

**Seasonal,
sub-seasonal and
spatial fluctuations**

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T. A. Probyn

Seasonal, sub-seasonal and spatial fluctuations in oxygen-depleted bottom waters in an embayment of an eastern boundary upwelling system: St Helena Bay

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Received: 30 June 2015 – Accepted: 3 August 2015 – Published: 19 August 2015

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Published by Copernicus Publications on behalf of the European Geosciences Union.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Abstract

The considerable impact of oxygen deficient waters on marine resources in St Helena Bay has generated interest in exploring the vulnerability of South Africa's largest and most productive bay to further deoxygenation in response to climate change. Seasonal, sub-seasonal and spatial fluctuations in bottom dissolved oxygen (DO) are examined in St Helena Bay to facilitate better interpretation of historical data. DO measurements in relation to physical, chemical and biological variables were made between November 2013 and November 2014. Alongshore bay characteristics were assessed through comparison of variables along the 50 m depth contour. A mean *coefficient of variation* of 0.35 provided a measure of the relative variability of near-bottom DO concentrations along this contour. Across-shelf transects captured the seasonal development of hypoxia in relation to the distribution of phytoplankton biomass. DO was lowest in autumn in the south of the bay prior to winter ventilation of the bottom waters. Exceptional dinoflagellate blooms forming extensive subsurface thin layers preceded the autumn DO minima. The development of hypoxia at inner and central stations prior to expansion beyond the boundaries of the bay provided evidence of local drawdown. Coincident with the seasonal decline of DO within the bay was an increase in macronutrient concentrations which tended to mirror DO concentrations. Indication of denitrification in the suboxic waters in the south of the bay was provided through evidence of a nitrate deficit in autumn supported by elevated nitrite concentrations. Superimposed on the seasonal decline of DO concentrations in the bottom waters were sub-seasonal events of hypoxia and anoxia linked to episodic deposition of organic matter as indicated by increases in bottom Chl *a* concentrations.

Seasonal, sub-seasonal and spatial fluctuations

G. C. Pitcher and
T. A. Probyn

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



1 Introduction

Available forecasts relating to global change and the future ocean indicate with some degree of confidence that dissolved oxygen (DO) levels in the ocean by the end of the 21st Century will be somewhat lower than at present (Duarte, 2014). Eastern Boundary Upwelling Systems (EBUS) in particular are considered to be strongly affected by the stressors of rising temperatures, ocean acidification and ocean deoxygenation making them potential hotspots of change (Gruber, 2015). Here these stressors are expected to act not only in isolation but simultaneously, and even in part synergistically. Recent observations of decreasing oxygen levels in the California Current System (Bograd et al., 2008; Chan et al., 2008), the Humbolt Current System off Peru and in the Canary Current System (Stramma et al., 2008) support these forecasts.

In the Benguela Current System, oxygen depletion in the northern Benguela is more severe and widespread than that in the southern Benguela, as is evident from the rapid and progressive increase of continental shelf DO values along the 200 m isobath south of the major upwelling cell at Lüderitz (Dingle and Nelson, 1993). Oxygen depleted waters in the southern Benguela tend also to be more localized and generally confined to depths of < 150 m on the Namaqua shelf where DO concentrations have been shown to be lowest in St Helena Bay (Fig. 1; De Decker, 1970; Bailey and Chapman, 1985, 1991; Monteiro and van der Plas, 2006; Jarre et al., 2015) the largest and most productive embayment on the South African coast (Pitcher and Weeks, 2006; Weeks et al., 2006). Here oxygen depletion has been considered a consequence of local drawdown (Bailey, 1991; Monteiro and van der Plas, 2006) and is therefore defined in the scheme of Kemp et al. (2009) as *persistent seasonal hypoxia* in which oxygen depletion is confined to the bottom layer and driven by: (1) summer stratification sufficient to isolate the bottom layer from surface waters and to impede downward mixing of oxygen; (2) the stimulation of high algal production in surface waters driven by considerable input of inorganic nutrients; and (3) a high rate of delivery of labile organic matter to the bottom layer through sedimentation of the algal production in the overlying waters.

Seasonal, sub-seasonal and spatial fluctuations

G. C. Pitcher and
T. A. Probyn

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Seasonal, sub-seasonal and spatial fluctuations

G. C. Pitcher and
T. A. Probyn

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



More recently, a second category of oxygen-deficient waters has been distinguished in St Helena Bay referred to in the scheme of Kemp et al. (2009) as *episodic anoxia* (Pitcher and Probyn, 2011, 2012; Pitcher et al., 2014). Occurring in shallow, nearshore environments *episodic anoxia* follows the decay of high biomass dinoflagellate blooms, termed red tides, that accumulate nearshore under conditions of persistent downwelling. The exceptional phytodetrital production associated with their decay in the reduced volume of water within the confines of shallow nearshore environments, results in localized depletion of oxygen through the entire water column.

These forms of oxygen-deficient waters have been identified as having the greatest environmental impact on living marine resources in the Benguela Current System (van der Lingen, 2006). In St Helena Bay *episodic anoxia* has specifically been considered the cause of repeated rock lobster mortalities (Cockcroft, 2001), leading ultimately to a major decline in the rock lobster resource within the region (Cockcroft et al., 2008), and also major fish mortalities (Matthews and Pitcher, 1996). These impacts have generated interest in exploring the vulnerability of the region to further deoxygenation in response to climate change.

Environmental monitoring that has included measures of DO has been carried out in the St Helena Bay region since the 1950s and there have been several attempts to evaluate these data in the assessment of long-term change in the southern Benguela. Whereas Hutchings et al. (2009) provided evidence of a 35 % long-term decline in DO concentrations in sub-thermocline waters since 1961, Pitcher et al. (2014) claimed no notable change in bottom water DO concentrations over the past 50 years. Others have suggested that DO variability in St Helena Bay is dominated by inter-annual and decadal signals (Hutchings et al., 2012; Jarre et al., 2015). However, limited knowledge of short-term and spatial fluctuations of bottom DO concentrations in the bay limit the interpretation of these historical data sets which are further compromised by temporal and/or spatial bias in the collection of these data over the past 60 years.

