Identifying biologically important areas for iconic species and apex predators in the Great Australian Bight

Final Report GABRP Project 4.2

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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.

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1. EXECUTIVE SUMMARY

Apex marine predators respond to changes in their environment in several measurable ways and therefore can be valuable bio-indicators of the functioning of entire ecosystems. Project 4.2 of the Great Australian Bight (GAB) Research Program, *Identifying biologically important areas for iconic species and apex predators in the GAB*, presents the first attempt to regionally integrate available electronic tracking data for 602 individuals across 20 years between 1995 and 2016. Tracking technologies included a range of satellite and GPS tags deployed on nine species from three different guilds (seabirds, pinnipeds and pelagic fish). Aerial and boat-based survey data, opportunistic sightings data and historical whaling data provided information on the distribution of two additional species from a fourth guild (cetaceans). The species assessed were the Australian sea lion, Australian fur seal, long-nosed fur seal, little penguin, short-tailed shearwater, white shark, blue shark, shortfin mako, southern bluefin tuna, pygmy blue whale and sperm whale. These species provide a good representation of the diversity of predators using the GAB, across the ecological spectrum from resident to highly migratory species. The data-streams from these 11 species were combined to describe the spatial and temporal use of the GAB region, which is characterised by high variability in environmental and oceanographic conditions. Assemblage of multi-species predators with diverse life-histories that changes at a local scale over time reveals the importance of the region in terms of biodiversity and biological activity. This information is critical for ecosystem-based management.

The objectives of this project were to: i) develop at-sea distribution and foraging habitat models for iconic species and apex predators in the GAB, ii) identify high use areas and key regions of inter-specific distribution and foraging overlap, iii) attempt to relate these areas/key regions to biological and physical oceanographic features, and iv) investigate the potential seasonal patterns in foraging habitat selection by migratory species in the GAB.

Data collected over the last 20 years (4,924 tracks, and 15,698 observations from aerial surveys, sightings and historical whaling data) clearly show differences in use of the GAB region by species that are resident for their entire life-cycle versus those that are migratory and use the region periodically and seasonally for feeding or breeding. The development of species distribution models (SDMs) revealed the distribution at-sea and the foraging habitats for the 11 species across the GAB region. The integration of abundance estimates into the models, especially for populations of central-place foragers (seal, seabirds), enabled spatial patterns in the amount of use by some species in the GAB region to be assessed. Seasonal patterns of use of the region by migratory species were also investigated. Regions of high use in oceanic, shelf-slope and neritic habitats, were identified using a combination of inter-species overlap models.

Two regions favoured by marine predators were identified in continental shelf and slope areas: the Bonney Coast, Kangaroo Island and Eyre Peninsula (Region 1), and the south coast of Western Australia (Region 2). While these two regions have common features including relatively narrow shelves and steep slopes, they are influenced by different oceanographic features. Seasonal coastal upwelling occurs along the Bonney Coast and off Kangaroo Island and the Eyre Peninsula. The enhancement of primary and secondary production during upwelling supports relatively higher production of nekton, small pelagic fish and squid, which in term underpins important predator foraging areas within these regions. In the western GAB, the important shelf and slope area is largely influenced by the Leeuwin Current. Different mechanisms are known to affect seasonal nutrient supply and production in this system.

In these two regions, the central-place foragers are mainly concentrated over the continental shelf near the mainland coast. In contrast, the migratory species concentrate on the shelf break, using it
both as a foraging area and as a migration corridor. The different foraging groups (benthic, pelagic and surface feeders) found in all areas indicate that the region likely provides food resources from the sea bottom to the surface for the different predators. However, the south coast of Western Australia, although as rich in biodiversity of marine predators as the other regions, has lower biomass, which suggests that production in the eastern GAB (enriched through upwelling) is greater than that in the western GAB. The seasonality in the environmental conditions in the two regions of high use is expected to influence the community of predators present in the GAB. Migratory species may be more prevalent in summer when the level of productivity increases. However, the two high-use regions remain important during the rest of the year since many resident species still forage and/or breed there in winter.

The present study explicitly addressed the use of the GAB by many marine predators and identified regions of high use that are associated with the unique and complex oceanographic features of the GAB. The environmental variability in these regions is likely to impact migratory patterns, distribution, abundance and residency times, and lead to marked variation in apex predator community structure, and the locations and extent that high-use regions are used in both space and time.
2. INTRODUCTION

2.1 Background and need

During the past 10 years, the need to conserve ecologically and biologically sensitive areas has become increasingly more critical due to the surge of human activities in the marine environment (Douvere 2008). However, a major issue faced by decision makers is the paucity and/or patchiness of biological data needed to inform management, which remains difficult to obtain in the marine environment. One method to overcome this data deficiency is the use of indicator species, which are usually top consumers in marine foodwebs. Monitoring the biology of key indicator species can provide information on the entire system and offer opportunities to detect and assess changes in biological and physical environmental parameters (e.g. Bost and Le Maho 1993). Integrative studies further this approach by synthesising information from diverse sources using integrated modelling approaches (e.g. Melbourne-Thomas et al. 2017), providing the foundation of ecosystem-based management (e.g. McLeod and Leslie 2009).

Integrative approaches, and especially multispecies analyses, are more commonly being used in fishery-based management of marine ecosystems that focus on commercial fish species (Hollowed et al. 2000, Whipple et al. 2000, Fulton et al. 2003, Koen-Alonso and Yodzis 2005). In comparison, the number of multispecies studies of marine apex predators (seabirds, marine mammals, etc) is relatively low, and those that exist have generally integrated data from independent studies conducted on different species at different times over a number of years (e.g. Brooks et al. 2001, Garson et al. 2002, Margules et al. 2002, this study). Integration of such data allows the identification of assemblages of multiple species of predators and reveals regions of high, medium or low use by predator communities, thereby providing a valuable approach for determining important marine habitats (Worm et al. 2003, Block et al. 2011, Hindell et al. 2011, Raymond et al. 2014), identifying conservation priorities (e.g. Lucifora et al. 2011) and developing conservation and management policy. High-use regions used by multiple species can indicate regions of high prey abundance and/or diversity of prey species that are typically underpinned by key physical features (e.g. submarine canyon) and/or related oceanographic processes (e.g. upwellings) (Block et al. 2002, 2011, Palacios et al. 2006, Yen et al. 2006, Morato et al. 2010, Santora et al. 2010, Hindell et al. 2011). As such, the diversity of predators aggregating in space and time can be indicative of the structure and function of the entire marine ecosystem.

Regions used by multiple species or communities of predators that overlap in space are commonly referred to as ‘hot-spots’ (Worm et al. 2003, Block et al. 2011, Davoren 2013). ‘Hot-spot’ has been applied in a range of contexts and defined in different ways, including ‘sites of critical ecosystem linkages between trophic levels’ (Sydeman et al. 2006); a ‘relatively small area in which we expect to find animal aggregations repeatedly’ (Piatt et al. 2006); and ‘areas where high abundance of species overlap in space and time’ (Davoren 2007). Santora and Veit (2013) attempted to quantify both ‘abundance hotspots’ for individual species, and ‘richness hotspots’ to describe species diversity within communities of marine predators. Hindell et al. (2011) and Patterson et al. (2016) restricted the definition of ‘hotspots’ to areas used for foraging (as opposed to migration) as either ‘areas of ecological significance’ (AES) or ‘high foraging value’. Overarching commonalities within these definitions include the concepts of spatio-temporal persistence, and elevated abundance and/or species richness (Gende and Sigler 2006, Piatt et al. 2006, Sydeman et al. 2006, Davoren 2007, Santora et al. 2010, Nur et al. 2011, Sigler et al. 2012, Suryan et al. 2012). Globally, most of the hotspots of marine predator diversity are located in coastal regions over the continental shelves (Worm et al. 2003, Block et al. 2011, Hindell et al. 2011, Lucifora et al. 2011, Raymond et al. 2014).
The Great Australian Bight (GAB) region is an area of high marine conservation significance (e.g. Spalding et al. 2007), and includes more than 130,000 km² of marine parks and other marine reserves from 120°E to 146°E (Edyvane 1999). Marine predators (e.g. marine mammals, seabirds, sharks and large pelagic fish) are common in the GAB (Goldsworthy et al. 2013). Occupying the highest trophic levels, these predators play an important role in the ecosystem. They can be highly influential in structuring marine food webs through ‘top-down’ processes, but equally can be affected by processes operating at lower trophic levels (‘bottom up’), including oceanographic processes that may control the availability of key prey species (Becker et al. 2007, Cury et al. 2008).

The GAB marine ecosystem is supported by complex and contrasting interactions between oceanographic and biological processes. These include: i) seasonal upwelling in coastal, shelf and shelf slope waters (especially in the eastern GAB) linked to the world’s only northern boundary current (Kämpf et al. 2004, van Ruth et al. 2010), ii) down-welling in the coastal, shelf, and shelf slope habitats in the central GAB (Middleton and Cirano 2002, Kämpf 2007, Middleton and Bye 2007), and iii) fronts between water masses in the oceanic waters and the warm in-flowing tropical Leeuwin Current over the narrow shelf in the western GAB (McClatchie et al. 2006). Spatial and temporal variations in meteorological and oceanographic conditions are known to be the main drivers of these processes. Indeed, the supply of nutrients and irradiance are both involved in underpinning productivity and food web structure, including the apex predator communities of these ecosystems. However, it is poorly understood how the different components of the food web and the predator communities respond to such marked spatial and temporal variability in production. For individual species, such variability may affect migratory patterns, distribution, abundance and residency times, leading to variation in community structure and the locations and extent of ecologically important areas in both space and time.

A combination of aerial survey and satellite telemetry (tracking) data collected over the last 20 years, suggests the GAB region contains the greatest density and biomass of predators in coastal Australian waters (Goldsworthy et al. 2013). These predators use the GAB in a range of different ways, either periodically for feeding and/or breeding as part of broad-scale migrations or as residents in the region for their entire life-cycle (Goldsworthy et al. 2011). Key iconic and apex predator species that occur in the GAB region include toothed whales (e.g. killer whales (Orcinus orca)), white sharks (Carcharodon carcharias), Australian sea lion (Neophoca cinerea), long-nosed fur seals (Arctocephalus forsteri) and Australian fur seals (Arctocephalus pusillus doriferus) (Shaughnessy et al. 2010, 2011, 2016). The area also supports an important seabird assemblage that includes several albatross and shearwater species (Puffinus spp.), little penguins (Eudyptula minor), terns (Sterna spp.), several diving petrels and gannets, and two species of giant petrels (Copley 1996, Einoder and Goldsworthy 2005, Einoder et al. 2011). The region also supports a large number of large pelagic fish and shark species, including southern bluefin tuna (Thunnus maccoyii), blue sharks (Prionace glauca), common thresher sharks (Alopias vulpinus), shortfin mako sharks (Isurus oxyrinchus) and porbeagle sharks (Lamna nasus) (Bruce et al. 2006, Bestley et al. 2008, 2009, Patterson et al. 2008, Rogers et al. 2015, Rogers and Bailleul 2015), and resident populations of common (Delphinus delphis) and bottlenose dolphins (Tursiops spp.) (Kemper et al. 2005). The GAB region is also home to Australia’s largest feeding aggregation of pygmy blue whales (Balaenoptera musculus brevicauda), which form feeding groups in mid-shelf and slope waters of the eastern GAB during summer and autumn (Gill et al. 2011). The GAB is also Australia’s largest breeding site for southern right whales (Eubalaena australis), which visit the region in winter to breed and nurse calves. The GAB, particularly its major submarine canyon systems, is also known to be important to whale species such as sperm (Physeter macrocephalus) and pilot (Globicephala melaena) (Bannister 1968, Carroll et al. 2014, Johnson et al. 2016).
Given the diversity and abundance of apex predators in the GAB, the region may represent an area of national and global importance for many of the region’s key species. However, there is limited knowledge and understanding of the key features of the region that explain its importance to communities of marine predators, since no multi-species synthesis has been done in the GAB. Key knowledge gaps about the ecology of marine predators in the GAB region have been identified (Rogers et al. 2013). These include information on the distribution and abundance of iconic and apex predators in the GAB, the physical and biological oceanographic processes that make the GAB important to predators, the influence of these processes on the ecology (e.g. distribution, foraging, migration) of the predators, the responses of predators to potential environmental changes, and the localisation of habitats shared by multiple species.

Project 4.1 ‘Status, distribution, and abundance of iconic species and apex predators in the Great Australian Bight’ explicitly addressed the paucity of baseline information on iconic and apex predator species’ distributions, status and trends in abundance (Goldsworthy et al. 2017). Project 4.2 of the GAB Research Program aims to describe: i) the pattern of use of the region by a range of marine predator species (marine mammals, seabirds, pelagic sharks and fishes), ii) the seasonal and spatio-temporal context of this use by individuals, and iii) the range of predators using the GAB across the ecological spectrum from resident to highly migratory species. The multi-species analysis is used to identify regions of high-, medium- and low-use, and determine if high-use habitats are characterised by particular physical or biological processes.

Project 4.2 uses advanced techniques in spatial distribution modelling to integrate all the available satellite telemetry and survey data collected in the region. Species distribution models (SDMs) relate species occurrence data at known locations with information on the environmental and/or spatial characteristics of those locations (Elith and Leathwick 2009, Franklin 2010). They are widely used in conservation, biology and ecology, as they can provide understanding and/or predict the species’ distribution across a landscape (Elith and Leathwick 2009). The use of SDMs requires a clear distinction of the differences between potential and realised distributions (Soberón, 2007). Potential distribution refers to the places where a species could live (i.e. where conditions are suitable for survival of the species), while realised distribution refers to the places where a species actually lives (i.e. areas where the species is known to be absent are excluded). These aspects are considered in this study.

The objectives of Project 4.2 directly address the key knowledge gaps and lead to a key outcome of the project, which is: ‘the identification of shared oceanic, shelf-slope and neritic habitats for apex predators and iconic species that constitute important areas in the eastern, central and western GAB’.

2.2 Objectives

The objectives of the project were to: i) develop at-sea distribution and foraging habitat models for predator species in the GAB, ii) identify high use areas and key regions of inter-specific distribution and foraging overlap based on these models, iii) attempt to relate these areas/key regions to the biological and physical oceanographic features of the region, and iv) investigate the potential seasonal patterns in foraging habitat use by migratory species in the GAB.
3. METHODS

3.1 Study area

The Great Australian Bight (GAB) extends from Cape Otway in Victoria in the east (144°E) to Albany (WA) in the west (117°E) (Figure 1), based on the model domain area developed for the Atlantis whole of ecosystem model (see Project 7.1 report for details).

