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GREAT AUSTRALIAN BIGHT RESEARCH PROGRAM

The Great Australian Bight Research Program is a collaboration between BP, CSIRO, the South Australian Research and Development Institute (SARDI), the University of Adelaide, and Flinders University. The Program aims to provide a whole-of-system understanding of the environmental, economic and social values of the region; providing an information source for all to use.

CONTENTS

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1. EXECUTIVE SUMMARY

Theme 2 has produced significant advances in knowledge of pelagic ecosystem structure and function in the eastern and central Great Australian Bight (GAB). It represents the first detailed study of the influence of variations in enrichment processes on lower trophic ecosystem dynamics in shelf, slope and offshore waters in the GAB, and characterised the biota from sizes of microns to metres. Sampling biota from microbes to tuna requires a large diverse team, using a wide range of technologies and methodologies. Inherent to this study were the multiple spatial and temporal scales that affect the composition, distribution and abundance of species. Given this complexity and the complexities and precision of any one sampling method, a multiple-lines-of-evidence approach was adopted. This study uncovered distinct spatial and temporal differences in enrichment, food webs and productivity of the eastern and central GAB.

Shelf enrichment processes were the focus of Project 2.1 which examined temporal patterns in the data rich eastern GAB region, and available datasets for the central GAB. These data, collected over a variety of spatial and temporal scales, were used to address key project hypotheses in an approach that first characterised variation in water masses and enrichment processes in shelf waters across the GAB. The associated responses of organisms at the base of the food web (microbes (viruses, bacteria), phytoplankton (pico- (< 2 µM), nano- (2 – 5 µm), and micro-phytoplankton (>5 µm)) and meso-zooplankton size) were then examined.

Significant advances in knowledge of offshore pelagic ecosystem structure and function in Project 2.2 were made possible with the voyage on the MNF *RV Investigator* (Kloser et al. 2016). A key finding being the higher than expected production in the central upper slope region driven by biological processes. It was also noteworthy that there were more similarities than differences between the offshore central and eastern GAB regions. Novel use of bioacoustics and Continuous Plankton Recorder (CPR) sampling provided greater spatial and temporal coverage and improved the generalisation of the findings.

Combining the findings from the two projects provides new insights into lower and middle trophic ecosystem dynamics in the GAB that are critical for the development of trophodynamic models for the region. We developed conceptual and quantitative models of pelagic ecosystem processes that provide a basis for understanding potential future changes in ecosystem structure and function, whether driven by anthropogenic or climate related factors. A key finding of this work is the fact that the central GAB plays a more important role in overall GAB ecosystem productivity than previously thought. This is reflected in the base nitrogen and reworked nitrogen trophic transfer to zooplankton and micronekton. This new knowledge should be reflected in future plans to monitor and manage marine resources in the region. For example monitoring of the central GAB region should be considered where higher production and micronekton biomass were found than previously expected.

2. INTRODUCTION

2.1 Overview

The Great Australian Bight (GAB) is part of the world's only northern boundary current system, the Flinders Current System, which extends from western Tasmania to south-western Western Australia. The eastern GAB shelf is characterised by enhanced primary and secondary productivity that is underpinned by coastal upwelling in the austral summer (Middleton and Cirano 2002, Kämpf et al. 2004, McClatchie et al. 2006, Middleton and Bye 2007, van Ruth et al. 2010a, b). Increased productivity supports large populations of small pelagic fish, including sardine and anchovy (Ward et al. 2001a, b, 2006, 2011), and important populations of large marine species, including southern bluefin tuna (Hobday et al. 2009, Fujioka et al. 2010, Basson et al. 2012), Australian sea lions (Goldsworthy et al. 2013) and pygmy blue whales (Gill et al. 2011). The GAB is a region of global conservation significance, supporting valuable fishing and aquaculture industries and important regional ecotourism industries (GABRP Theme 6.3). Future management of this economically and ecologically important region requires a thorough understanding of variations in the lower trophic levels of the food web which underpin overall ecosystem productivity (microbes, phytoplankton, zooplankton) in an area under increasing pressure from anthropogenic activities and a changing climate.

Important information about ecosystem structure and function can be derived from the taxonomic composition and size distribution of microbial and plankton assemblages and their variations in response to such key ecosystem drivers as nutrient enrichment through upwelling. In other systems, high autotrophic biomass and productivity in response to enrichment of the euphotic zone is associated with the dominance of large phytoplankton (diatoms), and the prevalence of an efficient 'classical' food web (i.e. diatoms to zooplankton to fish; Ryther 1969, Cushing 1989). In the absence of significant enrichment through physical processes, when well-lit waters become devoid of nutrients, a less efficient 'microbial' food web underpinned by picophytoplankton dominates, with high rates of nutrient recycling by microbes providing minimal enrichment via biological means. This study represents the first investigation of the influence of variations in physical/biological enrichment processes on primary productivity and food web dynamics in the GAB, and the implications these changes may have for overall ecosystem productivity.

As outlined in the most recent and comprehensive background review of the GAB ecosystem (Rogers et al. 2013), there is limited data and conceptual understanding of ecosystem structure and food web function, especially in the deep-water habitats of the central GAB. Data are needed on the microbial, planktonic and micronekton communities of the GAB to develop conceptual and numerical models of ecosystem function and inform future impact assessments. Data on patterns of regional, intra- and inter-annual variability are needed to enable discrimination between long-term trends and rapid changes in ecosystem structure and food web function. This information is also needed to explain patterns in the distribution, abundance and migration of apex predators and their vulnerability to anthropogenic impacts. These knowledge gaps need to be addressed in both the central GAB (where exploratory drilling and potentially other oil and gas activities may occur) and in shelf and slope waters of the eastern GAB that may be impacted.

The scientific review of the GAB (Rogers et al. 2013) identified that contrasting ecological processes predominate in the shelf and offshore eastern and central GAB. These are driven by spatial and temporal variations in meteorological and oceanographic processes, which govern the supply of nutrients and light that underpin the productivity of these ecosystems. Quantifying differences in pelagic ecology and food web structure will provide conceptual insights into how these systems function, and facilitate the development of tools and protocols for monitoring ecological indicators of the pelagic ecosystem. Monitoring is vital to assess potential impacts of anthropogenic and climate-driven environmental variation on the pelagic ecosystem of the GAB. This will assist in promoting the sustainable management of its marine resources. To underpin sustainable management, regarding the ecosystem structure, function and dynamics the following knowledge gaps were identified in the literature review (Rogers et al. 2013):

1. Micro- and macro-nutrient concentrations, sources and sinks

2. Microbial, phytoplankton, zooplankton and ichthyoplankton abundance and community composition

3. Macro-zooplankton and micronekton diversity, distribution, abundance and trophic linkages to iconic and apex predators.

