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Foraging preferences of an apex marine predator revealed through stomach content and stable isotope analyses



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ABSTRACT

Insights into the food habits of predators are essential for maintaining healthy predator populations and the functioning of ecosystems. Stomach content and stable isotope analyses were used to investigate the foraging habits of an apex predator, the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) in south-western Australia. A total of 2,594 prey items from 26 families were identified from the stomachs of 10 deceased stranded dolphins. Fish otoliths from stomach contents were used to identify fish to family or species level. Ninety-three percent of identified stomach contents were perciforme fishes, however, perciformes comprised only 30% of the catch during prey sampling. Gobiidae species, small fish generally <100 mm in total length, were the most prevalent family identified in dolphin stomachs, accounting for 82% of identified prey, yet Gobiidae accounted for 12.7% of the catch during prey sampling. For stable isotope analyses, tissue samples from 14 free-ranging dolphins were analyzed for nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) ratios. From stable isotope analyses and boat-based dolphin photo-identification surveys ($n = 339$, 2007–2011), results indicated niche differentiation between coastal and inshore (bay and estuarine habitat) dolphins. Carbon signatures showed that coastal dolphins had a more pelagic diet compared to a benthic diet observed in the inshore dolphins. Whereas, nitrogen signatures of inshore dolphins showed higher nitrogen levels than coastal dolphins, likely attributed to feeding on enriched prey typical of estuarine environments. Overall, these results indicated that bottlenose dolphins in the study area were selective foragers and that their foraging is specialized by the habitats most frequently used.

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1. Introduction

The charismatic appeal of marine mammals aids in public campaigns aimed at sustaining biodiversity and ecosystem function (Sergio et al., 2006). As top predators, dolphins are indicators of marine ecosystem health and as such, are

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conservation priorities (Sergio et al., 2006). To conserve top-level predators such as dolphins effectively, it is imperative that basic biological information is known, such as prey preferences (Bax, 1998). Prey availability can drive movement patterns (e.g. Heimlich-Boran, 1986; Benoit-Bird and Au, 2003; García-Rodríguez and Aurioles-Gamboa, 2004), population growth rates (e.g. Lindström, 1988; O'Donoghue et al., 1998), and social interactions (e.g. Baird and Dill, 1996; Patterson and Messier, 2001). Therefore, in order to effectively conserve a predator population, it is crucial to understand its food resources.

Predation pressure is an important influence on the long term viability of lower trophic level populations and has ecosystem level effects (Bax, 1998; Kiszka et al., 2015). In turn, the preservation of top predators is strongly dependent on healthy prey populations. To effectively manage such prey populations, it is important to increase our understanding of the diets of predators, and how human actions directly and indirectly affect those prey species (Dunsha et al., 2013; Secchi et al., 2017). Furthermore, information on marine mammal diets is important for tracking how predators adapt to climate variability and anthropogenic changes (Bowen and Iverson, 2013; Sprogis et al., 2017b). Since predator distribution is related to the distribution of prey (Gaskin, 1982; Womble et al., 2005; Xavier et al., 2006; Sveegaard et al., 2012; Degradi et al., 2013), the distribution of critical prey species can be used as a proxy for predicting distribution patterns of predators, such as cetaceans (Similä et al., 1996; Lambert et al., 2014).

Observations of prey consumption in most marine mammals are rare due to their capture and consumption of prey under the surface of the water (Walker et al., 1999; Tyack et al., 2006; Bowen and Iverson, 2013). Prey parts found in stomach contents and scat provide critical information for ascertaining the diet of marine predators (Walker et al., 1999). Stomach content analyses are an informative tool for determining the diet of cetaceans, as cetacean faeces do not contain visually identifiable hard parts (Dunsha et al., 2013). In most cases, stomach content analyses are confined to hard parts of the digested prey species, specifically otoliths of teleost fish and beaks of cephalopods, which can be used to identify prey species, age and size (Clarke and Roper, 1998; Kemp et al., 2011).