3.2 Datasets

The at-sea movement and census data available to this project fall into three categories (Table 1): i) those from land-breeding species, such as seals and seabirds, where movement data are derived from satellite and GPS tags; ii) those from pelagic species, such as the tunas and pelagic sharks, where movement data have been derived from archival, pop-up and fin-mounted satellite tags; and iii) aerial survey or historical (whaling) data for large whales (e.g. pygmy blue and sperm whales).

A total of 11 species from four different groups (marine mammals, seabirds, pelagic sharks and a pelagic teleost (tuna)) were considered in this study. Occurrence data were available and suitable for analyses for five species of marine mammals (three seals and two cetaceans), two species of seabirds, three species of pelagic shark and one pelagic teleost (Table 1 and 2). These were: Australian sea lion (*Neophoca cinerea*) (ASL), long-nosed fur seal (*Arctocephalus forsteri*) (LNFS) and Australian fur seal (*Arctocephalus pusillus doriferus*) (AFS), pygmy blue whale (*Balaenoptera musculus brevicauda*) (BW) and sperm whale (*Physeter macrocephalus*) (SW), short-tailed shearwater (*Puffinus tenuirostris*) (STSW) and little penguin (*Eudyptula minor*) (LP), white shark (*Carcharodon carcharias*) (WS), blue shark (*Prionace glauca*) (BS) and shortfin mako shark (*Isurus oxyrinchus*) (SM) and southern bluefin tuna (*Thunnus maccoyii*) (SBT).

Although available, tracking data for crested terns were limited to 21 individuals from the same colony during the same season and were not suitable for conducting general distribution models for the entire GAB region. Sightings of pilot whales, beaked whales and dolphin sp. during aerial surveys were too scarce or too limited in space to conduct spatial distribution analyses on these species.
Figure 1: Map of the GAB region. The continental shelf (shallower than 250 metres depth) is represented in light grey. The shelf break is represented in dark grey (250m to 2000m depth). KI = Kangaroo Island. TAS = Tasmania.
Table 1: Synthesis of occurrence data used in this study.

<table>
<thead>
<tr>
<th>Species</th>
<th>Type of species</th>
<th>Type of data</th>
<th>Data features</th>
<th>Data type</th>
<th>Time period covered by the data</th>
<th>Number of tracks or observations</th>
<th>Number of individuals</th>
<th>Number of colonies</th>
</tr>
</thead>
<tbody>
<tr>
<td>Australian sea lions</td>
<td></td>
<td>Argos, GPS</td>
<td>Presence only</td>
<td>2003-2015</td>
<td>4051 tracks</td>
<td>196</td>
<td>34</td>
<td></td>
</tr>
<tr>
<td>Australian fur seals</td>
<td>Central place forager</td>
<td>Argos</td>
<td>Presence only</td>
<td>1995-2003</td>
<td>415 tracks</td>
<td>38</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Long-nosed fur seals</td>
<td></td>
<td>Argos, GPS</td>
<td>Presence only</td>
<td>2000-2007</td>
<td>161 tracks</td>
<td>87</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Little penguins</td>
<td></td>
<td>Argos</td>
<td>Presence only</td>
<td>2004-2009</td>
<td>108 tracks</td>
<td>94</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Short tailed shearwater</td>
<td>TRACKING</td>
<td>Argos</td>
<td>Presence only</td>
<td>2006-2007</td>
<td>33 tracks</td>
<td>31</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Blue sharks</td>
<td></td>
<td>Argos</td>
<td>Presence only</td>
<td>2015-2016</td>
<td>8 tracks</td>
<td>8</td>
<td>NA</td>
<td></td>
</tr>
<tr>
<td>Shortfin mako</td>
<td></td>
<td>Argos</td>
<td>Presence only</td>
<td>2008-2015</td>
<td>18 tracks</td>
<td>18</td>
<td>NA</td>
<td></td>
</tr>
<tr>
<td>White sharks</td>
<td></td>
<td>Argos</td>
<td>Presence only</td>
<td>2015</td>
<td>5 tracks</td>
<td>5</td>
<td>NA</td>
<td></td>
</tr>
<tr>
<td>Southern bluefin tuna</td>
<td>Non central place forager</td>
<td>Geoloc</td>
<td>Presence only</td>
<td>1998-2011</td>
<td>125 tracks</td>
<td>125</td>
<td>NA</td>
<td></td>
</tr>
<tr>
<td>Sperm whales</td>
<td></td>
<td>Aerial / Boat / Historical whaling</td>
<td>Presence only</td>
<td>1958-2016</td>
<td>15579 obs</td>
<td>-</td>
<td>NA</td>
<td></td>
</tr>
</tbody>
</table>
Table 2: References to data sources used in this study.

<table>
<thead>
<tr>
<th>Species</th>
<th>Type of data</th>
<th>Source of Data Organisations*</th>
<th>Source of Data References</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Australian fur seals</strong></td>
<td></td>
<td>PINP</td>
<td>Kirkwood et al. 2006; Kirkwood &amp; Arnould 2012</td>
</tr>
<tr>
<td><strong>Little penguins</strong></td>
<td></td>
<td>SARDI</td>
<td>Bool et al. 2007; Goldsworthy et al. 2011; Wiebkin 2012</td>
</tr>
<tr>
<td><strong>Short-tailed shearwater</strong></td>
<td></td>
<td>SARDI</td>
<td>Einoder and Goldsworthy 2005; Einoder 2010, 2011</td>
</tr>
<tr>
<td><strong>Blue sharks</strong></td>
<td></td>
<td>SARDI</td>
<td>Roger et al. 2016</td>
</tr>
<tr>
<td><strong>Shortfin mako</strong></td>
<td></td>
<td>SARDI</td>
<td>Rogers et al. 2015; Rogers and Bailleul 2015</td>
</tr>
<tr>
<td><strong>White sharks</strong></td>
<td></td>
<td>SARDI (BP 4.1)</td>
<td>GAB RP 4.1</td>
</tr>
<tr>
<td><strong>Southern bluefin tuna</strong></td>
<td></td>
<td>CSIRO (BP 4.3)</td>
<td>Bestley et al. 2008, 2009; Patterson et al. 2008; Basson et al. 2012</td>
</tr>
<tr>
<td><strong>Pygmy blue whales</strong></td>
<td>SURVEYS</td>
<td>BWS (BP 4.1)</td>
<td>Gill et al. 2011; GAB RP 4.1</td>
</tr>
<tr>
<td><strong>Sperm whales</strong></td>
<td></td>
<td>BWS (BP 4.1)/SAM/OZCAM/AADC/OBIS/NWDSSD/NS/RPS/IFAW/IWC</td>
<td>GAB RP 4.1 for aerial and boat-based surveys</td>
</tr>
</tbody>
</table>

*SARDI = South Australian Research and Development Institute; IMOS = Integrated Marine Observing System; PINP = Phillip Island Nature Park; FRDC = Fisheries Research and Development Corporation; BP = British Petroleum; CSIRO = Commonwealth Scientific and Industrial Research Organisation; BWS = Blue Whale Study; SAF = South Australia Fauna; OZCAM = Online Zoological Collections of Australian Museums; AADC = Australian Antarctic Data Centre; OBIS = Ocean Biogeographic Information System; NWDSSD = National Whale and Dolphin Sightings and Strandings Database; NS = Nerites Swift; IFAW = International Fund for Animal Welfare; IWC = International Whaling Commission.
3.3 Data processing

Occurrence data were derived from a range of different tracking and survey methods which were: satellite telemetry, satellite linked GPS and light-based geolocation tags, aerial survey and historical sightings data. Occurrence data obtained from most of these methods required some level of pre-processing before they could be analysed. This is briefly detailed below.

Satellite telemetry data are obtained from satellite transmitter (Platform Terminal Transmitter, PTT) tags, which transmit a message to polar orbiting satellites when animals fitted with a tag are at the surface. ARGOS data are categorised into six quality classes (3, 2, 1, 0, A, B) based on the number of uplinks from transmitter to satellite, the time between these uplinks, and the time since a previous location was estimated (Austin et al. 2003). The estimation errors associated with these quality classes vary through time.

GPS telemetry data obtained from Fastloc-GPS tags provide location data similar to the accuracy from traditional GPS receivers (e.g. when an animal fitted with a tag breaks the surface for a very short time). Fastloc-GPS receivers take a quick (i.e. fraction of a second) snapshot of the radio signals produced by overhead GPS satellites. Signals are processed by the tag and compressed into a snapshot containing the satellite ID numbers; the accuracy of GPS location is dependent on the number of GPS satellites detected. Calibration studies indicate that 95% of locations are accurate to ±55 m with a mean error <150 m (Bryant 2007). Given the high level of accuracy of GPS locations, we did not post-process or filter data from these tag deployments.

Light data transmitted by miniature pop-up satellite archival tags (mini-PAT on white sharks) were processed using the GPE3 (state space model based) processor available through the Wildlife Computers user portal (http://wildlifecomputers.com).

The geolocation method uses measurements of light levels recorded by small Global Location Sensing (GLS) archival tags to estimate locations on southern bluefin tuna. Recording light levels over time produces data that can be used to estimate the latitude and longitude of an animal during long-distance movements. Position estimates were aggregated into counts within 0.5 x 0.5 degree squares by month within the study area (CSIRO unpublished data). Data were aggregated across the total number of years because of their uneven distribution across individual years (see Project 4.3 for details). Data used in this study (Project 4.2) were therefore in the form of grids representing the time spent by sectors (TPS).

Aerial survey data and historical sightings data included positions for each observation. These positions were not pre-processed as no accuracy estimate was available, but they were used directly as presence-only records in the analyses as done in other studies (e.g. Johnson et al. 2016).

3.4 Data analysis

Satellite telemetry derived position estimate data were filtered using the class-based location quality estimates provided by Argos (based on the precision and accuracy of location estimates) from correlated random walk modelling within a state-space framework. The errors in satellite-derived locations provided by Argos were incorporated into estimates of likely position, and their precision was estimated using either Bayesian (Jonsen et al. 2005, Patterson et al. 2009) or maximum likelihood methods (Jonsen et al. 2008). State-space models allow unobserved states and biological parameters to be estimated from location estimate data, and enable biological and statistical complexities from satellite telemetry data to be incorporated. The ARGOS-derived locations are observed irregularly
through time, which imposes an artificial perspective on the movement processes. We used models that account for these features of the data and allow filtering spatial positions (Jonsen et al. 2005). Models were fitted using JAGS 3.1.0 (Just Another Gibbs Sampler, http://martynplummer.wordpress.com; http://mcmc-jags.sourceforge.net) accessed from R (R Core Team 2015) using the package ‘bsam’ (Jonsen et al. 2013). Two Markov chains with a total of 50,000 simulations were computed, only keeping one out ten samples to minimise sample autocorrelation. The analyses assume a time-step of 2h and generate 25,000 samples per chain for each position.

GLS: Daylight length (the time between dawn and dusk) is generally used to determine latitude, while the mid-time between dawn and dusk is used to determine longitude. Position estimates were obtained using the “twilight likelihood” method and required pre-processing. Details of the method and processing of these data are provided in section 3.2.4 of Project 4.3 and Basson et al. (2012, 2016) but briefly involved a state-space modelling approach to estimate the likelihood (i.e., the probability density) of the light data given any location on the globe.

3.5 Model development and selection

Multiple methods are available in the field of species distribution modelling but data types vary among methods. Where presence/absence species data are recorded during systematic surveys regression methods, such as generalised linear models (GLMs; Guisan et al. 2002), generalised additive models (GAMs; Wood 2006), regression trees (e.g. random forests (Breiman 2001), boosted regression trees (BRT; Friedman 2001), or Support Vector Machines (Vapnick 1998) are generally used. However, for most species or regions, systematic survey data tend to be sparse and/or limited in coverage, and absences cannot be inferred with certainty. This is typically the case for individual tracking data or aerial surveys in the marine environment, where animals can be present but cryptic (e.g. when diving). Therefore, occurrence data consists of presence-only records, and requires adapted modelling methods to estimate species distribution. The maximum entropy model (Maxent; Phillips et al., 2006, 2009) is one such method that has been extensively used for modelling species distributions. The method is particularly efficient in handling complex interactions between response and predictor variables (Elith et al. 2006, 2011). Elith et al. (2006) demonstrated that Maxent performs as well as other methods in term of predictive performance. Moreover, Maxent appears to be suitable for estimating potential distribution as well as realised distribution (Jiménez-Valverde et al. 2008). Finally, after testing and comparing different methods, we observed that some models provided good estimation of the distribution for some species but did not converge for others (e.g. GAM) and were generally very time consuming to configure and implement. In contrast, Maxent suited the entire available tracking and survey dataset of this study, and the recent development of software (e.g. “dismo” in R, 2017) makes this method relatively easy to implement. For these reasons, and in order to limit the biases related to the use and the comparison of different methodologies, the Maxent model was chosen as the preferred method to model species distributions and habitat selection.

3.5.1 The Maxent model

Maxent is a machine learning algorithm that applies the principle of maximum entropy (where entropy is a measure of dispersal) to predict the distribution of species from presence-only data. The principle of maximum entropy states that the prior probability distribution which best represents the current observed data is the one closest to uniform (i.e. with the largest measure of unpredictability of the current observation). The method can be described as comparing probability densities in covariate space and calculating conditional probability of occurrence (Elith et al. 2011). Giving insight about
what features are important and estimating the relative suitability of one place versus another is the core of the Maxent model output (Elith et al. 2011).

The main problem with presence-only data is the lack of absences to counterbalance the presences. One attempt to solve this problem is to assess how much the model predictions differ from random expectation. Background data (e.g. Phillips et al. 2009) refers to locations randomly generated within the study area and used to characterise the environment in the GAB region. In this sense, background is the same, regardless of where the species has been found. The occurrence data possibly exhibit a strong spatial bias related to survey effort, meaning simply that some sites are more likely to be surveyed than others because of easier access or the known presence of a species in an area. Such biases are known to influence model outputs. If not accounted for appropriately, a fitted model may end up being a model of survey effort, rather than a model of a species true distribution (VanDerWal et al. 2009). The main alternative for dealing with biased data is to generate background data with similar biases to those in the presence data (Phillips et al. 2009, Elith et al. 2010). Thus, we selected background data for each species in an area defined by computing the Minimum Convex Polygon estimator based on the presence data. This method calculates the smallest convex polygon enclosing all the locations/observations of a species.