The purpose of this study was to quantify seasonal, sub-seasonal and spatial fluctuations of DO in St Helena Bay through intensive sampling of the region over the course

of a year. In addition to measurements of DO in relation to various physical properties, the development of hypoxia and/or anoxia was followed in relation to changes in phytoplankton biomass; macronutrients were also measured to assess local biogeochemical shifts in response to varying DO concentrations.

2 Methods

The study was undertaken within the St Helena Bay region between November 2013 and November 2014 and included: (1) regular sampling of 4 transects comprising a grid of 28 stations, and (2) deployment of bottom moored instrumentation at a single location at 50 m depth (Fig. 1). DO concentrations of $< 1.42 \text{ mL L}^{-1}$ are defined as hypoxic and $< 0.02 \text{ mL L}^{-1}$ as anoxic. The four seasons are defined to include the following months: spring – September to November, summer – December to February, autumn – March to May, and winter – June to August.

2.1 Transects

Transects located off the Olifants River, Lambert's Bay, Elands Bay and the Berg River, were sampled on 8 occasions at intervals ranging from 5–10 weeks (26–28 November 2013, 20–23 January 2014, 3–6 March 2014, 7–10 April 2014, 18–21 June 2014, 28–31 July 2014, 8–11 September 2014, 20–23 October 2014) (Fig. 1). The transects comprised 8 stations except for the transect off the Olifants River which consisted of only 4 stations. The distance between transect stations was 2 nautical miles.

A SBE-19 Seacat CTD with integrated SBE 43 oxygen sensor and WETLabs fluorometer (WETStar) was used to profile the water column at each station. Surface (1 m) and near-bottom water (within 2 m of seafloor) samples were collected by NIO (National Institute of Oceanography) bottles. Surface water samples were subject to fluorometric analysis of Chl *a* as detailed by Parsons et al. (1984) and used to calibrate in situ fluorescence profiles. Surface samples were also fixed in buffered formalin for

BGD

12, 13283–13309, 2015

Seasonal, sub-seasonal and spatial fluctuations

G. C. Pitcher and
T. A. Probyn

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



enumeration of phytoplankton by the Utermöhl method (Hasle, 1978). Surface and bottom water samples were subjected to manual nutrient analysis after filtration through Whatman GF/F filters. NO_3^- and NO_2^- were analysed according to Nydahl (1976), and NH_4^+ , PO_4^{3-} and SiO_4^{2-} according to Grasshoff et al. (1983), scaled down to 5 mL samples. Arbitrary surface and bottom water samples were subject to determination of DO content by means of the Winkler method (Carpenter, 1965) for the calibration of oxygen sensors.

2.2 Bottom mooring

High-resolution time series data from the southern region of the bay was obtained through deployment of a Wet Labs WQM (Water Quality Monitor) at station 6 on the Berg River transect at 50 m depth from 28 November 2013 to 27 November 2014 (Fig. 1). The WQM utilizes the conductivity, temperature, and depth (CTD) and DO sensors of SBE, and a WETLabs combination fluorometer and turbidity sensor (FLNTU). The CTD components of the WQM are fortified for long-term deployment by incorporating multiple active and passive antibiofouling technologies. The pump-controlled, TC-ducted system delivers a constant flow rate across the sensors that maximizes data coherence during sampling, and enhances the protection offered by two antibiofouling devices located on the inlet and outlet flow ducts. A SBE 43 DO sensor, explicitly engineered for pumped CTD applications provides stable, rapid-response DO measurements. The SBE 43 is a redesign of the Clark electrode sensor, which undergoes an 18-point automated calibration procedure at the factory (3 oxygen concentrations at 6 temperatures), and is characterized with temperature, pressure and salinity in the calibration equations. The SBE 43 is plumbed in-line with the CTD and benefits from the same passive biofouling protection provided in the CTD. The FLNTU uses a dual-LED single detector system and chlorophyll fluorescence is excited with a 470 nm LED. The FLNTU was configured for a chlorophyll measurement range of 0.02–50 mg m^{-3} .

BGD

12, 13283–13309, 2015

Seasonal, sub-seasonal and spatial fluctuations

G. C. Pitcher and
T. A. Probyn

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



2.3 Measured DO, DO equilibrium and Apparent Oxygen Utilization

Comparison of DO concentrations as measured by the integrated oxygen sensors of the WQM and CTD showed good correspondence. The measurements from these sensors were on average within 12% of the Winkler measurements. Apparent Oxygen Utilization (AOU) was determined as the difference between the equilibrium, or solubility value of oxygen and the measured concentration. The solubility value of the water was determined according to Garcia and Gordon (1992) as influenced by the temperature and salinity of the water.

3 Results

3.1 Variability along the 50 m depth contour

Alongshore bay characteristics were assessed through comparison of near-bottom variables (except for Chl *a*) along the 50 m depth contour as determined from linear interpolation (Fig. 2); a measure of *relative variability* along the contour was provided for each variable by a *coefficient of variation* (V ; Table 1). Mean V showed the physical variables of temperature (mean V 0.032) and particularly salinity (mean V 0.0006) to demonstrate the least variation, followed by the nutrient concentrations of NO_3^- , PO_4^{3-} and SiO_4^{2-} (mean V 0.12–0.18). The biological variable of Chl *a* demonstrated the greatest variation (mean V 0.63) and DO concentrations demonstrated intermediate variation (mean V 0.35).

