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Marine Isoscapes for trophic and animal movement studies in the southwest Pacific Ocean

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EXECUTIVE SUMMARY

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The ZBD2014-04 project aim was to produce validated, modelled, southwest Pacific Ocean and Southern Ocean carbon and nitrogen isotopic maps, referred to as “isoscapes”, to improve understanding of species biogeography, functional links, and movements between ecosystems. The first stage was to develop data-derived regional nitrogen and carbon isoscapes from historical baseline data (surface particulate organic matter - SPOM) collected from the northeast shelf and slope of New Zealand. The second phase was to collaborate with overseas colleagues to develop basin and global modelled nitrogen and carbon isoscapes. A nitrogen isoscape for the southwest Pacific Ocean and Southern Ocean was generated using a new Model of Ocean Biogeochemistry and Isotopes (MOBI). The output was derived from a three-dimensional ocean circulation model, forced with fixed monthly climatological winds and was coupled to a marine biogeochemical ecosystem model component, of a Global Earth System Climate Model. It incorporated key biological and chemical processes at the base of the food web from surface waters to seafloor sediments. A more accurate data-driven output of this model was produced for the central and eastern Pacific Ocean by using physical-statistical modelling and forcing the model with sediment $\delta^{15}N$ values from the region. The MOBI was further validated by collaborators using bulk isotope SPOM, and yellowfin tuna muscle data, as well as compound specific isotope analysis of amino acid data.

The two models produced low $\delta^{15}N$ values (-1 to -2‰) indicative of nitrogen fixation in the Archipelagic Deep Basins and the Pacific Equatorial Divergence. High $\delta^{15}N$ values, relating to regions of upwelled nitrate, were observed in the South Pacific Subtropical Gyre (8–10‰) and the Warm Pool (10–14‰). Nitrogen isotope values in the Southern Ocean were low (-1 to 1‰), largely because this is a High Nutrient Low Chlorophyll (HNLC) region with high current flows, turbulence and well-mixed water masses. A carbon isoscape was produced for the southwest Pacific Ocean and Southern Ocean using a process-based, coupled physics-biogeochemistry model (NEMO-MEDUSA), which was then validated with $\delta^{13}C$ SPOM data. Both modelled and data-derived outputs showed strong latitudinal $\delta^{13}C$ gradients of -16‰ at the Equator, gradually decreasing to -32‰ along the Antarctic shelf. This gradient is largely driven by changes in temperature and solubility of aqueous carbon dioxide ($[CO_2]$aq). Deviations from this predictable latitudinal pattern occurred where coastal processes, upwelling and biological effects over-rode the physical temperature drivers of $\delta^{13}C$ values in phytoplankton.

Generating modelled and data-derived isoscapes for coastal environments presents more challenges than for open ocean systems. This is largely due to highly dynamic coastal processes and variable isotopic sources and inputs to near-shore ecosystems. However, nitrogen and carbon isoscapes generated in northeast coastal New Zealand show promise for interpreting movements of resident cetaceans, seabirds, and fish that forage in the shelf and slope region. The utility of these isoscapes is dependent, in part, on the resolution at which consumers integrate prey isotopic signals relative to the spatial resolution of the isoscape. Overall, the value of this approach is greatly enhanced when there is a good understanding of the animal’s life history traits and physiology, and when the method is coupled with other tools, including additional chemical tracers (such as trace metals and compound specific isotopes), direct observations, demographic census of individuals or populations, and tagging programmes. Using compound specific stable isotope analysis of amino acids of animal tissues to generate baseline isotope values will further advance our abilities to validate modelled isoscapes and integrate field data into the models to produce more robust information on ecosystem structure and animal movements. There is still much work to be done in terms of infilling data gaps and further validation of modelled isoscapes. In the meantime, the global and coastal isoscapes generated in this research project are being used to improve our understanding of the trophic status and movements of animals to inform conservation and management strategies. Focussing on a multi-tool approach, we

now have the capability to better determine: i) connectivity between populations or sub-populations, ii) mixing rates between oceanic regions, iii) migratory routes between critical life history stages (e.g., movements between spawning/breeding and foraging grounds) and iv) migration pathways through high-risk routes (e.g., fishing, low productivity regions, ship strikes, and resource exploration).

1. INTRODUCTION

1.1 Rationale

Managing and conserving marine animal populations and biodiversity is a major societal goal as outlined in the New Zealand Biodiversity Strategy and Action Plan 2016–2020 (Department of Conservation, 2016) and the Aichi Biodiversity Targets adopted by the Convention on Biological Diversity (https://www.cbd.int/sp/targets/). However, this work is hampered by a lack of understanding of the movements and function of these animals in the open ocean (Block et al. 2011). Developing management policies for open ocean marine food webs is challenging, partly because they are taxonomically complex and difficult to sample. Increasingly, regulators are moving to spatially-based management tools such as marine protected areas (MPAs) and no-take zones. These are only effective, however, if they are in regions critical to different life stages, if they are of an appropriate size with respect to the movements of the animals to be conserved, and if regulations are enforced. Thus, more than ever, there is a need for reliable, cost-effective, and ideally retrospective methods to identify spatial and temporal movements of fish and other marine animals. Stable isotope analysis of animal tissues, coupled with spatial maps of isotope values (known as "isoscapes", first presented by West et al. 2010) offers one such solution. The goal of this project was to develop models that can predict the isotopic spatial variability in the ocean around New Zealand, so that from stable isotope analysis of tissue samples, animals can be accurately geolocated to specific regions, where they have previously foraged (Somes et al. 2010; Young et al. 2015a).

The movements and habitat use of animals in the open ocean determines the extent and degree of exposure they might have to a range of anthropogenic effects, including commercial fishing, pollution, and a changing climate. In turn, these interacting processes affect our ability to determine appropriate management practices and conservation measures (Gilman et al. 2016). These anthropogenic influences can impact species function, distribution and the overall marine food web structure and function (Young et al. 2015b; Britten et al. 2017). For example, habitat range contractions of marine animals may have occurred when species numbers significantly declined, such as reduced baleen whale numbers due to historical whaling practices and commercially important fish species nearing their estimated maximum sustainable yield (Meyer & Worm 2003; Worm & Tittensor 2011). Furthermore, highly dispersed species and populations may rebound from localised impacts, whereas species with a greater degree of residency are expected to take longer to replenish their population (Worm & Tittensor 2011). Current research suggests that there are significant changes in the range distributions of cetaceans and large pelagic predators caused by warming ocean conditions (Rasmussen et al. 2007; MacLeod 2009; Hoegh-Guldberg & Bruno 2010; Worm & Tittensor 2011; Young et al. 2015b). Marine animals that travel long distances can be exposed to a greater range and frequency of anthropogenic impacts. Warming conditions and changing oceanic conditions could not only affect marine animal movements in terms of range expansions (Deutsch et al. 2015; Burgess et al. 2017), but could shift prey composition and availability in different regions. A better understanding of marine animal trophic status and movements in the open ocean is then paramount to their effective management and conservation, especially with changing climate conditions (Hobday & Lough 2011; Burgess et al. 2017). This has important implications for Pacific Island and Pacific rim nations, as many of these migratory animals are important food/protein resources or are critical to their tourism industries.

1.2 Background and Project Approach

The combination of a vast habitat and the challenging and expensive sampling coordination required, limits the ability to track animal movements in the open ocean. Here, we apply stable isotope techniques to assess animal movements, without expensive and intensive tagging programmes, albeit that the combination of the two would have been ideal. Traditionally, stable isotope values have been used as a tool to provide information on the time-integrated, assimilated diets of marine animals (Minagawa & Wada 1994; Post 2002). Stable isotope analysis, although often unable to resolve the taxonomic composition of a predator's diet, indicates a predator's trophic position, because the isotope ratios of nitrogen, i.e., $^{15}N/^{14}N$ ($\delta^{15}N$) increase in a predictable stepwise manner with each trophic position (Figure 1; DeNiro & Epstein 1981; Minagawa & Wada 1994). For nitrogen isotope values an animal's tissue has been found to be 2–5‰ more enriched than its diet (Peterson & Fry 1987; Post 2002) and this difference is referred to as a trophic enrichment factor (TEF). More recent studies indicate that for marine species the TEF is on average around 3‰ (Graham, 2008; Olson et al. 2010). Carbon isotope values are not significantly affected by trophic variation (TEF about 0.4–1.0‰) and, therefore, carbon is a relatively conservative tracer (DeNiro & Epstein 1978; Goericke & Fry 1994). However, establishing the TEF and the animal's trophic position requires knowledge of the nitrogen isotopic values at the base of the food web, (i.e. primary producers), which exhibit different $\delta^{15}N$ values depending on the nitrogen source to the food web (Figure 1). Therefore, one must consider nitrogen baseline values when interpreting the isotope values of marine animals.

Assessing the spatial patterns of baseline isotope values in the ocean is key to understanding the biogeochemistry, nutrient cycling and production in present marine ecosystems (Altabet 2001; Sigman et al. 2009; Somes et al. 2013; Rafter & Sigman 2016). Isotopic baseline values can vary considerably in time and space and are dependent on a number of biogeochemical and physical variables. Broadly, carbon isotope values decrease with increasing latitude (Figure 2; Goericke & Fry 1994; Laws et al. 1995) and shift with changes in the dominant species of primary producers and the extent of primary production (Popp et al. 1999). Nitrogen isotope values vary spatially, and are affected by the dominant nitrogen source, its pool size and the extent of nutrient utilisation by local primary producers (Altabet 2001; Rafter & Sigman 2016). The degree of nitrogen fixation in oceanic waters also affects baseline nitrogen values. For example, a HNLC region with high levels of diazotrophs that fix nitrogen, will have lower $\delta^{15}N$ values than an area dominated by deep, upwelled waters with high nitrate concentrations (Figures 1 and 2; Graham et al. 2010). Therefore, knowledge of these geographical variations in the isotopic baseline is key to applying the isoscapes approach to tracking movements of animals in the open ocean.

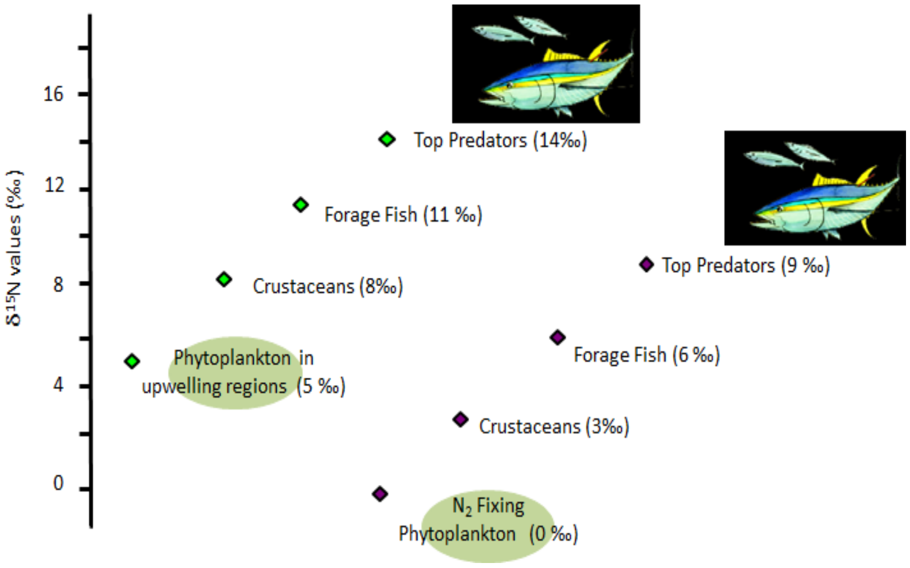

Figure 1: Schematic diagram of the trophic enrichment (i.e. the 3‰ increase in nitrogen isotope ($\delta^{15}N$) values) that occurs with each trophic level, in two separate geographical regions, where primary productivity is driven by different nitrogen sources (upwelling, green-filled diamonds; and nitrogen fixation, black-filled diamonds). The figure illustrates that the isotopic value of the oceanic baseline (i.e. primary producers, such as phytoplankton) determines the $\delta^{15}N$ values of foraging organisms at subsequent trophic levels of the food web. Thus, a "trophic level two" crustacean could have a $\delta^{15}N$ value ranging from 3 to 8‰, depending on the oceanic $\delta^{15}N$ baseline within its foraging habitat.