The selection of predictor variables (or covariates) was based on the availability of environmental data over the entire study area and study period. Although a large set of environmental variables could influence the distribution of the different species, the broad temporal range of the presence data used in the models precluded, most of the time, the use of temporally and spatially dynamic variables. Therefore, predictor variables were restricted to static variables. Ecological knowledge of individual species was used to reduce a priori the candidate predictor set.

3.5.2 Model performance and precision estimates

Model performance was evaluated using Area Under the receiver operating characteristic Curve (AUC), which is defined as the probability that a known presence location for a tracked animal is ranked above a random background location (Phillips et al., 2006). AUC values were calculated by partitioning the presence data to create 75% training and 25% test data sets. Training data were used to construct a model, which was then applied to the test data to measure performance. To use all the data for creating the model and evaluating its performance, a process of cross-validation was conducted by withholding one subset of the data in turn. AUC scores were successively calculated and averaged to provide an overall value. Final models were constructed using all available data.

The relative confidence in habitat suitability predictions was estimated using a bootstrap technique to produce spatially explicit measures of uncertainty. The modelling process was repeated 100 times changing the sample size of background data in steps from 100 to 10,000. Model uncertainty for each cell of the model domain was calculated by the variance in the bootstrap outputs. This uncertainty estimate was included in the prediction, since each predictive distribution model was weighted by the variance resulting from the bootstrap process as follows:

\[
\text{Prediction} = \text{probability of distribution } \times \left(1 - \frac{\text{var}}{\text{max(var)}}\right)
\]

3.6 Model outputs

The modelling was an iterative process involving several steps of model refinement: i) estimating the overall potential distribution of a species by including all available location data, ii) correcting
distribution models by the weighted abundance for central-place foraging species (seals and seabirds) breeding site abundance data, iii) estimating the potential foraging habitat for species where foraging locations could be predicted, and iv) developing separate sex and/or season models where inter-sexual and/or inter-seasonal differences in the distribution of a species were apparent. These steps are detailed below.

3.6.1 Overall potential distribution

Overall potential distribution of a species was estimated by including all available location data in the Maxent model. Environmental predictors were selected according to the species from the following list of variables: bathymetry, slope and aspect (both characteristics of the sea bottom), distance from the main shore, distance from the shelf break, distance from the subtropical front, mean sea surface temperature in summer, and mean annual sea surface temperature (Tables 3 and 4).

For southern bluefin tuna we used the coordinates of grid cell node where TPS was non-null as an index of presence to estimate the general distribution.

3.6.2 Corrected by weighted abundance

For central-place foragers, the potential at-sea distribution was further corrected by weighting the predicted distributions by estimates of colony/population abundance where available. The resultant estimates of spatial distribution of abundance using colony abundance estimates, were assumed to reflect the density at-sea. A grid of abundance at-sea was created drawing a circle around each colony. Values of abundance estimates were attributed to the circle. In order to use the abundance estimates for the colonies where no tracking was available, the diameter of the circle was set to the same value for all the colonies (species specific), and corresponded to the mean maximum distance travelled from all the colonies. When circles overlapped in space, values of abundance estimates were summed. Weighted distribution was obtained by multiplying the predicted distribution by the abundance estimates at-sea, and was used to estimate the realised distribution of the different species of central-place foragers.

For non-central-place foragers, no correction was applied on the predicted distributions. Based on current knowledge, a high number of observations and/or the broad spatial coverage of the dataset, the predicted distributions were considered as likely representative of the distribution of the entire population for each of those species.

3.6.3 Corrected for potential foraging habitat

Survey data didn’t allow foraging habitat to be identified. To identify and localise the foraging behaviour of the different species where satellite tracking data were available, we used the method developed by Benhamou and Cornelis (2010) based on a kernel density estimation. The kernel density approach was first used to estimate the utilization distribution (UD, van Winkle 1975) of an animal, which takes the form of a two dimensional (x,y) probability density function that represents the probability of finding an animal in a defined area within its home range. We modified this approach, following Benhamou and Riotte-Lambert (2012), to estimate intensity distribution (ID), a measure of residence time. The ID can be used as an indicator of foraging effort, as the more profitable areas tend to be exploited more intensively during a given visit and involves a longer residence time. The contour limits of the ID estimates enable the identification of patches where an animal spent a long period of time. All locations inside the 30% isopleth were considered as highly resident and assumed to be indicative of foraging areas (Benhamou and Riotte-Lambert 2012). Maxent models were then used on the foraging locations to predict the distribution of potential foraging habitats of species.
For SBT, the time spent by sector analyses were considered indicative of foraging since the more profitable areas will be those with higher residence times. The foraging habitat model for SBT was developed using a generalized additive model (GAM), with log-transformed time spent in a grid cell as the response variable and non-correlated environmental variables as explanatory variables. Environmental variables were selected depending on their biological relevance and availability in the study area. These variables were standardised to improve algorithm convergence. We checked for collinearity by calculating all pairwise Spearman rank correlation coefficients ($r_s$). When pairs of predictor variables were strongly correlated ($|r_s| > 0.7$), we constructed univariate models and only retained the predictor that led to the lowest Akaike Information Criteria (AIC) (Burnham and Anderson 2003). We assessed all possible linear combinations of explanatory variables. Model selection was performed using a maximum-likelihood approach to select the best model with the lowest AIC (Burnham and Anderson 2003).

For central-place foraging species, maps depicting the potential foraging distribution were weighted by estimates of colony/population abundance using the method outlined above (Section 3.6.2) to estimate their potential realised foraging habitats.

3.6.4 Corrected by sex or by season

Separate sex and/or season models were developed, where inter-sexual and/or inter-seasonal differences in the distribution of a species were apparent. Thus, males and females were considered as two separate entities for Australian sea lions and long-nosed fur seals, while inter-seasonal differences in distribution were observed for adult female long-nosed fur seals, blue sharks and southern blue fin tuna.

3.7 Identifying regions of high, medium and low use

In order to identify the spectrum of use of the GAB region by multiple species of predators, we overlapped the maps of predicted probabilities obtained for each species and calculated the mean predicted probability values at each cell node. Although there is a spectrum of use by predator species from low to high in the GAB, we defined three categories of use to facilitate interpretation of results: high, medium and low. This was achieved by dividing the range of mean probabilities into three equal intervals.

To establish criteria to identify regions of high use, we explored different combinations of distribution overlapping, including overlapping the potential general distribution, the realised general distribution (i.e. weighted by abundance), the potential foraging habitats, and the realised foraging habitats (i.e. weighted by abundance). Then, for each of these combinations, we did an additional sub-division only considering central-place foraging species or non-central-place foraging species. Finally, we considered seasonality for some migratory species where different spatial distribution patterns were observed between summer and winter.

3.8 Identifying the biological and physical oceanographic characteristics of regions of high use

Environmental factors like sea bottom depth (Australian 0.0025 decimal degree bathymetry and topography grid, June 2009, Geoscience Australia), distance from coast and shelf slope, sea surface temperature (SST, NOAA Optimum Interpolation Sea Surface Temperature) and environmental layers provided through Theme 1 (GABRP Projects 1.1 and 1.2) like temperature derived from high resolution hydrodynamic models were used to assess the biological and physical characteristics of the key regions.
identified. In addition, vertically generalised production models (VGPM) obtained from data collected from animal borne CTD/Fluorometer tags deployed as part of the Integrated Marine Observing System (IMOS) were integrated into the description of the bio-physical processes occurring in the key regions. The physical characterisation of the key regions was conducted from the average of the individual potential distribution probabilities as it includes all of the 11 species and corresponds to the most general representation of the GAB region use by marine predators.
4. RESULTS

A total of 11 species, 4,924 tracks and 15,698 observations from aerial surveys and/or historical data were analysed and synthesised (Figures 2 and 3). Tracking data and observations indicate that most of the species are localised over the continental shelf and slope, while some also use the adjacent oceanic waters, especially in the eastern GAB (Figure 3). The overall dataset reflects both the presence of the species in the GAB region as well as the effort directed towards obtaining observations (through tagging and/or survey).

4.1 Presence of the different species in the GAB versus data available

The species in this study use the GAB in different ways. Some are resident for their entire life-cycle, while others visit the GAB at particular times of the year as part of regular large-scale migrations. Many of the migratory species are present in the GAB region year-round, while others show seasonality and are only present in summer/autumn (e.g. short-tailed shearwaters and pygmy blue whales) (Figure 2). However, our dataset does not necessarily reflect a clear pattern in use of the GAB at particular times of the year for migratory species. Rather, the location data indicate that even migratory species can be present all year round in the GAB, probably because of different individual strategies (e.g. within the migratory species there is between-individual variation ranging from highly migratory contingents to mobile semi-residential). In addition, factors such as tagging effort (especially the time of the year when the tagging occurred), moult timing, project schedules, and other factors driving seasonal patterns in availability can potentially bias the distribution pattern of the different species (e.g. tagging effort occurring only in summer can limit the information on the distribution in winter).

The temporal presence and degree of residency displayed by the eleven predator species, as well as the temporal distribution of tracking and sighting observations used in spatial analyses, highlight that for some species there is a good and even spread of observational data throughout the year in the GAB region (e.g. Australian sea lions, SBT, mako and blue shark), while for others the spread of observational data was spatially and temporally patchy (e.g. little penguins, white shark, short-tailed shearwaters) (Figure 2). Interestingly, the spread of observations indicates that even migratory species (e.g. blue sharks, mako sharks, SBT) are present year-round in the GAB, although the seasonal peak in activity (based on observations) suggests inter-specific differences (SBT peaking in April, mako in June, blue shark in July) (Figure 2). For many species, the bias in observations relates to life-history constraints or the periods when they are accessible for telemetry studies. For example, satellite telemetry data are only available for little penguins and short-tailed shearwaters during the nesting and chick rearing periods, and in long-nosed and Australian fur seals, most telemetry data have only been collected in the months immediately following moult and prior to the next breeding season (e.g. April through to October) (Figure 2). White shark telemetry data are only available during winter months, even though the species is known to be present in shelf waters year-round. For pygmy blue whale, sighting data are typically restricted to the period of coastal upwelling between November and May (Figure 2). Sighting data of sperm whales suggests they are present year round, but their level of residency remains unclear.

The models predicting the spatial distribution of species are presented in successive figures for each species. Precision estimates for each model were included in the prediction since each predictive model presented in the figures is weighted by the variance resulting from the bootstrap process (see Section 3.5.2 in methods for details).
Figure 2: Schematic of the 11 predator species arranged by their relative degree of residency (resident to highly migratory). The temporal distribution of observations (tracking and sightings data) used in analyses are presented for each species as violin plots. A violin plot is a combination of a box plot and a kernel density plot. The thick black lines represent the interquartile range and the white square the median. Blue and red shaded background indicate when the species are known or supposed to be present in the GAB (CPF = central-place forager (red); blue = non central-place forager; diagonal stripes = absent). ASL = Australian sea lions; AFS = Australian fur seals; LP = Little penguins; LNFS = Long-nosed fur seals; SW = Sperm whales; WS = White sharks; BS = Blue sharks; SM = Shortfin mako sharks; SBT = Southern Bluefin Tuna; BW = Pygmy blue whales; STSW = Short-tailed shearwater.
Figure 3: Tracking and observation data for ten different species. For clarity and because of a different data format (gridded), Southern Bluefin Tuna are not represented in this figure. Magenta: Australian sea lions; White: Long-nosed fur seals; Blue: Australian fur seals; Cyan: Blue sharks; Green: Mako sharks; Orange: White sharks; Yellow: Sperm whale; Black: Pygmy blue whale; Red: Little penguins; Brown: Short-tailed shearwater. The dashed line represents the 250 m isobath and marks the extent of the continental shelf.
4.2 Australian sea lions

4.2.1 Distribution of observations
Observational data for Australian sea lions (ASLs) consisted of 4051 satellite/GPS telemetry tracks from 196 individuals and 34 sites in the GAB (Table 1). A total of 2633 tracks from 116 adult females were recorded from 16 sites in the eastern GAB off South Australia and from 32 females from nine sites in the Recherche Archipelago in the western GAB off the south coast of Western Australia (Figure 4a). A total of 1418 tracks from 45 males were recorded from 16 sites in the eastern GAB and from three males from three sites in the western GAB (Figure 4b).

Differences in distribution between adult males and females were previously reported (Goldsworthy et al. 2009b, Lowther et al. 2011, Lowther et al. 2012a, 2012b) and models were therefore developed for each sex.

Tracking observations identified the importance of coastal and continental shelf waters to Australian sea lions.

4.2.2 Potential distribution at-sea
Adult female ASL were distributed in coastal and continental shelf waters inside the 250 m depth contour (Figure 5a). The distribution model predictions were based on three environmental predictor variables; bathymetry, distance from shelf break and distance from coast. The distribution model suggests that habitat suitability is explained by bathymetry (73%), distance from the shelf break (19%) and distance from the coast (8%). Suitable habitats are likely to be located in shelf waters of the central GAB (124°E to 134°E), southern Spencer Gulf and Investigator Strait (137°E), south-east to Kangaroo Island (139°E) and in western Bass Strait north to Tasmania (145°E) (Figure 5a). The model performance (AUC) was estimated to be 0.720.

The contribution of the three environmental predictors differed for the male model with bathymetry contributing 40% of the explained variability, distance from the shelf break 30% and distance from the coast 30%, suggesting that suitable habitats for males are located further away from the coast and nearer the shelf break, especially in the eastern GAB between 129°E and 137°E (Figure 5b). The model performance (AUC) was estimated to be 0.690.

4.2.3 Potential foraging habitats
Suitable foraging habitats for adult female ASL are distributed both inshore and offshore (Figure 6). The model’s prediction, based on three static environmental predictors, indicates that the distribution of foraging habitats is mainly explained by distance from the shelf break (62%), distance from the coast (36%) and bathymetry (2%). The shoreline of the central GAB (129°E–135°E) might not be used as intensively as other shorelines in the GAB. The model performance (AUC) was estimated to be 0.693.

Suitable foraging habitats for males are located further away from the coast and nearer the continental shelf break, between 124°E and 134°E and between 137°E and 139°E (Figure 6). The contribution of the three environmental predictors differs from the female model as distance from the coast contributes 66%, distance from the shelf break 33% and bathymetry 1% of the explained variability predictions. The model performance (AUC) was estimated to be 0.684.