To address these knowledge gaps several key hypotheses were proposed to be tested:

1. That the microbial food web is the dominant planktonic food web in shelf waters of the eastern GAB and that the more efficient classic food web only occurs in the eastern GAB during periods of nutrient-rich upwelling. Spatial and temporal shifts in the influence of upwelling and downwelling in the eastern GAB trigger shifts in food web structure between the microbial loop and the classic diatom dominated food web.
2. That shifts in food web structure will have implications for the size structure of the zooplankton community in shelf waters of the eastern GAB and, consequently, the biomass of upper trophic levels.
3. The “microbial food web” is the dominant planktonic food web over the deep GAB continental margin, particularly in the central GAB where year-round downwelling is thought to be the prevailing cross-margin flow, and that the more efficient “classic food web” only dominates in the eastern GAB during periods of nutrient-rich upwelling.
4. That the zooplankton and micronekton communities of the central GAB continental margin have lower biomass, smaller species, different composition and longer trophic pathways than those on the eastern GAB. This is due to the nutrient source being “microbial loop” dominated in the central GAB and “classical” food web dominated in the eastern GAB.

Two projects were designed to address the identified knowledge gaps and test the hypotheses to provide new insights into ecosystem dynamics in the GAB that were seen as critical for the development of trophodynamic models for the region: The two projects were based on the shelf and offshore GAB:

- Project 2.1: Spatial and temporal variability in shelf microbial and plankton communities in the Great Australian Bight; addressing hypotheses 1 and 2 above.

- Project 2.2: Characterise spatial variability of offshore/slope plankton, and micronekton communities; addressing hypotheses 3 and 4 above.

Knowledge gained from these two projects will assist future developments and potential impacts to be placed in a regional and global context.

3. PROJECTS

3.1 Project 2.1: Spatial and temporal variability in shelf microbial and plankton communities in the Great Australian Bight.

3.1.1 Objectives

Project 2.1 was designed to address two key hypotheses (hypotheses 1 and 2) with the following objectives:

1. Identify and compare inter-annual, seasonal and spatial variability in the taxonomic composition and size distribution of the microbial, phytoplankton and zooplankton assemblage in shelf waters of the eastern and central GAB to test the hypothesis that spatial and temporal shifts in the influence of upwelling and downwelling in these regions trigger shifts in food web structure between the microbial loop and classic diatom dominated food web.

2. Derive empirical relationships between taxonomic composition and size structure of plankton to test the hypothesis that shifts in food web structure will have implications for the size structure of the zooplankton community and, consequently, the biomass of upper trophic levels.

3. Identify key environmental drivers of observed variability in species composition and size spectrum of microbes and plankton (e.g. upwelling strength, nutrient concentrations, primary productivity).

4. Compare inter-annual patterns in microbial and planktonic ecosystem structure and sardine egg densities.

3.1.2 Key results and discussion

Project 2.1 was primarily focused on the analysis of temporal patterns in existing physical, chemical and biological data from the data rich eastern GAB region. However, we also examined available datasets for the central GAB, to complement work conducted in Project 2.2 to investigate spatial patterns in food web dynamics across the GAB. These data, collected over a variety of spatial and temporal scales, were used to address key project hypotheses in an approach that first characterised variation in water masses and enrichment processes in shelf waters across the GAB, then examined the associated responses of organisms at the base of the food web (microbes (viruses, bacteria), phytoplankton (pico- (< 2 µm), nano- (2 – 5 µm), and micro-phytoplankton (>5 µm)) and meso-zooplankton). Our work provides new insights into lower trophic ecosystem dynamics in the GAB that are critical for the development of trophodynamic models for the region. We developed

conceptual and quantitative models of pelagic ecosystem processes that provide a basis for understanding potential future changes in ecosystem structure and function, whether driven by anthropogenic or climate related factors. Key findings, and their role in the evaluation of project hypotheses and objectives, are outlined below.

Environmental drivers

" Identify key environmental drivers of observed variability in species composition and size spectrum of microbes and plankton (e.g. upwelling strength, nutrient concentrations, primary productivity)."

A ten-year data set of wind stress and remote sensed primary productivity, was coupled with a five-year data set of *in situ* water column measurements (temperature, salinity, irradiance and dissolved nutrients) to assess key drivers of variations in enrichment and primary productivity in the eastern GAB. Consistent with previous research (Kämpf et al. 2004, Middleton and Bye 2007, van Ruth et al. 2010a, b) we found that:

- Seasons can be characterised by the dominant alongshore windstress (AWS), with upwelling favorable winds prevailing through summer (November-April), and downwelling favourable winds dominant in winter (May-October).
- Inter- and intra-seasonal variability in AWS drove marked variation in seasonal primary productivity between years.
- More importantly, our results provided new information regarding the timing, intensity and duration of upwelling, and the potential influence of upwelled waters on primary productivity.

Specifically, key findings were that:

- The length of an upwelling season did not dictate its intensity or productivity, and long, intense seasons were not necessarily the most productive.
- It was important to differentiate between upwelling events (indicated from AWS) and enrichment events (as indicated by $NO_x > 2$ µM; temperatures < 15°C and salinities < 35.6 psu in the euphotic zone). Specifically, AWS was not a good indicator of enrichment in the euphotic zone in the early upwelling season (November-December).
- The early upwelling season represents a pre-conditioning period that is critical in governing the intensity of enrichment in the euphotic zone during the late upwelling season. The intensity and number of upwelling/downwelling events through the pre-conditioning period dictate the volume of nutrient rich water drawn onto the shelf in the Kangaroo Island pool that is available to be brought into the euphotic zone during subsequent, late season upwelling events.
- The eastern GAB can be considered a region subject to moderate enrichment and, generally, moderate rates of primary productivity on a global scale.

With a clearer understanding of the influence of event scale variations in upwelling and downwelling on enrichment and primary productivity in the eastern GAB, we propose a refined conceptual model for the region, building on the work of van Ruth et al. (2010a, b). The model details five different meteorological/oceanographic scenarios that are likely to occur in the eastern GAB, and their influence on lower trophic ecosystem dynamics and productivity (Fig. 3.1-1):

- Winter-mixing: downwelling conditions, well mixed water column, no enriched water entering the euphotic zone. Pico-phytoplankton underpinning a microbial food web, and low primary productivity.

