stages of the 1941 El Niño.

3.2. The effect of time-of-day on near-surface net samples

The *Warreen* observations that are analysed in this paper are the vertical hauls from 50 m to the surface and horizontal tows near the surface. Many deeper tows were undertaken but the inconsistency in their deployment does not lend itself to the analysis undertaken here. Of the 392 50-m vertical hauls and near surface horizontal tows considered in this paper, 277 were taken during daylight hours, and 115 at night. Before analysing the day and night time samples together, it is worth considering the effects of time-of-day.

The mean concentrations of zooplankton groups during day and night sampled by the vertical haul and horizontal tow are given in Table 1. Euphausiids have been shown to undertake diel migration between the surface and deeper waters in the Tasman Sea (Griffiths, 1979a, b), and this behaviour is confirmed in the

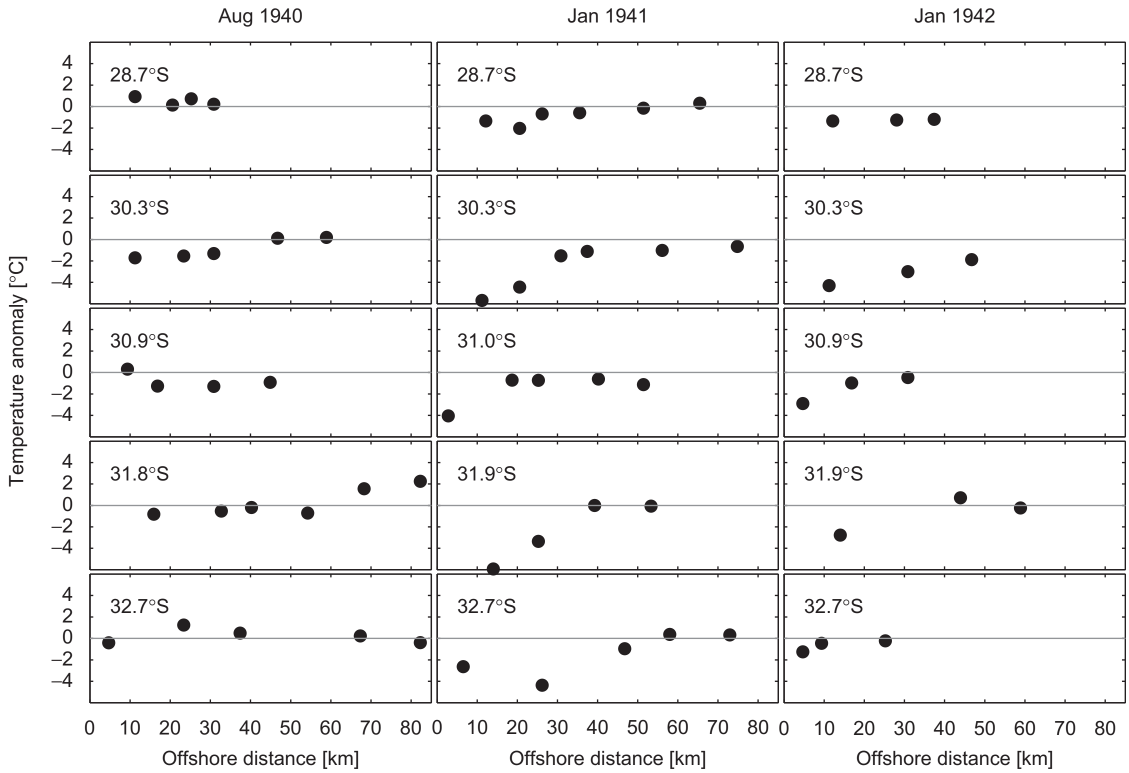

Fig. 4. Temperature anomalies [°C] of surface *in situ* observations relative to the CSIRO Atlas of Regional Seas 2006a version from cross shelf transects during the *Warreen* cruises off northern NSW in August 1940 (left column), January 1940 (centre column) and January 1941 (right column). This figure replots data from Fig. 3A to improve readability.

Table 1
Mean $\pm\sigma/n$ for all *Warreen* plankton observations from 1938–42 for vertical hauls of the N70 net between 50 m to the surface (V50_0) and horizontal surface tows (H_0).

Tow	Biovolume (mm^3 m^{-3})	Euphausiacea (ind. m^{-3})	Thaliacea (ind. m^{-3})	Larvacea (ind. m^{-3})	Chaetognatha (ind. m^{-3})	*n*
V50_0 day	2269 ± 25	1.59 ± 0.03	16.5 ± 0.2	16.2 ± 0.2	2.38 ± 0.03	156
V50_0 night	2080 ± 66	2.47 ± 0.10	16.1 ± 0.9	24.4 ± 0.9	2.30 ± 0.05	61
H_0 day	422 ± 7	0.028 ± 0.001	2.71 ± 0.04	2.52 ± 0.03	0.53 ± 0.01	121
H_0 night	329 ± 6	1.01 ± 0.074	2.35 ± 0.08	2.13 ± 0.07	0.56 ± 0.02	54

Estimates of whether it is day or night are based on orbital cycles (Brock, 1981) assuming no daylight savings in the recorded tow times and correcting for the difference between the local time-zone (for AEST defined at 150°E) and the local mean time or sundial time (i.e. correcting for sunset at 149°E being 4 min after sunset at 150°E).

Warreen observations with lower abundance found during the daylight hours in both vertical and surface horizontal nets (Table 1). The extremely low abundance of euphausiids in the horizontal tows may also be due to net avoidance (Griffiths, 1979a). For the purpose of this paper, analysis of abundance of euphausiids is not undertaken across all locations because of the confounding effects of time of day. Euphausiid abundance from individual net tows are referred to occasionally.

The abundance of chaetognaths, larvaceans and salps and the sample biovolume is similar at day and night. For the salps this can be explained by the numerical dominance of the non-migrating species *T. democratica* (Heron, 1972). By counts (for all nets at all stations) *T. democratica* outnumbered combined counts of all other salp species (Thompson, 1948).