Upwelling was most intense during late spring (November) with the coldest and least saline waters present in the south of the bay (off Elands Bay and the Berg River, Fig. 2a and b). Phytoplankton biomass maxima as indicated by subsurface Chl *a* maxima along the 50 m depth contour peaked in autumn also in the south of the bay (off the Berg River, Fig. 2c). As bottom temperatures and salinities increased during the course of summer and autumn, DO content declined with a corresponding increase in

BGD

12, 13283–13309, 2015

Seasonal,
sub-seasonal and
spatial fluctuations

G. C. Pitcher and
T. A. Probyn

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Seasonal, sub-seasonal and spatial fluctuations

G. C. Pitcher and
T. A. Probyn

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

AOU (Fig. 2d and e). During this period DO was always lowest in the south of the bay. Minimum DO concentrations were measured in April ranging from 0.11 mL^{-1} (Berg River) – 0.88 mL^{-1} (Lambert's Bay), representing an 8-fold variation along the 50 m contour. Winter mixing in June and July resulted in a marked increase in bottom temperature, salinity and DO with a drop in AOU. The transition to spring was evident in the appearance of colder, oxygen depleted water with a sharp increase in AOU. Winter Chl *a* minima were followed by increases in biomass in spring in the northern regions of the bay (off the Olifants River and Lambert's Bay).

Coincident with the seasonal drawdown of near-bottom DO within the bay was an increase in macronutrient concentrations. Mean bottom nutrient concentrations of NO_3^- and PO_4^{3-} tended to be highest during autumn (mean NO_3^- of 27.9 mmol m^{-3} in March; mean PO_4^{3-} of 2.74 mmol m^{-3} in April); with the highest concentrations occurring in the south of the bay. Concentrations of SiO_4^{2-} were highest in the spring (mean of 46.4 mmol m^{-3} in September). Winter mixing served to dilute bottom nutrient concentrations with minima in either June or July (mean NO_3^- of 14.9 mmol m^{-3} in July, mean PO_4^{3-} of 1.39 mmol m^{-3} and mean SiO_4^{2-} of 21.6 mmol m^{-3} in June).

3.2 Near-bottom DO concentrations as related to depth

Near-bottom DO concentrations are plotted against the depth at which they were measured during each of the 8 field studies (Fig. 3). Inshore stations ($< 20 \text{ m}$) were generally subject to greater variability in bottom DO. During late spring (November) bottom DO ranged from $1.30\text{--}2.82 \text{ mL}^{-1}$, and in summer (January) from $0.58\text{--}2.68 \text{ mL}^{-1}$, apart from a shallow inshore station off Lambert's Bay where DO exceeded 4 mL^{-1} . A marked downward shift in DO was evident in autumn (March and April). DO concentrations at stations $> 20 \text{ m}$ depth ranged from $0.16\text{--}1.51 \text{ mL}^{-1}$ in March and from $0.10\text{--}1.7 \text{ mL}^{-1}$ in April. The lowest DO concentrations ($0.10\text{--}0.22 \text{ mL}^{-1}$) were found in April at the central stations on the Berg River transect at depths between 31 and 69 m. During winter (June and July) bottom waters $< 68 \text{ m}$ depth were well ventilated

($\geq 3.1 \text{ mL L}^{-1}$), with DO concentrations $\leq 0.94 \text{ mL L}^{-1}$ confined to the outer limits of the bay at depths $> 79 \text{ m}$. With the onset of spring DO concentrations at depths $> 20 \text{ m}$ tended to decline to $\leq 2.45 \text{ mL L}^{-1}$ in September and $\leq 1.95 \text{ mL L}^{-1}$ in October. The lowest DO concentrations ranging from $0.22\text{--}0.46 \text{ mL L}^{-1}$ in October were again located on the Berg River transect between 28 and 61 m depth.

3.3 Temperature, nutrient and oxygen relationships

Temperature– and nutrient–oxygen relationships are presented for all surface and near-bottom data (Fig. 4). A positive correlation is found between temperature and DO with the lowest concentrations clearly associated with a narrow range in temperature centered around 9.9°C (Fig. 4a). Colder water with a higher DO content tended to be found towards the fringes of the bay particularly during spring (e.g., water of $< 9^\circ\text{C}$ and a DO concentration of $> 2 \text{ mL L}^{-1}$ was only found at a depth of $> 80 \text{ m}$). Also deviating from the general trend were several points depicting relatively warm water with a lower than expected DO content. These points represent either bottom waters off the Berg River in autumn (April) or off the Olifants River in spring (September).

Coincident in waters with high oxygen utilization and low DO are high macronutrients. Consequently a general negative correlation is evident in the relationships between NO_3^- , PO_4^{3-} , SiO_4^{2-} and DO. In examining the NO_3^- – DO relationship a high number of anomalous points were evident in depicting oxygen depleted water with relatively low NO_3^- concentrations (Fig. 4b). These points generally represented bottom waters off the Berg River; the anomaly was particularly evident during autumn (April).

Concentrations of NO_2^- were generally low ($< 1 \text{ mmol m}^{-3}$) in both surface and bottom waters irrespective of DO concentration (Fig. 4c). Notable exceptions occurred in bottom waters off the Berg River in autumn (April) and in surface waters of the inner stations off the Berg River in winter (June). The high NO_2^- concentrations ($1.33\text{--}6.61 \text{ mmol m}^{-3}$) in the bottom waters in April were confined to oxygen depleted waters

BGD

12, 13283–13309, 2015

Seasonal, sub-seasonal and spatial fluctuations

G. C. Pitcher and
T. A. Probyn

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



($\leq 0.32 \text{ mL L}^{-1}$), whereas the elevated concentrations ($1.38\text{--}1.90 \text{ mmol m}^{-3}$) in the surface waters in June were found in well-oxygenated waters ($\geq 4.27 \text{ mL L}^{-1}$).