4.2.4 Realised distribution at-sea (weighted by abundance)
A total of 70 breeding colonies have been surveyed in the GAB region during the last 20 years (Shaughnessy et al. 2011) (an exhaustive survey was recently conducted in South Australia as a part of the GAB Project 4.1, Goldsworthy et al. 2017). The number and size of ASL breeding sites is greater
in the eastern GAB compared to the western GAB (Figure 7), with the ASL population in the eastern GAB accounting for almost 90% of the total GAB population (Goldsworthy et al. 2017).

When weighted by abundance, the suitable habitats for female ASL are concentrated along the coast in the eastern GAB, south-east to Kangaroo Island and southern Spencer and St Vincent Gulfs from 134°E to 140°E (Figure 8a).

As for females, the abundance estimates constrain the suitable habitats for male ASL in the eastern GAB from 133°E to 137°E, but males were distributed further away from the coast and nearer the shelf break (Figure 8b).

4.2.5 Realised foraging habitats (weighted by abundance)

When weighted by abundance, the suitable foraging habitats for female ASL are located over the continental shelf in the eastern GAB from 134°E to 140°E (Figure 9a).

As for females, the integration of abundance estimates suggests that suitable foraging habitats for male ASL are located in the eastern GAB from 133°E to 140°E, but males generally appear to forage further away from the coast near the shelf break (Figure 9b).
**Figure 4**: Tracking data for a) female and b) male Australian sea lions showing the importance of the coastal and continental shelf waters to the species in the GAB. The dashed line represents the 250 m isobath and marks the extent of the continental shelf.
Figure 5: Standardised probability of potential distribution at-sea in the GAB of a) adult female Australian sea lions (ASL) and b) adult male ASL. The warmer colours indicate a higher probability of occurrence. Suitable habitats for females are located in shelf waters of the central GAB, southern Spencer Gulf and the Investigator Strait, south-east to Kangaroo Island and in western Bass Strait north to Tasmania, while suitable habitats for males are located further away from the coast and nearer the shelf break, especially in the eastern GAB.
Figure 6: Standardised probability of potential foraging habitats of a) adult female Australian sea lions (ASL) and b) adult male ASL. Warmer colours indicate a higher probability of occurrence of foraging. Suitable foraging habitats for females are distributed both inshore and offshore. The shoreline of the central GAB might not be used as intensively as other shorelines in the GAB. Suitable foraging habitats for males are located further away from the coast, and nearer the shelf break, in the central GAB and south-east to Kangaroo Island.
Figure 7: Population estimates of Australian sea lions in the GAB region. A total of 70 breeding colonies have been surveyed. The size of the circles is proportional to the size of the colonies. The grey line represents the 250 m isobath and marks the limit of the continental shelf.
Figure 8: Standardised probability of realised occurrence at-sea (weighted by abundance) of a) adult female Australian sea lions (ASL) and b) adult male ASL. Warmer colours indicate a higher probability of occurrence. Suitable habitats for females are located along the coast in the eastern GAB, south-east to Kangaroo Island, and in southern Spencer and St Vincent Gulfs, while suitable habitats for males are mainly located in the eastern GAB, further away from the coast and nearer the shelf break.
Figure 9: Standardised probability of occurrence of realised foraging habitats (weighted by abundance) of a) adult female Australian sea lions (ASL) and b) adult male ASL. The warmer colours indicate a higher probability of occurrence of foraging. Suitable foraging habitats for females are located over the continental shelf in the eastern GAB, while suitable foraging habitats for males are located in the eastern GAB, further away from the coast and nearer the shelf break.
4.3 Long-nosed fur seals

4.3.1 Distribution of observations

Observational data for long-nosed fur seals (LNFS) consisted of 161 satellite telemetry tracks from 87 individuals and six sites in the GAB (Table 1). A total of 116 tracks from 62 adult females were recorded from four sites (Figure 10a) and 45 tracks from 25 males were recorded from two sites in the eastern GAB (Figure 10b). Tracking observations identified the importance of both continental shelf and oceanic waters for females and the continental shelf for males (Figure 10).

Because of these potential different distributions, models were developed for each sex. Moreover, females shift between shelf waters and oceanic waters seasonally (Page et al. 2005, 2006, Baylis et al. 2008a, 2008b). Therefore, we developed additional models to predict the distribution of females during summer versus winter.

4.3.2 Potential distribution at-sea

The distribution model predictions for adult female LNFS were based on three environmental predictor variables: bathymetry, distance from shelf break and distance from Subtropical Front. The distribution model suggests that habitat suitability is explained by distance from the Subtropical Front (41%), distance from the shelf break (41%), and bathymetry (18%). This suggests that suitable habitats are likely to be located over all the GAB continental shelf and along the shelf break, except in the central GAB, and in oceanic waters (Figure 11a). The model performance (AUC) was estimated to be 0.806.

The contribution of the three static environmental predictors for males differed from the female model as bathymetry contributes 56% of the model prediction, while distance from Subtropical Front and distance from the shelf break contribute 23% and 21%, respectively. Model results suggest that suitable habitats for males are restricted to the continental shelf and shelf break, especially in the eastern and western GAB, while the central GAB appears not to be suitable (Figure 11b). The model performance (AUC) was estimated to be 0.956.

4.3.3 Potential foraging habitats

Suitable foraging habitats for adult female LNFS are located over the continental shelf, along the shelf break and in oceanic waters, especially in the eastern GAB (Figure 12a). Model predictions, based on three environmental predictors, indicates that occurrence of foraging habitats is mainly explained by distance from the shelf break (74%), while bathymetry and distance from the Subtropical front contribute 21% and 5%, respectively. The model performance (AUC) was estimated to be 0.640.

Highly suitable foraging habitats for males are located over the continental shelf and shelf break, especially in the eastern and western GAB, while the central GAB appears not to be suitable (Figure 12b). The contribution of the three static environmental predictors used in the model differs from the female model as bathymetry contributes 60% of the explained variability, while distance from the shelf break and distance from the Subtropical Front contribute 33% and 7%, respectively. The model performance (AUC) was estimated to be 0.800.

4.3.4 Realised distribution at-sea (weighted by abundance)

A total of 56 LNFS breeding colonies have been surveyed during the last 20 years (Shaughnessy et al. 2016). As for sea lions, the population size is much higher in the eastern GAB than in the western GAB. No breeding colonies were found in the central GAB (Figure 13).
When weighted by abundance, the suitable habitats for female LNFS are located over the shelf, along the shelf break and in oceanic waters in the western and eastern GAB. The central GAB does not appear to be suitable for female LNFS (Figure 14a).

The suitable habitats weighted by abundance for male LNFS are located over the shelf and along the shelf break in the western and eastern GAB. The central GAB does not appear to be suitable for male LNFS (Figure 14b).

4.3.5 Realised foraging habitats (weighted by abundance)

When weighted by abundance, the highly suitable foraging habitats for female LNFS are located over the shelf, along the shelf break and in the oceanic waters, especially in the eastern GAB. The central GAB does not appear to be suitable for foraging for female LNFS (Figure 15a).

The suitable habitats weighted by abundance for male LNFS are located over the shelf and shelf break, mainly in the eastern GAB. The central GAB does not appear to be suitable for foraging for male LNFS (Figure 15b).

4.3.6 Seasonality in female’s distribution

In summer, suitable habitats for adult female LNFS are distributed over the continental shelf in the western GAB and in the eastern GAB, north-west and south-east of Kangaroo Island, and along the Bonney coast (Figure 16a).

In winter, suitable habitats for females are distributed over the continental shelf in the western GAB, and over the continental shelf, along the shelf break and in the oceanic waters in the eastern GAB (Figure 16b).
Figure 10: Tracking data for a) female and b) male long-nosed fur seals showing the importance of both continental shelf and oceanic waters for females and continental shelf for males in the GAB. The dashed line represents the 250 m isobath and marks the extent of the continental shelf.
Figure 11: Standardised probability of potential occurrence at-sea of a) adult female long-nosed fur seals (LNFS) and b) adult male LNFS. The warmer colours indicate a higher probability of occurrence. Suitable habitats for females are located over all the GAB continental shelf and shelf break, except in the central GAB, and in oceanic waters, while suitable habitats for males are restricted to the continental shelf and shelf break, especially in the eastern and western GAB, while the central GAB does not appear to be suitable.
Figure 12: Standardised probability of potential occurrence of foraging habitats of a) adult female long-nosed fur seals (LNFS) and b) adult male LNFS. The warmer colours indicate a higher probability of occurrence of foraging. Suitable foraging habitats for females are located over the continental shelf, along the shelf break and in the oceanic waters, especially in the eastern GAB. Suitable foraging habitats for males are located over the continental shelf and shelf break, especially in the eastern and western GAB, while the central GAB does not appear to be suitable.
Figure 13: Population estimates of long-nosed fur seals in the GAB region. A total of 56 breeding colonies have been surveyed. The size of the circles is proportional to the size of the colonies. The grey line represents the 250 m isobath and marks the limit extent of the continental shelf. No breeding colonies were found in the central GAB.
Figure 14: Standardised probability of realised occurrence at-sea (weighted by abundance) of a) adult female long-nosed fur seals (LNFS) and b) adult male LNFS. The warmer colours indicate a higher probability of occurrence. Suitable realised habitats for female LNFS are located over the shelf, along the shelf break and in the oceanic waters in the western and eastern GAB. The suitable realised habitats for male LNFS are located over the shelf and shelf break in the western and eastern GAB. The central GAB does not appear to be suitable for neither female nor male LNFS.
Figure 15: Standardised probability of occurrence of realised foraging habitats (weighted by abundance) of a) adult female long-nosed fur seals (LNFS) and b) adult male LNFS. The warmer colours indicate a higher probability of occurrence of foraging. Suitable realised foraging habitats for female LNFS are located over the shelf and shelf break and in the oceanic waters, especially in the eastern GAB, while the suitable realised habitats for male LNFS are located over the shelf and shelf break. The central GAB does not appear to be suitable for foraging for either female or male LNFS.
Figure 16: Standardised probability of potential occurrence of adult female long-nosed fur seals during a) summer and b) winter. The warmer colours indicate a higher probability of occurrence. In summer, suitable habitats for females are distributed over the continental shelf in the western GAB and in the eastern GAB, north-west and south-east to Kangaroo Island and along the Bonney coast. In winter, suitable habitats for females are distributed over the continental shelf in the western GAB and over the continental shelf, along the shelf break and in the oceanic waters in the eastern GAB.
4.4 Australian fur seals

4.4.1 Distribution of observations

Observational data for Australian fur seals (AFS) consisted of 415 satellite telemetry tracks from 38 individuals (27 females + 11 males) and three sites in the GAB (Table 1). Tracking observations identified the importance of the continental shelf and shelf break (Figure 17). No sex difference in distribution was observed, so both males and females were pooled together in the analyses. The models were based on the 415 tracks recorded (Figure 17).

4.4.2 Potential distribution at-sea

The distribution model predictions for AFS were based on three environmental predictor variables: bathymetry, distance from shelf break and distance from coast. The distribution model suggests that habitat suitability is explained by bathymetry (52%), distance from the shelf break (28%) and distance from the coast (20%). Suitable habitats for adult AFS are distributed over the continental shelf break between 117°E and 124°E, south-west to Kangaroo Island (136°E), over the continental shelf break between 139°E and 145°E and along the coast north to Tasmania (144°E – 146°E) (Figure 18). The model performance (AUC) was estimated to be 0.756.

4.4.3 Potential foraging habitats

Highly suitable foraging habitats for adult AFS are distributed over the continental shelf break between 117°E and 124°E, south-west to Kangaroo Island (136°E-137°E) and extended north-west along the Eyre Peninsula till 134°E, over the continental shelf break between 139°E and 145°E and along the main coast north to Tasmania (144°E – 146°E) (Figure 19). Bathymetry contributes 46% of the explained variability, while distance from the coast contributes 33% and distance from the shelf break 21%. The model performance (AUC) was estimated to be 0.81.

4.4.4 Realised distribution at-sea (weighted by abundance)

Abundance estimates for AFS were available for five different breeding colonies far to the east of the GAB. The largest colonies were found further east than 140°E, while smaller colonies are located in the south of Kangaroo Island and south of the Eyre Peninsula (136°E) (Shaughnessy et al. 2010) (Figure 20).

When weighted by abundance, the highly suitable realised habitats for AFS are located in the far east of the GAB over the continental shelf break, and along the mainland coast north to Tasmania (Figure 21).

4.4.5 Realised foraging habitats (weighted by abundance)

When weighted by abundance, the highly suitable realised foraging habitats for AFS are located in the far east of the GAB over the continental shelf and shelf break (139°E – 145°E), and along the mainland coast north to Tasmania (Figure 22).
Figure 17: Tracking data for Australian fur seals showing the importance of the continental shelf and shelf break in the eastern GAB. The dashed line represents the 250 m isobath and marks the extent of the continental shelf.

Figure 18: Standardised probability of potential occurrence at-sea of adult Australian fur seals. The warmer colours indicate a higher probability of occurrence. Model results suggest that suitable habitats are likely distributed over the continental shelf and shelf break in the western and eastern GAB, southwest of Kangaroo Island, and along the mainland coast north of Tasmania.
Figure 19: Standardised probability of potential occurrence of foraging habitats of adult Australian fur seals. The warmer colours indicate a higher probability of occurrence of foraging. Suitable foraging habitats are distributed over the continental shelf and shelf break in the western and eastern GAB, south-west to Kangaroo Island, extending north-west along the Eyre Peninsula, and along the mainland coast north of Tasmania.

Figure 20: Population estimates of Australian fur seals in the GAB region. Abundance estimates were available for five different breeding colonies in the eastern GAB. The size of the circles is proportional to the size of the colonies. The grey line represents the 250 m isobath and marks the extent of the continental shelf.
Figure 21: Standardised probability of realised occurrence at-sea (weighted by abundance) of Australian fur seals (AFS). The warmer colours indicate a higher probability of occurrence. Suitable realised habitats for AFS are located far in the east of the GAB over the continental shelf break and along the mainland coast north of Tasmania.

Figure 22: Standardised probability of realised occurrence of foraging habitats (weighted by abundance) of Australian fur seals (AFS). The warmer colours indicate a higher probability of occurrence of foraging. Suitable realised foraging habitats for AFS are located in the far east of the GAB over the continental shelf and shelf break and along the mainland coast north of Tasmania.
4.5 Little penguins

4.5.1 Distribution of observations

Observational data for little penguins (LP) consisted of 108 satellite telemetry tracks from 94 individuals tagged at eight sites in the GAB (Table 1). Tracking observations identified the importance of the continental shelf in the vicinity of the mainland coast (Figure 23). No information on sex was recorded.