The similar abundance of chaetognaths, larvaceans and salps and biovolume during the day and night in surface nets allows us to analyse all samples together, thus increasing the data set over day or night alone.

As a further note of caution when comparing nets, the mean mixed layer depth for the NSW shelf is less than 50 m from October to April (Condie and Dunn, 2006). Thus, while the horizontal surface tows are sampling the surface mixed layer only, the vertical haul from 50 m will often sample water from below the mixed layer.

3.3. Northern NSW

Plankton observations on the northern NSW coast were concentrated during the spring of 1938, late autumn and winter of both 1939 and 1940, and the summers of 1941 and 1942 (Fig. 1). Of these cruises, the design of the cross-shelf transects of August 1940 (highlighted in Fig. 1), and repeated in 1941 and 1942, allows the best interpretation of the physical environment. The analysis of water masses on the northern NSW coast takes advantage of the strong gradient in salinity along the shelf from 30°S to 34°S to infer the strength of the EAC (Fig. 2). Negative salt anomalies (fresher, shown in blue in Fig. 3B) are indicators of the EAC penetrating further south than the climatological average.

July 1939: In July 1939 shelf temperature (Fig. 3A) and salinity (Fig. 3B) were close to the 1938–2006 climatology, and with weak winds from the southwest (Fig. 5, top row). These conditions are typical of the northern NSW coastline in winter. The dominant zooplankton taxon was copepods. The biovolume caught in the

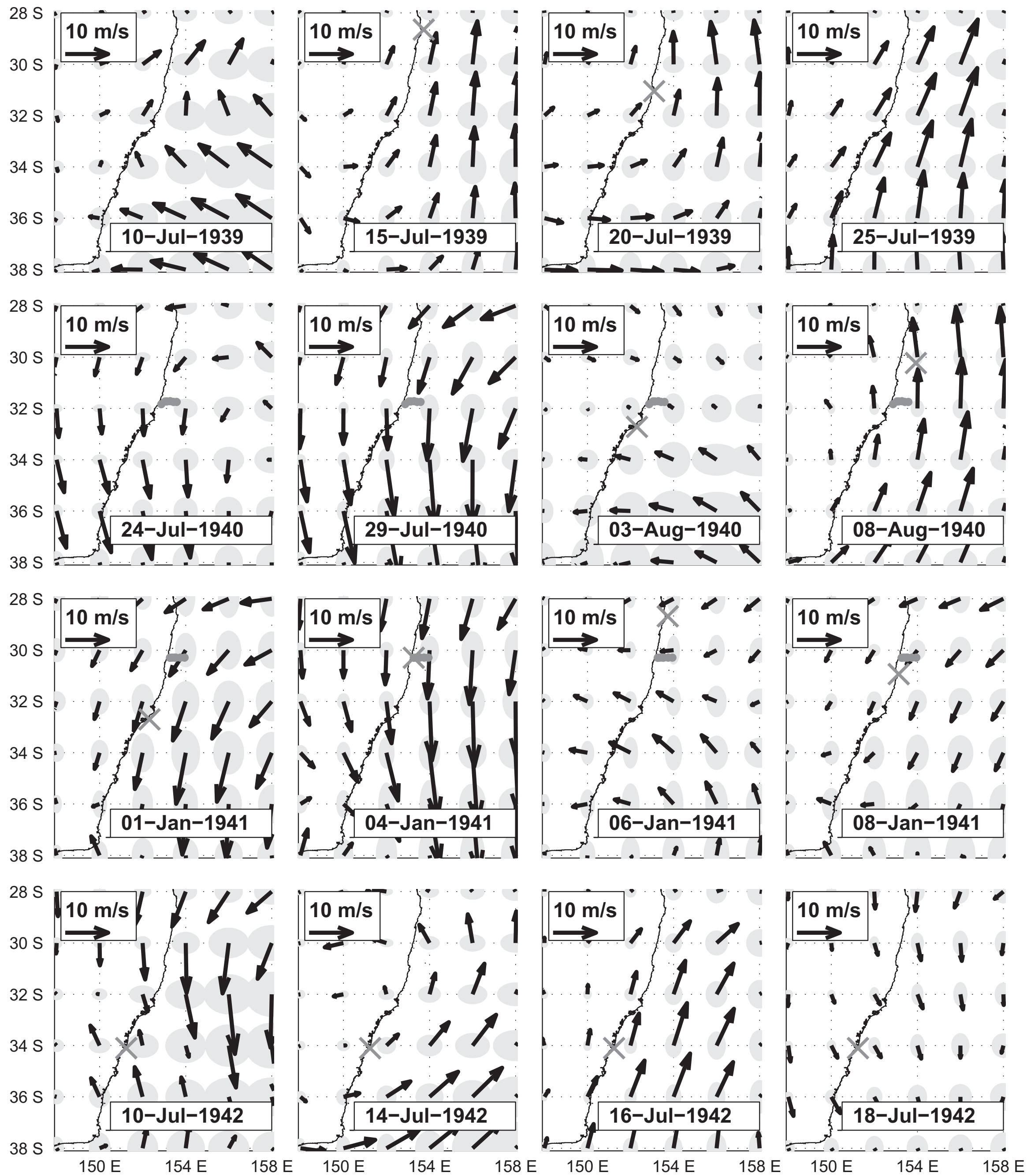

Fig. 5. Surface wind field from NOAA-CIRES 20th century atmospheric reanalysis provided by the NOAA/OAR/ESRL PSD, Boulder, CO, USA, from their Web site at http://www.cdc.noaa.gov/. Reanalysis details are described in Compo et al. (2006). The images show the ensemble mean daily average field from 6 hourly output on a $2^\circ \times 2^\circ$ horizontal grid. The ensemble mean is derived from a 56 member ensemble, the spread of which is shown by the grey ellipses at the tail of the vector. The *x*- and *y*-axes of the ellipse have radii equal to the ensemble spread in the *x* and *y* directions. The grey × symbols give the location of the *Warreen* on the day. The thick grey line in the 1940 and 1941 panels gives the location of the Diamond Head (31°45′S) and Coffs Harbour transect (30°18′S) shown in Fig. 9.