- Preconditioning: Upwelling favorable winds with an enriched bottom layer of water on the shelf, but no enrichment of euphotic zone. Pico-phytoplankton underpinning a microbial food web, and low primary productivity.
- Moderate upwelling: Upwelling favorable conditions, moderate enrichment of the ~bottom third of the euphotic zone. Micro-phytoplankton underpinning a classic food web and higher primary productivity, with a microbial food web in overlying waters.
- Strong upwelling: Upwelling favorable conditions with significant enrichment of the ~bottom two thirds the euphotic zone, at times approaching the surface. Micro-phytoplankton underpinning a classic food web and highest primary productivity, with a microbial food web in overlying waters.
- Suppression: downwelling conditions, enhanced mixing, suppression of enrichment, with a multivorous food web based on pico- and micro-phytoplankton, and reduced primary productivity.

Total ecosystem productivity in the eastern GAB depends on the combination of these scenarios in a given season/year, and will be further influenced by variations in the duration and intensity of individual events (i.e. within scenario variation).

Further information on water mass characteristics and spatial variations in the influence of upwelling and downwelling across the wider GAB shelf region was provided through the analysis of over 10 years of data obtained from Conductivity Temperature and Depth (CTD) instruments that were attached to Australian sea lions. About 20,000 temperature and salinity profiles were recorded across ~ 1,000 km of shelf, covering up to 10 months of the year, including 4–6 months through the upwelling season. All the data are free to access, and stored on the Ocean Current web portal of the Australian Integrated Marine Observing System (IMOS; see http://oceancurrent.imos.org.au/aatams.php). This dataset was critical for evaluating the objectives of this project as it represents the only source of sub-surface data available in some areas of the GAB, especially the more remote regions in the central GAB where there is a paucity of ship-based CTD profiles, and the only source of near-real time sub-surface observations in the GAB. Key findings regarding spatial and temporal variations in water mass characteristics across the broader GAB shelf include:

- The water column was well-mixed from surface to bottom during winter (June to September). The set-up of stratification occurred in Spring (November), with wide spread stratification of the water column over the shelf in Summer (December to February). The breakdown of stratification occurred in Autumn (March to May).
- Cold water originating from the slope was present on the shelf south of Eyre Peninsula in December, which then moves north-westerly toward Cape Bauer by March/April, after which slope water was no longer observed on the shelf.
- The rare occurrence of cold (< 15°C) water reaching the surface during the upwelling season, a phenomenon that was not observed in the other long-term datasets analysed for the project.
- The maximum spatial extent of upwelled water occurs over the GAB shelf during March and April.
- The westward extent of upwelled water reaches along the coast as far as ~133.5°E.
- The long time-series of data analysed confirm that the upwelled water mass, and thus significant enrichment of waters in the euphotic zone, is restricted to the eastern GAB, and areas close to the coast as far west as Cape Bauer. Aside from these nearshore regions, water mass characteristics in the central GAB reveal little evidence of upwelled water

(temperatures < 15°C and salinities < 35.6 psu), which implies the absence of significant enrichment from physical processes in the region.

Community structure

" Identify and compare inter-annual, seasonal and spatial variability in the taxonomic composition and size distribution of the microbial, phytoplankton and zooplankton assemblage in shelf waters of the eastern GAB to test the hypothesis that spatial and temporal shifts in the influence of upwelling and downwelling trigger shifts in food web structure between the microbial loop and the classic diatom dominated food web."

Project 2.1 represents the first holistic examination of lower trophic ecosystem dynamics in the Eastern GAB. An ~ 8 year time series of chemical and biological parameters was used to capture the responses of organisms at the base of the food web (microbes (viruses, bacteria), phytoplankton (pico- (< 2 µm), nano- (2 – 5 µm), and micro-phytoplankton (>5 µm)) and meso-zooplankton) to changes in hydrographic conditions, and the degree of enrichment of waters in the euphotic zone. Each sampling event in the time-series was assigned to one of five met/ocean scenarios likely to occur in the eastern GAB, as defined in the refined conceptual model (Fig. 3.1-1). We then compared observed community biomass, abundance, composition, and size-structure with predictions made in the conceptual model, and found inconsistencies between the hypothesised and observed plankton community. Key findings were as follows:

- During winter-mixing, when a pico-phytoplankton community was hypothesised to dominate, nano-phytoplankton comprised the bulk of autotrophic biomass, with high numbers of flagellates and dinoflagellates. The dominant food web during winter would be better described as multivorous, rather than strictly microbial.
- Moderate to high levels of autotrophic biomass were observed during pre-conditioning, with highest abundances of micro-phytoplankton (diatoms and flagellates), in contrast to predictions from our conceptual model. We hypothesise that this represents a previously undocumented (for this region) "spring bloom" scenario, which is stimulated during the winter/spring transition by increasing irradiance and stratification. Coincident high zooplankton abundances and biomass suggest efficient trophic transfer from primary producers to secondary consumers.
- A classic food web dominates during moderate and strong upwelling, in agreement with our hypotheses in the refined conceptual model, with a co-dominance of pico- and micro-phytoplankton.
- During suppression, our hypothesised multivorous food web was somewhat matched with observations. However, this food web would be better described as microbial/multivorous, given the dominance of nano-phytoplankton (as biomass), and relatively high numbers of the small pico-phytoplankton at this time.

Other novel findings included:

- Possible additional SiO_2 sources in the eastern GAB, not linked to upwelled water (e.g. groundwater intrusion, benthic resuspension).
- The importance of nano-phytoplankton to overall phytoplankton biomass and food web dynamics year-round in eastern GAB shelf waters.

- The occurrence of relatively high numbers of dinoflagellates which appear to be mixotrophic/heterotrophic, and are proposed as an important trophic link between pico-, nano- and micro-plankton and copepods and other zooplankton taxa.
- Viruses likely exert, at times, strong pressures on the bacteria, picophytoplankton and nanophytoplankton communities.
- The microbial food web is a persistent feature of the eastern GAB, with growth and biomass build-up of larger phytoplankton concomitant with smaller cells during periods of enrichment (i.e. not replacement of small cells with larger cells).
- Efficient biomass transfer from primary to secondary producers occurs during preconditioning, strong upwelling and, at times, at the end of the upwelling season.
- The importance of the winter to spring transition period for "kick starting" productivity and trophic transfer in the system.