Stomach content analysis provides valuable insights into the diet of predators, ecosystem dynamics, and foraging behavior (Kemp et al., 2011). However, there are limitations and biases of using prey hard parts to elucidate a predator's diet. To list a few, identification of species to the lowest taxonomic level can be difficult or impossible due to variation in digestion rates which are influenced by meal size, otolith structure, predator activity, and stomach size (Gibbs et al., 2011; Kemp et al., 2011). These differential rates of digestion degrade the shape and definition of hard parts (Heise, 1997; Pusineri et al., 2007; Kemp et al., 2011; Buckland et al., 2017). Digestive action also leads to under representation of soft bodied prey (Barros and Clarke, 2009), while over-representing prey with chitinous structures and fish otoliths (Bowen, 2000; Sheffield et al., 2001). Furthermore, empty stomachs yield no diet data, and secondary prey i.e. prey consumed by the primary prey species, may confound conclusions based on studies of hard parts (Santos et al., 2001). Stomach contents are temporally limited in that they represent what has been ingested on the scale of hours to days, perhaps weeks (Davis et al., 2012). In an experiment examining the digestive rates of otoliths from Red Rock Cod (*Pseudophycis bachus*) and Bearded Rock Cod (*Pseudophycis barbata*), Kemp et al. (2011) found that 58.3% of Red Rock Cod but only 25% of three Bearded Rock Cod otoliths were completely digested after 12 h in the stomach of 62 Australian fur seals (*Arctocephalus pusillus doriferus*). Likewise, Murie and Lavigne (1986) found that 99% of ingested herring were completely digested within 12 h by the seven pinniped species in the controlled study. The quantity of prey intake and the feeding rate also influence the retention and degradation of hard parts in the stomach of marine mammals (Bowen and Iverson, 2013).

Typically, few cetacean stomachs are analyzed due to the dependence of these studies on stranded or bycaught animals, which inherently have biases of how accurately those animals represent the population as a whole (Leatherwood, 1975; Heise, 1997). Stomach samples of stranded animals may not represent an accurate picture of diet if the stranded animals were sick, or otherwise physically compromised, prior to stranding (Barros and Odell, 1990). Whereas stomachs of bycaught animals may also represent a skewed picture of diet if the dolphin was feeding on fish from fisheries operations that would not otherwise occur in the diet (Gibbs et al., 2011). Studies comparing stranded and net-caught marine mammals have produced conflicting results. For example, research in the Atlantic coast of the United States and Spain found comparable frequencies of the most abundant fish species in both stranded and net-caught dolphins (Leatherwood, 1978; Santos et al., 2007). In contrast, a study in the waters off South Africa found differences in the composition of prey in stomachs of stranded versus net-caught dolphins – stranded animals had a higher proportion of cephalopod beaks than net-caught animals, which the author attributed to slower digestion of cephalopod beaks compared to fish otoliths (Ross, 1984). However, the difference could also have been attributed to regional differences in cephalopod abundance as the animals came from different areas (Ross, 1984).

While stomach contents represent specific species consumed over a short temporal scale, tissue stable isotope analyses provide a longer term, but less specific representation of diet (Abend and Smith, 1997; Mahfouz et al., 2017). Stable isotope ratios of carbon ($\delta^{13}\text{C}$) reflect the primary sources of carbon in the foraging habitat, e.g. freshwater versus marine primary production, while those of nitrogen ($\delta^{15}\text{N}$) reflect the source of nitrogen and the trophic level of the prey (Abend and Smith, 1997; Rossman et al., 2016). Generally, the nitrogen isotope values increase by $\sim 3\text{‰}$ – 4‰ with each increasing step in the food chain (Kelly, 2000; Rossman et al., 2015a). Thus, combining both stomach content and stable isotope analyses in studies increases our understanding of a predators' diet by investigating both ingested and assimilated prey (Giménez et al., 2017).

Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) are distributed throughout the tropical and sub-tropical Indo-Pacific region in coastal and shallow offshore waters (generally < 30 m depth) (Hale et al., 2000; Amaral et al., 2017). However, there is strong evidence that each population of bottlenose dolphin is genetically and behaviorally distinct from other sympatric populations, including foraging behaviors and diet preferences (Sargeant et al., 2005; Allen et al., 2011; Sprogis et al., 2016a).

While similar, or the same, families of prey may be available to different populations of bottlenose dolphins (*Tursiops* spp.) in different parts of the world, each population appears to have a unique diet (Berens McCabe et al., 2010; Rossman et al., 2015a, 2015b; Giménez et al., 2017; Ronje et al., 2017). Even within an overlapping geographic area in South Australian waters, two *Tursiops* species have differing diets, which appear to be based on differences in home range habitats, and thus the availability of demersal versus pelagic prey (Gibbs et al., 2011).