SiO_4^{2-} and particularly PO_4^{3-} were more tightly correlated with DO than either NO_3^- or NO_2^- (Fig. 4d and e). Of interest was that the highest PO_4^{3-} concentrations were found in the low DO environment off the Berg River in autumn (April). There was no clear difference between surface and bottom NH_4^+ concentrations and no relationship with DO concentration. However, there was a tendency for elevated NH_4^+ concentrations to be found at shallow inner stations in either surface or bottom waters (Fig. 4f).

3.4 Across-shelf bay biomass and DO

Across-shelf transects off the Berg River capture the seasonal evolution of the intensity and distribution of hypoxia in relation to phytoplankton biomass distribution (Fig. 5). Upwelling was most intense during November and was characterized by the intrusion of a large volume of $< 10^\circ\text{C}$ water penetrating to within 5 m of the surface at some of the inner stations. A high biomass phytoplankton bloom evident at the outer stations in November (Chl *a* maxima $> 55 \text{ mg m}^{-3}$ located between 2 and 4 m depth at stations 7 and 8) intensified at the central and inner stations of the bay in January (Chl *a* maxima $> 100 \text{ mg m}^{-3}$ between 3 and 4 m depth at stations 2, 4 and 5). In March the bloom was present as a thin layer of exceptional biomass in association with intense stratification (Chl *a* maxima of between 100 and 135 mg m^{-3} centered between 9 and 12 m depth extended from station 3 to 7). At this time the phytoplankton assemblage in the surface waters was dominated by the dinoflagellate *Prorocentrum triestinum* (data not shown). Phytoplankton biomass declined from March through to July at which time Chl *a* concentrations through the water column were found to be $< 10 \text{ mg m}^{-3}$ at most stations. Of interest in April were the high Chl *a* concentrations within 1 or 2 m of the seafloor particularly at stations 5 and 7. In September elevated phytoplankton biomass was again observed offshore (subsurface Chl *a* maxima $> 20 \text{ mg m}^{-3}$ at stations 7 and

BGD

12, 13283–13309, 2015

Seasonal, sub-seasonal and spatial fluctuations

G. C. Pitcher and
T. A. Probyn

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



8) and by October high biomass was evident at the inner stations of the transect (Chl *a* maximum > 100 mg m⁻³ at 11 m depth at station 2).

During the period of intense upwelling in November the 10 °C isotherm was closely aligned to the 2 mL⁻¹ oxygen contour except at the outer stations of the transect. By January DO concentrations were < 0.5 mL⁻¹ in a small volume of bottom water at the inner stations. By March the volume of this oxygen depleted water had increased and expanded to include central stations as stratification increased and the oxycline strengthened. Downwelling and a general deepening of the oxycline during autumn caused the ventilation of bottom waters at the inner stations (1 and 2). By April the pool of bottom water of < 0.5 mL⁻¹ DO extended beyond the outer limits of the transect. In June and July winter mixing caused isothermal conditions and ventilation of bay bottom waters. The intrusion of bottom water of < 10 °C in early September indicated the transition to upwelling conditions and was again accompanied by DO concentrations of < 2 mL⁻¹. Towards the end of October uncharacteristic downwelling was associated with bottom DO concentrations of < 0.5 mL⁻¹ specifically at the central stations of the transect.

3.5 Bottom mooring time series

A time series is presented of temperature, salinity, DO, DO solubility, AOU and Chl *a* measured hourly at 50 m depth at station 6 of the Berg River transect from 28 November 2013 to 27 November 2014 (Fig. 6). A steady increase in temperature and salinity was observed during summer and autumn following the minimum values of 8.66 °C and 34.66 ppt measured in late November (Fig. 6a). During this time there was a general decrease in DO, coincident with a small decrease in DO solubility, in the development ultimately of anoxic (< 0.02 mL⁻¹) conditions in late March 2014 (Fig. 6b; note reversal of DO solubility axis). The relatively small change in DO solubility ensured that trends in AOU at this time closely followed those of observed DO (Fig. 6c; note reversal of AOU axis).

BGD

12, 13283–13309, 2015

Seasonal, sub-seasonal and spatial fluctuations

G. C. Pitcher and
T. A. Probyn

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



**Seasonal,
sub-seasonal and
spatial fluctuations**G. C. Pitcher and
T. A. Probyn

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

The general decline in DO in summer and autumn was marked by abrupt dips in DO clearly associated with episodic increases in bottom water Chl *a* concentrations (Fig. 6d). The peaks in near-bottom fluorescence are presumed to indicate the sinking of organic matter, and signal periods of increased oxygen utilization. The first and second of these events in mid-December and early-January were clearly linked to the development of hypoxic conditions ($< 1.42 \text{ mL L}^{-1}$). Similarly the development of anoxic conditions towards the end of March corresponded to an episodic increase in bottom Chl *a* concentration of even greater magnitude. The conditions of bottom anoxia were further maintained by similar increases in bottom Chl *a* concentrations in early May.

Bottom waters were abruptly ventilated ($\text{DO} > 5 \text{ mL L}^{-1}$) at the end of May by deep mixing as revealed by a coincident increase in bottom temperature. The increased DO concentrations, despite further decreases in DO solubility, resulted in closer alignment of observed DO concentrations and estimates of AOU. Mid-winter cooling of bottom waters was associated with a decline in bottom DO prior to further mixing in late July. Bottom waters remained ventilated until a sharp decline in temperature, salinity and DO in early September signified the spring transition to the upwelling season. Again events of very low DO in early October ($< 0.1 \text{ mL L}^{-1}$), late October and in November ($< 0.05 \text{ mL L}^{-1}$) appear to be coupled to episodes of increased bottom Chl *a* concentrations.