The idea of using isoscapes to examine animal movements in the open ocean was first developed by Schell et al. (1989) to determine the movements of bowhead whales (*Balaena mysticetus*) in the north Pacific Ocean. These researchers used samples selected along the baleen to determine the seasonal movements and migratory routes of the whales within the Bering, Chukchi and Beaufort seas. At its simplest, if the stable isotope value of a predator reflects the local signal, that marine animal can be regarded as resident; if a marine animal exhibits a stable isotope value that is inconsistent with the local baseline value, then that individual must have migrated from another, isotopically-distinct region (Cherel & Hobson 2007; Lorrain et al. 2009; Ramos & Gonzales-Solis 2012; Trueman et al. 2012; McMahon et al. 2013). Since Schell et al.'s (1989) pioneering work, isoscapes have been developed to examine movements of seabirds in the Southern Ocean (Quillfeldt et al. 2005; 2010), tuna in the Pacific Ocean (Graham, 2008; Lorrain et al. 2015), top predators in the tropical Indian Ocean (Ménard et al. 2009) and pelagic predators along the eastern coast of Australia (Young et al. 2010, 2015a).

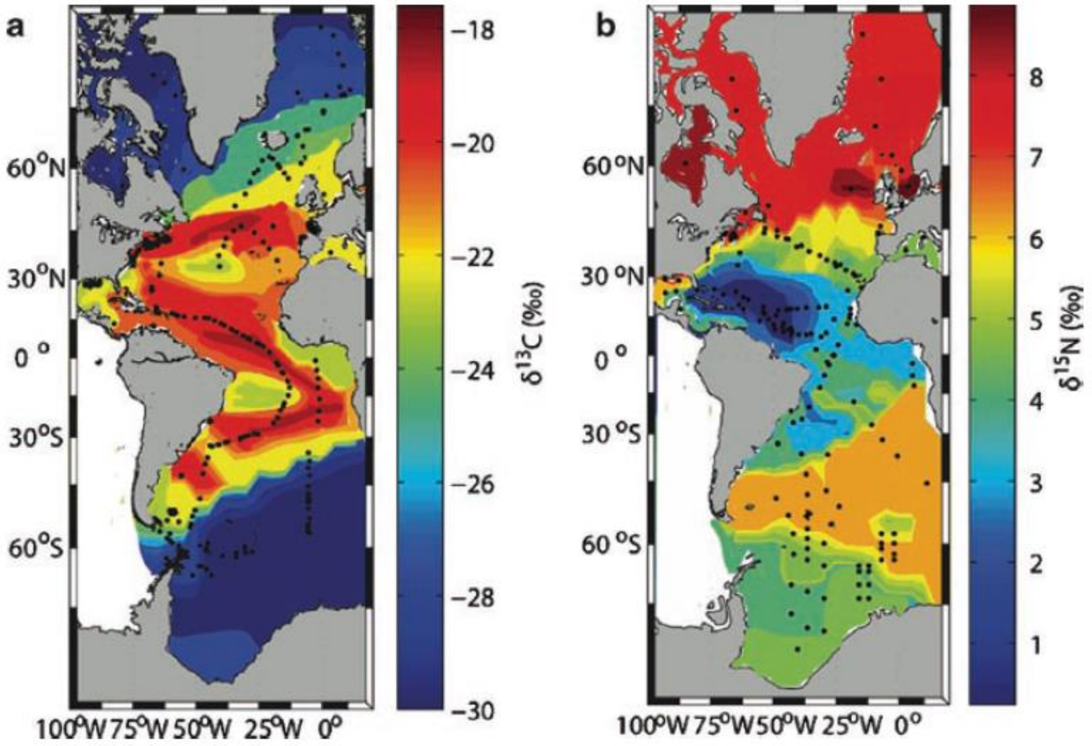

Figure 2: Contour plots of the stable isotope values or isoscapes of the Atlantic Ocean from a meta-analysis of published data in, (a) δ^{13}C values of plankton, and (b) δ^{15}N values of zooplankton. Black dots indicate sample locations. From Graham et al. (2010).

There are several key requirements for this method to be successful in tracking animal movements using stable isotope techniques and isoscapes. The animals need to have moved between distinct isotopic regions (see Figure 2) and have foraged in these regions to incorporate the isotopic signal. Additionally, it is important to have some knowledge of the turnover, or metabolism of the analysed tissues to understand the time period over which isotopic information was incorporated (i.e., incorporation rate). Tissue turnover rates can be determined either by conducting captive diet studies, or observing distinct, rapid diet shifts in nature (Graham et al. 2007; Kitagawa & Fujioka 2017). There are several studies of the turnover rates of a range of tissues in tuna, sharks, pinnipeds, seabirds, and sea turtles (Hobson et al. 1996; Graham 2008; Kim et al. 2012; Madigan et al. 2012; Olin et al. 2013; Tomaszewicz et al.

2017). To date, this can be a challenge for large marine animals, because diet shift experiments are often not possible, and therefore, some inferences need to be made, such as understanding the animal's metabolism and life history stages. The selection of the tissue type can be the key factor to being able to link an animal's movements to isoscapes. Different tissues that have been sampled include muscle, blood, feathers, shells (sea turtles), whiskers (pinnipeds), bone collagen and spines (billfish) (e.g., Estrada et al. 2006; Votier et al. 2010; Acosta-Pachon et al. 2015; Hanson et al. 2017; Tomaszewicz et al. 2017). Tissues that are more metabolically active, such as liver and blood, represent a shorter diet integration period, compared to more slowly metabolically active tissues, such as muscle and bone collagen. Isotopic variability in animal bone collagen is likely to be lower than other tissues, because bone collagen is integrating a much longer period of foraging (e.g., the lifetime of the animal), compared to relatively fast turning-over tissues, such as plasma and whole blood, which integrate over days to weeks respectively, and muscle, a mid-range metabolic tissue, which integrates over months (see review in Fry 2006). Selecting and appropriately sampling materials that grow incrementally, such as pinniped whiskers and billfish dorsal spines, can help resolve seasonal and annual movements in these animals (Graham et al. 2010; Acosta-Pachon et al. 2015). Due to variations in tissue turnover rates and animal movements, and isotopic spatial variability in many study regions, the selection of study organisms and research locations requires careful consideration. Using isoscapes and stable isotope techniques is most successful if the spatial scale at which baseline isotopic variation occurs, is less than the geographic scale at which the animal moves. With these considerations, we developed isoscapes at several spatial scales (coastal to basin-wide) and used case studies to examine the strengths and limitations of the approaches, with emphasis placed on the southwest Pacific Ocean and the Southern Ocean.

1.3 Project Specific Objectives:

1) Development of a marine nitrogen isoscape, collaborating with expert modellers in the field
2) Validation of modelled nitrogen isoscape using field data from the Southern Ocean, New Zealand waters and the tropics, making necessary adjustments to isoscape models to improve accuracy.
3) Identification and infilling of nitrogen isotope data gaps at a resolution required to examine marine animal movements.
4) Development of a marine carbon isoscape, collaborating with expert modellers in the field
5) Validation of modelled carbon isoscape using field data from the Southern Ocean, New Zealand waters and the tropics, making necessary adjustments to isoscape models to improve accuracy.
6) Identification and infilling of carbon isotope data gaps at a resolution required to examine marine animal movements.
7) Utilisation of validated isoscapes to determine and assess the movements of migratory animals in the south-west Pacific Ocean, within existing and future funded projects.

2. METHODS

2.1 Geographical Region

In this project, data was incorporated into isoscapes to further develop them for the southwest and western central Pacific Ocean. We also developed isoscapes for the Southern Ocean and off the northeast coast of New Zealand. Ocean biogeochemistry, and in turn, baseline isotopic values are affected by physical oceanography (water masses, currents), nutrient chemistry, and biological processes (see review by Sigman et al. 2009). Southwest Pacific Ocean oceanography is summarised in Menkes et al. (2015) and Southern Ocean oceanography and biological processes are reviewed by Chiswell et al. (2015) and Boyd (2002), respectively. Physical and biogeochemical processes in the Hauraki Gulf and the northeast shelf of New Zealand have been summarised by Zeldis (2004), Zeldis et al. (2004), Hall et al. (2006) and Bury et al. (2012). These regions are impacted to varying degrees by climatic shifts, such as El-Niño-La Nina or El-Niño Southern Oscillation (ENSO) events which affect the physical oceanography and have impacts on the marine food web and animal distributions (Cane 1983; Rasmussen et al. 2007; Lehodey et al. 1998).

2.2 Development of marine nitrogen isoscapes, collaborating with expert modellers in the field (Objective 1)

2.2.1 *Basin-level, modelled nitrogen isoscape*

The modelled nitrogen isoscape used in this project was based on Somes et al. (2013), which was developed using the Model of Ocean Biogeochemistry and Isotopes (MOBI), which is an extension of the original nitrogen isoscape model of Somes et al. (2010). The MOBI (Somes et al. 2013) is currently the most powerful tested nitrogen isoscape available (Young et al. 2015a). The output is derived from a three-dimensional ocean circulation model, forced with fixed monthly climatological winds. It is coupled to a marine biogeochemical ecosystem model component, of a Global Earth System Climate Model. This model incorporates phytoplankton, zooplankton, sinking detritus, nutrients (nitrate and phosphate) and dissolved oxygen concentrations, along with nitrogen fixation, water column dentification, and benthic denitrification processes (Somes et al. 2013). The nitrogen isotope model simulates the two stable nitrogen isotopes (^{14}N and ^{15}N) in all nitrogen species included in the MOBI.

Incorporating sediment δ^{15}N values from Altabet (2001), using a method applied in Graham (2008), enabled the forcing of a more accurate output of the Somes et al. (2013) model (MOBI) for the central and eastern Pacific Ocean. This process used Bayesian techniques, known as physical-statistical modelling (Berliner 1991; Campbell 2005; Wikle & Berliner 2007; Parslow et al. 2013; Pagendam et al. 2014). The modelling provided a framework, whereby prior knowledge of physical processes (incorporated in the MOBI) was assimilated with observational data (sediment δ^{15}N values), to improve confidence in the modelled δ^{15}N predictions. The process acknowledges all sources of uncertainty and is useful in that it can provide guidance on sampling efficiency. It should be noted that although the MOBI output is suited for the open ocean system, it has not been parametised for, and therefore cannot be reliably used for, coastal systems. The same applies to all other oceanic models presented in this project.