A population of Indo-Pacific bottlenose dolphins is distributed off Bunbury, south-western Australia (Fig. 1; Smith et al., 2013; Sprogis et al., 2016b). The abundance of the dolphin population varies seasonally, with an estimated maximum of 185 dolphins in the austral summer months and a minimum of 76 dolphins in the winter (Smith et al., 2013; Sprogis et al., 2016b). Bunbury has one of the fastest growing commercial ports in Western Australia, supports extensive recreational fishing, and maintains a strong tourist dependency on the dolphins (eco-cruises and swim-with dolphin tours) (Arcangeli and Crosti, 2009; Jensen et al., 2009; Senigaglia et al., 2019). The area is also subject to human impact through dredging, coastal development, industry, vessel traffic, and terrestrial runoff (Hillman et al., 2000; Semeniuk et al., 2000; Hugues-dit-Ciles et al., 2012). The long-term viability of the Bunbury dolphin population is projected to potentially decline by half over the next two decades (Manlik et al., 2016), mainly due to low female reproductive output (Senigaglia et al., 2019; Senigaglia and Bejder, 2020). Natural and anthropogenic pressures increase the need to better understand basic life history patterns, including prey preferences, to better manage this dolphin population. As large predators, marine mammals also act as sentinel species, making it particularly important to understand their ecology as they inhabit coastal waters impacted by human pressures (Rossman et al., 2015a). Knowledge of specific prey species is useful for informing fisheries management as well as preserving habitats important to the life history of those prey species.

The aims of this study were to 1) determine the main dietary items of dolphins in Bunbury, and 2) assess the sources of nutrients for this dolphin population and whether they vary between individuals that primarily occupy inshore waters versus coastal and offshore waters. We used records from long-term systematic dolphin photo-identification surveys to determine whether specific individual dolphins were predominately 'coastal' or 'inshore' dolphins. To elucidate diet, we identified prey

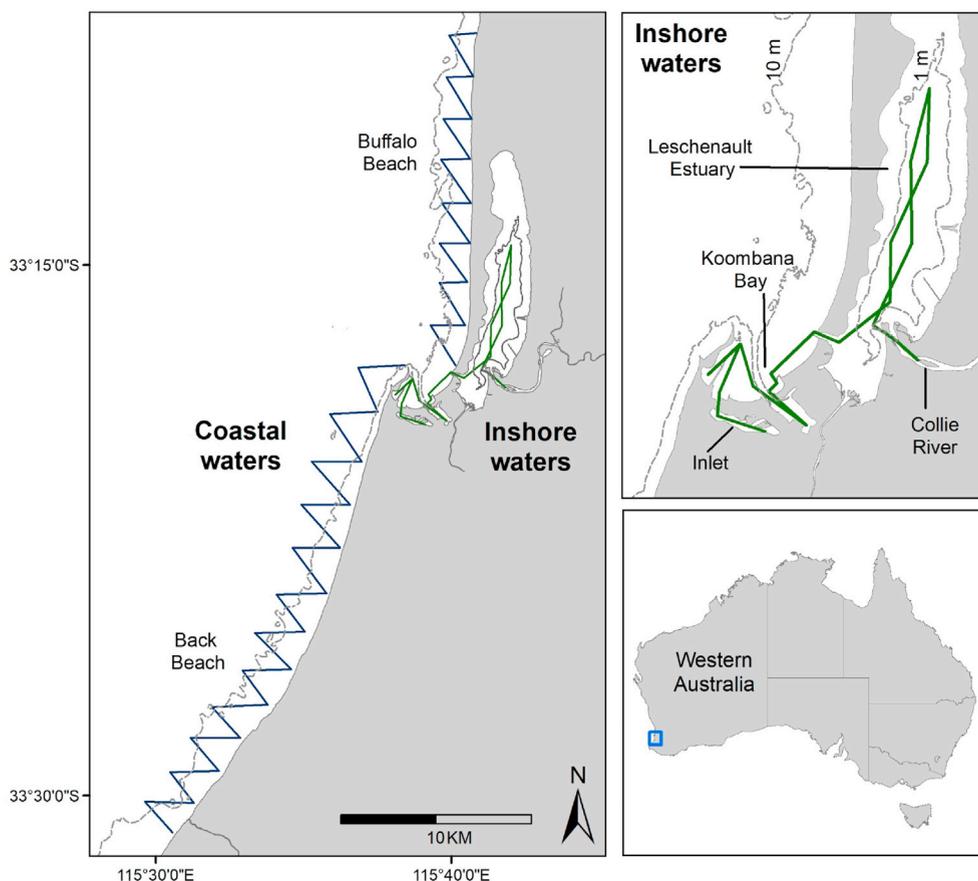


Fig. 1. The study area of Bunbury, Western Australia showing the transect survey lines in inshore and coastal waters. The inshore waters include the Leschenault Estuary, Leschenault Inlet, Collie River and Koombana Bay. The coastal waters refer to the waters west of Koombana Bay, specifically along Back Beach and Buffalo Beach. Solid zig-zag lines depict the transect survey lines (blue for coastal water surveys, green for inshore waters). Dashed lines depict the 10 and 1 m depth contours, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

parts from dolphin stomachs, and analyzed stable isotope ratios of nitrogen and carbon across the food web to ascertain trophic level and foraging habitat preferences. We were able to compare the observed diet with the abundance and calorific value of fish sampled in the nearshore waters determined by [McCluskey et al. \(2016\)](#).