4 Discussion

4.1 Spatial and seasonal variability in DO

St Helena Bay is formed by Cape Columbine, a promontory that modulates the upwelling process by influencing across-shelf structure in alongshore flow creating a zone of retention in the lee of the Cape (Duncan and Nel, 1969; Holden 1985; Penven et al., 2000; Fawcett et al., 2008). Upwelling is intensified off the cape and the resulting upwelling plume formed off Columbine tends to isolate the nearshore area from the

BGD

12, 13283–13309, 2015

**Seasonal,
sub-seasonal and
spatial fluctuations**G. C. Pitcher and
T. A. Probyn[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

offshore domain, inducing retention on the coastal side of the plume. Increased residence time within the cape-associated embayment is apparent through the presence of warmer water and increased water column stratification which function to enhance productivity (Pitcher and Weeks, 2006; Weeks et al., 2006). The exceptional levels of phytoplankton biomass present during this study confirm these observations and are considered a major driver of seasonal hypoxia within the area. The significant contribution of dinoflagellates to the high biomass observed during late summer and autumn also serves to support previous observations of a high incidence of red tides within the bay which have been shown to cause events of episodic anoxia (Pitcher and Probyn, 2011; Pitcher et al., 2014)

Isolation of the bay from the shelf region through limited across-shelf exchange is also apparent in the bottom oxygen regime in that the relationship between DO and temperature in the bay does not follow the structure of these properties offshore (Pitcher et al., 2014; Lamont et al., 2015). Across-shelf observations during the present study further showed that seasonal hypoxia develops within the inner and central regions of the bay, coincident with the seasonal development of exceptional phytoplankton blooms, and indicative of the local drawdown of DO (Fig. 5). The pool of hypoxic bottom water was shown to expand seasonally to extend beyond the boundary of the bay during autumn. Wind mixing to a depth of around 70 m reoxygenated most of the bay in winter (Fig. 3). At this time oxygen depleted waters were confined to deeper waters at the outer limits of the bay. The incursion of colder bottom water with the spring transition to upwelling conditions was again associated with lower DO concentrations.

Apart from the identification of cyclonic circulation within St Helena Bay (Holden, 1985), current patterns within the bay remain poorly described. Patterns of cyclonic circulation have nevertheless been supported by the model output of Penven et al. (2000) and these circulation patterns are shown to contribute to the creation of a dynamic boundary between the coastal and offshore domains. However, the location and dynamics of the cyclonic eddy important in determining the outer and northern boundaries of the bay require further investigation. These circulation patterns are likely to

contribute to the considerable alongshore and across-shelf variation described in this study. The tendency for the highest Chl *a* concentrations and the lowest bottom water DO concentrations to occur in the southern regions of the bay is considered to reflect diminished wind-driven vertical mixing, weaker circulation, reduced lateral exchange and enhanced retention.

4.2 Evidence of denitrification

Oxygen is consumed during respiration and remineralization of organic matter, nitrification, and redox reactions (Peña et al., 2010). The remineralization of organic matter consumes oxygen both directly through oxic respiration and indirectly through oxidation of a variety of metabolites. In shelf environments such as St Helena Bay remineralization of particulate organic input is likely to be the main consumer of oxygen in sub-surface waters and water column hypoxia or anoxia arises from the imbalance in the transport rates of organic matter and oxygen into these waters.

As DO concentrations in bottom waters approach levels of anoxia major changes in biogeochemical cycles occur and respiration becomes sequentially based on oxidized forms of inorganic nitrogen, manganese, iron and other trace constituents prior to the onset of sulfate (SO_4^{2-}) reduction (Codispoti et al., 2005). Under these conditions of oxygen deficiency the process of denitrification in which bacteria use nitrogen oxides (NO_3^- , NO_2^- , NO and N_2O) as terminal acceptors in their metabolism is probably the single most important respiratory pathway in the water column. This process permits organisms to continue what is essentially a form of respiration in which the end product is dinitrogen (N_2) although intermediates sometimes accumulate. At this time NO_3^- is the most abundant electron acceptor; for this reason denitrification is a function of available NO_3^- but is also inhibited by the presence of oxygen occurring only when DO concentrations are $< 0.1\text{--}0.2\text{ mL L}^{-1}$, i.e. suboxic conditions (Codispoti et al., 2005).

Denitrification leaves an imprint on water properties in terms of a NO_3^- deficit as described for other parts of the Benguela upwelling system; whereby NO_3^- concentra-

BGD

12, 13283–13309, 2015

Seasonal, sub-seasonal and spatial fluctuations

G. C. Pitcher and
T. A. Probyn

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



**Seasonal,
sub-seasonal and
spatial fluctuations**G. C. Pitcher and
T. A. Probyn[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

tions are significantly less than predicted by the Redfield ratio (Tyrrell and Lucas, 2002). Denitrification in St Helena Bay was clearly evident through its influence on the NO_3^- –DO and NO_2^- –DO relationships in near-bottom waters (Fig. 4). The general asymmetry in the scatter of points in the NO_3^- –DO relationship (not observed in the PO_4^{3-} – and SiO_4^{2-} –DO relationships) is indicative of a NO_3^- deficit as a consequence of denitrification. This NO_3^- deficit is particularly evident in autumn (April) off the Berg River where DO concentrations are at their lowest at this time of the year (Fig. 4b). Chemical features of water column suboxia present at that time also included NO_2^- maxima (Fig. 4c). NO_2^- is an intermediate in the denitrification process; hence the elevated NO_2^- concentrations off the Berg River in autumn (April). Similar observations of elevated NO_2^- have been observed off the coast of Peru under conditions of intense denitrification when oxygen concentrations were $< 0.2 \text{ mL L}^{-1}$ (Codispoti et al., 1986).

Although the large flux of particulate organic matter into the bottom waters of St Helena Bay and its remineralisation are expected to enhance NO_3^- concentrations, the enrichment of NO_3^- at least in the southern part of the bay is likely to be reduced in autumn by denitrification. Suboxic electron acceptors such as NO_3^- are also considered to significantly delay the onset of anoxia and sulfide production (Codispoti et al., 2005).