N70 50 m to the surface vertical haul was $\sim 1000\,\mathrm{mm}^3\,\mathrm{m}^{-3}$ (Fig. 6A). There was a low abundance of salps (Fig. 6B) and chaetognaths (Fig. 7A), with average abundance of larvaceans (Fig. 7B).

August 1940: In August 1940 the waters off northern NSW were on average 0.08 fresher (Fig. 3B) than the 1938–2006 climatology. In August a 0.07 decrease in salinity represents 2° of latitude further penetration of the EAC southward along the NSW shelf (Fig. 2). Off the shelf at 31°45′S waters were 1.55 and 2.24 °C warmer than climatology (Figs. 3A and 4). Warming and freshening of the offshelf waters indicates a strengthening of the EAC.

Late July 1940 was a period of northerly winds on the northern NSW coast (Fig. 5, 2nd row). The 1957–2003 mean winds for 9 am at the Hill St, Port Macquarie weather station (31°26′S, 152°55′E) are in the westerly octant 48% of the time, with the combined totals of northerly, north-easterly and easterly octants of less than 5%. The anomalously northerly (alongshore in a poleward direction) component of the winds in late July 1940 is upwelling-favourable.

The physical properties along the cross-shelf transect at Diamond Head (31°45′S) from the 5 August 1940 can be compared with the climatology (Fig. 8). The lifting of the 14 and 15 °C isotherms onto the inner shelf, and the elevated nitrate concentrations, confirm coastal upwelling. The presence of low-nutrient 19 °C water in the top 50 m of the offshore waters is also indicative of a stronger than average EAC. The combination of upwelling-favourable winds and a stronger than average EAC that imposes an upwelling favourable bottom stress produced unseasonal coastal upwelling.

These anomalous conditions off the northern NSW coast in August 1940 have occurred with high abundance, relative to the more typical July 1939, of salps (Fig. 6B) and larvaceans (Fig. 7B) in the northern NSW region, but only average biovolume concentration (Fig. 6A). The dominant zooplankton, as was the case in July 1939, was copepods.

January 1941: In January 1941 the coastal stations from 30°S to 32°30′S are between 5 and 6 °C cooler than the climatology (Figs. 3A and 4). From 1–5 January 1941 there were strong alongshore winds in a poleward direction (Fig. 5, 3rd row) which are upwelling favourable along the eastern Australia seaboard. At 32°48′S the coldest station is slightly offshore (Figs. 3A and 4). This distribution of cold surface water is typical of an upwelling event between 30 and 32°30′S with a filament of cold water being advected south and offshore at Port Stephens (32°40′S; Cresswell, 1994; Baird et al., 2007).

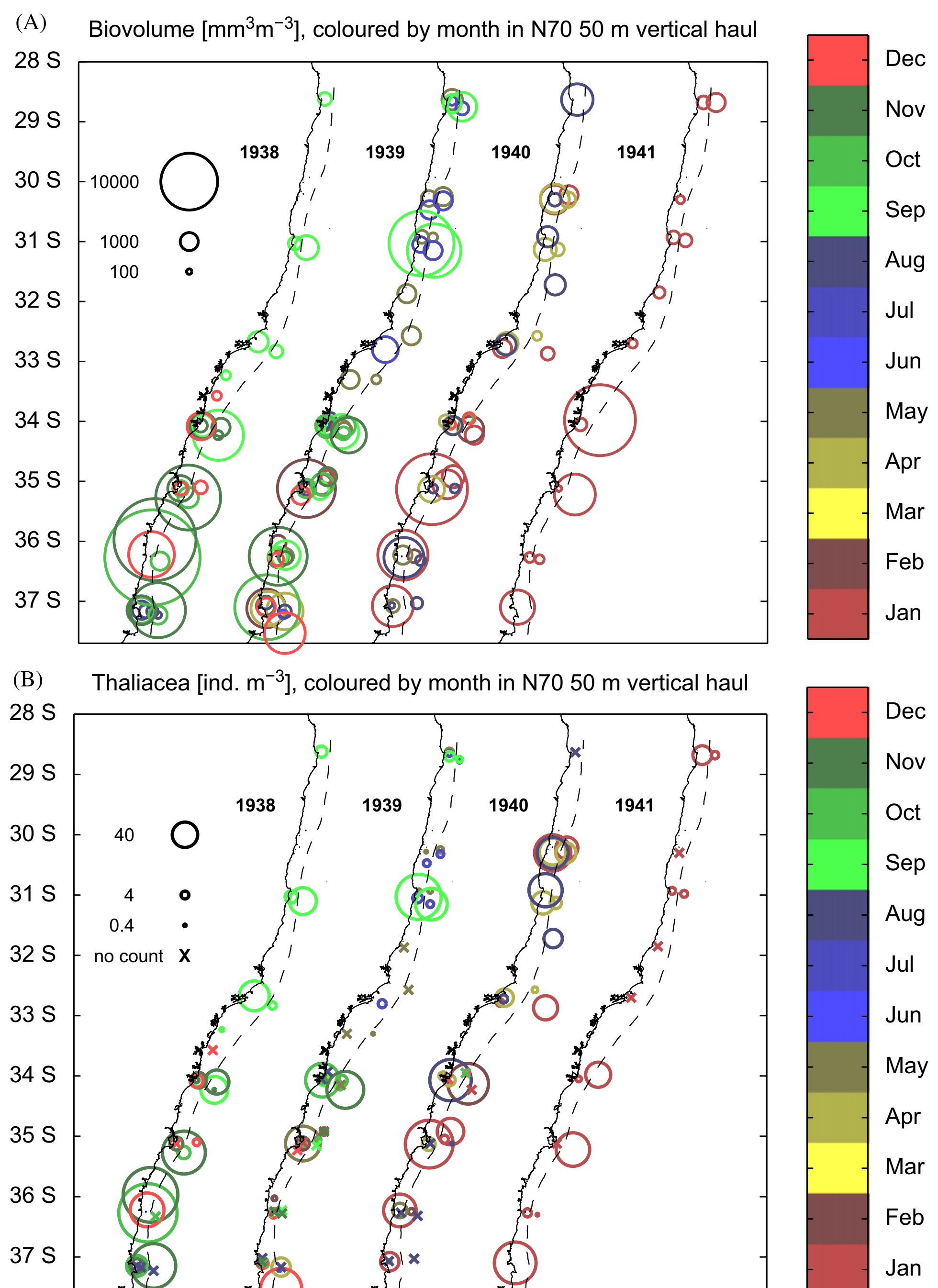

Fig. 6. (A) Biovolume [mm^3 m^{-3}] and (B) Thaliacea abundance from vertical hauls of the N70 net from 50 m to the surface. Symbol area gives the biovolume/abundance and symbol colour identifies the month of sampling. One count in the haul gives an abundance of 0.52 ind. m^{-3}.