Plankton size structure and sardine egg densities

"Derive empirical relationships between taxonomic composition and size structure of plankton to test the hypothesis that shifts in food web structure will have implications for the size structure of the zooplankton community and, consequently, the biomass of upper trophic levels."

"Compare inter-annual patterns in microbial and planktonic ecosystem structure and sardine egg density."

Archived samples from SARDI sardine biomass surveys were re-processed through a Laser Optical Particle Counter (LOPC) to provide a suite of parameters (abundances, biomass and size distributions) to characterise variation in the meso-zooplankton community. These were used, together with associated environmental data, to improve our understanding of the factors influencing the distributions and densities of sardine eggs across shelf water of the eastern and central GAB.

Key results for the meso-zooplankton community showed that there were:

- Differences in the size distributions of meso-zooplankton in the central and eastern GAB; with the meso-zooplankton comprised of smaller individuals in the central GAB, and larger individuals in the eastern GAB. These results suggest a longer 'microbial' food web was dominant in the central GAB and a shorter, more efficient, classic food web was occurring in the east during upwelling.
- Clear annual differences in the meso-zooplankton community present in the GAB during the upwelling season. For example, a significantly larger sized meso-zooplankton community occurred in 2013 compared to any other year. In 2014, the highest meso-zooplankton abundance and biomass recorded for the study period was reflected in a meso-zooplankton community dominated by relatively smaller sized individuals than in 2013.
- Temperature was a key driver overall of meso-zooplankton abundance, biomass and size distribution, as shown in previous studies (e.g. van Ruth and Ward 2009; van Ruth 2009).

The key findings for sardine egg densities were that:

- Highest sardine egg densities occurred in the central GAB shelf in 2014, coinciding with highest meso-zooplankton abundances and biomass, with the community dominated by smaller organisms.
- The key enviromental drivers of fluorescence and temperature (at the mixed layer depth), together with the increased meso-zooplankton abundance, provided a significant yet, overall low (19%) explanatory power for describing sardine egg densities distributions.

Together these results highlight the difficulty in unravelling the responses of lower trophic organisms by environmental drivers occurring over various time scales (i.e. days to weeks). However these results support previous findings of the link between cold upwelled water, increased phytoplankton biomass, increased zooplankton biomass and increased sardine egg densities (Ward et al. 2006).

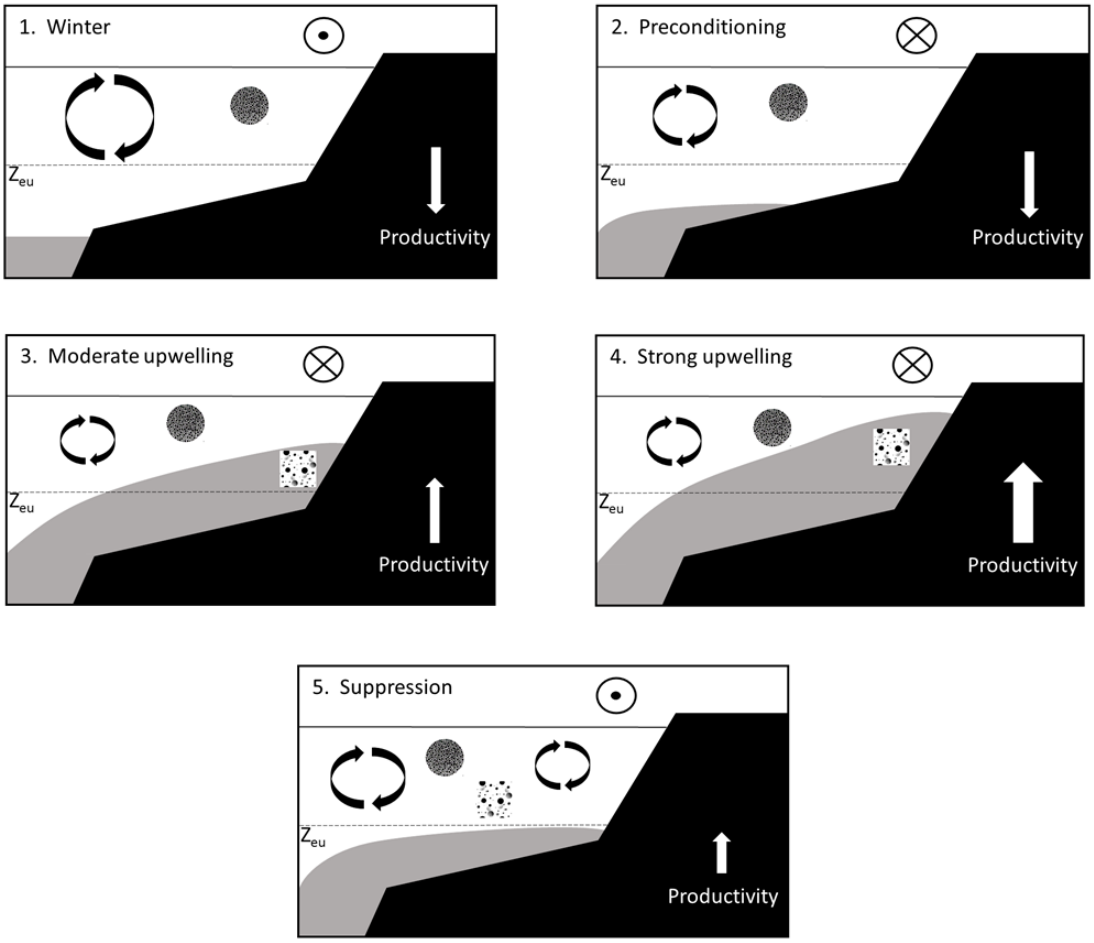

Figure 3.1-1 A refined conceptual model of variation in the influence of upwelling/downwelling on mixing, water mass characteristics, primary productivity and food web dynamics in shelf waters of the eastern Great Australian Bight. = wind coming out of the page (i.e. south westerly), = wind going into the page (i.e. south easterly). = pico-phytoplankton, = microphytoplankton. The black shape denotes the shoreline and the shelf, the grey shape denotes enriched upwelled water. The dashed line indicates the euphotic depth (Z_{eu}). Black arrows indicate mixing, white arrows indicate the expected level of primary productivity. See text for full description of the 5 different scenarios.