2.2.2 Coastal*, data-derived nitrogen isoscape*

In addition to the oceanic-scale nitrogen isoscape produced, an extra output of ZBD201404 was the development of a coastal nitrogen isoscape for the Hauraki Gulf slope and shelf region in the northeast of New Zealand. This isoscape was based on historical stable isotope values of SPOM (S. Bury, NIWA, unpublished data), collected along gridded transects from early spring 1996 through to late summer 1997, during a cross-shelf primary productivity study (Bury et al. 2012). Sample collection is detailed in Bury et al. (2012) and methods for stable isotope analysis are provided below (Section 2.4). The data presented are from the spring period and include the average nitrogen isotope values for the upper surface waters (0–20 m). The isoscape was generated using R (v. 3.4.2) (R Core Team, 2015) and followed a method previously used to develop isoscapes linked to a tropical tuna study in the Pacific Ocean (Graham et al. 2010). The latitude and longitude of the sample locations were transformed into uniform surface arrays that were then used to fit a surface Z, where Z is the isotope value interpolated for a location. Data were gridded using a triangle-based linear interpolation and the Z surface always bisected the measured data points.

2.3 Validation of modelled nitrogen isoscape using field data from the Southern Ocean, New Zealand waters and the tropics, making necessary adjustments to isoscape models to improve accuracy (Objective 2)

2.3.1 Western Central Pacific Ocean data-derived nitrogen isoscape

Collaboration with research scientists at IRD, New Caledonia, led to further data validation of the MOBI (Somes et al. 2013) in the southwest Pacific Ocean. Estimates of trophic position derived from bulk isotope SPOM data (combination of new data and literature values), and muscle tissue analyses of tropical tuna (analysed at IRD), combined with compound-specific isotope analyses of amino acids (analysed at NIWA) were used to validate the ecosystem model (Houssard et al. 2017). A generalised additive model (GAM) was used to generate smooth spatial contour maps of SPOM and yellowfin and bigeye tuna $\delta^{15}N$ values.

2.4 Identification and infilling of nitrogen isotope data gaps at a resolution required to examine marine animal movements (Objective 3)

Gaps in nitrogen isotope baseline data are more extensive than for carbon data, mostly due to past analytical capabilities of elemental analysers and mass spectrometers. Particulate nitrogen concentrations in the ocean are much lower than carbon concentrations (C:N mass ratio 6:1; Redfield 1958), which means that many of the analyses of nitrogen in SPOM were below the detection limits of analytical equipment. There is thus a relative paucity of reliable nitrogen SPOM data to validate nitrogen modelled isoscapes compared to carbon. This was the case for isotope data reported in Quilfelldt et al. (2010) where only carbon data were presented. With the advance of analytical technologies and lower detection limits, nitrogen data availability is improving and will enable more data-derived nitrogen isoscapes to be compiled in the future. NIWA is currently undergoing a data retrieval exercise with archived marine sediment, sediment trap material and SPOM nitrogen isotope data spanning the last 20 years of analyses, to retrospectively calibrate low nitrogen data sets, using new improved analytical technologies. These data will then be made available for the development of future data-derived nitrogen isoscapes and data validation of modelled isoscapes. Currently, however, literature nitrogen isotope data for SPOM are relatively sparse, particularly for the Southern Ocean.

The nitrogen baseline isotope gaps in the south Pacific Ocean are predominantly south of 30°S, encompassing the oceanic and coastal waters around New Zealand, and the Sub-Antarctic region. There are also large tracts of the Southern Ocean, for which there is little field measured nitrogen isotope baseline data. Of these regions, oceanographic voyages of opportunity were only available to the Sub-Antarctic and Southern Ocean (see below and Section 2.6.1). Nitrogen baseline isotopic data were collected on two Research Vessel (RV) *Tangaroa* oceanographic voyages in 2016 and 2017 from the east coast of the South Island of New Zealand to the Auckland Islands in the Sub-Antarctic. SPOM samples were collected on RV *Tangaroa* during times when no trawling was occurring. Underway surface water samples were taken from 5.5 m beneath the ship via the RV *Tangaroa* Underway Flow Through System. Two to three litres of water were filtered in duplicate onto 0.7 µm pore size, 25 mm Whatman® glass microfibre filters (grade GF/F) for particulate organic carbon, particulate organic nitrogen, $\delta^{13}C$ and $\delta^{15}N$ analysis. GF/F filters were pre-ashed at 450°C for five hours and stored in tin foil prior to use, to minimise contamination from organic material and achieve low blank values. Filter blanks were generated for each batch filtration, by placing a filter on the filtration manifold and rinsing with 0.2 µm filtered seawater, to replicate the filtration of water samples. All filters were placed in clean six-well plates and stored frozen at -20°C, until ready for analysis, when they were oven dried at 60°C overnight.

Bulk Stable Isotope Analysis: SPOM filters were subsampled and prepared into tin boats before carbon and nitrogen bulk isotope analysis at NIWA's Environmental Stable Isotope Laboratory. Analysis was carried out on a Delta V Plus continuous flow, isotope ratio mass spectrometer (IRMS) coupled to a Flash 2000 elemental analyser (Thermo-Fisher Scientific, Bremen, Germany). Repeat analysis of National Institute of Standards and Technology (NIST) and laboratory standards had a precision of better than 0.2‰ and 0.1‰ for $\delta^{15}N$ and $\delta^{13}C$ values, respectively. Stable carbon and nitrogen isotope ratios are reported in standard δ-notation as per mil (‰) using this equation: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$ where X is ^{13}C or ^{15}N and R is the ratio ^{13}C:^{12}C or ^{15}N:^{14}N (Fry 2006) versus an international standard. The carbon and nitrogen standards used are calibrated against National Bureau of Standards

19 – calcite (NBS19-calcite) (which is calibrated against the original international carbon standard Vienna Pee Dee Belemnite: VPDB, which is now exhausted) and atmospheric nitrogen, respectively.

2.5 Development of marine carbon isoscapes, collaborating with expert modellers in the field (Objective 4)

2.5.1 *Basin-level, modelled carbon isoscape*

Colleagues at the National Oceanography Centre, University of Southampton, UK developed predictive models of stable carbon isotope compositions using ocean surface temperature and $[CO_2]aq$ (MacKenzie et al. 2011; Trueman et al. 2012). Their models were constructed to build isoscapes in northern hemisphere ocean basins to examine fish movements. The model used in this project (Magozzi et al. 2017), was developed building on the earlier models of MacKenzie et al. (2011) and Truman et al. (2012). The model is a process-based, coupled physics-biogeochemistry model (NEMO-MEDUSA) and is currently the most robust carbon isoscape model available. It is most accurate in higher latitudes, such as the northern Atlantic or southern Pacific oceans. Code from this model was shared with this project for adaptation and application to specific New Zealand focussed projects. Modelled carbon isotope baseline data from the southwest Pacific Ocean from Magozzi et al. (2017) were compared to marine animal carbon isotope values in an MPI highly migratory species project (Graham, unpublished data). The model can be configured to produce outputs of various resolutions. A coarser-scale output was selected to avoid over-interpretation of minor changes in the baseline values. The model is less reliable (i.e. has reduced accuracy) in coastal and nearshore regions, due to the dynamic nature and potential of multiple and varied isotopic sources in such areas.

2.5.2 *Coastal, data-derived carbon isoscape*

See 2.2.2 above: the coastal, data-derived carbon isoscape for the shelf and slope of northeast New Zealand was produced using the same method as that used to generate the nitrogen isoscape.

2.6 Validation of modelled carbon isoscape using field data from the Southern Ocean, New Zealand waters and the tropics, making necessary adjustments to isoscape models to improve accuracy (Objective 5)

2.6.1 *Southern Ocean data-derived carbon isoscape*

Carbon baseline isotopic data were collected during four RV *Tangaroa* oceanographic voyages (in 2010, 2015, 2016 and 2017); two to the Southern Ocean and two to the Sub-Antarctic region. SPOM samples were collected on RV *Tangaroa* at six-hourly intervals from New Zealand to the Ross Sea on south-bound and north-bound transects in February-March 2010 and 2015 (S. Bury, NIWA, unpublished data). SPOM isotope samples collected during the Sub-Antarctic RV *Tangaroa* voyages were collected less regularly, being restricted to time periods when no trawling was occurring. Underway surface water sampling and filtration procedures were as reported in Section 2.4. A SPOM dataset, compiled from 20 voyages (Fischer et al. 1998; Quillfeldt et al. 2010) were combined with the two RV *Tangaroa* datasets to produce a data-derived Southern Ocean isoscape. The isoscape was produced using the Geostatistical Analyst Package in ArcMap and ordinary kriging, employing the default kriging model. The isoscape was generated as an exploratory output for the purpose of data visualisation of amalgamated carbon baseline field data. Carbon isotope data obtained during the 2010 RV *Tangaroa* voyage transect from New Zealand to the Ross Sea were plotted as an interpolated isotope track using a Global Information System (GIS) arc inverse distance weighting interpolation.

2.7 Identification and infilling of carbon isotope data gaps at a resolution required to examine marine animal movements (Objective 6)

As stated in Section 2.4, there are relatively sparse biogeochemical and stable isotope datasets available for the higher latitudes of the South Pacific Ocean, and infilling data gaps is a costly, time consuming and complex process. During this project, we researched what datasets were available in the southwest Pacific Ocean and Southern Ocean region and identified oceanographic voyages of opportunity. These voyages included Southern Ocean (Ross Sea) multi-objective ecosystem voyages and Sub-Antarctic and New Zealand fisheries survey voyages. Acquiring baseline and fisheries isotope samples from these significantly under-sampled areas was an important component of this project, as these are key regions for commercial fisheries and top predator habitat. See Section 2.4 above, for details of oceanic sampling, bulk stable isotope sample processing, and analysis to infill carbon isotope data gaps in modelled and data-derived isoscapes.

2.8 Utilisation of validated isoscapes to determine and assess the movements of migratory animals in the south-west Pacific Ocean, within existing and future funded projects (Objective 7)

Several aligned research projects have been completed, where isoscapes and associated stable isotope techniques have been utilised to assess the trophic status and movements of migratory animals. Isoscapes, compound-specific stable isotope analysis of amino acids (CSIA-AA), satellite tagging, and a GAM have been used to examine the trophic status and feeding behaviour of yellowfin (*Thunnus albacares*) and bigeye (*Thunnus obesus*) tunas (Houssard et al. 2017). Research on highly migratory species (HMS) has determined their trophic status and movements (Graham, unpublished data). Isoscapes were also used to examine the movements of humpback whales (*Megaptera novaeangliae*) that breed in the south central tropical Kermadec Islands and forage in the Southern Ocean (ZBD201308; Constantine 2016).

3. RESULTS

3.1 Development of marine nitrogen isoscapes (Objective 1)

3.1.1 Development of marine basin nitrogen isoscape

Figure 3 shows the output of the modelled nitrogen isoscape from MOBI (Somes et al. 2013), which was tailored for the southwest Pacific Ocean for this project and was driven by regional sediment $\delta^{15}N$ values. The nitrogen isoscape has both strong latitudinal and longitudinal structure between the equator and 45°S, and 130°E to 150°W. The strongest longitudinal gradient exists in the tropics between 0–10°S where $\delta^{15}N$ values of 3–5‰ off the northeast Australian coast in the Coral Sea, and off Papua New Guinea, in the Solomon Sea, gradually increase in a westerly direction to reach values of around 10‰ between 160–150°W. A region of elevated $\delta^{15}N$ values of 12‰ occurs around the Gilbert Islands which span three degrees north and south of the Equator between 172–174°E. In the subtropics (15–30°S), a tongue of depleted $\delta^{15}N$ values exists, which decrease from 1‰ around 160°E to -2‰ between 175°W to 150°W. Nitrogen isotope values range from 1 to -2‰ across the Antarctic region south of 55°S.