4.3 Episodic bottom anoxia

Key ecological controls in bottom water hypoxia and anoxia involve the production and delivery of labile organic matter to these waters. Oxygen depletion in most stratified coastal systems is ultimately supported by high rates of particulate organic input from algal production in overlying waters driven in turn by inputs of inorganic nutrients (Kemp et al., 2009). The seasonal decline in DO in St Helena Bay is well documented and has been considered to be driven by a seasonal supply of organic matter to the bottom waters of the bay (Bailey, 1991; Pitcher et al., 2014). However, the sharp declines in DO as observed in this study, superimposed on the more gradual seasonal decline in DO have not been previously reported. These events of hypoxia and anoxia were as-

sociated with episodic deposition of organic matter as indicated by increases in bottom Chl *a* concentrations (Fig. 6a).

The flow and fate of photosynthetically fixed organic matter is often determined by the manner in which phytoplankton die, which in turn may constrain water column biogeochemistry (Bidle, 2014). The observations in St Helena Bay of large, abrupt increases in bottom fluorescence indicate events of phytoplankton mortality and rapid vertical flux of particulate matter to the sediment. Phytoplankton death in response to adverse abiotic or biotic environmental conditions serves to mediate bloom-to-postbloom transitions which play an important role in the biogeochemical fate of phytoplankton by critically influencing their coupling to the marine ecosystem pathways of grazing, sinking and the microbial loop as well as the biogeochemistry of the water column. Cell death has traditionally been considered to invoke cell lysis, the release of DOM, and stimulation of the microbial loop in the upper water column. However, programmed cell death, transparent exopolymer production and aggregate formation have now been suggested to provide a mechanistic role in the vertical flux of organic matter into deeper waters (Bidle, 2104). The role of such mechanisms in determining the fate of the exceptional blooms observed in St Helena Bay and in dictating rapid increases in bottom AOU and consequent sub-seasonal events of hypoxia and anoxia requires further investigation.

5 Conclusions

Considerable across-shelf and alongshore variability in bottom DO concentrations in the St Helena Bay region is attributed to circulation patterns that contribute to a dynamic boundary between the bay and shelf domains. Cyclonic circulation is considered to result in the very high level of phytoplankton biomass observed in late summer and autumn in the southern region of the bay. Here concentrations of DO are consistently lower during the upwelling season and the suboxic environment present in autumn results in a biogeochemical shift to denitrification. In addition to the seasonal drawdown of DO, sub-seasonal fluctuations in DO leading to events of hypoxia and/or

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12, 13283–13309, 2015

Seasonal, sub-seasonal and spatial fluctuations

G. C. Pitcher and
T. A. Probyn

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



anoxia were observed in response to episodic deposition of organic matter dictated by cell death processes. The observations of this study contribute to a greater understanding of the scales of oxygen depletion in St Helena Bay and will further contribute to interpretation of historical data sets in the future assessment of long-term change.

5 In monitoring the response of the bay to climate change the need for implementation of a consistent sampling protocol with respect to sampling intervals and station positions is clearly evident.

Acknowledgements. Andre du Randt and Lisa Mansfield are thanked for their extensive contribution to data collection in the field.

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Seasonal, sub-seasonal and spatial fluctuations

G. C. Pitcher and
T. A. Probyn

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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Seasonal, sub-seasonal and spatial fluctuations

G. C. Pitcher and
T. A. Probyn

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Seasonal, sub-seasonal and spatial fluctuations

G. C. Pitcher and
T. A. Probyn

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Seasonal, sub-seasonal and spatial fluctuations

G. C. Pitcher and
T. A. Probyn

Table 1. *Coefficients of variation (V)* providing a measure of relative variability for 8 variables along the 50 m depth contour within St Helena Bay as determined during 8 field studies undertaken between 26 November 2013 and 20 October 2014.

	26–28 Nov 13	20–23 Jan 14	3–6 Mar 14	7–10 Apr 14	18–21 Jun 14	28–31 Jul 14	8–11 Sep 14	20–13 Oct 14	Mean V	Range V
Temperature	0.067	0.036	0.025	0.018	0.010	0.044	0.024	0.028	0.032	0.010–0.067
Salinity	0.0014	0.0005	0.0004	0.0006	0.0007	0.0005	0.0004	0.0003	0.0006	0.0003–0.0014
Chl <i>a</i>	0.68	0.42	0.89	0.89	0.52	0.41	0.99	0.25	0.63	0.25–0.99
DO	0.28	0.15	0.52	0.56	0.11	0.21	0.28	0.68	0.35	0.11–0.68
AOU	0.19	0.07	0.10	0.06	0.15	0.41	0.06	0.10	0.14	0.06–0.41
NO ₃ ⁻	0.10	0.13	0.06	0.20	0.25	0.34	0.03	0.04	0.14	0.03–0.34
PO ₄ ³⁻	0.12	0.07	0.06	0.16	0.15	0.23	0.08	0.09	0.12	0.06–0.23
SiO ₄ ²⁻	0.15	0.13	0.27	0.21	0.21	0.11	0.19	0.18	0.18	0.11–0.27

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)