2. Materials and methods

2.1. Study area

The study area consisted of the marine and brackish waters around Bunbury, Western Australia, (33.326° S, 115.640° E, [Fig. 1](#)). The coastal waters consisted of exposed beaches: Buffalo Beach and Back Beach. The inshore waters included the Leschenault Estuary, the mouth of the Collie River, Koombana Bay, and the Leschenault Inlet. The inshore area is relatively shallow: the average depth of the Estuary is 1.5 m in the middle and lower reaches and <1.5 m in the upper Estuary. Koombana Bay has an average depth of approximately 6–8 m in the non-dredged sections, and an average depth of 10–15 m in the dredged channel that connects the coastal waters to the Port of Bunbury ([McCluskey et al., 2016](#)).

3. Data collection

3.1. Boat-based surveys to document individual dolphin habitat use

To document individual dolphins as either inshore or coastal dolphins, we conducted year-round dolphin photo-identification surveys between March 2007 and August 2013. Only sightings before a dolphin was biopsied were used to determine distribution and classification of the dolphin as inshore or coastal. Surveys were systematic and followed pre-determined zig-zag transect lines ([Fig. 1](#), for details see [Smith et al. \(2013\)](#) and [Sprogis et al. \(2016b\)](#)). Upon a dolphin group sighting, a photograph of every dolphin's dorsal fin was taken wherever possible, and the Global Positioning System (GPS) location, time, and group composition were recorded. Photographic images of dorsal fins were used to identify individuals by unique nicks and notches along the fins' trailing edge ([Wursig and Wursig, 1977](#)). Sighting histories and data were available on individual dolphins (including sex and age class) from a long-term research program (2007 onwards) focused on the Bunbury dolphin population ([Smith et al., 2013](#); [Sprogis et al., 2016a,b](#)).

Dolphins were assigned as being inshore or coastal based on the region where they were sighted >60% of the time, standardized by survey effort, prior to being biopsy sampled (see below). The number of sightings of each dolphin during coastal water transects was divided by the number of coastal transects during the period of March 2007 until the date of biopsy. This procedure was also used to calculate the proportion of sightings in inshore waters i.e. total number of sightings/number of inshore transect surveys. This gave a standardized proportion of sighting events of each dolphin in each of the locations categorized as inshore and coastal. Coastal waters included the open water areas off Back Beach and Buffalo Beach, while inshore waters included Koombana Bay, the Leschenault Estuary, and the Leschenault Inlet ([Fig. 1](#)).

3.2. Sample collection for stable isotope analyses

Samples for stable isotope analyses were taken across the breadth of the food web, and in both coastal and inshore waters ([Fig. 1](#); see below). Samples included plankton, macroalgae and seagrass, fish species, invertebrate species, and dolphin skin. Samples of fish, invertebrates, plankton, and algae for stable isotope analyses were collected during the austral summer months of January–March 2010. Biopsied skin samples of dolphins were collected in February and March 2010.

3.3. Plankton sampling

Plankton was collected by towing surface plankton nets of two mesh sizes: fine (100 µm), and coarse (300 µm) at random locations in both inshore and coastal waters. A minimum of six plankton tows were undertaken in each sampled region (inshore estuary and bay, and coastal waters). The plankton samples were pumped through filter paper and dried in the same manner as the tissue samples (see below). Plankton samples were divided into two replicate groups: one group was treated with acid to remove inorganic carbonates prior to carbon analysis, and the other group was left untreated. Dried plankton samples were placed in a desiccator containing 32% hydrochloric acid and left to fumigate for 24 h. [Bunn et al. \(1995\)](#) found that acid washing enriched the $\delta^{15}\text{N}$ values for shrimp tissues to a degree that could confound food web interpretation. However, the authors found that the $\delta^{13}\text{C}$ values of the shrimp tissue were not affected by acid washing and concluded that acid washing was not necessary to remove non-dietary carbon from the exoskeleton of shrimp tails. For carbonate-rich samples, acid washing prior to $\delta^{13}\text{C}$ analyses has been found to be beneficial, and non-acid washed samples are typically used for $\delta^{15}\text{N}$ analyses ([Jacob et al., 2005](#); [Carabel et al., 2006](#); [Mateo et al., 2008](#); [Serrano et al., 2008](#)).