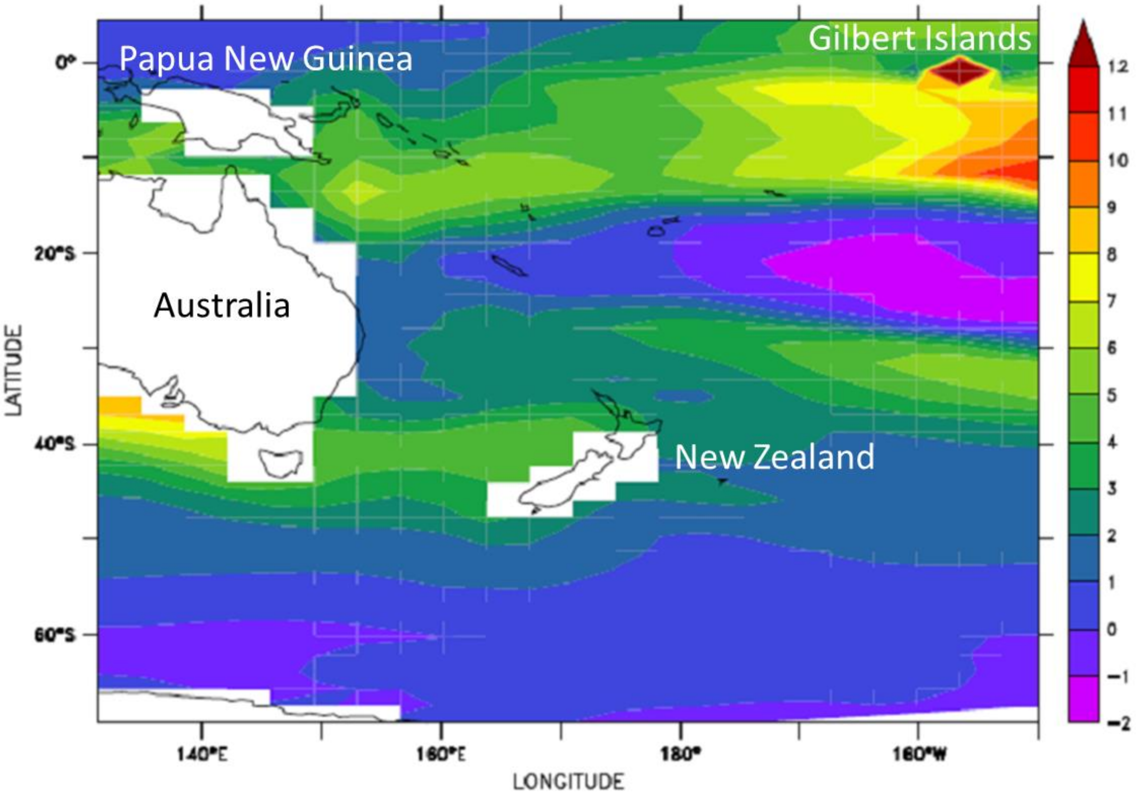

Figure 3: Nitrogen modelled isoscape for the south Pacific Ocean based on the Somes et al. (2013) MOBI. See Section 2.2.1 for model details (Objective 1). The scale bar on the right indicates the δ^{15}N value (‰) of the modelled particulate organic matter.

3.1.2 Development of a coastal, data-derived nitrogen isoscape

A data-derived nitrogen isoscape was developed for the Hauraki Gulf shelf region based on the stable isotope values of particulate organic matter collected from surface waters (Figure 4). Strong nitrogen isotopic gradients occur across the shelf-slope region. In the near-shore region of Auckland harbour, δ^{15}N values are around 9‰, with values gradually and systematically decreasing to 2–3‰ in the coastal oceanic waters off the northeast shelf. There is a well-defined plume of elevated δ^{15}N values northwards of Auckland harbour, extending out to offshore of Bream Bay.

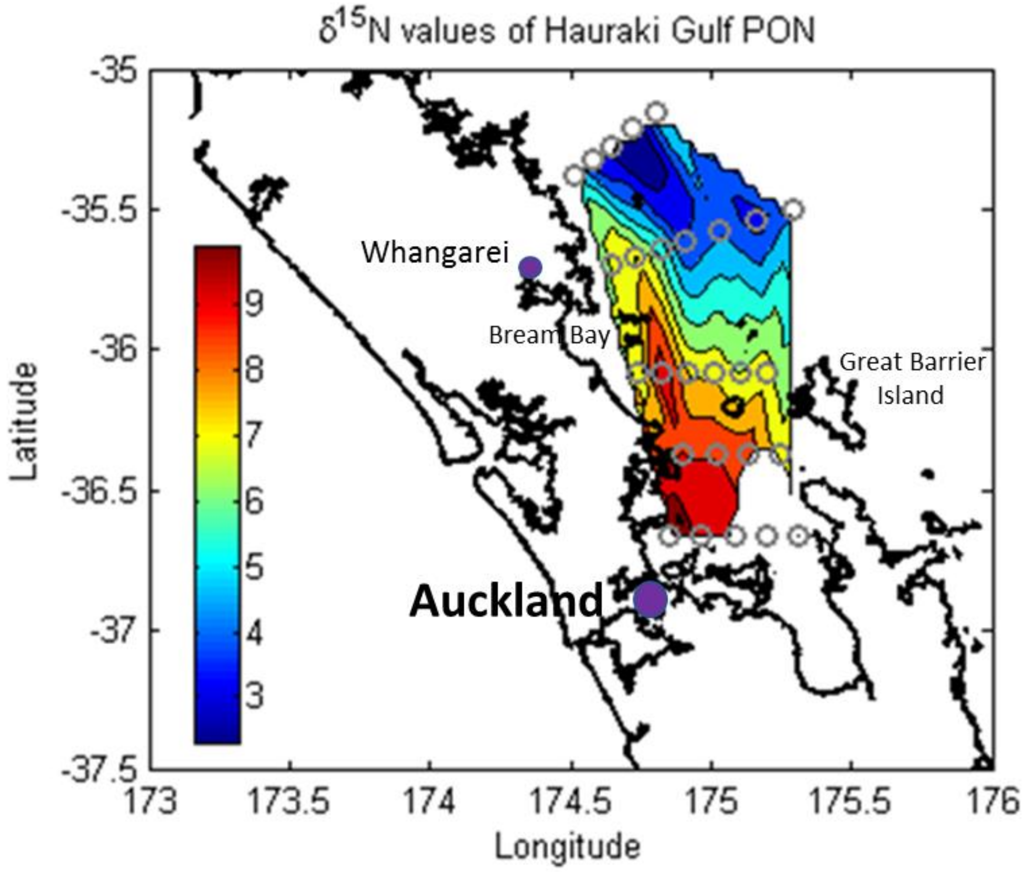

Figure 4: Nitrogen data-derived isoscape of SPOM collected during spring 1996, in the northeast shelf and slope of New Zealand (see Bury et al. (2012); S. Bury, NIWA unpublished data). Nitrogen isotope values represented in the coloured legend are in units of ‰ (Objective 1).

3.2 Validation of modelled nitrogen using field data (Objective 2)

3.2.1 Western Central Pacific Ocean data-derived nitrogen isoscape

The Houssard et al. (2017) study aimed to improve the MOBI output for the subtropical western Pacific Ocean, where the Somes et al. (2013) model did not effectively capture the extent of N_2 fixation empirically measured in the region (Menkes et al. 2015). This is the first data-driven baseline nitrogen isoscape that has been produced for the western and central Pacific Ocean. Five biogeochemical regions were identified, as shown in Figure 5, based on distinct particulate organic matter $\delta^{15}N$ values. The Warm Pool (WARM) region to the east of Papua New Guinea and the north Pacific Equatorial Counter Current (PNEC) region in the central Pacific Ocean, both showed little isotopic variability, with surface baseline nitrogen values of 6-8‰. The Pacific Equatorial Divergence (PEQD) region south of the PNEC, and the Archipelagic Deep Basins (ARCH) area to the east of Australia, both displayed vast areas of very low nitrogen isotope values ranging from -1 to 2‰. Large tracts of the southwest Pacific Ocean have little variation in nitrogen isotope values, however the South Pacific Subtropical Gyre (SPSG) region showed large latitudinal variability, with $\delta^{15}N$ values ranging from 4‰ in the north of the area around 10°S, to 14‰ in the south (at about 20°S).

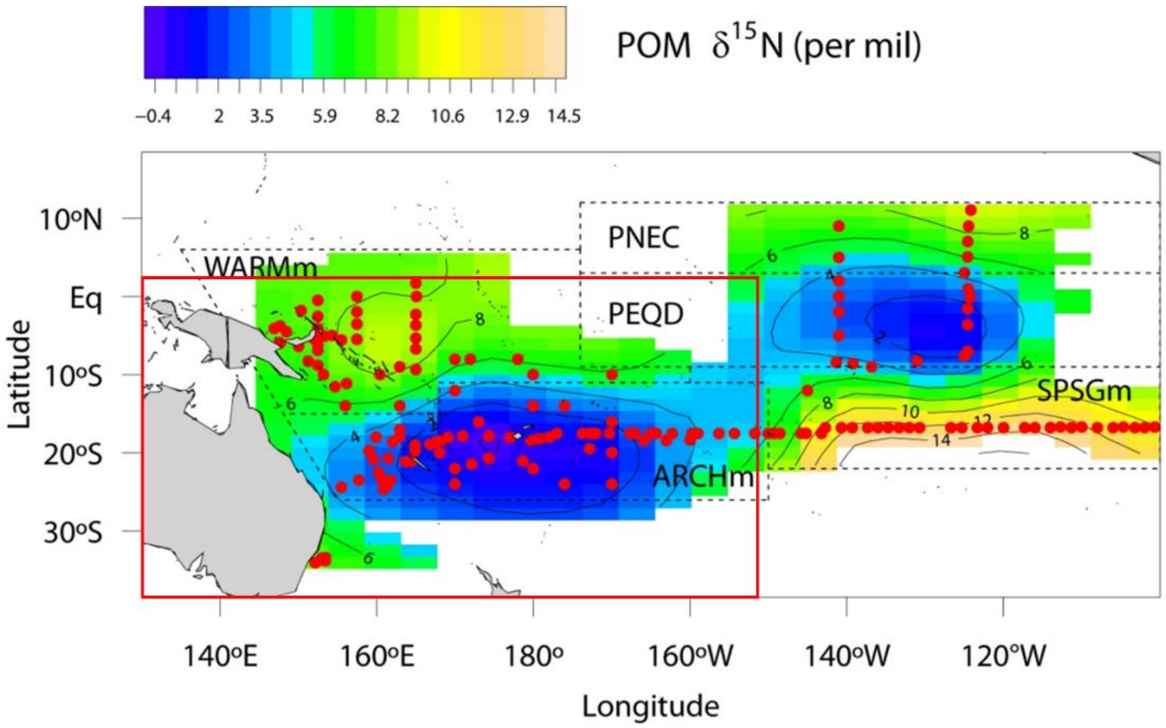

Figure 5: The equatorial and South Pacific Ocean nitrogen isoscape based on SPOM measured from oceanographic voyages in the Longhurst biogeographical providences: Warm Pool modified (WARMm), PEQD, Archipelagic Deep Basins modified (ARCHm), PNEC and the South Pacific Subtropical Gyre modified (SPSGm) (Longhurst 2007). The red dots represent where SPOM was measured and the dotted lines delineate the five biogeochemical regions based on distinct particulate organic matter δ^{15}N values. The red rectangular box marks the spatial coverage of the MOBI model represented in Figure 3. A GAM was used to generate the smoothed spatial contour maps of these values. Further details about the model and approach can be found in Houssard et al. (2017). This figure is adapted from figure 2 of Houssard et al. (2017).