3.2 Project 2.2: Characterise spatial variability of offshore/slope plankton, and micronekton communities

3.2.1 Objectives

The objectives of project 2.2 were designed to address hypotheses 3 and 4 to characterise seasonal and spatial variability of plankton and micronekton communities with the following objectives:

1. Describing the community structure, dynamics, biodiversity and endemism of microbes (i.e., viruses and bacteria), plankton (i.e., phytoplankton, zooplankton, ichthyoplankton) and micronekton (including squids, small pelagic and mesopelagic fish and gelatinous organisms).
2. Testing the hypothesis that the "microbial food web" is the dominant planktonic food web over the deep GAB continental margin, particularly in the central GAB where year-round downwelling is thought to be the prevailing cross-margin flow, and that the more efficient "classic food web" only dominates in the eastern GAB during periods of nutrient-rich upwelling.
3. Compare the eastern and central GAB continental margin zooplankton and micronekton communities in terms of their species composition, size range, biomass, nutrient source/trophic pathways and habitat. Describe how differences could affect the distribution and abundance of key species.

3.2.2 Key results and discussion

Significant advances in knowledge of the pelagic ecosystem structure and function were made possible with the voyage on the MNF *RV Investigator* (Kloser et al. 2016). Sampling biota from microbes to tuna requires a large, diverse research team, using a wide range of technologies and methodologies, and is only possible on a large research vessel. Inherent to this study were the multiple spatial and temporal scales that affect the composition, distribution and abundance of species. Given this complexity, and the complexities and precision of any one sampling method, a multiple-lines-of-evidence approach was adopted. The potential for bias in interpretation due to fast turnover (days – months) of microbes and plankton influenced by small scale local environmental changes, was augmented by characterising slow turn over (years) micronekton species. Similarly, studies of micronekton may be biased by gear selectivity and behaviour, and its temporal and spatial variability.

This synthesis of knowledge is based on historic data for temporal and spatial context, and new data collections made through this project, principally on a shared voyage in December 2015 on *RV Investigator* and collections of bioacoustics and CPR data to address the key questions/hypotheses as outlined below in italics.

Community structure

"Describing the community structure, dynamics, biodiversity and endemism of microbes (i.e., viruses and bacteria), plankton (i.e., phytoplankton, zooplankton, ichthyoplankton) and micronekton (including squids, small pelagic and mesopelagic fish and gelatinous organisms)."

Microbes (viruses and bacteria) and plankton (picophytoplankton, phytoplankton, and zooplankton) were sampled for the first time for shelf, slope and offshore waters of the eastern and central GAB in summer, highlighting differences in community composition and dynamics with major findings:

- No statistical differences were detected in the abundance and composition of the microbial communities between the central and eastern GAB;
- Highest phytoplankton biomass always occurred below surface, with the biomass peak ~20-30 m deeper in the central GAB than in the east;
- Picoplankton (< 2 µm) (e.g. *Synechococcus* and *Prochlorococcus*) dominated phytoplankton biomass in the central GAB and nanoplankton (2 – 5 µm) (e.g. Prymesiophytes and Chlorophytes) dominated phytoplankton biomass in the east;
- Diatoms and dinoflagellates dominated the larger micro-phytoplankton (> 5 µm) across the region, with Prasinophytes the next dominant taxa in the central GAB, and Chryptophytes the next dominant taxa in the eastern GAB; and
- The zooplankton community in the eastern GAB was dominated by copepods, with appendicularians, cladocerans, chaetognaths, echinoderms and the predatory dinoflagellate *Noctiluca* other dominant taxa. In the central GAB, copepods were also dominant, with appendicularians and thaliaceans the other dominant taxa;

Large zooplankton and micronekton were investigated for the first time in the central and eastern GAB with a combination of net, acoustic and optical sampling. This study highlights the dynamics of these organisms between regions, water depth and day-night gradients. The main findings are:

- Based on net catches 319 taxa were identified where fish dominated the taxon richness showing that central and eastern GAB regions were similar in diversity and evenness;
- 18 new records of gelatinous organisms for the GAB that include 2 species new to science, 3 species newly reported to the Southern Hemisphere, 3 to Australia and 10 new species for the GAB, bringing the known gelatinous species to 140; and
- A newly developed Profiling Lagrangian Acoustic Optical Probe (PLAOS) highlighted the behaviour of micronekton to sampling gear and quantified the abundance and size with depth. The imagery from PLAOS provided the first depth referenced images of fragile gelatinous organisms and their diel migration patterns.

Planktonic food webs

"The "microbial food web" is the dominant planktonic food web over the deep GAB continental margin, particularly in the central GAB where year-round downwelling is thought to be the prevailing cross-margin flow, and that the more efficient "classic food web" only dominates in the eastern GAB during periods of nutrient-rich upwelling."

Physical, chemical, microbial, and planktonic data, together with information on rates from associated physiological processes, were synthesised to address the question/hypothesis above, and place those data in a regional context. In summary, the GAB enrichment mechanisms driving primary productivity were found to differ between the eastern and central GAB at the time of the voyage (i.e. during the upwelling season). These can be summarised as being driven by physics (upwelling in summer) in the east, where enrichment is sporadic, but at times intense, and biological processes have a limited influence. In contrast, in the central GAB there is a stronger influence of biological

processes (e.g. nitrification), with only intermittent input from turbulent fluxes at the shelf edge, resulting in a more constant but constrained enrichment.

The physical and chemical environment reflects the differences in food web dynamics that characterised the eastern and central GAB during the upwelling season, summarised below.

- East:
  - Deep Chlorophyll Maximum (DCM) and nutricline ~40 – 60 m, Z_{eu} ~80 - 90 m.
  - Low nitrification rates.
  - Abundant high dimethylsulfoniopropionate (DMSP) producing phytoplankton (Dinoflagellates, prymnesiophytes).
  - Nano-phytoplankton dominate the autotrophic community.
  - High productivity driven by large volume of nutrient rich water above the euphotic depth, which contributes a significant proportion of total primary productivity in the euphotic zone.
  - More abundant meso-zooplankton community with higher grazing rates.
  - Higher rates of grazing on larger cells.

    ➔ Short food web underpinned by upwelled nitrogen.
- Central:
  - DCM ~80 - 90 m, nutricline ~100 m, Z_{eu} ~80 - 90 m.
  - High nitrification rates.
  - Abundant non/low DMSP producing phyto-plankton (smaller pico-phytoplankton, diatoms).
  - Pico-phytoplankton dominate the autotrophic community.
  - Productivity highest at the base of the euphotic zone, which makes a minimal contribution to total primary productivity in the euphotic zone.
  - Less abundant meso-zooplankton community with low grazing rates.
  - Higher rates of grazing on small cells.