Seasonal, sub-seasonal and spatial fluctuations

G. C. Pitcher and
T. A. Probyn

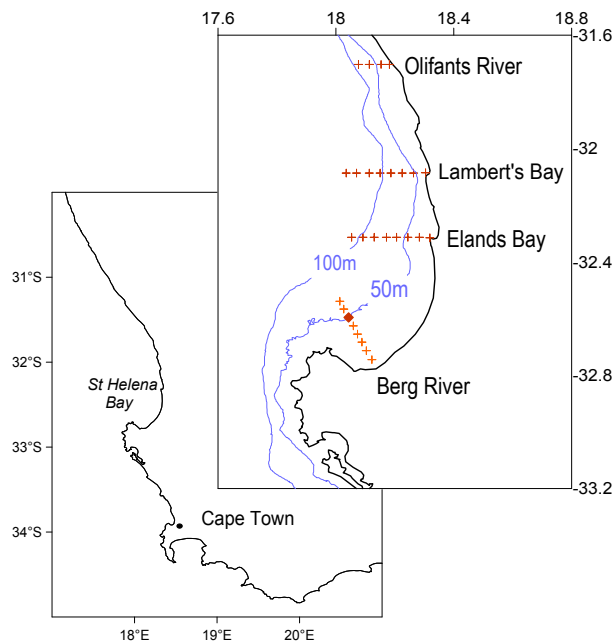


Figure 1. Map indicating station positions in St Helena Bay of 4 transects sampled at intervals ranging from 5–10 weeks between November 2013 and October 2014. A Wet Labs WQM (Water Quality Monitor) was moored on the seafloor at station 6 on the Berg River transect from 28 November 2013 to 27 November 2011.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[◀](#)
[▶](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)


Seasonal, sub-seasonal and spatial fluctuations

G. C. Pitcher and
T. A. Probyn

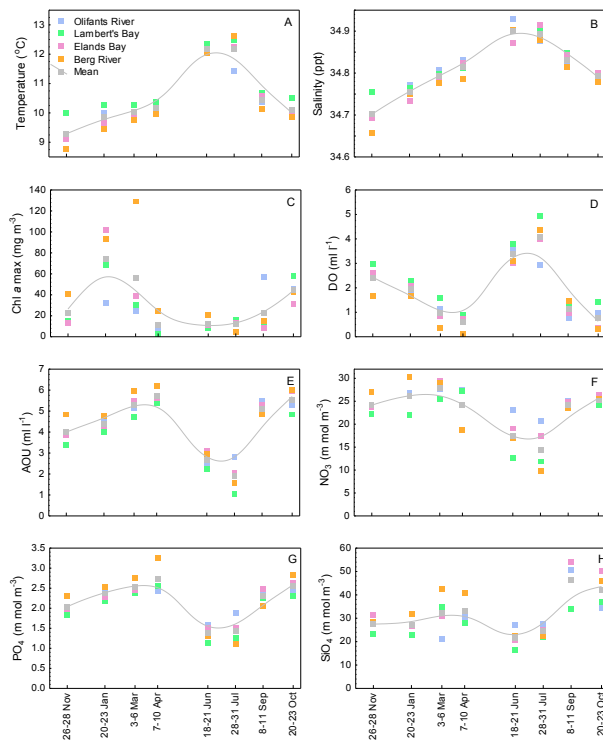


Figure 2. A time series of near-bottom (a) temperature and (b) salinity, (c) the water column Chl *a* maximum, and near-bottom (d) DO, (e) AOU, (f) NO₃⁻ (g) PO₄³⁻ and (h) SiO₄²⁻ concentrations from the 50 m depth contour along the Olifants River, Lambert's Bay, Elands Bay and Berg River transects. A distance weighted least squares fit is applied to the mean values.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

Seasonal, sub-seasonal and spatial fluctuations

G. C. Pitcher and
T. A. Probyn

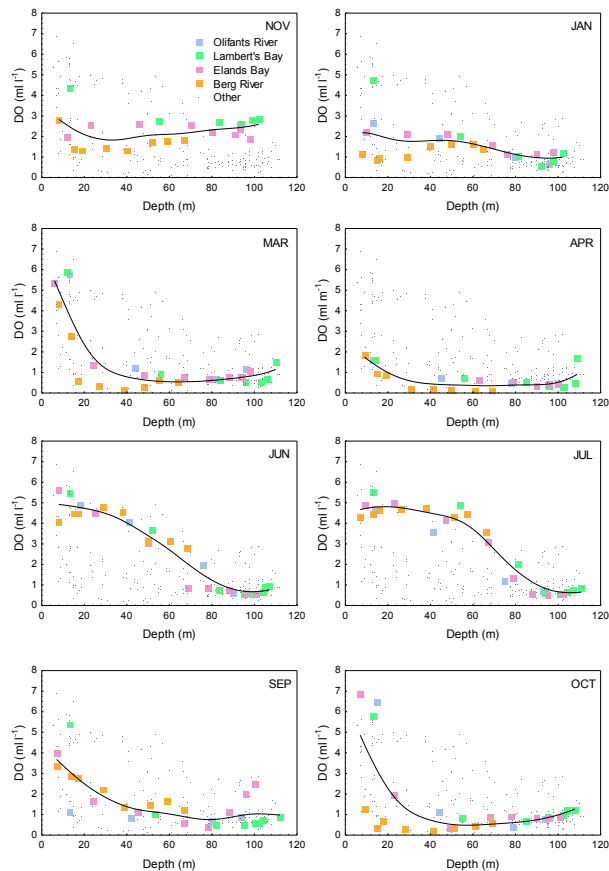


Figure 3. Near-bottom DO concentrations for all stations (depths) as determined during 8 field studies: **(a)** 26–28 November 13, **(b)** 20–23 January 14, **(c)** 3–6 March 14 **(d)** 7–10 April 14, **(e)** 18–21 June 14, **(f)** 28–31 July 14, **(g)** 8–11 September 14 and **(h)** 20–23 October 14 (fit: distance weighted least squares).