3.2.2 Identification and infilling of nitrogen isotope data gaps at a resolution required to examine marine animal movements (Objective 3)

There were limited opportunities to infill nitrogen isotope data gaps given the low number of oceanographic voyages of opportunity to the southwest Pacific Ocean and Southern Ocean. However, using the developed nitrogen isotope model (Somes et al. 2013) and interpolating between datasets of the south Pacific Ocean, a better understanding of this region's geographical isoscape has been achieved. Nitrogen isotope data in the Sub-Antarctic region were obtained and SPOM δ^{15}N values from a voyage in February 2016 (Roberts et al. 2018) are plotted in Figure 6. There was a large degree of variability in SPOM δ^{15}N values in the shelf waters along the eastern side of the South Island. Nitrogen isotope values were enriched in waters off Banks Peninsula (4.4 to 7.3‰), were depleted in waters just north of Campbell Plateau (-1.9 to -1.0‰), and ranged from -0.9 to 4.3‰ in Sub-Antarctic waters to the east and northeast of the Auckland Islands. The average δ^{15}N value was 1.5 ± 2.8‰ (standard deviation).

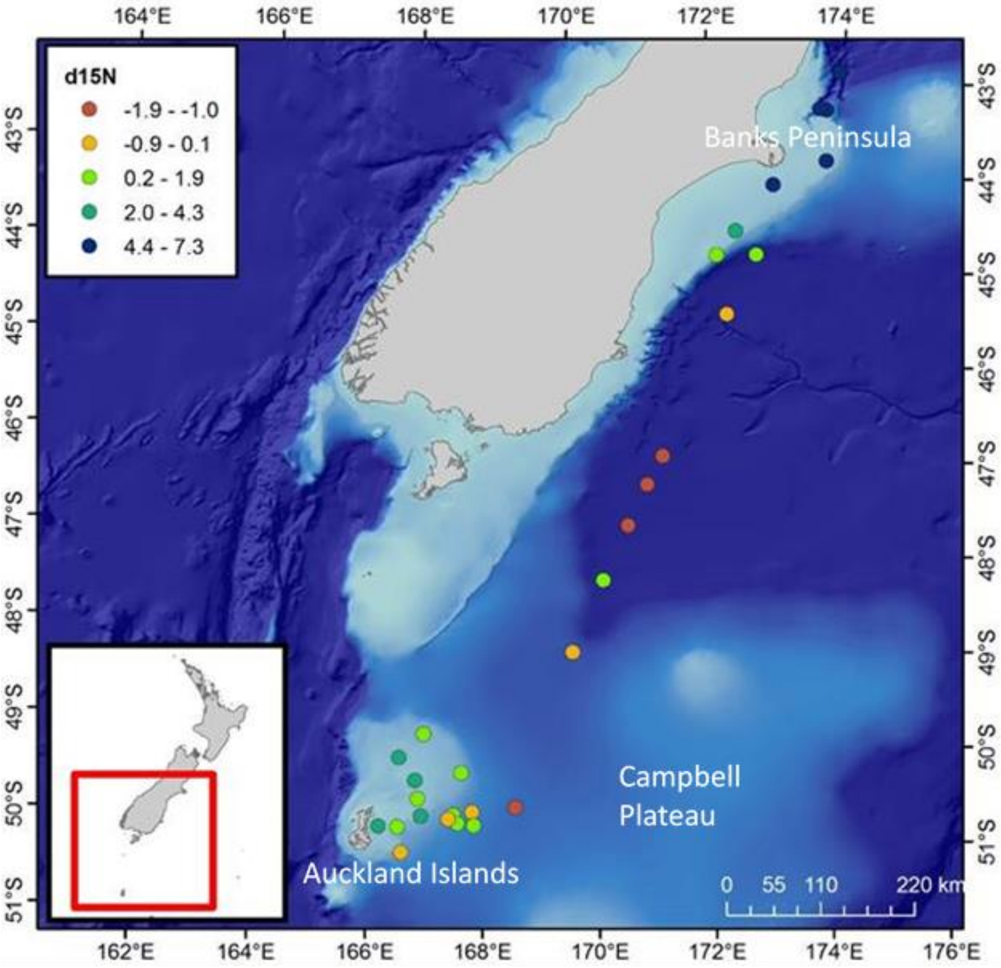

Figure 6: Nitrogen isotope ($\delta^{15}N$) values (‰) of SPOM collected around New Zealand during a fisheries voyage (TAN1614), to Sub-Antarctic waters, during February 2016 (Objective 3).

3.3 Development of marine carbon isoscapes collaborating with expert modellers in the field (Objective 4)

3.3.1 Basin-level, modelled carbon isoscape

Figure 7 is a modified, coarse resolution output of the Magozzi et al. (2017) model, which was tailored for the southwest Pacific Ocean. There is a classic strong latitudinal gradient in $\delta^{13}C$ values, with values of around -16‰ occurring at the Equator, which gradually decrease in open ocean areas to reach -32‰ along the Antarctic shelf. South of 40°S there is very little longitudinal variation in $\delta^{13}C$ values. Carbon values show variability off the southeast coast of Australia (-27 to -16‰) and around the coast of New Zealand (-32 to -19‰). Tropical waters spanning the Equator from 10°N to 10°S are more or less isotopically homogeneous, with carbon isotope values ranging from -19 to -21‰ across huge tracts of the open ocean. Enriched carbon isotope values of -19 to -16‰ occur around the coast of Papua New Guinea. A region of more depleted $\delta^{13}C$ values (-26 to -24‰) occurs to the east of Australia around 25°S and to the west of Australia between 20–30°S.

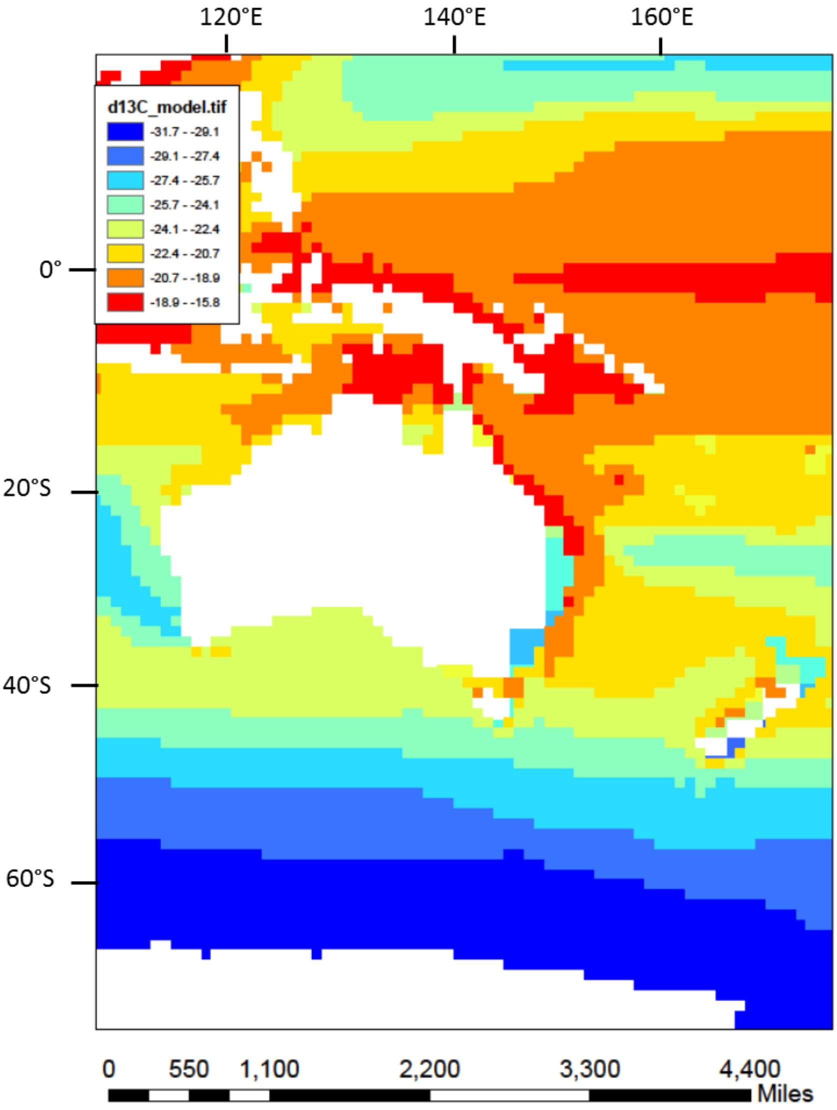

Figure 7: Modelled δ^{13}C isoscape for the south Pacific Ocean. Modified coarse resolution output of the Magozzi et al. (2017) model, tailored for the southwest Pacific region (Objective 4).

3.3.2 Coastal, data-derived carbon isoscape

A data-derived carbon isoscape (Figure 8) was developed for the Hauraki Gulf shelf region based on the stable isotope values of SPOM collected from surface waters (see Bury et al. 2012). Strong isotopic gradients were observed in the δ^{13}C values, with enriched carbon isotope values (-18‰) observed off the coast of Whangarei and Bream Bay and out to Great Barrier Island. There were isotopically distinct areas within the northeast New Zealand shelf and slope region: the Hauraki Gulf area had carbon isotope values of -22 to -21‰, whilst offshore slope waters had more depleted values of -24 to -22‰.

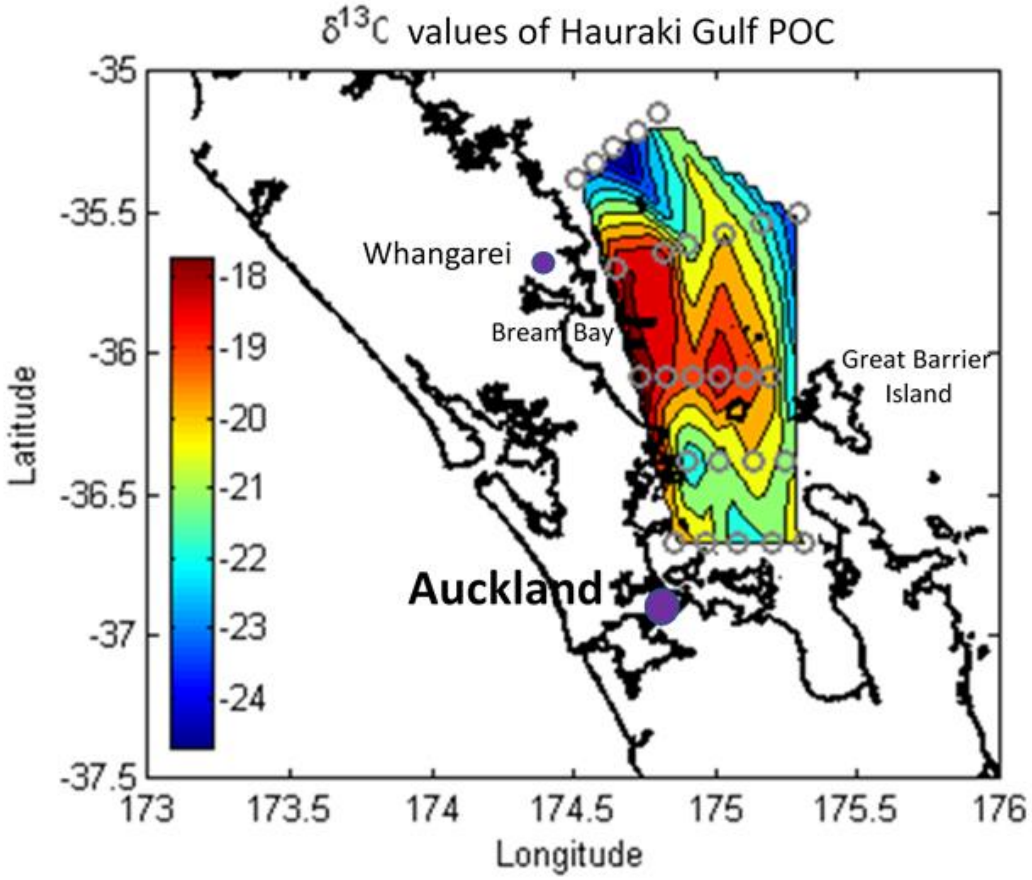

Figure 8: Carbon data-derived isoscape of SPOM collected during spring 1996 (see Bury et al. 2012; S. Bury, NIWA, unpublished data). (Objective 4). Carbon isotope values represented in the coloured legend are in units of ‰.