    ➔ Longer food web underpinned by regenerated nitrogen.

Despite these differences, long-term mean levels of remote sensed primary productivity were similar between the two regions. Primary productivity in the east is at times very high, but intermittent and variable, whereas in the central GAB primary productivity is more moderate and constant. Remote sensed data, which rely on surface measurements, likely under estimate total primary productivity in the eastern GAB by neglecting significant sub-surface primary productivity. However, our results indicate that the central GAB ecosystem is an important contributor to overall GAB productivity.

Zooplankton and Micronekton

"That the zooplankton and micronekton communities of the central GAB continental margin have lower biomass, smaller species, different composition and longer trophic pathways than those on the eastern GAB. This is due to the nutrient source being "microbial food web" dominated in the central GAB and "classical" food web dominated in the eastern GAB."

Zooplankton and micronekton samples were used to address the above question and place those data in a regional context. In summary, nutrient sources and trophic pathways (food web) were investigated for the first time in the offshore GAB using the compound-specific stable isotope

analysis (CSIA) method. The results highlight the complexity of predator-prey interactions of species within/between regions and depths with the main findings being:

- Clear evidence of a difference in source nitrogen between the eastern and central GAB upper slope crustacean species;
  - Eastern GAB source nitrogen indicative of upwelled or higher latitude water mass,
  - Central GAB source nitrogen indicative of atmospheric fixed nitrogen,
  - Longer trophic pathways in the central GAB for a high number of dominant species, and
  - These findings complement the plankton and primary production findings;
- Mesopelagic fish have same or higher trophic position as sampled tuna, hence mesopelagic fish are not a significant prey of those tuna; and
- Meso-zooplankton size and biovolume is consistent with plankton, production and isotope evidence that the eastern GAB upper slope is a distinct habitat consistent with upwelled nutrients:
  - meso-zooplankton communities can be characterised with the new precise size-based method to characterise developed.

While there were multiple lines of evidence to support dominant differences in nutrient enrichment and trophic pathways between the eastern and central GAB in summer, the assumed ecological response for zooplankton and micronekton of lower biomass, smaller species and different composition was difficult to assess. Zooplankton and micronekton biomass, size and species composition were similar between the east and central GAB but differed between species groups and sampling device, with highlights below:

- Meso-zooplankton size was smaller with higher biomass in the eastern upper slope GAB due to inferred recent nutrient enrichment;
- Micronekton size ranges did not differ significantly between the eastern and central GAB;
- Macro zooplankton and micronekton biomass was higher in the eastern than central GAB but highly variable with limited sampling:
  - Shelf break and upper slope dominated by important krill prey species, and
  - Gelatinous community is an important component of the system, highest in the central GAB;
- Micronekton fish communities of the GAB have bio-geographic affinities with the Subtropical Convergence habitat zone:
  - No detectable east to central GAB differences in communities;
- Multi-frequency acoustic estimate of biomass was similar (within 30%) between regions;
- Profiling Lagrangian Acoustic Optical System (PLAOS) results infer slightly higher biomass with larger individuals in the central upper slope compared to the eastern GAB upper slope; and
- Large number of fish schools (hence biomass) in the central upper-slope and offshore GAB observed from acoustics highlights that the central GAB has a production source to support them.

Spatial and temporal knowledge of zooplankton and micronekton distribution and abundance were investigated with Continuous Plankton Recorder (CPR) and bioacoustics methods. These methods are part of the Australian Integrated Marine Observing System (IMOS) and incorporating these methods enhanced this monitoring to place the GAB in an Australian and global context. These sampling methods also represented the most cost effective method of sampling at the time. Our sampling can also be placed in context with the overall oceanographic setting, temporal changes (e.g. in the Leeuwin Current) and variation in inferred production (ocean colour time series). Of note was the very weak Leeuwin Current prior to the December 2015 voyage but of normal strength during the voyage (GABRP, Theme 1). The influence of this on-transport of nutrients and biota from the western GAB could not be explored in this study as it may have contributed to the lower micronekton biomass in December 2015 compared to previous years. Based on the limited spatial and temporal context, this study provided a comprehensive state of the offshore environment that can be used to compare future environmental states.

The prevailing hypothesis prior to this study was that the central GAB upper slope was an area of constant downwelling, implying low nutrients and hence low production and biomass that explained the sparse (low biomass) benthic fauna when compared to the upwelling eastern and western GAB regions (Middleton et al., 2014, fig. 8). This study questions the validity of this hypothesis with the following observations:

- yearly production in the central GAB was similar to the eastern region based on remote sensed net primary productivity analysis, and
- high levels of micronekton biomass observed in the central GAB were similar to the eastern GAB and other moderate production regions in Australia.

As a result of this study, we hypothesise that the central and eastern GAB have similar production, sustained by the biology in the central and eastern GAB and for the eastern upper slope and shelf enrichment driven by the physics (during the summer upwelling season). In support of this we found that production and trophic transfer in the central region is more constant and appears to be dominated by regenerated nitrogen while the eastern region also receives pulses of upwelled nitrogen. This is reflected in the base nitrogen and reworked nitrogen trophic transfer to zooplankton and micronekton (Figure 3.2-1).

The findings in this work would benefit from longer temporal sampling to improve their significance. Clear differences in nutrient sources between the eastern and central upper slope at the time of sampling were highlighted from multiple lines of evidence. An understanding of the significance of these findings over a longer time frame is required to test our conclusions. We hypothesise, based on our findings, that the central GAB has lower but more consistent production supporting the micronekton schools observed by acoustics. Interestingly, our initial work on predator interactions using the CSIA method raises more questions than answers. The variability and complexity in these results highlights the difficulty in deriving simple functional relationships, but suggests that many mesopelagic fish are operating as top predators, with no overlap with the sampled tuna diet for this region. More detailed investigation of trophic interactions using stomach analysis and CSIA species specific trophic enrichment factors would assist in unravelling the complexities of the mesopelagic communities and their role in supplying food to other more charismatic “top predators”.