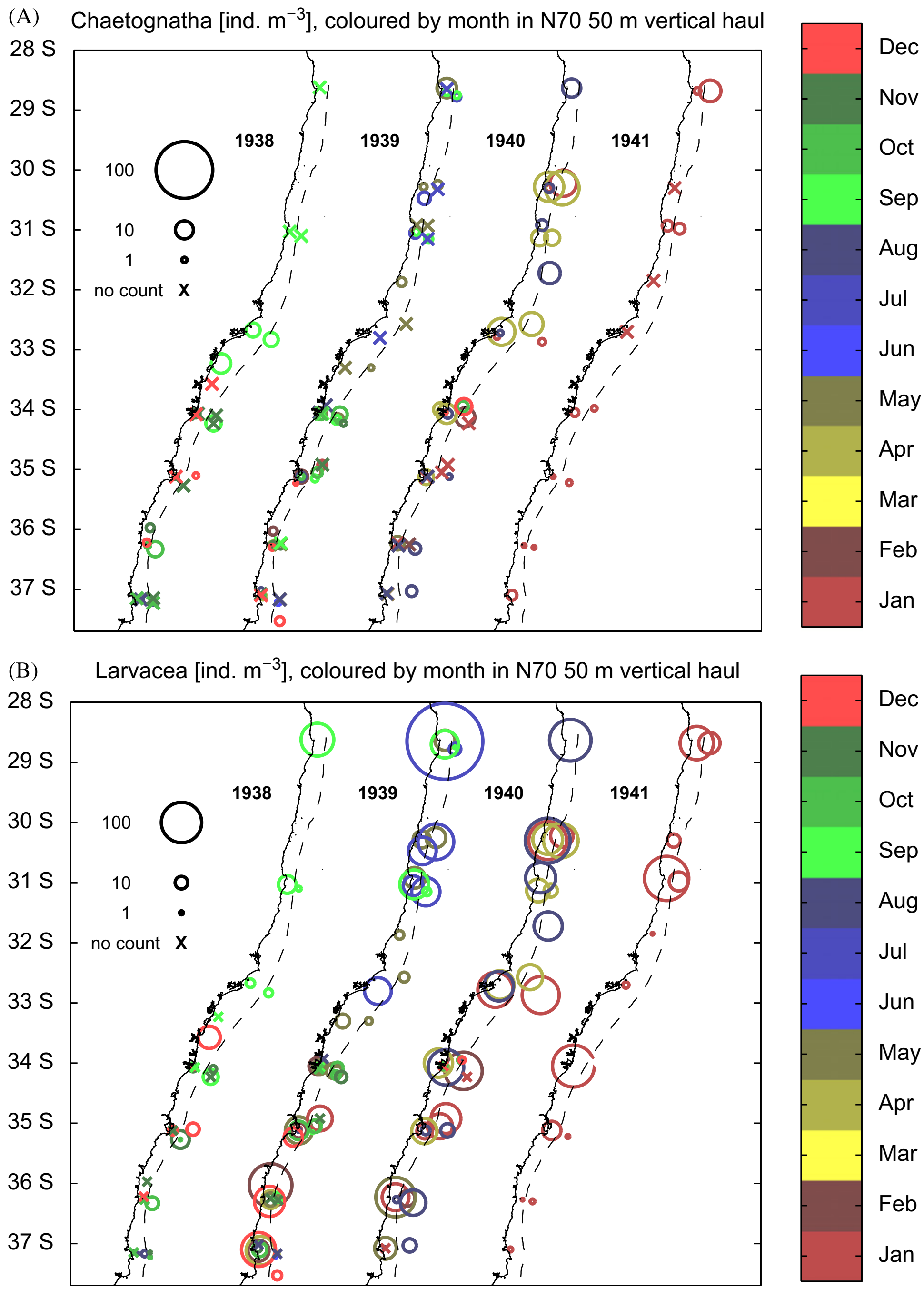

Fig. 7. (A) Chaetognatha and (B) Larvacea abundance from vertical hauls of the N70 net from 50 m to the surface. Symbol area gives the abundance and symbol colour identifies the month of sampling. One count in the haul gives an abundance of 0.52 ind. m^{-3}.

More details are revealed in the cross-shelf transect at Coffs Harbour (Fig. 9). The movement of slope water onto the shelf can be seen in the temperature and nitrate fields on a cross-shelf transect and is typical of a coastal upwelling event. The *Warreen* transects did not show elevated bottom-water nitrate concentrations as was found in November 1998 under similar summer upwelling favourable conditions at 30°30′S (Roughan and Middleton, 2002, Fig. 6 Urunga Station). The deepest *Warreen* samples were taken at 14, 19 and 33 m off the bottom for the inner shelf, mid-shelf and outer shelf stations, respectively. The deepest sample at the outer shelf station was too shallow to sample the bottom boundary layer (~ 20 m thick). The mid-shelf station bottom sample does show the hint of elevated nitrate. The inshore station bottom sample is sufficiently shallow for phytoplankton to remove nutrients from the water column, possibly explaining the low nitrate concentrations.