3.4 Validation of modelled carbon isoscape using field data from the Southern Ocean, New Zealand waters and the tropics, making necessary adjustments to isoscape models to improve accuracy (Objective 5)

3.4.1 Southern Ocean data-derived carbon isoscape

The Southern Ocean data-derived carbon isoscape is presented in Figure 9. Southern Ocean transect SPOM data generated during the 2010 Antarctic Whale Expedition, which were included in the modelled output of Figure 9, are shown in Figure 10. Both Figures 9 and 10 illustrate a consistent decrease in δ^{13}C values with increasing latitude, with values of around -20‰ in the sub-tropical waters around New Zealand to just below -30‰ in Antarctic waters. The data-derived model indicated that more depleted carbon values exist along the Ross Sea shelf and slope region extending as far as the boundary of the Bellingshausen Sea, and in the Weddell Sea. North of 65°S and the Southern Antarctic Circumpolar Front, there is very little longitudinal isotopic variability, until 50°S is reached, where elevated δ^{13}C values (around -20‰) exist in the tropical waters between the Chatham Islands east of New Zealand to South America. More depleted values of around -25‰ occur to the east of Australia in the Coral and Tasman seas and into the central Pacific Ocean as far as the Equator. These values are similar to carbon values predicted in Sub-Antarctic waters north of the Sub-Antarctic Front around 50°S.

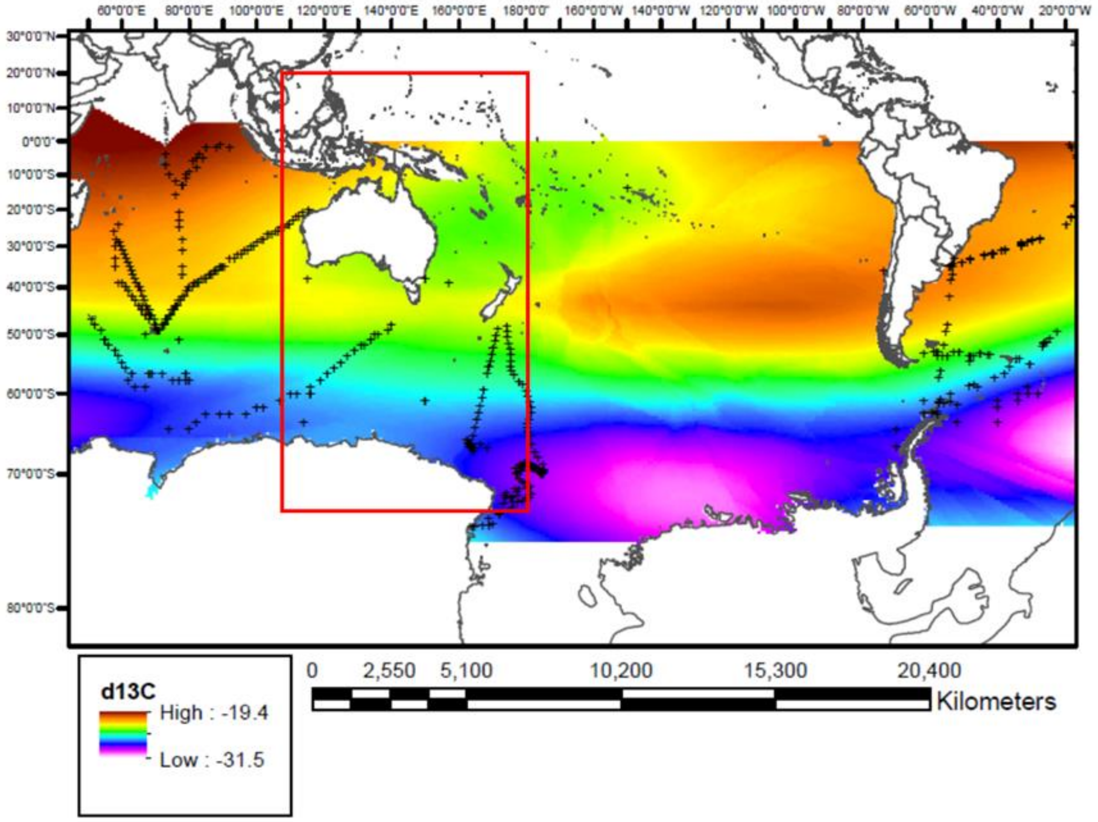

Figure 9: Southern Ocean data-generated carbon isoscape based on SPOM isotope values collected from over 15 oceanographic cruises from 1970–1990 (Quillfeldt et al. 2010; Fischer et al. 1998) and from the two RV *Tangaroa* voyages from New Zealand to the Southern Ocean in 2010 and 2015 (S. Bury, NIWA, *unpublished data*) (Objective 5). The red rectangular box marks the spatial coverage of the Magozzi et al. (2017) model represented in Figure 7. The carbon isoscape was generated by Katie St John Glew using the Geostatistical Analyst Package in ArcMap using kriging.

3.5 Identification and infilling of carbon isotope data gaps at a resolution required to examine marine animal movements (Objective 6)

As described in Sections 2.7 and 3.4.1, SPOM carbon isotope data collected on two voyages from New Zealand to the Ross Sea, Antarctica, were used to infill the sparse carbon isotope data set in this region of the southwest Pacific Ocean and Southern Ocean. These data were used to constrain the output of the data-derived carbon isoscape (Figure 9) presented above. Carbon isotope data shown in Figure 10 illustrate the very strong latitudinal effect on δ^{13}C values. In subtropical waters east of New Zealand, δ^{13}C values are around -18 to -22‰ and steadily decrease with increasing latitude and decreasing water temperatures to values of -32‰ between 160°E–160°W south of 65°S. Elevated δ^{13}C values of -24 to -22‰ occur in waters around the Balleny Islands around 165°E.

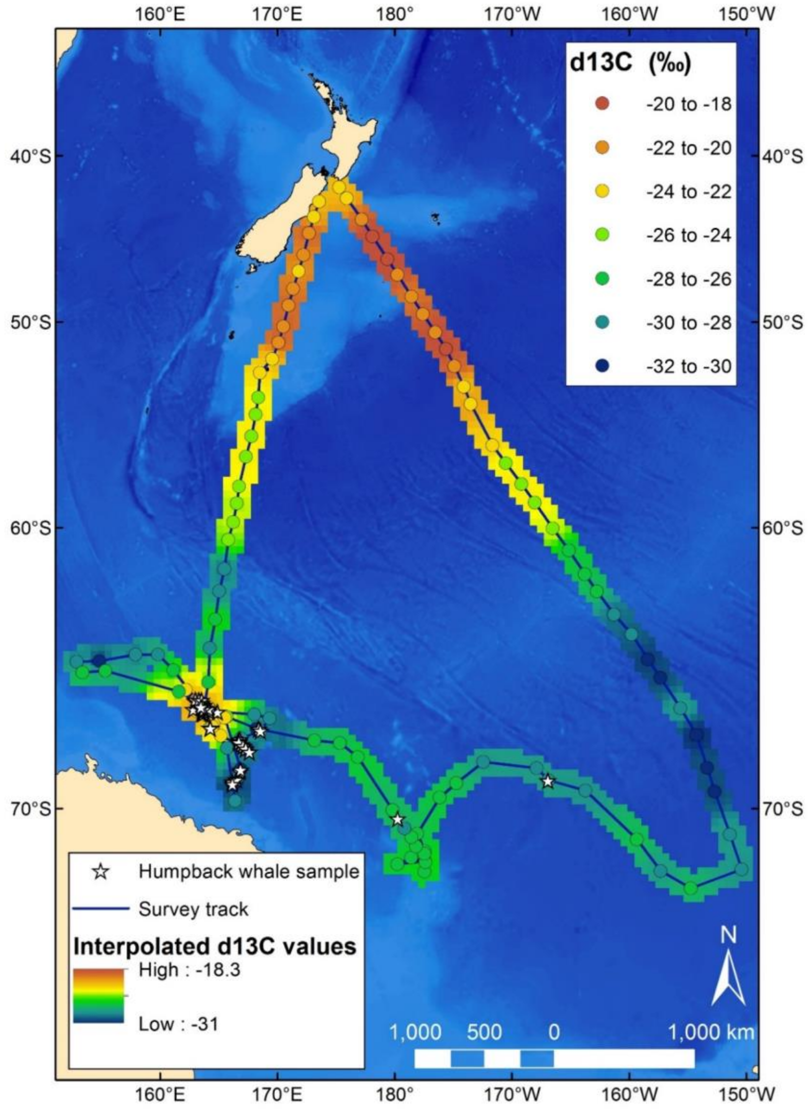

Figure 10: The interpolated δ^{13}C isoscape track of the 2010 Antarctic Whale Expedition voyage, generated by Leigh Torres using GIS arc inverse distance weighting interpolation (S. Bury, NIWA, *unpublished data*) (Objective 6). Humpback whale sightings are superimposed on the tracks. These data were included in the isoscape illustrated in Figure 9.

Carbon isotope values of SPOM collected on a voyage in February 2016 (Roberts et al. 2018) are plotted in Figure 11. A large degree of variation was observed in the carbon isotope values of SPOM, particularly in nearshore regions. Carbon isotope values ranged from -27 to -18‰ in waters to the east and northeast of the Auckland Islands in the Sub-Antarctic, to values of -27 to -22‰ offshore of Banks Peninsula. There was no distinctive decrease in δ^{13}C with increasing latitude. Carbon values were more stable across the open ocean transect, exhibiting δ^{13}C values of between -22 to -24‰.