4.5.2 Potential distribution at-sea

The distribution model predictions for LP were based on two environmental predictor variables: bathymetry and distance from the coast. The distribution model suggests that bathymetry contributes 52% of the explained variability and distance from the coast 48%. Model results suggest that suitable habitats are distributed all along the coast of the GAB region, with the most suitable habitats between 120°E and 124°E, 135°E and 137°E, and 144°E and 146°E (Figure 24). The model performance (AUC) was estimated to be 0.674.

4.5.3 Potential foraging habitats

The most suitable foraging habitats for little penguins are distributed all along the shoreline (Figure 25). Model predictions, based on two environmental predictors, indicate that distance from the coast and bathymetry contribute to 74% and 26% respectively to the explained variability. The model performance (AUC) was estimated to be 0.701.

4.5.4 Realised distribution at-sea (weighted by abundance)

The abundance estimates for LP were available for 65 different sites. However, no recent overall GAB survey has been conducted on this species, and some estimates were found in the literature from very old studies. Based on the available information, it appears that the largest colonies are located in the eastern GAB (Figure 26).

When weighted by abundance, the highly suitable realised habitats for LP are located along the west of the Eyre Peninsula (around 134°E, 34°S) (Figure 27).

4.5.5 Realised foraging habitats (weighted by abundance)

When weighted by abundance, the highly suitable realised foraging habitats for little penguins are located along the west of the Eyre Peninsula (around 134°E, 34°S) and are very similar to the predicted habitats based on the general realised distribution (Figure 28).
Figure 23: Tracking data for little penguins showing the importance of the continental shelf in the vicinity of the coast in the eastern GAB. The dashed line represents the 250 m isobath and marks the extent of the continental shelf.

Figure 24: Standardised probability of potential occurrence at-sea of little penguins. The warmer colours indicate a higher probability of occurrence. Suitable habitats are distributed along the entire coast of the GAB region, with the most suitable habitats between 120°E and 124°E, 135°E and 137°E and 144°E and 146°E.
Figure 25: Standardised probability of potential occurrence of foraging habitats of little penguins. The warmer colours indicate a higher probability of occurrence of foraging. Suitable foraging habitats are distributed along the entire shoreline in the GAB.

Figure 26: Population estimates of little penguins in the GAB region. The abundance estimates for little penguins were available for 65 different sites. However, no recent overall GAB survey was conducted on this species and some estimates were found in the literature from very old studies. Based on the available information, it appeared that the largest colonies were located in the eastern GAB. The grey line represents the 250 m isobath and marks the extent of the continental shelf.
**Figure 27:** Standardised probability of realised occurrence at-sea (weighted by abundance) of little penguins. The warmer colours indicate a higher probability of occurrence. Suitable realised habitats are located in the west of the Eyre Peninsula.

**Figure 28:** Standardised probability of realised occurrence of foraging habitats (weighted by abundance) of little penguins. The warmer colours indicate a higher probability of occurrence of foraging. Suitable realised foraging habitats are located in the west of the Eyre Peninsula and are very similar to predicted habitats based on the general realised distribution.
4.6 Short-tailed shearwater

4.6.1 Distribution of observations

Data for short-tailed shearwaters (STSW) consisted of 33 satellite telemetry tracks from 31 individuals and two sites in the GAB (Table 1). STSW undertake short foraging trips in the mid-outer shelf waters of the GAB alternately with longer trips in Southern Ocean waters off the GAB region during their breeding season (Raymond et al. 2010, Einoder 2011). In the present study, we only considered the short trips occurring within the GAB. Tracking observations identified the importance of both continental shelf and oceanic waters (Figure 29). No information on sex was recorded.

4.6.2 Potential distribution at-sea

The distribution model predictions for STSW were based on three environmental predictor variables: bathymetry, sea bottom slope and summer (December-March) mean temperature. The distribution model suggests that annual mean sea surface temperature contributes 63% of the explained variability, bathymetry 30% and sea bottom slope 7%. Model results suggest that suitable habitats for STSW are distributed over the continental shelf break in the south-west of Kangaroo Island (136°E) (Figure 30). The model performance (AUC) was estimated to be 0.90.

4.6.3 Potential foraging habitats

Suitable foraging habitats for STSW are distributed over the continental shelf break south to Kangaroo Island (136°E–138°E) (Figure 31). The predictions from the distribution model and foraging model are very similar. The foraging model, based on three environmental predictors, indicates that mean sea surface temperature contributes 56% of the explained variability, bathymetry 35% and sea bottom slope 9%. Model performance (AUC) was estimated to be 0.93.

4.6.4 Realised distribution at-sea (weighted by abundance)

The abundance estimates STSW were available for 33 different sites. However, no recent overall GAB survey has been conducted for this species and some estimates were found in the literature from very old studies. Based on the available information, it appears that the largest colonies are located in the central/eastern GAB (Figure 32).

When weighted by abundance, the suitable realised habitats for STSW are mostly located in the west and north-west of Kangaroo Island and Eyre Peninsula (134°E–137°E). An area in oceanic waters (36°S) might be of interest for STSW as well (Figure 33).

4.6.5 Realised foraging habitats (weighted by abundance)

When weighted by abundance, suitable realised foraging habitats for STSW are mostly located in the west and north-west of Kangaroo Island and along the western shore of Eyre Peninsula. A foraging area in the oceanic waters (36°S) might be of interest for STSW as well (Figure 34). The realised general distribution model and realised foraging model give very similar predictions.
Figure 29: Tracking data for short-tailed shearwaters showing the importance of both continental shelf and oceanic waters in the eastern GAB. The present study only considered short trips occurring within the GAB. The dashed line represents the 250 m isobath and marks the limit extent of the continental shelf.

Figure 30: Standardised probability of potential occurrence at-sea of short-tailed shearwaters. The warmer colours indicate a higher probability of occurrence. Suitable habitats are distributed over the continental shelf break in the south-west of Kangaroo Island.
Figure 31: Standardised probability of potential occurrence of foraging habitats of short-tailed shearwaters. The warmer colours indicate a higher probability of occurrence of foraging. Suitable foraging habitats are distributed over the continental shelf break south of Kangaroo Island.

Figure 32: Population estimates of short-tailed shearwaters in the GAB region. The abundance estimates were available for 33 different sites. However, no recent overall GAB survey has been undertaken on this species, and some estimates were found in the literature from very old studies. Based on the available information, the largest colonies were located in the central/eastern GAB. The grey line represents the 250 m isobath and marks the extent of the continental shelf.
Figure 33: Standardised probability of realised occurrence at-sea (weighted by abundance) of short-tailed shearwaters. Warmer colours indicate a higher probability of occurrence. Suitable realised habitats are mostly located in the west and north-west of Kangaroo Island and Eyre Peninsula. An area in oceanic waters (36°S) might also be of interest for STSW.

Figure 34: Standardised probability of realised occurrence of foraging habitats (weighted by abundance) of short-tailed shearwaters. Warmer colours indicate a higher probability of occurrence of foraging. Suitable realised foraging habitats are mostly located in the west and north-west of Kangaroo Island and along the west shore of the Eyre Peninsula. Area in the oceanic waters (36°S) might also be of interest.
4.7 Blue sharks

4.7.1 Distribution of observations

Observational data for blue sharks (BS) consisted of eight satellite telemetry tracks from eight individuals in the GAB (Table 1) (Figure 35). Tracking observations identified the importance of continental shelf break and oceanic waters for this species (Figure 35). No information on sex was recorded. However, differences in distribution between seasons were observed. In consequence, we developed additional models to predict the distribution of blue sharks during summer versus winter. No model on realised distribution was conducted as no data on abundance were available for non-central-place forager species.

4.7.2 Potential distribution at-sea

The distribution model predictions for BS were based on four environmental predictor variables: bathymetry, sea bottom aspect, sea bottom slope and annual mean sea surface temperature. The distribution model suggests that habitat suitability is explained as much by bathymetry as by annual mean sea surface temperature (both 46%), then by sea bottom aspect (6%) and sea bottom slope (2%). Although, BS are pelagic animals in oceanic waters, model results suggest that suitable habitats in the GAB are located over the continental shelf break (Figure 36). The model performance (AUC) was estimated to be 0.642.

4.7.3 Potential foraging habitats

The most suitable foraging habitats for BS are located over the continental shelf break (Figure 37). Model predictions, based on four environmental predictors, indicate that bathymetry and annual mean sea surface temperature contribute more than 90% of the explained variability (71% and 20%, respectively), while aspect and slope contribute 6% and 3%, respectively. The model performance (AUC) was estimated to be 0.76.

4.7.4 Seasonality in potential distribution

In summer, suitable habitats for BS are mainly distributed over the continental shelf break in the GAB, but oceanic waters may be of interest for the species as well during this season. (Figure 38a).

In winter, suitable habitats for BS are distributed almost exclusively over the continental shelf break in the central GAB and in the eastern GAB (Figure 38b).
Figure 35: Tracking data for blue sharks showing the importance of continental shelf break and oceanic waters in the GAB. The dashed line represents the 250 m isobath and marks the extent of the continental shelf.

Figure 36: Standardised probability of potential occurrence at-sea of blue sharks. The warmer colours indicate a higher probability of occurrence. Suitable habitats in the GAB are located over the continental shelf break.
Figure 37: Standardised probability of potential occurrence of foraging habitats of blue sharks. The warmer colours indicate a higher probability of occurrence of foraging. Suitable foraging habitats are located over the continental shelf break especially in the central and eastern GAB.
Figure 38: Standardised probability of potential occurrence of blue sharks during a) summer and b) winter. The warmer colours indicate a higher probability of occurrence. In summer, suitable habitats are mainly distributed over the continental shelf break in the GAB but oceanic waters may be important for the species as well. In winter, suitable habitats are distributed almost exclusively over the continental shelf break in the central GAB and in the eastern GAB.
4.8 Shortfin mako sharks

4.8.1 Distribution of observations

Observational data for shortfin mako sharks consisted of 18 satellite telemetry tracks from 18 individuals in the GAB (Table 1) (Figure 39). Tracking observations identified the importance of the continental shelf and shelf break for this species (Figure 39). No information on sex was available.

4.8.2 Potential distribution at-sea

The distribution model predictions for shortfin mako sharks were based on four environmental predictor variables: bathymetry, sea bottom aspect, sea bottom slope, and summer (December-March) mean sea surface temperature. The distribution model suggests that habitat suitability is explained by bathymetry (89%), summer mean sea surface temperature (8%), sea bottom aspect (3%), while the contribution of sea bottom slope is near zero (0.2%). Model results suggest that suitable habitats in the GAB are located over the continental shelf and shelf break (Figure 40). The model performance (AUC) was estimated to be 0.682.

4.8.3 Potential foraging habitats

The most suitable foraging habitats for shortfin mako sharks are located over the continental shelf and near the shelf break in the western GAB from 117°E to 121°E, in the central GAB from 125°E to 133°E, and in the eastern GAB from 135°E to 142°E (Figure 41). Model predictions, based on four environmental predictors, indicate that bathymetry contributes the most to the explained variability (88%), while summer mean sea surface temperature contributes 10%, aspect 2%, and slope contribution is near zero (0.8%). The model performance (AUC) was estimated to be 0.94.
Figure 39: Tracking data for shortfin mako sharks showing the importance of continental shelf and shelf break in the GAB. The dashed line represents the 250 m isobath and marks the extent of the continental shelf.

Figure 40: Standardised probability of potential occurrence at-sea of shortfin mako sharks. The warmer colours indicate a higher probability of occurrence. Suitable habitats in the GAB are located over the continental shelf and shelf break.
Figure 41: Standardised probability of potential occurrence of foraging habitats of shortfin mako sharks. The warmer colours indicate a higher probability of occurrence of foraging. Suitable foraging habitats are located over the continental shelf and near the shelf break in the western GAB from 117°E to 121°E, in the central GAB from 125°E to 133°E and in the eastern GAB from 135°E to 142°E.
4.9 White sharks

4.9.1 Distribution of observations

Observational data for white sharks (WS) consisted of five satellite telemetry tracks from five individuals in the GAB (Table 1) (Figure 42). Tracking observations identified the importance of the continental shelf and shelf break for this species (Figure 42). No information on sex was recorded.

4.9.2 Potential distribution at-sea

The distribution model predictions for WS were based on three environmental predictor variables: bathymetry, distance from the coast and sea bottom slope. The distribution model suggests that habitat suitability is explained by distance from the coast (80%), bathymetry (17%) and sea bottom slope (3%). Model results suggest that suitable habitats for WS in the GAB are located in the eastern GAB over the continental shelf and shelf break from 134°E to 145°E, and in the Spencer and St Vincent Gulfs (Figure 43). The model performance (AUC) was estimated to be 0.905.

4.9.3 Potential foraging habitats

The most suitable foraging habitats for WS are located over the continental shelf and near the shelf break in the eastern GAB from 134°E to 137°E, and in Spencer Gulf (Figure 44). Other suitable habitats appear over the shelf break along the Bonney Coast (Figure 44). Model results, based on three environmental predictors, indicate that distance from the coast contributes 74% of the explained variability, bathymetry 19%, and sea bottom slope 7%. The model performance (AUC) was estimated to be 0.964.
Figure 42: Tracking data for white sharks showing the importance of the continental shelf and shelf break in the GAB. The dashed line represents the 250 m isobath and marks the extent of the continental shelf.

Figure 43: Standardised probability of potential occurrence at-sea of white sharks. The warmer colours indicate a higher probability of occurrence. Suitable habitats are located over the continental shelf and shelf break in the eastern and western GAB and in Spencer and St Vincent Gulfs.
Figure 44: Standardised probability of potential occurrence of foraging habitats of white sharks. The warmer colours indicate a higher probability of occurrence of foraging. Suitable foraging habitats are mainly located over the continental shelf and near the shelf break in the eastern GAB from 134°E to 137°E and in Spencer Gulf.
4.10 Southern Bluefin Tuna

4.10.1 Distribution of observations

Observational data for southern bluefin tuna (SBT) consisted of position estimates from geolocators deployed on 125 individuals between 1998 and 2011 (Table 1). Difference in distribution between seasons was observed, and we developed additional models to predict the distribution of SBT during summer versus winter. No information on sex was recorded.