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

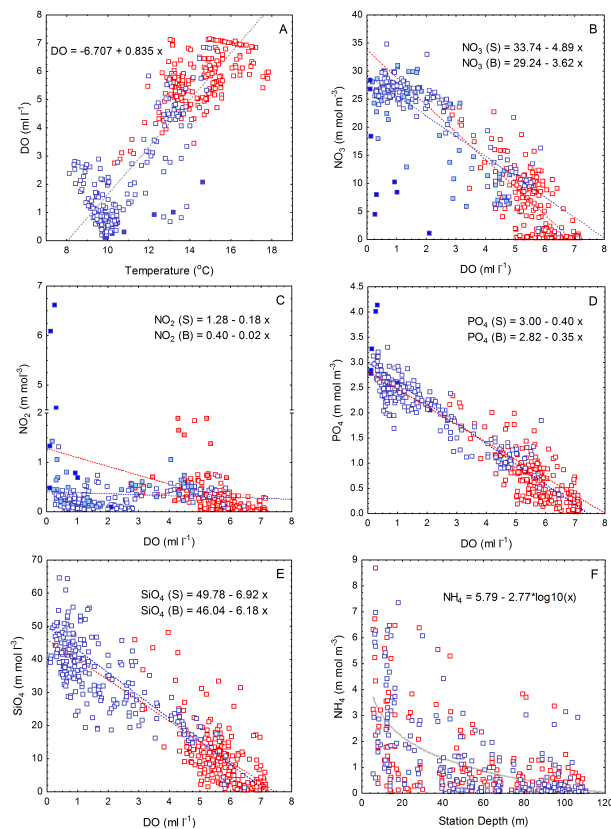
Seasonal,
sub-seasonal and
spatial fluctuationsG. C. Pitcher and
T. A. Probyn

Figure 4. Relationships between DO and **(a)** temperature **(b)** NO_3^- **(c)** NO_2^- **(d)** PO_4^{3-} **(e)** SiO_4^{2-} , and between station depth and **(f)** NH_4^+ . Red squares represent surface and blue squares near-bottom measurements. Shaded squares indicate measurements off the Berg River and solid squares indicate measurements off the Berg River in April.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



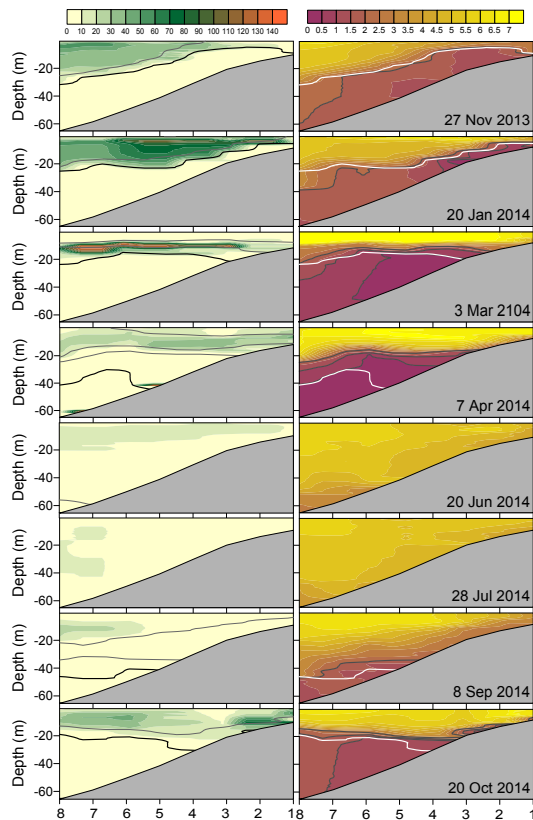


Figure 5. Across-shelf structure of Chl *a* (left panel) and DO (right panel) along the Berg River transect determined during 8 field studies between the 27 November 2013 and 20 October 2014. On the left isolines depict temperatures at 2°C intervals with the isoline in bold depicting a temperature of 10°C. On the right the black contours represent DO concentrations of 2, 1 and 0.5 mLL⁻¹ and the white isoline a temperature of 10°C. Chl *a* scale bar units are mg m⁻³ and DO scale bar units are mLL⁻¹.

Seasonal,
sub-seasonal and
spatial fluctuations

G. C. Pitcher and
T. A. Probyn

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



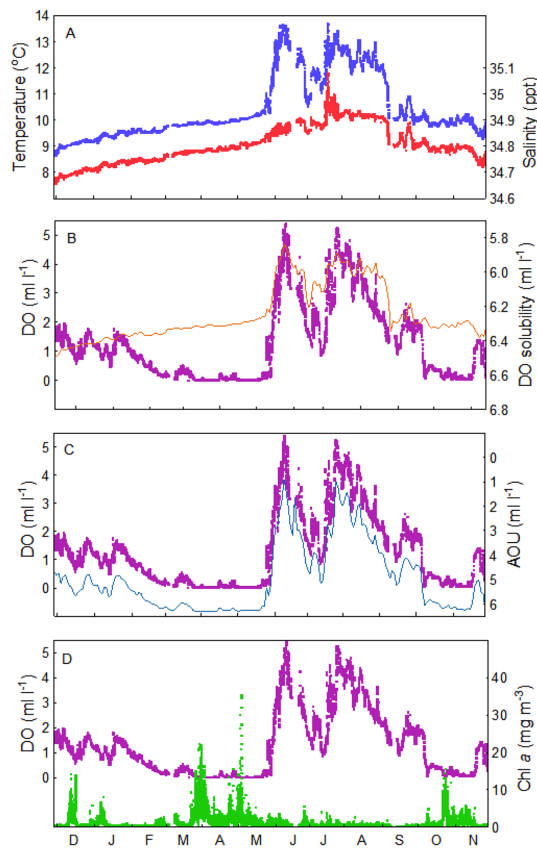


Figure 6. A time series of **(a)** temperature (blue) and salinity, **(b)** observed DO (purple) and DO solubility, **(c)** DO and AOU and **(d)** DO and Chl *a* concentrations measured hourly at 50 m depth at station 6 of the Berg River transect from 28 November 2013 to 27 November 2014. Note reversal of DO solubility and AOU axes.

Seasonal, sub-seasonal and spatial fluctuations

G. C. Pitcher and T. A. Probyn

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