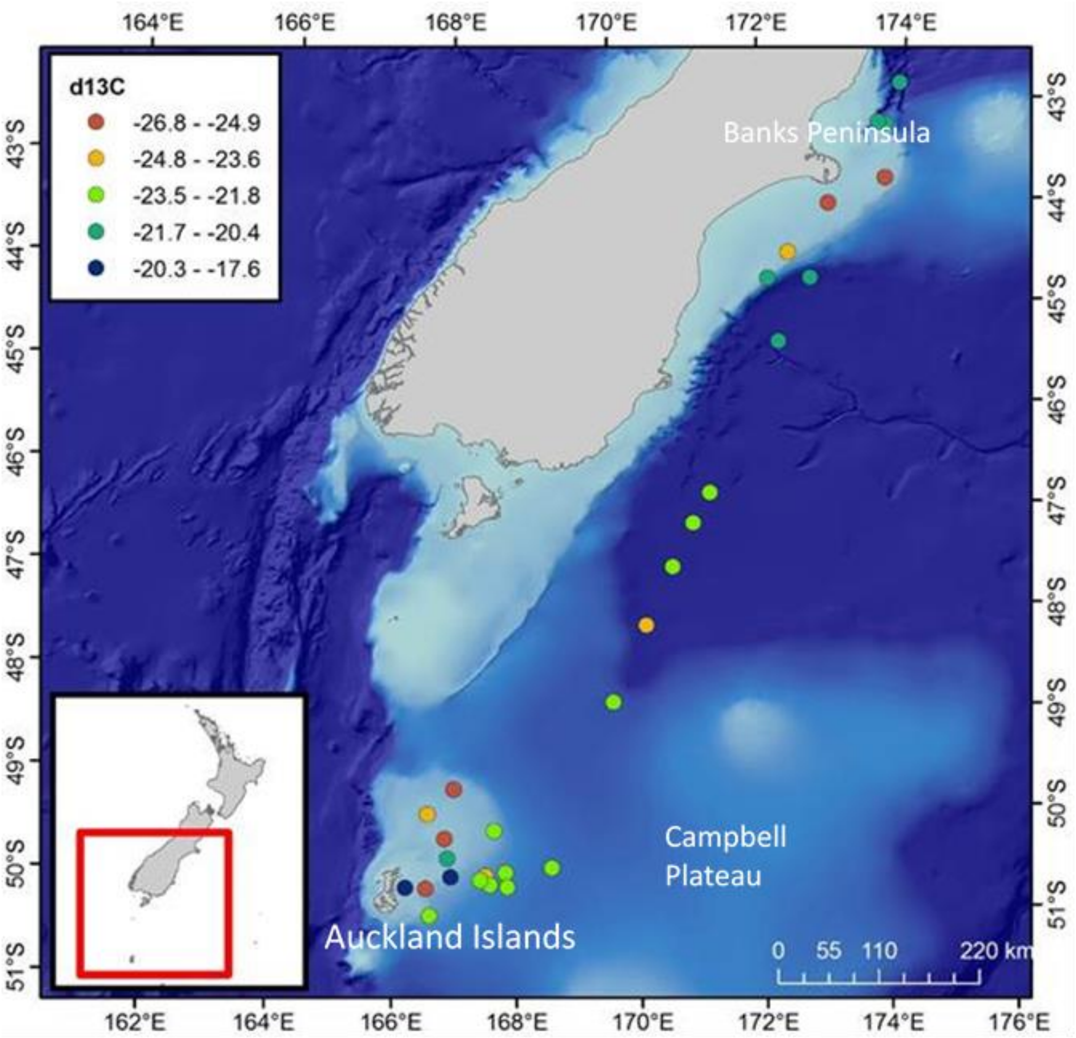

Figure 11: Carbon isotope ($\delta^{13}C$) values (‰) of SPOM collected around New Zealand during a fisheries voyage (TAN1614, sea lion prey survey) to Sub-Antarctic waters, in February 2016 (Objective 6).

3.6 Utilisation of validated isoscapes to determine and assess the movements of migratory animals in the southwest Pacific Ocean, within existing and future funded projects (Objective 7)

Results and applications related to this objective are covered in the Discussion below under Sections 4.1, 4.3 and 4.4.

4. DISCUSSION

4.1 Overview

The combination of an extensive three-dimensional sampling region, modest research budgets and large requirements of ship time, limit the ability to track animal movements in the open ocean. Here, an emerging approach using marine isoscapes has been developed to address this issue. The difficulty of directly observing marine animals, and the expanse of their pelagic habitat, have both hindered our understanding of their movements, and of the locations of critical habitat, such as feeding and mating grounds. These challenges have spurred development of recent technologies and novel methods to remotely examine animal movements, especially by tracking fish carrying acoustic or satellite tags (Holland & Sibert 1994; Brill et al. 1999; Block et al. 2011; Francis et al. 2012; Leroy et al. 2015). These electronic tagging studies are generally limited to studying the detailed movements of a few individuals, but recently the launch of extensive electronic and traditional tagging programmes have circumvented some of the difficulties of over-interpreting the movements of a few individuals in the population (e.g., Leroy et al. 2015; Block et al. 2011). In this project, isoscapes and stable isotope techniques were shown to be a useful, complementary tool to examine animal movements. For this tool to be used most successfully, baseline isoscapes must be developed, both to provide information on animal movements and trophic status. This project produced baseline isoscapes developed in collaboration with international researchers, that were both model-derived and data-driven, and which covered regional, basin, and global scales. These models are now enabling animal movements to be tracked in the open ocean and are more accurately determining the trophic status of marine animals when they reside in a region long enough to acquire the local baseline signal (Best & Schell 1996; Lee et al. 2005; Graham et al. 2010; Trueman et al. 2012; Young et al. 2015a; Houssard et al. 2017).

4.2 Baseline isotopic variability in the southwest and central Pacific Ocean and the Southern Ocean

The model-derived (Figure 3) and data-driven (Figure 5) nitrogen isoscapes both showed low baseline δ^{15}N values (-1 to -2‰) in the ARCH of the southwest Pacific Ocean, indicating high levels of nitrogen fixation in this area (Menkes et al. 2015). The data-driven Houssard et al. (2017) isoscape, which depicted a wider coverage of the southwest Pacific Ocean, also showed similar low baseline values in the PEQD. Higher δ^{15}N values were obtained in the SPSG and WARM: 10–14‰ and 8–10‰, respectively (Longhurst 2007; Houssard et al. 2017), where upwelling of deep currents introduced high nitrate levels to the surface waters. Nitrogen isotope values in the Southern Ocean were relatively homogeneous and low (-1 to 1‰), largely because this is a HNLC region with high current flows, turbulence and well-mixed water masses. In addition to local oceanographic drivers of hydrography, surface water nutrient chemistry and phytoplankton community composition, which together determine the nitrogen baseline values (Montoya 2007; Graham et al. 2010; Lorrain et al. 2015; Young et al. 2015a; Houssard et al. 2017), there are larger scale climatic processes, such as ENSO events, that also modify the δ^{15}N values and their spatial distributions (Lehodey et al. 1998; Menkes et al. 2015).

The two models (Somes et al. 2013, Figure 3 and Houssard et al. 2017, Figure 5) compare relatively well in terms of the details of the δ^{15}N output values, in that they both demonstrate a similar expansive area of low δ^{15}N nitrogen fixation values in the southwest Pacific Ocean off the east coast of Australia to 170°W. The highly enriched nitrogen baseline values (12‰) around the Gilbert Islands and the longitudinal variability south of the islands are only depicted in the Somes et al. (2013) model output, as the Houssard et al. (2017) output was devoid of SPOM data in this area. The strong carbon latitudinal variability, which was observed in the modelled (Figure 7) and data-derived isoscapes (Figures 9, 10), is largely driven by changes in temperature and the solubility of CO_2(aq) (Goericke & Fry 1994; Laws et al. 1995; Popp et al. 1999; Graham et al. 2010; Trueman et al. 2012). This coherent and predictable carbon isotope latitudinal gradient enables us to use carbon isotopes to evaluate movements of animals, such as fish, seabirds and marine mammals, in north-south directions between tropical waters and Antarctica. In the Southern Ocean, strong circumpolar currents and a high degree of mixing produces a relatively homogeneous isotopic water mass in the east-west direction. Therefore, interpreting east-west movements in such regions with little longitudinal isotopic structure is more challenging. There were sections in the field data of the carbon isotope latitudinal transect where carbon isotope values deviated from the predicted modelled values driven by the positive δ^{13}C-temperature relationship – these were in locations close to the New Zealand coastline and around the Balleny Islands, north of the Ross Sea slope. These regions are where coastal processes, upwelling and biological effects can all play a part in over-riding the physical temperature drivers of δ^{13}C values in phytoplankton.

The Magozzi et al. (2017) model output (Figure 7) compared well to the data-derived model of Katie St John Glew (Figure 9) and the interpolated isotope field data (Figure 10) in terms of general spatial structure. However, the SPOM $\delta^{13}C$ data from the 2010 Antarctic Whale Expedition voyage were more enriched than the model data throughout the latitudinal transect. For example, measured values just south of New Zealand were around -22 to -20‰, whereas modelled values were -24 to -26‰. Carbon values from the data-derived model (Figure 9) were in closer alignment to the measured values, as one might expect, which strengthens the argument for field data to be embedded within models to generate more accurate outputs. Having accurate modelled outputs is critical to the correct assignment of animals to their feeding locations in migration studies.

4.3 Coastal isoscapes – strengths and limitations

Generating modelled and data-derived isoscapes for coastal environments presents more challenges than for open ocean systems. This is largely due to highly dynamic coastal processes and variable isotopic sources and inputs to near-shore ecosystems. Such systems tend to be more spatially and temporally heterogeneous than open ocean systems. However, a recent study by Kurle & McWhorter (2017) demonstrated that in some regions, coastal isoscapes can be temporally robust. The more localised, sample-based isoscapes generated in the northeast New Zealand shelf-slope area within this project (Figures 4, 8) also produced coastal isoscapes with distinct isotopic gradients. The nitrogen isoscape showed a well-defined plume of enriched $\delta^{15}N$ values discharging northwards into the Hauraki Gulf from the port of Auckland, and a strong nitrogen gradient with $\delta^{15}N$ values declining with increasing distance from the shore. This reflects the extent of terrestrial and anthropogenic inputs to the Hauraki Gulf and shelf/slope region. Similarly, the strong carbon isotope gradient with higher $\delta^{13}C$ isotope values off the coast of Whangarei and Bream Bay out to Great Barrier Island indicates isotopically distinct regions within the northeast New Zealand shelf. These distinct isotopic regions could be used to track resident animals in this region and to interpret their small-scale movements and trophic status.

The isoscapes from the northeast coastal region of New Zealand and Hauraki Gulf show strong spatial isotopic structure that may be uncommon in such marine environments. The spatial trends are most likely driven by the influence of land-based and anthropogenic nutrient inputs from Auckland and other highly populated regions. Nutrients added to agriculture and forestry systems have stable isotope values that can have "point" source, unique isotope signals (Fry 2006) and it is possible to trace these inputs into marine systems Where multiple point source or "endmember" input sources to a coastal environment can be identified, it is possible through mixing models to estimate relative proportions of different inputs to marine systems (Phillips 2001; Phillips & Gregg 2003; Gibbs 2008; Inger et al. 2010; Parnell et al. 2010; Gibbs 2014; Mabit et al. 2018). Further work needs to be conducted to see how temporally and spatially stable coastal isoscapes are, as there is great potential for applying coastal isoscapes to understand fish, mammal and seabird movements in New Zealand waters with benefits to marine resource management and conservation.

Under the current project, a hypothetical approach was developed to delineate potential foraging regions for seabirds, based on the coastal isoscapes developed in the northeast shelf and slope region of New Zealand (Figure 12). A simple collation of local $\delta^{13}C$ and $\delta^{15}N$ values for a predicted diet, given the seabird feather isotope values, corrected for trophic enrichment (see figure caption), can define the likely space the seabirds or other marine animals foraged in, so long as those animals have a feeding home range within the developed isoscape. Currently, several researchers are interested in using these isoscapes to determine seabird and delphinid foraging grounds in the Hauraki Gulf (S. Ismar, M. Rayner; K. Stockin, *pers. comm.*)

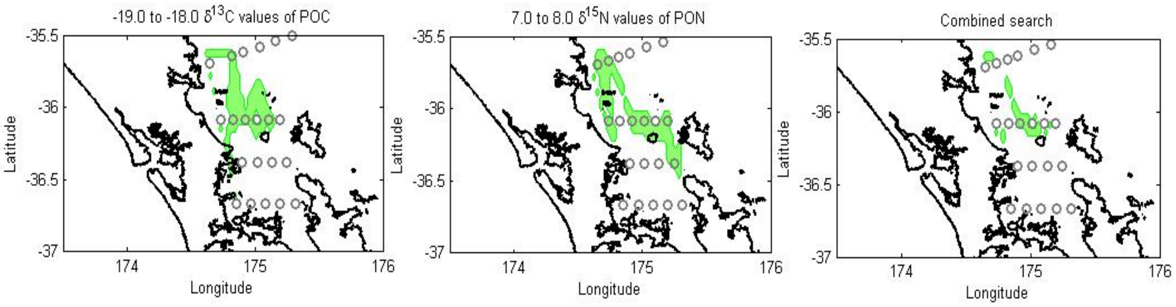

Figure 12: Application of the Hauraki Gulf shelf and slope isoscape to determine foraging grounds for a hypothetical seabird. The left graph shows the δ^{13}C values of a seabird measured between -19 to -18‰, after correcting for trophic level fractionation using 1‰ TEF. The middle graph is a similar graph, but of the seabird δ^{15}N values measured between 7 to 8‰, after correcting for trophic level fractionation using 3‰ TEF. The right graph is a search of the isoscape, where both the carbon and nitrogen isotope values match those measured in this hypothetical seabird. In theory, this is the likely foraging area of this seabird, if foraging was confined to within this geographical region only (B. Graham, S. Bury, NIWA, unpublished data).