4.10.2 Potential distribution at-sea

The distribution model predictions for SBT were based on four environmental predictor variables: bathymetry, sea bottom aspect, sea bottom slope and distance from the shelf break. The distribution model suggests that habitat suitability is explained by bathymetry (66%), distance from the continental shelf break (12%), sea bottom slope (12%) and sea bottom aspect (10%). Suitable habitats are mainly located in the central and eastern GAB over the continental shelf and near the shelf break (Figure 45). The model performance (AUC) was estimated to be 0.59.

4.10.3 Potential foraging habitats

The most suitable foraging habitats for SBT are mainly distributed over or near the continental shelf break, especially between 121°E and 126°E, 131°E and 134°E and between 136°E and 139°E (Figure 46). GAM model predictions, based on four environmental predictors, indicate a significant contribution of bathymetry and distance from the shelf break. The model explained 79.7% of the total deviance ($R^2 = 0.797$).

4.10.4 Seasonality in potential distribution

In summer, suitable habitats for SBT are distributed over the continental shelf near the shelf break. The highest probability of occurrence is located between 131°E and 136°E (Figure 47a).

In winter, suitable habitats for SBT are distributed over the continental shelf break in all the GAB region (Figure 47b).
Figure 45: Standardised probability of potential occurrence at-sea of southern bluefin tuna. The warmer colours indicate a higher probability of occurrence. Suitable habitats are mainly located in the central and eastern GAB over the continental shelf and near the shelf break.

Figure 46: Standardised probability of potential occurrence of foraging habitats of southern bluefin tuna (SBT). The warmer colours indicate a higher probability of occurrence of foraging. Suitable foraging habitats for SBT are mainly distributed over or near the continental shelf break, especially between 121°E and 126°E, 131°E and 134°E and between 136°E and 139°E.
Figure 47: Standardised probability of potential occurrence of southern bluefin tuna (SBT) during a) summer and b) winter. The warmer colours indicate a higher probability of occurrence. In summer, suitable habitats for SBT are distributed over the continental shelf near the shelf break. The highest probability of occurrence is located between 131\(^{\circ}\)E and 136\(^{\circ}\)E. In winter, suitable habitats for SBT are distributed over the continental shelf break over the entire GAB region.
4.11 Pygmy blue whales

4.11.1 Distribution of observations

A total of 119 pygmy blue whales (BW) were observed during four different aerial surveys. A position estimate was assigned to each observation and used as an indication of presence for the species. No map of the locations of this species is presented, in compliance with an agreement with “Blue Whale Study”, who provided the data. Potential foraging habitats couldn’t be predicted from survey data.

4.11.2 Potential distribution at-sea

The distribution model predictions for BW were based on four environmental predictor variables: bathymetry, sea bottom aspect, sea bottom slope and summer (December–March) mean sea surface temperature. The distribution model suggests that habitat suitability is explained by bathymetry (75%) and sea bottom aspect (23%). The summer mean sea surface temperature and the sea bottom slope have a very low contribution to the model predictions (both 1%). Model results suggest that suitable habitats for BW in the GAB are mainly located over the continental shelf break between 134°E and 138°E (Figure 48). However, the entire continental shelf break in the GAB may be used by BW (Figure 48). The model performance (AUC) was estimated to be 0.894.

Figure 48: Standardised probability of potential occurrence at-sea of pygmy blue whales. The warmer colours indicate a higher probability of occurrence. Suitable habitats may be located over the continental shelf break in the GAB.
4.12 Sperm whales

4.12.1 Distribution of observations

More than 15,500 records of the location of sperm whales (SW) were available over the last 50 years from the GAB region. These records included data from systematic surveys, opportunistic sightings data and records provided by the International Whaling Commission on the location of SW catches by commercial whalers (Table 1). Positions recorded from systematic aerial surveys, boat based surveys and opportunistic sightings data were combined with positions reported in historical whaling data to estimate the distribution of suitable habitats for this species. SW locations recorded in these dataset indicate the importance of the continental shelf break for this species (Figure 49). Potential foraging habitats couldn’t be predicted from survey data.

4.12.2 Potential distribution at-sea

The distribution model predictions for SW were based on three environmental predictor variables: bathymetry, sea bottom aspect and sea bottom slope. Habitat suitability is explained by bathymetry (77%), sea bottom aspect (13%) and sea bottom slope (10%). Model results suggest that suitable habitats for SW in the GAB are mainly located over the continental shelf break, but more specifically, over the sub-marine canyons (inferred from sea bottom aspect) (Figure 50). The model performance (AUC) was estimated to be 0.880.

Figure 49: Location of observations of sperm whales from aerial surveys and historical whaling data showing the importance of the continental shelf break in the GAB for this species. The dashed line represents the 250 m isobath and marks the extent of the continental shelf.
Figure 50: Standardised probability of potential occurrence at-sea of sperm whales. The warmer colours indicate a higher probability of occurrence. Suitable habitats are located over the continental shelf break in the GAB, and more specifically, over the sub-marine canyons.
4.13 Distribution at-sea and foraging habitat models synthesis

Bathymetry contributes the most to explaining the general distribution of many species, and indicates the importance of the continental shelf for top predators in the GAB (Table 3). Predictor variables contributing to foraging habitat models indicate a strong influence of bathymetry and indicate the importance of the continental shelf for many species, especially the shelf slope and the vicinity of the mainland coast (Table 4).
Table 3: Synthesis of predictor variable contributions to general distribution models for each individual species and model performance. Predictors that contribute the most in the models are shaded in grey. Dashes indicate that variables have not been tested.

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Table 4: Synthesis of predictor variable contributions to foraging habitat models for each individual species and model performance. Predictors that contribute the most in the models are shaded in grey. Dashes indicate that variables have not been tested.

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4.14 Identification of areas of high, medium and low use

GENERAL DISTRIBUTION

4.14.1 Inter-species overlap of general distribution models

The overlap between the potential distribution models for the 11 species highlights two different regions of the GAB that are highly used by predators. The first is located over the continental shelf and shelf break in the eastern GAB extending along the Bonney coast and the mainland coast north of Tasmania (134°E–145°E). The second is located over the continental shelf and shelf break in the western GAB (117°E–126°E) (Figure 51). The 11 species included in the identification of these regions were: ASL, AFS, LNFS, LP, STSW, BS, SM, WS, SBT, SW and BW.

4.14.2 Inter-species overlap of general distribution models weighted by abundance

When replacing the potential distribution models for central-place foragers (i.e. ASL, AFS, LNFS, LP, STSW) by the realised distribution models (weighted by abundance) for these species, only one region over the continental shelf break in the eastern GAB (132°E–145°E) appears highly used by predators (Figure 52). The same 11 species (than in section 4.14.1) were included here.

4.14.3 Inter-species overlap of general distribution models only for central-place forager species.

Overlap of the potential distribution models for central-place foragers (five species: ASL, AFS, LNFS, LP, STSW) shows two different regions highly used by these predators. One region is located in the eastern GAB extending along the Bonney coast and along the mainland coast north of Tasmania (134°E–146°E). A second region is located in the western GAB (117°E–124°E). In these two regions, the continental shelf in the vicinity of the mainland coast is mostly used (Figure 53).

4.14.4 Inter-species overlap of general distribution models weighted by abundance only for central-place forager species

The overlap of the realised distribution models (weighted by abundance) for central-place foragers (five species: ASL, AFS, LNFS, LP, STSW) shows three different highly used regions. All three are confined to the eastern GAB. One region is located over the shelf and shelf break west to Kangaroo Island (132°E–137°E). A second region is located in the open sea (131°E–134°E; 36.5°S) and the third region is located over the shelf in the far east GAB along the Bonney coast and along the mainland coast north of Tasmania (139°E–146°E) (Figure 54).

4.14.5 Inter-species overlap of general distribution models only for non-central-place foragers species

The overlap of the general distribution models for non-central-place foragers (six species: BS, MS, WS, SBT, SW, BW) shows that the continental shelf break in the whole GAB is highly used by these predators (Figure 55). However, the eastern GAB (134°E–145°E) and the western GAB (117°E–130°E) are the most intensively used regions.
Figure 51: Multi-species overlap calculated as the average of the potential occurrence from the 11 species of the study. Two different regions highly used by the predators are identified: i) the continental shelf and shelf break in the eastern GAB extending along the Bonney coast and the mainland coast north of Tasmania, ii) the continental shelf and shelf break in the western GAB. Species included in the identification of these regions are: Australian sea lions, Australian fur seals, Long-nosed fur seals, Little penguins, Short-tailed shearwater, Blue shark, Shortfin mako sharks, White sharks, Southern Bluefin Tuna, Sperm whales and Blue whales.
Figure 52: Multi-species overlap calculated as the average of the occurrence from the 11 species including the realised distribution (weighted by abundance) for central-place foragers. One region over the continental shelf break in the eastern GAB is highly used by the predators. Species included are: Australian sea lions, Australian fur seals, Long-nosed fur seals, Little penguins, Short-tailed shearwater, Blue shark, Shortfin mako sharks, White sharks, Southern Bluefin Tuna, Sperm whales and Blue whales.
Figure 53: Multi-species overlap calculated as the average of the potential occurrence from the five central-place forager species. Two different regions highly used by these predators are identified: i) the eastern GAB extending along the Bonney coast and the mainland coast north of Tasmania, ii) the western GAB. In these two regions, the continental shelf in the vicinity of the mainland coast is mostly used. Species included are: Australian sea lions, Australian fur seals, Long-nosed fur seals, Little penguins and Short-tailed shearwater.
Figure 54: Multi-species overlap calculated as the average of the realised occurrence (weighted by abundance) from the five central-place forager species. Three separate, highly used regions are identified in the eastern GAB i) over the shelf and shelf break (132°E–137°E), ii) in the open sea (131°E–134°E; 36.5°S), and iii) over the shelf in the far east GAB along the Bonney coast and the mainland coast north of Tasmania. Species included are: Australian sea lions, Australian fur seals, Long-nosed fur seals, Little penguins and Short-tailed shearwater.
Figure 55: Multi-species overlap calculated as the average of the potential occurrence from the six non-central-place forager species. The continental shelf break in the whole GAB appears to be highly used by these predators. However, the eastern GAB (134°E–145°E) and the western GAB (117°E–130°E) are the most intensively used regions. Species included are: Blue shark, Shortfin mako sharks, White sharks, Southern Bluefin Tuna, Sperm whales and Blue whales.
FORAGING HABITATS

4.14.6 Inter-species overlap of foraging habitat models

The overlap of the potential foraging habitat models for the nine species where foraging information was available, highlights two regions that were highly used by predators. The location of these regions is very similar to those highlighted by overlapping the general distribution models as one is located over the continental shelf and shelf break in the eastern GAB extending along the Bonney coast and the mainland coast north of Tasmania (134°E – 144°E), and one is located over the continental shelf and shelf break in the western GAB (117°E – 126°E) (Figure 56). The nine species included are: ASL, AFS, LNFS, LP, STSW, BS, SM, WS, and SBT.

4.14.7 Inter species overlap of foraging habitat models weighted by abundance

When replacing the potential foraging habitat models for central-place foragers (i.e. ASL, AFS, LNFS, LP, STSW), by the realised foraging model (weighted by abundance) for these species, two regions appear highly used by predators. One is located over the continental shelf and shelf break in the eastern GAB extending along the Bonney coast and the mainland coast north of Tasmania and look very similar to the region identified in the previous section (see section 4.14.6 to compare). One is located over the continental shelf break in the western GAB (121°E – 126°E) (Figure 57). The same nine species (than in section 4.14.6) are included: ASL, AFS, LNFS, LP, STSW, BS, SM, WS and SBT.

4.14.8 Inter species overlap of foraging habitat models only for central-place forager species

The overlap of the potential foraging habitat models for central-place foragers (five species: ASL, AFS, LNFS, LP, STSW) shows three separate regions highly used by these predators. One region is located in the far east GAB along the Bonney coast and the mainland coast north of Tasmania (139°E – 146°E), one is located in the eastern GAB (134°E – 139°E), and one in the western GAB (117°E – 124°E). (Figure 58). In these three regions, the continental shelf in the vicinity of the mainland coast is mostly used.

4.14.9 Inter species overlap of foraging habitat models weighted by abundance only for central-place forager species

The overlap of the foraging habitat models weighted by abundance for central-place foragers (five species: ASL, AFS, LNFS, LP, STSW) highlights the same three separate highly used regions than in the previous section. However, the regions in the eastern GAB seem to be connected and the portion of the continental shelf near the main coast used by the predators in these regions appear to be broader than in the previous section (Figure 59).

4.14.10 Inter species overlap of foraging habitat models only for non-central-place forager species

The overlap of the foraging models for non-central-place foragers (four species: BS, SM, WS; SBT) shows that all but the far west and the far east of the continental shelf break in the GAB (123°E – 143°E) is highly used by these predators for feeding (Figure 60).
Figure 56: Multi-species overlap calculated as the average of the potential foraging habitats occurrence from the nine species where foraging information was available. Two regions highly used by predators are identified. The location of these regions is very similar to those highlighted by overlapping general distribution models. One is located over the continental shelf and shelf break in the eastern GAB and extends in to the far east GAB along the Bonney coast and the mainland coast north of Tasmania and one is located over the continental shelf and shelf break in the western GAB. Species included are: Australian sea lions, Australian fur seals, Long-nosed fur seals, Little penguins, Short-tailed shearwater, Blue shark, Shortfin mako sharks, White sharks and Southern Bluefin Tuna.
Figure 57: Multi-species overlap calculated as the average of the foraging habitats occurrence from the nine species including the realised foraging occurrence (weighted by abundance) for central-place foragers. Two different regions highly used by predators are identified. One is located over the continental shelf and shelf break in the eastern GAB extending along the Bonney coast and the mainland coast north of Tasmania and look very similar to the region identified in the previous figure. One is located over the continental shelf break in the western GAB. Species included are: Australian sea lions, Australian fur seals, Long-nosed fur seals, Little penguins, Short-tailed shearwater, Blue shark, Shortfin mako sharks, White sharks and Southern Bluefin Tuna.
Figure 58: Multi-species overlap calculated as the average of the potential foraging habitats probabilities from the five central-place forager species. Three regions highly used by predators are identified. In these three regions, the continental shelf in the vicinity of the mainland coast is mostly used. One region is located in the far east GAB along the Bonney coast and the mainland coast north of Tasmania, one is located in the eastern GAB and one in the western GAB. Species included are: Australian sea lions, Australian fur seals, Long-nosed fur seals, Little penguins and Short-tailed shearwater.
Figure 59: Multi-species overlap calculated as the average of the realised foraging habitats occurrence (weighted by abundance) from the five central-place forager species. The same three highly used regions than in the previous figure are highlighted. However, the regions in the eastern GAB seem to be connected and the portion of the continental shelf near the main coast used by the predators in these regions appear to be broader than in the previous figure. Species included are: Australian sea lions, Australian fur seals, Long-nosed fur seals, Little penguins and Short-tailed shearwater.
Figure 60: Multi-species overlap calculated as the average of the potential foraging habitats occurrence from the four non-central-place forager species. All but the far west and the far east of the continental shelf break in the GAB appears to be highly used by these predators. Species included are: Blue shark, Shortfin mako sharks, White sharks and Southern Bluefin Tuna.
SEASONALITY

4.14.11 Inter species overlap of foraging models for migratory species in summer

The overlap of the foraging models for the three species showing a seasonal pattern (i.e. adult female LNFS, BS and SBT) highlights two different regions highly used for foraging in summer, all mostly over the continental shelf. One is located in the eastern GAB (133°E – 145°E) extending in the far east along the Bonney coast, and one in the western GAB (117°E – 125°E) (Figure 61).