In the cool, upwelled water of early January 1941, 50–0 m vertical hauls were low in macrozooplankton biomass (Fig. 6A), salps (Fig. 6B) and chaetognaths (Fig. 7A), and the larvaceans abundance was highly variable (Fig. 7B). Low macrozooplankton abundance in coastal waters on the NSW mid-north coast during upwelling is consistent with coupled physical–biological model simulations of the region showing maximum zooplankton biomass downstream of the upwelling site (Baird et al., 2006).

At the Coffs Harbour inshore station (30°18′S,153°16′E), five tows were undertaken at 3.45 pm on the 5 January 1941. The

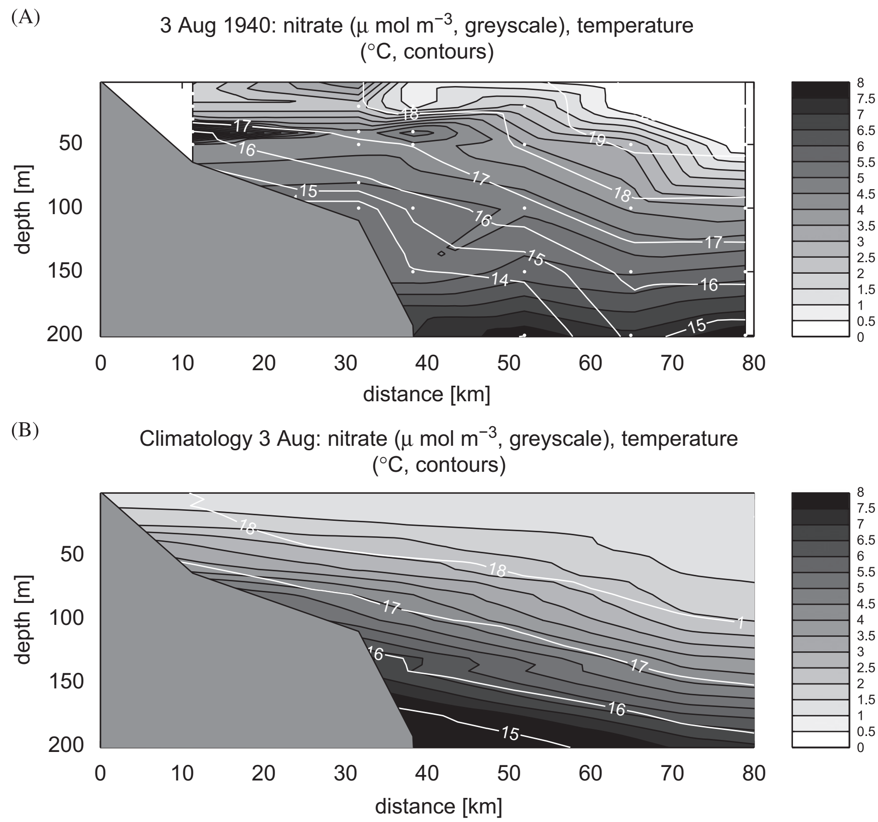

Fig. 8. (A) Cross-shelf transect at Diamond Head (31°45′S) of temperature and nitrate sampled in an offshore direction on the 4th–5th August 1940 (*Warreen* stations 70–75). (B) CSIRO Atlas of Regional Seas temperature and nitrate fields for the same transect on the 5 August obtained from historical four-dimensional interpolated data. Transect location shown in Fig. 5. The *x*-axis is distance in km from the coastline.

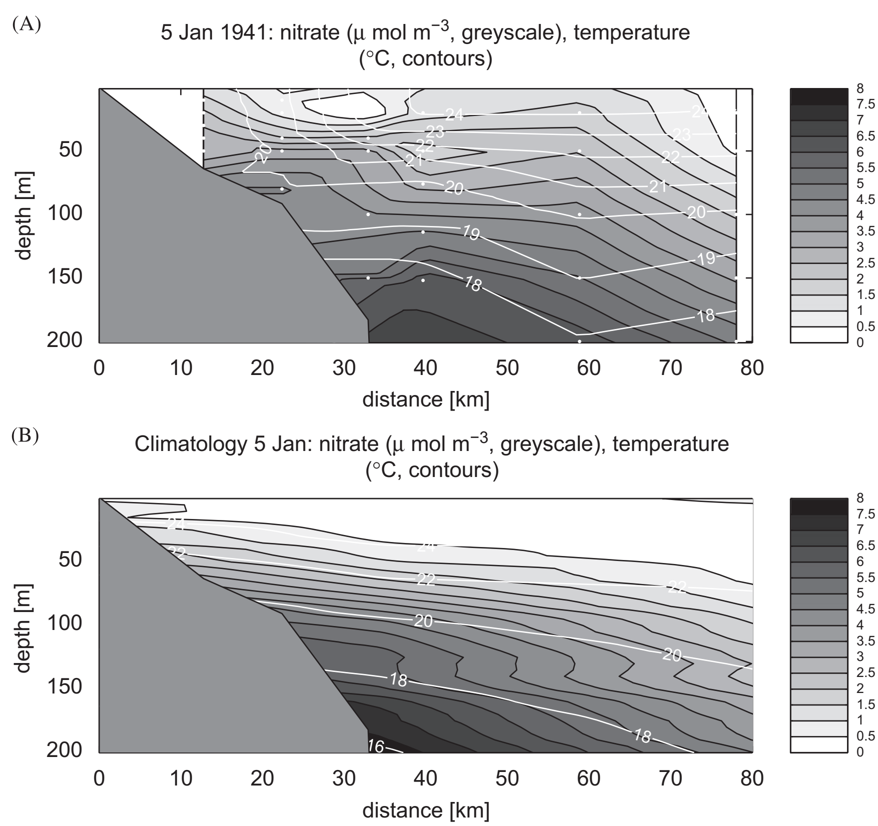

Fig. 9. (A) Cross-shelf transect at Coffs Harbour (30°18′S) of temperature and nitrate sampled in an offshore direction on the 4th and 5th January 1941 (*Warreen* stations 6–11). (B) CSIRO Atlas of Regional Seas temperature and nitrate fields for the same transect on the 5 January obtained from historical four-dimensional interpolated data. Transect location shown in Fig. 5. The *x*-axis is distance in km from the coastline.