In contrast to the smooth carbon and nitrogen isotopic gradients measured in the northeast region of New Zealand, data from voyages sampling SPOM along a transect from New Zealand's South Island to Sub-Antarctic waters showed great isotopic heterogeneity in both δ^{15}N (Figure 6) and δ^{13}C values (Figures 6, 11). This is most likely due to the highly dynamic oceanographic area where several water masses and fronts were transited, encountering transient eddy systems and variable nutrient sources and fluxes (Chiswell et al. 2015). Furthermore, local biological processes (e.g., phytoplankton blooms) can perturb the physical temperature effects that are usually the strongest determinants of δ^{13}C values in open ocean systems. Future work could sample further off shore in this region to see if the variability decreases, since greater stability in isotope values can be seen in the offshore data points (Figures 6, 10).

Finally, when applying these isoscape techniques to understanding the movements of marine animals at smaller scales some additional factors need to be considered. For example, it would be important to understand the animal's main prey range of depth, because isotopic values can vary considerably with depth in dynamic coastal and shelf ecosystems, as shown at two moorings south and north of the subtropical front over the Chatham Rise (S. Nodder, NIWA unpublished data). This depth variability is much less of an issue in stratified, open ocean ecosystems (e.g. Altabet 2001) and the variation is comparatively small, when compared to the geographical variations observed in the south Pacific region.

4.4 Isoscapes coupled with CSIA-AA

The power of isoscapes as a research tool is increased when this method is coupled with other chemical tracer methods. For example, using bulk isotope tissue analyses and isoscapes to track animal migration is strengthened by supplementing with direct observations or sightings of the animals, using data from electronic tagging programmes, and fisheries catch data for commercially important species. CSIA-AA is advancing the use of bulk isotope analysis and isoscape applications in both movement and trophic status studies. CSIA-AA can help to determine if a marine animal's stable isotope value is driven by variations in the baseline or in trophic position. The stable isotope values of specific amino acids (AAs) in a single tissue sample of an animal represent an internal indicator of the animal's trophic position (Popp et al. 2007; Chikaraishi et al. 2007, 2009; Lorrain et al. 2009). This method works because the δ^{15}N values of one group of AAs, the so-called source AAs (*sensu* Popp et al. 2007, e.g., phenylalanine, glycine), change little with each trophic transfer and can represent the isotopic baseline, whereas a second group of AAs, the trophic AAs (*sensu* Popp et al. 2007, e.g., glutamic acid and alanine), become enriched in ^{15}N with each trophic transfer and can provide an estimate of the consumer's trophic position (McClelland & Montoya 2002; Chikaraishi et al. 2007, 2009; Hannides et al. 2009). Thus, by comparing the isotope results from both source and trophic AAs sampled from the same individual consumer, one can determine if the individual has, a) resided in the region, but their diet has changed, or b) migrated from another region (see Ohkouchi et al. 2017 for the most recent review on the method, applications, and future directions). As this method simply requires a tissue sample of the individual, and not expansive sampling of the baseline, which often requires extensive at-sea measurements, CSIA-AA is growing exponentially in its application to assess animal movements and trophic positions. The most advanced nitrogen isoscape that combined all methods; isoscape models, bulk and CSIA-AA, demonstrated that bigeye and yellowfin tunas utilize different depths for foraging and adjust to the thermocline as they migrate in the tropical Pacific Ocean (Houssard et al. 2017). Bulk nitrogen isotope values of baseline particulate organic matter in the western and central Pacific Ocean (Figure 5) and CSIA-AA muscle data from bigeye and yellowfin tunas were integrated into the MOBI model (Somes et al. 2013) using a GAM to generate the final nitrogen isoscape (Houssard et al. 2017). In future work, combining all these methods, plus utilising data generated by satellite and conventional tags will allow us to best track marine animals in the open ocean and understand their utilisation of this three-dimensional, dynamic marine environment.

One application of using baseline modelled isoscapes to examine marine animal movements has been recently completed for MPI project HMS201502. The results from this project show that the carbon and nitrogen isotopic difference between the modelled baseline isoscapes, subtracted from the tissue isotope values of migratory species (e.g., tuna, pelagic sharks, billfish), show a large degree of variation in movements of each species. These movements indicate that there is considerable connectivity between the tropics, subtropics and New Zealand waters for some species (Graham, unpublished data). This work demonstrated that these isotope methods can successfully identify signals of latitudinal movements of marine animals that migrate into New Zealand waters. However, such signals can only be detected if the individuals foraged during their movements. Accordingly, this method provided limited success in determining migration routes of humpback whales prior to their arrival at the Kermadec Islands, as foraging is rare for this species whilst migrating (Constantine, 2016). Humpback whales feed almost exclusively in the Southern Ocean during the austral summer, and then migrate to the tropics to mate and give birth to their calves. This means that the whales which were biopsied in the Kermadec Islands retained an isotopic signature of their Southern Ocean feeding grounds, rather than regions that they moved through. Sampling baleen rather than whale skin may provide a better mechanism of determining whale migration routes and dietary behaviour, since baleen plates represent 3–5 years of growth, so that longer-term patterns of movements can be investigated (Eisenmann et al. 2016).

4.5 Future directions

Future studies will benefit if the modelled carbon isoscape is more closely coupled to sea surface temperatures around New Zealand coastal and shelf waters. In addition, using complementary datasets, a wider spatial coverage of nitrogen and carbon isoscapes will lead to the more successful application of the method. For example, utilizing the extensive surface sediment and sediment trap collections around New Zealand and the south Pacific Ocean would strengthen the models, because these samples would represent time-integrated δ^{15}N and δ^{13}C values, which would average out seasonal and episodic variability observed in the isotopic baseline in marine systems. In addition, sampling more offshore shelf and near-shore coastal systems will advance understanding of marine ecosystem structure and dynamics, including animal movements in these regions. Given the more dynamic nature of these regions, and the influence of land-based and anthropogenic activities, sediment samples would assist in generating more robust, time-integrated isoscapes.

In this project, baseline isoscapes were constructed in collaboration with international researchers which were both model-derived and data-driven. The spatial scale of the isoscapes ranged from coastal and basin, up to global scales. These isoscapes will now facilitate a diverse array of research projects to use isotopes to study marine ecosystem structure, in regions where baseline nitrogen values were hitherto unavailable, and to track animal movements in the coastal and open ocean. Further extensions of such isoscapes, particularly into coastal seas, will also enable researchers to establish point source inputs of pollutants and contaminants and determine proportions of different sediment sources to ecosystems.

Future applications of open ocean and coastal isoscapes include animal movement studies of a) Antarctic toothfish (*Dissostichus mawsoni*) and southern right whales (*Eubalaena australis*) in the Southern Ocean, b) common dolphins (*Delphinus delphis*) and bronzer sharks (*Carcharhinus brachyurus*) around New Zealand, c) mako sharks (*Isurus spp.*) in the subtropical Pacific Ocean, d) beaked whales around New Zealand, and e) seabirds in the Pacific Ocean. Due to their high trophic position, apex predators integrate complex processes at lower trophic levels and are ideal ecosystem sentinel species. Moreover, many of these species are either commercially important (e.g., tunas, hoki (*Macruronus* spp.), toothfish (*Dissostichus mawsoni*)) or threatened/recovering (e.g. marine mammals, seabirds). Overall, generating new insights into top predator trophic status and movements will contribute to our knowledge of key habitat use, environment and ecosystem structure, function and resilience and will assist in monitoring our changing marine ecosystem.

5. NON-TECHNICAL SUMMARY and APPLICATION

The carbon and nitrogen isoscapes generated and reviewed within ZBD200404, provide insight into present and past nutrient dynamics and drivers of primary productivity, and enable us to determine if there are changes in primary production at the base of the food web in the southwest Pacific Ocean and Southern Ocean. Combined with information on oceanographic and ecosystem trophic dynamics, we can relate environmental drivers to marine ecosystem processes. This research will advance our understanding of the functional links between the environment and the marine food web. In addition, having more knowledge of animal movements increases our ability to understand how individuals and populations may respond to future climate changes in marine ecosystems (Lehodey et al. 2006; Barange et al. 2018).

With a well-planned study, including (i) access to samples of the population(s) of interest, (ii) an understanding of some of their life history traits and physiology, and (iii) isoscapes of relevant geographic scale, stable isotope techniques can be a powerful and cost-effective method to refine inputs required for stock assessment models such as:

a) determine spatial connectivity between populations or sub-populations (Graham et al. 2010; Lorrain et al. 2015 Francis et al. 2015)
b) determine mixing rates of populations within and between oceanic regions (Livingston et al. 2002; Madigan et al. 2014)
c) determine migratory routes of animals between critical life history stages (e.g., movements between spawning/breeding and foraging grounds) (Livingston et al. 2002; Francis et al. 2012; Madigan et al. 2014; Francis et al. 2015; Thompson et al. 2015)
d) determine if movements or animal migration routes occur in regions with higher risks encountered by the species or population (e.g., fishing, low productivity regions, ship strikes, and resource exploration) (Abraham et al. 2015).

A study using isoscapes to determine the movements of New Zealand hoki would be valuable in determining their stock structure (e.g., Francis et al. 2011). Such a study could examine hoki movements from the west coast to east coast (e.g., Chatham Rise) and the movements from the Sub-Antarctic to the north (lower latitudes). This information would be vital to determine site fidelity to feeding grounds and spawning locations. As the distribution of tarakihi (*Nemadactylus macropterus*) is relatively continuous around New Zealand, many techniques cannot be applied to determine tarakihi stock structure and mixing rates (i.e., movements; Langley 2018). Using NZ-based isoscapes the movements of tarakihi around and between the North and South Island, New Zealand could provide insight into population connectivity and fidelity. However, as mentioned, considerable effort would be required to ground-truth a NZ-based isoscape coastal application as the isoscapes can be more spatially and temporally dynamic relative to open ocean isoscapes. Once NZ coastal isoscapes are established, historical changes in the movements and abundance of tarakihi in the Tasman and Golden Bays could be examined, as there is concern that it has varied in that region over time (M. Morrison, *personal communication*). The success of the isoscape approach is greatly enhanced when it is coupled with other tools and approaches, including tagging programmes, additional chemical tracers, and demographic census of populations. For example, Abraham et al. (2015) successfully combined counts made by fisheries observers around the Hauraki Gulf and Kermadec Island with satellite tracking data in two models to examine the overlap between black petrel and commercial fisheries. Stock assessments and marine management strategies have developed dramatically over the past thirty years and these management tools will only benefit by the addition of new techniques and datasets, including chemical tracers to examine marine animal movements (Annala 1996; Punt et al. 2000; Sippel et al. 2015).

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