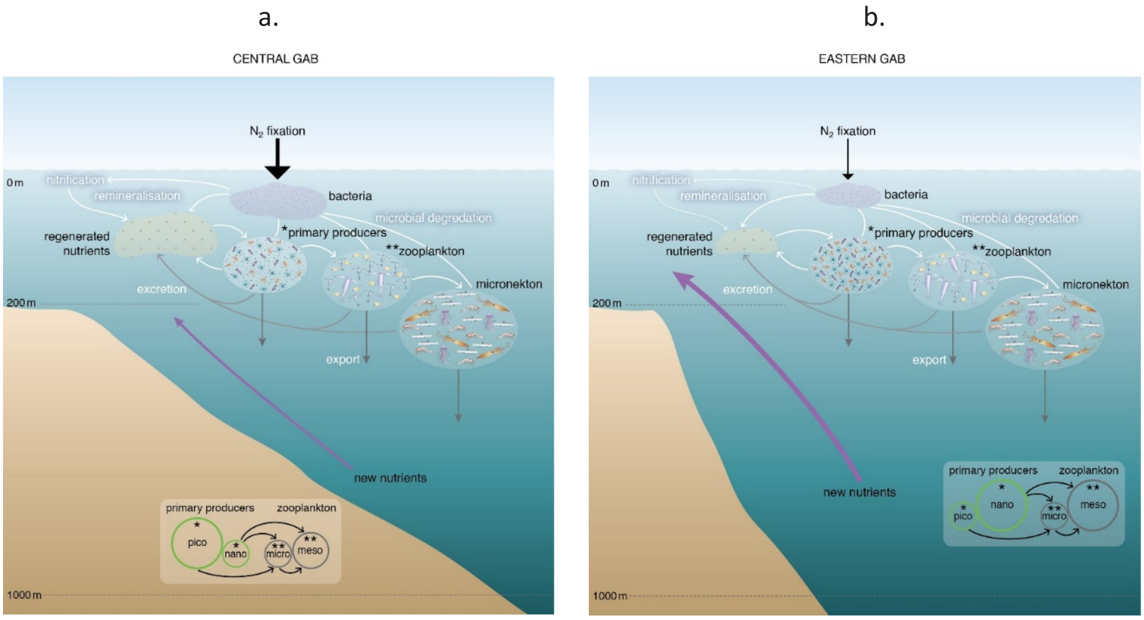

Figure 3.2-1 Diagram of functioning of the upper slope GAB highlighting dominant production drivers, (a). Central GAB where nutrient supply is constant but constrained and biological processes dominate nitrogen supply supporting production. (b), Eastern region where nutrient supply is characterized by addition of pulses of upwelled nutrients with a reduced pathway of biological processes. In general zooplankton and micronekton biomass is similar in the eastern and central region.

4. CONTRIBUTION TO THE GABRP

Theme 2 has produced significant advances in knowledge of pelagic ecosystem structure and function in the eastern and central GAB. It represents the first detailed study of the influence of variations in enrichment processes on lower trophic ecosystem dynamics in shelf, slope and offshore waters in the GAB, and characterised the biota from sizes of microns to metres. Sampling biota from microbes to tuna requires a large diverse team, using a wide range of technologies and methodologies. Inherent to this study were the multiple spatial and temporal scales that affect the composition, distribution and abundance of species. Given this complexity and the complexities and precision of any one sampling method, a multiple-lines-of-evidence approach was adopted. The potential for bias in interpretation due to fast turn over (days – months) of microbes and plankton, influenced by small-scale local environmental changes, was augmented by characterising slow turn over (years) micronekton species. Similarly, studies of micronekton may be biased by gear selectivity and behaviour, and its temporal and spatial variability. This work has uncovered distinct spatial and temporal differences in enrichment, food webs and productivity, which are summarised below with key knowledge gaps that have been identified during the study (Figures 3.1-1 and 3.2-1):

For the eastern GAB

- Nutrient enrichment from upwelling driven by the physics supports intense production at times.
- This production is exported to the shelf and has reduced impact on continental margin processes and biomass.
- Ensures that the shelf has large pulses of nutrients and production to support fisheries.
- Eastern zooplankton and micronekton species and biomass similar (slightly higher) than the central GAB.

For the central GAB

- Production is more constant and constrained by biological processes
- We hypothesise that shelf break upper slope production is influenced by import of fixed nitrogen and other nutrients from the west and/or from the shelf.
- Major finding is a potential mechanism of new nitrogen to guide future studies for sampling in the central GAB shelf waters.
- Offshore GAB identified to have a number of micronekton schools over large spatial scale need for future investigation as to their source and mechanisms for production.
- Other nutrient enrichment processes such as turbulence may be supplementing the constant production of the offshore GAB.

Knowledge gaps:

- Role of nitrogen fixation in the production of the shelf-slope central GAB .
- Production processes of the central GAB shelf.
- Role of mesopelagic organisms as a food source for iconic species.
- Longer term monitoring of the central GAB to confirm hypotheses generated from findings.

Our findings indicate that nutrient enrichment is a key environmental driver of variation in food web dynamics in the GAB. However, the situation is more complex than first thought, and our findings deviate somewhat from our hypotheses. There are three food webs operating in the GAB, all of which vary significantly in their influence on productivity in the region, and all of which are enhanced by enrichment (either via 1. upwelling of new nitrogen in the east, from 2. atmospheric fixed nitrogen in the central upper slope region, or 3. the production of regenerated nitrogen through microbial processes in the eastern and central GAB). The microbial food web is present year-round, and is the dominant food web in slope and offshore waters. In shelf waters it operates as a background signal underlying other important food webs in the region, effectively "keeping the lights on" in productivity terms. The dominant food web in shelf waters of the GAB, underpinning moderate rates of primary productivity year-round, is a previously undocumented (for GAB waters) food web based on nanophytoplankton and heterotrophic dinoflagellates. The efficient, classic food web only occurs in shelf waters of the eastern GAB during upwelling, when enrichment with new nutrients drives spikes in rates of primary productivity that are comparable to highly productive eastern boundary current upwelling systems. During periods of enrichment across the region, shifts in food web dynamics are not clearly delineated; growth and biomass buildup of larger phytoplankton occurs together with increased growth and biomass of smaller cells (i.e. not simply the replacement of small cells with larger cells, or the microbial food web with the classic food web). Despite these differences in food web dynamics, long-term patterns in primary productivity from remote sensed data are relatively similar between the regions, particularly on the upper slope. While primary productivity in the east can be high, it is intermittent and highly variable, with highest rates implicitly linked to upwelling. In the central GAB, primary productivity is more moderate, but linked to a more constant, biologically-mediated supply of nitrogen that ensures that these moderate rates can be maintained over longer periods of time. While remote sensed data, which rely on surface measurements, likely underestimate total primary productivity in the eastern GAB by neglecting significant sub-surface primary productivity, these results show that the central GAB is an important contributor to overall productivity in the wider GAB region.