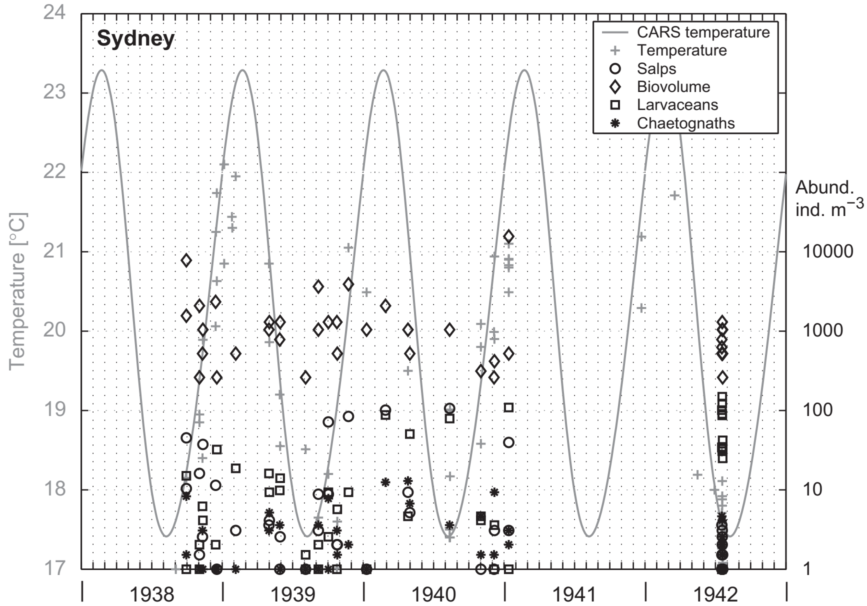

Fig. 10. Time series of observations at Sydney ($\sim$34°S). Climatological temperature (CARS at $\sim$34°S, 151°30′E) and *in situ* observations of surface temperature [°C], biovolume [mm^3 m^{-3}], and the abundance of Thaliacea, Larvacea, and Chaetognatha [ind. m^{-3}]. Minor ticks on the *x*-axis delineate months.

surface temperature and salinity were 19.50 °C and 35.53. Larvaceans dominated three of the tows (surface horizontal, 50–0 m vertical haul and an oblique 50 m tow). No counts were recorded for salps or chaetognaths.

The other station on the Coffs Harbour transect at which plankton observations were taken was 27 km further offshore in water of a total depth of $\sim$1200 m (30°18′S, 153°33′E at 7.30 am). At this location four tows were undertaken down to 200 m. Surface waters of 24.10 °C indicate that the tows were within the EAC. The surface salinity was 35.54. High abundance of salps, larvaceans and chaetognaths were found in both surface horizontal and 200 m to the surface oblique tows, but no euphausiids. The biovolume was consistently high (these observations do not appear in Figs. 6 and 7 because no vertical tows were taken). Clearly the offshelf station is within the EAC and had different physical and biological properties to the inshore upwelled waters.

3.4. Southern NSW

Plankton observations along the southern NSW coast are temporally more complete than northern NSW (Fig. 1) allowing seasonal signals to be investigated off Sydney ($\sim$34°S) and Eden ($\sim$37°S). At 34 and 36°S the annual cycle of temperature and salinity are similar (Fig. 2). The waters at 34 and 36°S are also the saltiest water along the coast. Thus, a fresh anomaly could be a result of water moving either north or south or an upwelling event. The best metric for these large water mass movements on the southern NSW continental shelf is temperature anomaly.

Sydney time-series: For Sydney ($\sim$34°S) the most striking trend is a positive correlation between biovolume and salps (Fig. 10) which has long been recognised for the region (Sheard, 1949, Fig. 2). When salps bloom they dominate the net biovolume. Salp blooms tend to occur in the spring and summer months. The spring–summer period may be characterized by 1–2 salp blooms, with low populations in the intervening periods following sudden collapses of the blooms.

The final *Warreen* cruise in southeast Australia involved 13 repeat stations at Port Hacking (34°6′S, 151°14′E) during daylight hours on the 17–19 July 1942. On the 18 July, as hindcast by the 20th century reanalysis (not shown), winds shifted from a southerly of $\sim$8 m s^{-1} to a weaker northerly of $<$5 m s^{-1}. Between the 17 and 19 July the bottom temperature dropped from 15.48 to 15.14 °C, bottom dissolved oxygen concentrations decreased by 0.13 ml l^{-1}, and bottom nitrate concentration increased from 34 to 71 mg m^{-3}. These changes are consistent with a shift to an upwelling favourable northerly wind. Over the three days biovolume ranged over 260–1300 mm^3 m^{-3}, salps over 0–2.6 ind. m^{-3}, larvaceans over 0–148 ind. m^{-3}, chaetognaths over 0–3.64 ind. m^{-3}, and the dominant organism shifted between tunicates and copepods. Although the three days were during a period when wind forcing shifted, there was no obvious change in surface water mass or zooplankton community (which likely lags the wind forcing). The large range of zooplankton abundance data illustrates short term variability (or spatial patchiness) in the zooplankton community that is occurring as a result of processes at scales than can be diagnosed using the available knowledge of synoptic conditions. Or alternatively are a result of ecological interactions rather than physical forcing.

Eden time-series: For Eden ($\sim$37°S) a seasonal cycle, which is not clear at Sydney and further north, is apparent (Fig. 11). Biovolume has a low in May to August and reaches the highest biovolume recorded during the *Warreen* cruises off NSW in spring (Fig. 6A). As with further north, biovolume follows salp abundance.

In the global ocean cooler waters generally favour nano- and micro-phytoplankton that would be more available to mesozooplankton grazers such as tunicates. Accordingly, in the cooler waters off Eden mesozooplankton dominated the tows. The only occasion of the visual dominance of crustaceans in the N70 50 m to surface haul occurred during the anomalously warm January 1941 at Montague Island ($\sim$36°S).