4.14.12 Inter species overlap of foraging models for migratory species in winter

The overlap of the foraging models for the three same species (i.e. adult female LNFS, BS and SBT) in winter shows that the two regions highly used for foraging are now located over the shelf break, while the shelf appears to be less used (compared to summer) (Figure 62).
Figure 61: Multi-species overlap calculated as the average of the potential foraging habitats occurrence in summer from the three species showing a seasonal pattern in distribution. Two different regions highly used for foraging in summer are identified. One is located the eastern GAB extending in the far east along the Bonney coast and one in the western GAB. Species included are: adult female long-nosed fur seals, Blue sharks, and Southern Bluefin Tuna.
Figure 62: Multi-species overlap calculated as the average of the potential foraging habitats occurrence in winter from the three species showing a seasonal pattern in distribution. Two different regions highly used for foraging are located over the shelf break in the eastern and western GAB. In these two regions, the continental shelf appears to be less used by these species (compared to summer). Species included are: adult female long-nosed fur seals, Blue sharks, and Southern Bluefin Tuna.
4.15 Physical oceanographic features of the key regions

Two different regions of the GAB were selected as key regions of interest (i.e. highly used by predators) based on the average potential occurrence of the 11 species (Figure 63). The first is located over the continental shelf and shelf break in the eastern GAB extending along the Bonney coast and the mainland coast north of Tasmania (134°E-145°E). The second is located over the continental shelf and shelf break in the western GAB (117°E–126°E) (Figure 63). Although the key regions share similar physical characteristics as they are all located in relatively narrow shelf waters in the vicinity of the shelf slope, as indicated by the bathymetry, distance from the coast and distance from the shelf slope in these areas (Figure 64a, b and c), they are influenced by different oceanographic processes, known to occur in these part of the GAB (e.g. Lewis 1981, Middleton and Cirano 2002, Middleton and Platov 2003, Middleton and Bye 2007). In summer, the region #1 is characterised by two similar but different upwelling systems and as such, can be distinguished between the east and west part of the region. The east part is influenced by the ‘Bonney Upwelling’, which is a predictable summertime upwelling (Lewis 1981) (Figure 65). In this system, cool waters are driven onto the continental shelf by southeast wind forcing and the resulting Ekman flux (Lewis 1981) (Figure 64d). The Bonney Upwelling is strongly influenced by the narrowness of the continental shelf in this location (≈ 30 km), the steep bathymetry and the presence of notable canyons. The west part is also influenced by an upwelling system. Cold water is brought from the ocean floor up to the continental shelf by localised sub-surface upwelling but remains in a Kangaroo Island “pool” until subsequent wind-driven upwelling events draw the water to the shallower and surface coastal regions, especially during summer (Middleton and Cirano 2002, Middleton and Platov 2003) (Figures 64d and 66). Both upwelling systems bring cool and nutrient-rich water to the surface in summer (Middleton and Cirano 2002, Middleton and Platov 2003), phytoplankton concentrations (primary production) increase (Figure 67) and attract upper trophic levels. The region #2 is influenced by the Leeuwin Current (LC). The LC is a warm current that originates in tropical waters and flows southwards along the continental shelf of Western Australia before turning eastwards around Cape Leeuwin and continuing into the GAB (Figure 68), with the strongest flow occurring during winter (Cresswell and Golding 1980, Ridgway and Condie 2004, Middleton and Bye 2007). This leads to warmer sea surface temperatures in the region #2 than observed elsewhere over the continental shelf (Figure 64e).

A large part of the continental shelf and shelf slope was calculated as medium use (Figures 63 and Figure 64a, b and c), while oceanic waters were generally calculated as low use (Figures 63 and Figure 64a, b and c).
Figure 63: Areas of overlap calculated as the average of the individual potential distribution probabilities of the 11 species (top map) and used to physically characterise the different regions used by multiple predators in the GAB (bottom map). High-use regions are divided into two different regions (region #1 is sub-divided into east and west).
Figure 64: Physical characteristics of areas used by top predators: a) bathymetry, b) distance from the coast, c) distance from the shelf slope, d) mean sea surface temperature in summer and e) mean sea surface temperature in winter. Colours match the areas presented in the Figure 63. The three red lines correspond to the three oceanographic systems influencing the high use regions (dotted line = area #1 east, dashed line = area #1 west, solid line = area #2). The green and blue lines correspond to the medium and low-use areas respectively. Given the large spatial coverage of the green area over the continental shelf and slope, the characteristics of this area (green lines) are used as reference to describe the average conditions over the continental shelf and slope.
Figure 65: Mean sea surface temperature in February (calculated from satellite remote sensing data over the last 30 years) illustrating the presence of two upwelling systems, one along the Bonney coast and another along the Eyre Peninsula coast.

Figure 66: Modelled mean bottom sea temperature in February (calculated from a local environmental model applied over the continental shelf over 4 years (2011-2014)) illustrating the Kangaroo Island (KI) pool (black circle) and the drift of cold water along the Eyre Peninsula coast. The spatial window represents the extent of the model.
Figure 67: Seasonality of productivity (austral summer to winter). a) Location of temperature, salinity and fluorescence profiles recorded by 2 adult male sea lions in 2016. b) and c) Primary productivity calculated from the data recorded by the two seals. The red curve is a smoothing indicating the general trend; i.e. a maximum in productivity occurring in summer (February, March), then a progressive decline till the end of April after which productivity stabilizes at a low constant level during winter.
Figure 68: Mean sea surface temperature in July (calculated from satellite remote sensing data over the last 30 years) illustrating the incursion of the Leeuwin current (LC) in the GAB region during winter. The LC can be identified as a narrow band of warmer water adjacent to the coast.
5. DISCUSSION

Our knowledge and understanding of the marine environment are limited, and the use of surrogates to assist in the identification of areas of high ecological value is one mechanism used to address and potentially overcome these limitations. Apex predators are likely to respond to changes in their environment and especially food supply. This connection makes them particularly appropriate as bio-indicators of the functioning of the entire ecosystem (e.g. Furness and Camphuysen 1997). Drawing upon a database spanning more than 20 years and containing thousands of records of apex predator locations from tracking and sighting data, this study assesses the combined distribution of predators as indicators for important biological areas in the Great Australian Bight.

As detailed in the introduction, there are no criteria for the identification of biologically important areas for marine predators beyond broad notions of spatio-temporal persistence, elevated abundance and species richness. For the GAB, the species vary enormously in the spatial and temporal scales that they use habitat, and the available datasets are complex and varied in their spatial and temporal extent, resolution and quality (due to performance and data streams collected by different electronic tag configurations, or survey methods). Because of these issues, it is difficult to define specific criteria (e.g. numbers of individuals/species, specific percentage in habitat use) by which biologically important areas should be defined a-priori. However, through the analyses of the broad and disparate data sets included in this study, a range of criteria have been explored, and the criteria used to define important biological areas clearly depend on the initial question. Thus, when predator habitat use is of interest, general distribution or foraging data to estimate potential occurrence should be used to understand what habitats could attract predators. However, if interest is focused on the actual areas used, the use of more specific information such as abundance to estimate realised occurrence is required.

Sufficient telemetry data and/or survey data were available to estimate potential distributions for 11 species. The most extensive tracking dataset was for Australian sea lions (ASL), and likely covered the entire range of habitats used by this species in the GAB. As central-place foragers, ASL remain dependent on land all year round either for breeding or moulting/resting. Previous studies have shown that distribution and/or foraging strategies for adult females were associated with either inshore or mid-outer shelf habitats within the GAB, in water depths rarely greater than 130 m, while adult males were more often associated with deeper waters (200–250 m) near the shelf break (Goldsworthy et al. 2009, Lowther et al. 2011, 2012). Being benthic foragers, ASL were never observed in oceanic waters. Oceanographic devices have been attached to adult male ASLs over the last ten years and have proved to be valuable for collecting data on physical and biological oceanic features at places and times not possible using other platforms. These data provided valuable information on the temporal variability in estimated productivity in an upwelling system.

For long-nosed fur seals (LNFS), telemetry data mainly come from deployments undertaken at the largest breeding colonies in the eastern GAB. Although breeding colonies are also present in Western Australia (Shaughnessy et al. 1994), no tracking data were available for this part of the GAB, which may lead to a potential bias in modelled distribution estimates for this species. However, our results are consistent with other studies that have shown that adult females tend to forage close to the colony in shelf and near shelf break waters in the eastern GAB during summer but switch to foraging in oceanic waters further south (associated with the subtropical front) during winter (Baylis et al. 2005, 2008a, 2008b, Page et al. 2005, 2006). The shift between these two foraging areas may coincide with the decline in productivity over shelf waters at the end of the upwelling season (Page et al. 2006, this study: see Figure 75). In contrast, adult males appear to forage in slope waters all year round (Page et
LNFS are central-place foragers and remain dependent on land year round for breeding or moulting/resting. When at-sea, they forage at depth in pelagic waters.

Both adult male and female Australian fur seals (AFS) are known to forage broadly across the continental shelf of the far east GAB, and females typically show strong site fidelity to foraging areas (Arnould and Kirkwood 2008, Kirkwood and Arnould 2011). Although most of the time, they forage locally around the breeding colonies that are mainly located on islands in Bass Strait; some individuals have been observed foraging further west. As demersal foragers, this species may compete with sea lions for food where foraging areas overlap (Kirkwood et al. 2006, Kirkwood and Arnould 2012). As with the two other seal species, AFS are central-place foragers.

Seabird telemetry data were available for little penguins and short-tailed shearwater (STSW). Little penguins are known to forage in pelagic inner shelf and lower gulf waters near their breeding colonies, likely year round (Bool et al. 2007, Goldsworthy et al. 2011, Wiebkin 2012). Distribution and foraging models from the present study are consistent with what has been found in the previous studies. Both seabird species are central-place foragers.

STSW undertake short foraging trips in the mid-outer shelf waters of the GAB alternating with longer trips in Southern Ocean waters off the GAB region (sometimes to the Antarctic icefront) during their breeding season (Raymond et al. 2010, Einoder 2011). In the present study, we only considered the short foraging trips that occurred within the GAB, which represent roughly 30% of their foraging effort during the breeding period (Einoder and Goldsworthy 2005, Einoder 2010). As central-place foragers, STSW remain dependent on islands in the GAB for nesting and raising chicks during their spring/summer breeding season.

Telemetry data recently revealed that shelf slope and outer shelf waters in the central and western GAB are critical foraging habitat for both shortfin mako sharks and blue sharks (Rogers 2013) following broad-scale oceanic migration phases off the GAB region. Both species may also use key oceanic habitats in the GAB. Similarly, the eastern GAB, especially around the Neptune Islands, is an important habitat for white sharks (Malcolm et al. 2001, Bruce et al. 2006). The distribution models from the present study agree with what is known about the main habitats for these species in the GAB.

Geolocation data for common threshers were inaccurate and unsuitable for any of the analyses conducted in this project.

Movement data have been collected over the last 10 or more years for southern bluefin tuna (SBT) in the GAB region. The migratory movements of SBT are complex and vary markedly between life-history stages. It is generally thought that SBT larvae are carried south from the spawning grounds in tropical waters by the Leeuwin Current shortly after hatching in spring, reaching the waters off southwest Australia in early summer (Carrey et al. 1981, Cresswell and Griffin 2004). The juveniles are assumed to move into the southern continental shelf waters off southern Western Australia, gradually moving eastwards into the GAB. The young SBT may remain throughout the winter in the GAB, while others move offshore and into the Indian Ocean (Hobday et al. 2009, Fujioka et al. 2010, Basson et al. 2012). Later, older juveniles undertake seasonal large-scale migrations, frequenting the GAB only during summer and autumn (arriving November-January). Seasonal upwelling and associated enhanced productivity in the GAB may drive SBT migration. Migration schedules are highly variable between individuals (Bestley et al. 2009, Basson et al. 2012), as they generally demonstrate highly plastic behaviours in response to their environment (Bestley et al. 2009).

Pygmy blue whales aggregate in mid-shelf and slope waters of the Bonney Coast during summer and autumn, where they forage at the surface (Gill et al. 2011). Links between coastal upwellings, krill and blue whales are likely in this region of southern Australia. During late autumn, winter and spring, the
upwelling is inactive, and blue whales appear to be absent from the region (Gill 2002). The huge dataset, collected from sperm whale historical catch data, opportunistic sighting data, and more recent location data from systematic aerial and boat-based surveys (Goldsworthy et al. 2017), confirms the shelf slope and topographic features, such as canyons, are areas where sperm whales can occur. However, given the extremely limited survey data for this species in the region, there is no information on what the spatial or temporal distribution, abundance or densities of sperm whales in the GAB are. Sightings of pilot whales, beaked whales and dolphins during aerial survey were too scarce or too limited in space to conduct any analyses.