Understanding the influence of upwelling on the lower trophic ecosystem in the eastern GAB shelf was a particular focus of Project 2.1. We discovered that the length of an upwelling season did not dictate its intensity or productivity, and that long, intense seasons were not necessarily the most productive. A key finding was the importance of differentiating between upwelling events and enrichment events. The former occurred in the early upwelling season (November-December) and drew cold, nutrient rich water onto the shelf, but not into the euphotic zone. The latter only occurred in the late upwelling season (January – April), and drew water upwelled in the early season into the euphotic zone where it was available for primary producers. We have detailed, for the first time, the importance of the November-December preconditioning period that characterises the early upwelling season in the eastern GAB in governing the intensity of enrichment in the euphotic zone during the late upwelling season. In addition, we have discovered a previously undocumented "spring bloom" scenario in the eastern GAB which develops during the winter-spring transition, and provides a critical "kick-start" for productivity and trophic transfer in the system. Physical and chemical drivers of this phenomenon are yet to be described. Future studies should focus on examining the influence of variations in the duration and intensity of individual upwelling events (i.e. within scenario variation) on enrichment, primary productivity, and food web dynamics in the eastern GAB, and the physical, chemical, and biological processes underlying the spring bloom. Spatially, our analyses confirmed that the upwelled water mass, and thus significant enrichment of

waters in the euphotic zone, was restricted to the eastern GAB. Water mass characteristics revealed no evidence for the presence of upwelled water on the central GAB shelf.

Differences in the structure and function of the central and eastern offshore regions was a focus of Project 2.2. Our analysis of lower trophic ecosystem community dynamics highlights similarities and differences between the eastern and central regions for gradients of distance from the shelf break, day to night, and depth. Most notable was the similarity rather than differences between the eastern and central GAB. Key differences were that pico-plankton dominated in the central GAB, with nano-plankton dominant in the east. Notable similarities were that micronekton fish dominated the taxon richness showing that the central and eastern GAB were similar in diversity and evenness. Highest sardine egg densities in the GAB were linked with years and locations having highest zooplankton abundances and biomass. Through this project, we have discovered that meso-zooplankton size distributions provide valuable information that improves our understanding of the drivers of sardine egg density distributions. The analysis of plankton “bycatch” collected during sardine biomass surveys will provide additional information that will assist in the management of this valuable fishery and the GAB marine ecosystem.

Nutrient sources and trophic pathways examined using the CSIA method showed that distinct differences between eastern and central upper slope habitats existed during the study. This was most evident for the crustaceans where source-nitrogen was indicative of an upwelled or higher-latitude water mass in the east, and biologically-fixed nitrogen in the central GAB. This observation reinforced the differences observed in the dominant production mechanisms. CSIA also showed there were longer trophic pathways in the central GAB for a high number of dominant species. Interestingly, many micronekton fish had a similar or higher trophic level using the CSIA method to the few tuna sampled using the same trophic enrichment factor.

While there were multiple lines of evidence to support dominant differences in nutrient enrichment and trophic pathways between the eastern and central GAB, the assumed ecological response for zooplankton and micronekton of lower biomass, smaller species and different composition was difficult to assess. Variations in the size structure of the zooplankton community in the GAB are implicitly related to the underlying dominant food webs, and shifts in food web dynamics drove changes in meso-zooplankton size structure. The meso-zooplankton community in shelf waters in the central GAB was smaller than that found in the east. In slope and offshore waters, however, zooplankton and micronekton biomass, size and species composition were similar between the eastern and central GAB, but differed between species groups and sampling device. The prevailing hypothesis prior to this study was that the central GAB upper slope was an area of constant downwelling, suggesting low nutrients, and hence low production and biomass that explained the sparse (low biomass) benthic fauna when compared to the upwelling eastern and western GAB regions. This study does not support this hypothesis where the yearly production derived from satellite ocean colour and micronekton biomass is similar between the regions and similar to other moderate production regions in Australia. These findings are also supported by the larger spatial and longer temporal CPR and bioacoustic sampling.

The two pelagic ecosystem structure and function projects of the GAB have improved important knowledge gaps identified at the start of the study. Firstly, the processes that drive high production from upwelling on the eastern GAB shelf have been quantified. Secondly, the production processes that support a high biomass of micronekton in the central GAB have been identified for a region previously thought to be of low production due to the constant downwelling environment. This information is needed to understand how the distribution and abundance of forage animals may potentially overlap with human uses. Importantly, uptake of this new knowledge will also accrue over time as it is incorporated into regional ecosystem models that will enable better predictions for scenarios regarding a changing climate and increased anthropogenic uses. In common with most studies, we have identified gaps in knowledge, most significantly the production mechanisms of the central GAB and the source of atmospheric fixed nitrogen and associated nutrients to promote the extra production observed. Another important gap concerns the ability to obtain observations over greater temporal and spatial sampling to support the generalisation of our findings. Key to any further understanding of the region is the need to have greater temporal and spatial sampling in a cost-effective way. In this way our significant usage of IMOS mooring, CPR and bioacoustics data was critical to reducing cost and facilitating longer term observations.

5. CONCLUSION

Our work highlights the influence of enrichment on biomass transfer from primary producers to primary and secondary consumers in GAB waters. The conceptual and quantitative models of pelagic ecosystem processes we have developed provide new insights into lower trophic ecosystem dynamics in the GAB that are critical for the development of trophodynamic models that will promote sustainable management of marine resources in the region. Our more detailed characterisation of natural variation in lower trophic ecosystem dynamics provides the knowledge required to monitor and manage potential future anthropogenic impacts. Enrichment mechanisms driving primary productivity in the GAB were found to differ between the eastern and central regions. These can be summarised as being driven by physics (upwelling) in the east, where enrichment is sporadic, but at times intense, and biological processes have a limited influence. In contrast, in the central GAB there is a stronger influence of biological processes (nitrification), with only intermittent input from turbulent fluxes at the shelf edge, resulting in a more constant but constrained enrichment. These differences have led to the evolution of three distinct food webs in the region, which vary in the size of the autotrophs that underpin them, and, thus, in the efficiency of energy transfer to higher trophic levels.

A key finding of this work is the fact that the central GAB plays a more important role in overall GAB ecosystem productivity than previously thought. This is reflected in the base nitrogen and reworked nitrogen trophic transfer to zooplankton and micronekton.

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