4. Discussion

4.1. Using Warreen observations to investigate climate-change impacts

Zooplankton populations will be affected by changes in ocean climate, and are likely to drive changes in other components of

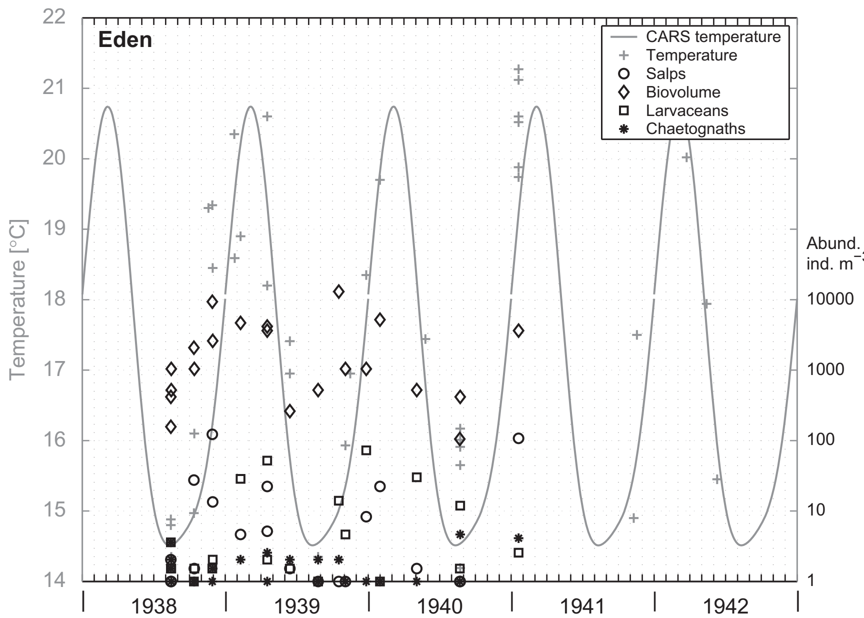

Fig. 11. Time series of observations at Eden (~37°S). Climatological temperature (CARS at ~37°S, 150°30′E) and *in situ* observations of surface temperature [°C], biovolume [mm^3 m^{-3}], and the abundance of Thaliacea, Larvacea, and Chaetognatha [ind. m^{-3}]. Minor ticks on the *x*-axis delineate months.

marine ecosystems (Hays et al., 2005; Hobday et al., 2006). There are no continuous zooplankton time-series along the southeast Australian coast (Hobday et al., 2006; Poloczanska et al., 2007). As a result, the *Warreen* observations provide key observations of the marine ecosystem off southeast Australia before the accelerating warming seen in the second half of the 20th century.

Despite 1742 samples, the *Warreen* observations are not sufficient to provide a complete picture, or 'baseline', of the marine ecosystem before the recent warming trend. Firstly, the observations were taken over a 5-year period, precluding the ability to identify 5+ year cycles that existed. In particular, the El Niño cycle, which affected the observations through a long-duration event in 1941, cannot be properly considered. Secondly, the observations were spread over a large geographical region, with few repeat observations to aid in statistical analysis. And thirdly, the clustering of observations tended to be over a week or so, approximately the time scale of regional oceanographic processes such as wind-driven coastal upwelling. So while a number of oceanographic events are well captured, this may not be representative of the other oceanographic processes that occurred during a particular season for which there are no observations.

The knowledge of synoptic conditions at the time of *Warreen* sampling does allow for the comparison with modern sampling under similar physical forcing. For example, as reported in Section 3.3 the *Warreen* observations off Coffs Harbour in January 1941 were undertaken in similar conditions to the R.V. Franklin cruise of November 1998 (Roughan and Middleton, 2002; Dela-Cruz et al., 2008). Frustratingly, the zooplankton sampling on the 1941 and 1998 expeditions were undertaken quite differently. Nonetheless, an extensive search of historical cruise records will no doubt find instances of comparable plankton observations under similar environmental forcing.

4.2. *Interpretation of previous ecological insights from the Warreen plankton observations*

The *Warreen* plankton observations have been analysed by a number of researchers since their collection. Given the importance of these studies in influencing both past and current understanding of the pelagic ecosystem off southeast Australia it is worth revisiting their findings in the context of synoptic oceanographic conditions.

Thompson and Kesteven (1942) used the observed zooplankton assemblages to infer circulation patterns, and concluded that 1939 and 1940 were abnormally warm years throughout southeast Australia. Removing the 20th century warming trend, our analysis suggests 1940 was warmer at the sampling locations due to a stronger than average EAC in August and the presence of warm water off Sydney in January, probably due to a warm core eddy (Tranter et al., 1986; Baird, 2011).

Thomson (1947) studied chaetognaths in the *Warreen* samples and identified five genera and 19 species. For each species identified he provides anatomical measurements and stages for the samples taken. Along the Australian east coast, eight tropical, seven temperate and two cold-water species were characterised by their observed distribution. Analysing the vertical distribution using vertical haul data with a N70 net, Thomson (1947) found approximately equal concentrations of chaetognaths in the top 50 and 50–100 m depth, decreasing by 40% between 100 and 250 m, and 83% between 250 and 500 m. Our analysis of day versus night sampling (Table 1) shows that chaetognaths do occur in equal numbers throughout a 24-h period, and suggests the Thomson (1947) study is not confounded by the lack of considering day/night differences.

Thompson (1948) authored a seminal taxonomic text on pelagic tunicates based on the *Warreen* samples. Thompson (1948) described the anatomy and ecology of 44 species of pelagic tunicates found during the *Warreen* cruises. Thompson found *T. democratica* to be the most common tunicate in southeast Australian waters, and there to be generally greater diversity and numbers of tunicates off the southeast Australian mainland than off the island of Tasmania further south. He suggested the period of 1939 to early 1940 was characterised by an unusual incursion of tropical and sub-tropical species of tunicates into southeast Australian waters. The comparison of the temperature and salinities observations taken at the time with the 20th century climatology of temperature and salinity agrees with Thompson.