Although extensive tagging and survey work has been undertaken for several species in the GAB region over decades, this research effort does not necessarily reflect the entire distribution of each species in the region (e.g. LNFS were only tagged in the eastern GAB but we know that the species is also present in the western GAB). Our use of species distribution models has enabled us to overcome some existing knowledge gaps of species distributions by integrating location data and environmental predictors. However, the quality and performance of the models is dependent on the spatial coverage of the location data, which was largely uneven between the species, relative to their entire range, and the relative contribution of the selected environmental predictors on each species distribution. In the present study, model performance was consequently not uniform since it is influenced by tagging effort, which varied markedly from one species to another and across the time-frame of the entire 20 years dataset. The seasonal, inter-annual or inter-individual variability inherent to the dataset added complexity in the modelling process, especially in the selection of relevant predictors. Nevertheless, the distribution models provide the best estimates of the likely suitable habitats for each species based on the data available and our current knowledge on the biology and ecology of the different species. McPherson and Jetz (2007) and Tsoar et al. (2007) demonstrated that the distribution data of species with restricted niches are modelled with higher accuracy than that of generalist species. We also found that predictions were more accurate for species with the smaller distribution ranges and higher habitat specificity (for instance restricted to the continental shelf). The overlap between the different distribution models has enabled the identification of two distinct shelf and slope regions of high preference used by multiple species: the Bonney Coast, the Kangaroo Island and Eyre Peninsula region (Region 1), and the south coast of Western Australia (Region 2). However, although the general distribution models were informative in highlighting these areas, they did not provide any information on how the regions were used.

The foraging habitat models provide an indication of key regions at-sea used by the different species within their overall distribution. Although, we have no evidence that what we defined as “foraging” was related to real feeding activity, we assumed that the index (i.e. time spent in an area) used in the modelling process was closely related to a real foraging activity for predators (Fauchald and Tveraa 2003). The limitations in the foraging model performance are the same as those detailed for distribution models. We assumed that the overlap of these models highlights high value areas in the GAB region based on their importance for providing food for multiple species. The same two areas as those identified using the general distribution model were identified as highly used by predators for foraging: the Bonney Coast, the Kangaroo Island and Eyre Peninsula region (Region 1), and the south coast of Western Australia (Region 2). The similarities between the regions highlighted indicate that, when at-sea (for central-place foragers) and/or present (for migratory species), the GAB region is largely used for foraging by marine predators.

Abundance, when available (i.e. only for central-place foragers when colony surveys have been undertaken), was integrated into the models. The highly used regions, revealed by these models may correspond to the realised distribution of these species. However, depending on the species, the
abundance surveys of the different colonies were not conducted concurrently, some of them were surveyed more than ten years ago (e.g. some seabirds colonies), while others were surveyed as a part of the GAB Research Program (e.g. sea lions). Nevertheless, the use of the abundance estimates reveals that the area identified along the south coast of Western Australia, although as rich as the others in term of species richness, might be less important in terms of biomass of central-place foragers.

Regardless of criteria used in the analyses (i.e. general distribution, foraging, abundance, group of species [e.g. central-place forager versus non central-place foragers]), the two regions described above (the Bonney Coast, Kangaroo Island and Eyre Peninsula region and the south coast of Western Australia) appear to be important for predators. These two regions all have relatively narrow shelves and steep slope areas, or the presence of offshore islands that provide breeding space for central-place foragers. However, the two regions are influenced by different oceanographic conditions. The Bonney Coast is known as a region of predictable summertime upwelling, referred to as the ‘Bonney Upwelling’. Southeast wind forcing and resulting Ekman flux is the primary driver of this system, but regional ocean circulation also influences the seasonal upwelling (Lewis 1981). The westward-flowing Flinders Current is strongest in the western GAB but still may enhance water mass exchange by raising the thermocline on the continental shelf, and so pre-conditions wind-driven, cool-water upwelling (Middleton and Cirano 2002, Middleton and Platov 2003). The Bonney Upwelling is also strongly influenced by local bottom topography (Baird 2003). The narrowness of the continental shelf at that location (≈ 30 km width), the steep bathymetry and the presence of notable canyons contribute to bring cool and nutrient-rich water to the surface, where phytoplankton concentrations then develop and attract upper trophic levels.

The eastern GAB west of Kangaroo Island, along the western coast of Eyre Peninsula and along the continental slope from 131°E to 137°E is also an upwelling region. However, although similar the upwelling process there differ from the Bonney coast, as the continental shelf is much wider in places (≈ 100 km width) and water is not drawn directly from the seafloor to the surface. Instead, the upwelling follows from a chain of processes, possibly starting south of Kangaroo Island, where cold water is brought from depth to the continental shelf by localised sub-surface upwelling. The upwelled water is likely to remain in a Kangaroo Island “cold pool” (McClatchie et al. 2006) until subsequent wind-driven upwelling events draw the water to the shallower coastal regions of south western Eyre Peninsula, and south western Kangaroo Island. The seasonal upwellings occur when high pressure cells are far enough south for their southeast wind component to be roughly parallel to this northwest-trending coast, i.e. between the months of November/December - March/April (Lewis 1981, Schahinger 1987). Although there are some differences in the general process, the surface upwellings off the Bonney Coast and the eastern GAB appear to be simultaneous. However, the Bonney coast upwelling is more prominent at the surface than the one in the eastern GAB, where the upwelling remains largely sub-surface. There, the nutrients are likely used by phytoplankton before reaching the surface, creating both a subsurface phytoplankton peak (van Ruth et al. 2010) and spatial and temporal spread of zooplankton (Baird 2003, van Ruth and Ward 2009). The enhancement of primary and secondary production is assumed to support the large populations of pelagic fish present in this region, and consequently, many marine predators.

In the western GAB, the highly used region over the continental shelf and further east over the continental slope is under the influence of the Leeuwin Current (LC). The LC is a warm poleward-flowing ocean current that originates in tropical waters off the North West Cape of Western Australia, and flows southwards along the edge of the continental shelf before turning eastwards around Cape Leeuwin and continuing into the GAB (Cresswell and Golding 1980, Ridgway and Condie 2004, Middleton and Bye 2007). Its strength varies seasonally, with the strongest flow occurring during
winter and the weakest during summer (Smith et al. 1991, Feng et al. 2003), mostly due to the seasonal variations of surface winds. Because of its tropical origin, the LC is relatively nutrient-poor. However, different mechanisms, from erosion of seasonal thermocline to eddy advection or local wind-driven upwelling (Feng et al. 2009), control seasonal nutrient supply and primary production and make the LC important for the local marine ecosystems. The LC and its inter-annual variability play a major role in the life histories of southern bluefin tuna and sardines by dispersing their eggs, larvae and juveniles. The LC is also used as a migration corridor for Australian salmon and herring (Cresswell 1990). High recruitment of the western rock lobster is also recognised to be influenced by a strong LC and the associated warmer water temperatures (Pearce and Phillips 1988). All these species at different stages of development represent a potential source of food for upper level predators.

The contribution of the different species in highlighting these two regions indicates that the central-place foragers, which remain dependent on land for breeding, moulting or resting, mainly concentrate in the physical systems over the continental shelf near the mainland coast. In contrast, the non-central-place foragers, most of which are highly migratory, are distributed on the shelf break. The shelf break is known to be used both as a foraging area and as a migration corridor by these species. We did not observe any evidence that one system more affects species richness than another. The groups of species (benthic, pelagic and surface feeders) represented in all these systems (upwellings, LC) only indicate that whatever the system, it provides food resources from the sea bottom to the surface for the different predators. However, if the population abundance estimates (for central-place foragers) are an indication of the level of productivity in the systems, the upwelling in the eastern GAB might be more productive than the Leeuwin Current in the western GAB, as the upwelling in the east supports larger populations than in the west.

The seasonality in the high-use regions influences the community of predators present in the GAB. The presence of most of the species, especially the migratory species, may be related to a high level of productivity in the regions in summer; however, these regions remain important for resident species throughout the year. Some species are present all the year round in the GAB and some of them breed either in summer or winter. For example, that ASL are present year round (Goldsworthy et al. 2015), sometimes breeding in summer (18-month reproductive cycle), when the system may be less productive. This indicates that food resources are still sufficient to support a demanding part of their life history. Moreover, although some species are specialist feeders, targeting one prey species, like blue whales whose presence in the GAB is related to the seasonally high abundance of krill (Gill 2002), others are generalist feeders and may change their diet according to the season. Spatial changes in high-use regions for blue sharks or adult female long-nosed fur seals may be related to some change in their diet (e.g. Page et al. 2006, Dudley and Cliff 2010).

The physical mechanisms influencing the high-use foraging regions (i.e. currents, upwelling) are strongly influenced by periodic climate events, such as La Nina and/or El Nino, making these systems potentially affected by global climate change (Feng et al. 2009). La Nina tends to reinforce the Leeuwin Current, while El Nino has the opposite effect. The thermocline during summer is raised in the eastern GAB during El Nino events, which may affect the upwelling system and primary production in this region, although the ecological implications are still unknown (Middleton et al. 2007). In the past 50 years, the sea surface temperature off the west and south coast of Australia has warmed up faster than the average trend of the global ocean (Pearce and Feng 2007). Climate model simulations suggest that a warming climate induces more El Nino-like conditions, which affect wind circulation, thermocline tilting and flow of water masses (IPCC 2007). The effects of global warming on the GAB ecosystem remain hard to predict, but they should be considered in the perspective of management/conservation of the ecologically/biologically important areas in the GAB.
Although some regions were not identified as high use, they may still be of importance for predators. For example, during summer, a front develops at the interface between high-salinity Spencer Gulf water and the strongly stratified shelf water in the eastern GAB (Hahn 1986). There, larval fish have been shown to aggregate, possibly as a result of convergent flows (Bruce and Short 1990), providing a potential food resource for marine predators. The central GAB appears to attract an important number of predators too. Nutrient enrichment process, and the associated ecosystem, are not related to upwelling in this part of the GAB. Rather, a downwelling process, resulting from convergence of deep-ocean and shelf slope water, may occur along the shelf break (Middleton and Platov 2003). The sub-tropical front also attracts a large number of predators, due to the localised downwelling of high concentrations of nutrients that lie the south (Rajakumar et al. 2009), though it was not highlighted as one of the highest used regions in this study. The reason for the sub-tropical front not to be identified as highly important for predators could be explained by the strong spatio-temporal variability in its location, which is not captured in our study. Another explanation could be the under-representation in this study of species targeting the front as a major foraging location, such as flying seabirds (e.g. albatrosses sp.).

Overall, the enhancement of productivity due to local oceanographic conditions in the high-use region explains the presence of all the predators in the GAB. However, the variability inherent to marine ecosystems (i.e. inter-individual, -colony, -species and inter-seasonal or -annual), makes the relationship between primary productivity and the upper trophic levels challenging to understand. The overall picture cannot be simply summarised as high productivity means presence of predators. The link between production and predator distribution is complex as many other factors need to be considered. Thus, considering the presence of apex predators in the GAB only in relation to foraging areas and the presence of productivity potentially misrepresents the importance of the region. For instance, some species, such as southern right whales, only use the GAB in winter for breeding and nursing calves, which means that other characteristics (shelter, water temperature), rather than food, will influence their distribution.

Key Knowledge Gaps

- Despite considerable effort over the last two decades, the extensive tagging/survey work does not necessarily reflect the overall distribution of the species studied in the GAB. The tagging effort is sometimes spatially biased (e.g. long-nosed fur seals were only tagged in the eastern GAB but some colonies are also present in the western GAB), which can affect the model performance and may make the predictions of species distribution inaccurate. A larger spatial coverage of the actual distribution of the different species could improve the accuracy of some models.
- Some species were under-sampled, particularly sharks (low number tracked) and whales/dolphins (not tracked) and a higher tagging effort for these species may provide more accurate predictions about their distribution in the GAB.
- Population assessments of many predators in this study are rare or non-existent, which makes the use of abundance to estimate the biomass of predators at-sea, impossible in this study.
- Some groups of species are under-represented in the study (e.g. flying seabirds) and for some other species only partial data on distribution are available (e.g. tracks only available during winter for little penguins). For these reasons, some key areas might be under-evaluated (e.g. the Subantarctic front).
- The physical oceanographic processes in the GAB have been well described and likely pathways for nutrient enrichment identified (GABRP project 1). In addition, through this
research program we have gained a better understanding of the processes that underpin productivity in the region, and what drives variations in the lower trophic ecosystem in space and time. However, the response of apex predators to variations in productivity and trophic ecosystem in the region remains difficult to estimate.

- The descriptors used to characterise marine predator ‘hotspots’ or ‘areas of ecological significance’ or ‘biologically important areas’ are limited and not clearly defined. Metrics for quantifying important biological regions are required.

6. CONCLUSION

This study represents the first regional integration of tracking and survey data available for many species of marine predators in the GAB. The main outcome of the project is the clear identification of key regions in the GAB highly-used by predators, especially for foraging. Biologically important regions identified appear to be underpinned by the unique and complex oceanographic features of the region. In particular, these include a combination of: 1) seasonal wind-driven coastal upwelling that is a feature of the eastern GAB; 2) shelf slope up- and down-welling associated with oceanic currents; and 3) frontal systems driven by seasonal intrusion of the Leeuwin Current that transports warm, well-mixed, tropical water masses south-ward into the GAB from the Indian Ocean. The presence of such a diversity of predators in these systems, especially during summer when productivity is strongly enhanced, implies the development of rich local ecosystems from the sea bottom to the surface. For individual species, environmental variability may impact migratory patterns, distribution, abundance and residency times, leading to marked variation in apex predator community structure and the locations and extent of highly used regions’ distribution in both space and time. Although the project includes important advances in knowledge about the occurrence and distribution of communities of predators in the GAB, basic information for many of the species is still rudimentary. The project has identified knowledge gaps, which if addressed, would significantly enhance our understanding of the functioning of key physical systems in the region, on which marine predators, and more broadly entire ecosystems, ultimately depend.
7. REFERENCES


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van Winkle, W., 1975. Comparison of several probabilistic home-range models. The Journal of wildlife management: 118-123.


### APPENDIX 1: DATA MANAGEMENT

<table>
<thead>
<tr>
<th>Data type / Species</th>
<th>Description</th>
<th>Raw or derived data</th>
<th>Data processing</th>
<th>Derived datasets created</th>
<th>Data format</th>
<th>Curation and archive</th>
<th>Metadata</th>
<th>Use agreements &amp; licensing</th>
<th>Data access</th>
</tr>
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<tbody>
<tr>
<td>Satellite tracking / Australian sea lions</td>
<td>Argos and GPS locations</td>
<td>Raw</td>
<td>Locations filtering / Species distribution modelling</td>
<td>Filtered tracks / predicted distributions</td>
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*1* A metadata record will be created and registered on the AODN catalogue for all raw and derived data sets generated as part of the GABRP. Where possible, data sets will be lodged with IMOS and made available through the AODN / IMOS Ocean portal.

*2* Where possible, data sets will to be made publically available (e.g. through the AODN / IMOS Ocean portal). In the event that a data set can’t be made publically available, an electronic copy of the data set will be supplied to BP Australia.