Sheard (1953) investigated the taxonomy, distribution and development of the euphausiids from the *Warreen* observations, supplemented by later cruises of the Discovery II. Sheard (1953) was able to distinguish different on-shelf and off-shelf populations (Sheard, 1953, Tables 4 and 5), with *Nyctiphanes australis* being the most abundant netric euphausiid. Sheard (1964) then published an analysis that grouped zooplankton assemblages according to their co-occurrence, and found a reasonable correspondence between zooplankton assemblages (using tunicates, euphausiids, hyperiidae, chaetognaths and pteropods) and water masses, as defined by temperature and chlorinity. While not conclusive, the correspondence with water mass (as opposed to say geographical position) is a result to be expected if synoptic oceanographic conditions play a large role in determining planktonic response.

Wood (1954) summarised the distribution of dinoflagellates around Australia based on estuarine sampling, the *Warreen* observations and other research cruises. As for the earlier work of Thompson some of the motivation of the study was to gain insights into circulation based on species distributions. With hindsight, he had mixed results. Wood (1954) erroneously inferred from dinoflagellate distributions that (1) 'the maximum intensity of oceanic warm-water influence (the EAC) normally lasts for 3–4 months, usually between April and July, or early August'—a summer maximum of 16 Sv and winter minimum of 7 Sv of southward EAC is now apparent from climatologies (Ridgway and Godfrey, 1997); and (2) 'water from the Tasmanian-Bass Strait region…is poor in nutrients [relative to EAC]'—mean annual surface nitrate values for east coast of Tasmania are $>2\,\text{mmol N m}^{-3}$ and less than $1\,\text{mmol N m}^{-3}$ off the NSW coast (CARS). Nonetheless, Wood (1954) is a significant work that attempts to correlate physical and biological oceanographic observations. The erroneous conclusions can be attributed to shortcomings in the physico-chemical data available.

From the surviving 964 samples of the *Warreen* now housed at the South Australian Museum, Zeidler (1998) detailed an exhaustive taxonomic study of the Hyperiidea, a suborder of marine amphipods. Zeidler (1998) found 89 Hyperiidean species, 21 of which are new for Australian waters, and two taxa new to science. The taxonomic studies of Zeidler (1998), Thompson (1948) and Thomson (1947) remain the most complete works for their taxon in Australian waters. Given the range of synoptic conditions encountered during the *Warreen* sampling, it is reasonable to assert that they sampled much of the diversity that existed.

4.3. Uncertainties in the wind field hindcast

This paper emphasises the importance of weather-band (week) scale events on the local oceanographic response that drives plankton dynamics. The robustness of 1940s wind field hindcasts can be assessed through measures of forecast skill that the hindcast produces, and by comparison with synoptic charts of the time.

The surface wind field estimates from the 20th Century atmospheric reanalysis in Fig. 5 are the mean of a 56 member ensemble from sequential 9-h forecasts. Uncertainty in initial conditions, and the divergence this drives in the 9-h simulations is quantified by the standard deviation of the wind fields for the ensemble. The grey shaded ellipses in Fig. 5 show that there is significant spread in the reanalysis fields. In general spread appears to be the largest in the offshore waters, tapering across the shelf to be the smallest on the Australian mainland. For July 1939 and July 1940 the spread is small relative to the wind fields (Fig. 5, top two rows). For the January 1941 and 1942 the spread is approximately 50% of the magnitude of the wind speed (Fig. 5, bottom two rows). It is still safe to assume that upwelling favourable winds were prevailing in early 1941. In January 1942 the ensemble spread approaches the magnitude of the mean wind for much of the domain. While it is still likely that upwelling winds occurred from the 4–12 January, they may have been twice as strong as the mean, or quite weak. Nonetheless, for the purpose of this study, the errors due to the spread of trajectories from uncertainties in initial state are sufficient small that the 20th century reanalysis provides a valuable insight into the atmospheric forcing of the ocean at the time of the *Warreen* observations.

Such a conclusion is supported by comparison with synoptic weather charts published at the time. In late July 1940, when unseasonal northerly winds were predicted by the reanalysis, the synoptic charts (Sydney Morning Hearld, 1940) showed a high pressure system moving across the NSW coast at $\sim 30^{\circ}$S that would explain the hindcast. The more commonly observed westerly winds in July 1939 and northerly winds in January 1941 are also consistent with the synoptic charts. Weather-band systems are important for interpretation of planktonic observations off southeast Australia. At the scales required to cause upwelling, winds are reliably reproduced by atmospheric reanalysis products.

4.4. Historical particle tracks

On an historical note, it is worth mentioning the sampling was undertaken in challenging conditions. The technical log of 16th November 1941 reads: '3.30 pm Stopped [sampling] after sighting a floating mine'. From 2 until 2.30 pm off Montague Island (36°16′S, 150°17′E) the crew had been deploying nets. The log then continues '8.20 pm Lost sight of mine, so got under way'. During the Second World War floating mines were generally released in the Coral Sea. A mine off Montague Island may be taken as evidence of the presence of the poleward extension of the EAC. At the time of the mine sighting, the surface temperature and salinity were 18.30 °C and 35.61, respectively. The climatological values for this time at 36°S and 34°S are 18.30 °C and 35.55, and 20.0 °C and 35.57, respectively. Accounting for the 0.45 °C shift in SST in 70 years, the surface properties at Montague Island are shifted towards that of waters typically found further north—again likely due to a poleward extension of the EAC. During the war years, the use of mine sightings may provide further water mass analysis information for interpreting planktonic observations. In terms of zooplankton, this time was noteworthy for a 'remarkable increase' of *Salpa maxima* (Thompson, 1948, p. 156).

4.5. Concluding thoughts

The zooplankton observations collected during the 1938–42 research cruises of the *Warreen* can provide valuable data for quantifying the impacts of climate change in the waters off southeast Australia. The historical regional oceanographic context that this paper provides ensures that such a quantification accounts for the natural variability driven by mesoscale processes that dominate the NSW continental shelf pelagic ecosystem. Further work to consider the effect of synoptic oceanography conditions on the large number of intermittent observations during the last 70 years provides the best opportunity of assessing climate change impacts on the pelagic ecosystem.

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