3.4. Algae and seagrass sampling

Macroalgae (*Hormophysa triquetra*, *Laurencia* sp., *Enteromorpha* sp.) and seagrass (*Heterozostera* sp.) were collected at fish sampling sites in the inshore and coastal waters (see McCluskey et al., 2016). Plant samples were dried and homogenized from each region.

3.5. Fish and invertebrate sampling

Tissue samples were taken from fish and invertebrates collected using beach seines, gill nets and trap nets, as described in McCluskey et al. (2016). Muscle tissue was also taken from fish caught by recreational fishers in coastal waters and from vessels fishing off the continental shelf approximately 160 km offshore from the study area. These included fish not commonly caught closer to shore, such as shark and dhufish (*Glaucosoma hebraicum*). Muscle tissue from the dorsal region of fish and general muscle from invertebrates was dissected with a sterilized scalpel and stored in liquid nitrogen, then transferred to an -80°C freezer until further analyses. Dorsal muscle tissue of fish was taken as it is commonly used in other studies, making direct comparisons more applicable (Hesslein et al., 1993; Pinnegar and Polunin, 1999; Pinnegar et al., 2003).

3.6. Dolphin skin biopsy sampling

Dolphin tissue samples were obtained from a research vessel by using a modified 0.22 biopsy rifle (PAXARMS biopsy system) following the methods of Krützen et al. (2002). On the vessel, biopsy samples were stored in ice, prior to freezing in liquid nitrogen upon return to land. The samples were transported in liquid nitrogen and transferred to a -80°C freezer until processing for analysis.

3.7. Sample processing

Tissues from all species were dried to constant weight at 60°C in a drying oven for 24–36 h. Once dried, the tissue was ground using a mortar and pestle, and divided into tin capsules for analysis in a continuous flow isotope-ratio mass spectrometer (Waters XEVO G2 qTOF) at the University of California Davis, USA. For small fish species, such as atherinids and gobies, individual fish captured at the same location were combined into groups of 10 and homogenized to ensure that sufficient tissue was available for each encapsulated sample. A minimum of four samples of each species and habitat combination were analyzed and a mean isotopic ratio (± 1 SD) for each sample type was calculated.

3.8. Sample collection from dolphin stomachs

Stranded deceased dolphins in the study region were retrieved wherever possible and immediately frozen for post mortem examination. Photographs of the dorsal fin and body morphological measurements were taken prior to freezing. To identify individual dolphins, dorsal fin features were compared to a long-term photo-identification catalogue focused on the Bunbury dolphin population (Smith et al., 2013; Sprogis et al., 2016b). Dolphin stomachs were removed and re-frozen at -25°C before being thawed and dissected.

Stomach contents were washed through a series of nested wire mesh sieves ranging from 0.5 to 4.0 mm. Contents from the fore stomach and main chamber were stored separately. Flesh and cephalopod beaks were separated from the contents and stored in 70% ethanol, while fish otoliths and invertebrate shell fragments were removed and stored dry in vials. Prey items and parts were identified to the lowest taxonomic level possible under a dissecting microscope. The minimum number of individuals (MNI) was recorded as the minimum number of either lower or upper cephalopod beaks (whichever number was higher), or right or left otoliths (whichever number was higher). If otoliths could not be classified as either right or left, they were considered unknown. Unknown otoliths were added to the side which had fewer otoliths (either right or left) until the sides had an even number. Any remaining unknowns were then divided evenly between the side categories. The MNIs of cephalopod beaks were calculated in the same way as otoliths using lower and upper beaks.

3.9. Stable isotope analyses

For stable isotope analyses, the means and standard deviations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were calculated for all prey and dolphin tissue samples, and means of coastal and inshore dolphins were tested for statistical difference using a *t*-test. Consumer and source isotope data were analyzed using the MixSIAR package in R (R Core Team, 2013; Stock and Semmens, 2016; Stock et al., 2018), where source data were composed of mean and standard deviation values of samples from prey species that were collected in both the inshore and coastal habitats. The MixSIAR package provides a framework for a Bayesian stable isotope mixing model to characterize diet proportion based on consumer isotope signatures of the dolphins from each habitat. The coastal and inshore habitats were included as fixed effects (Stock et al., 2018). The differentiation values used were $1.01 (\pm 0.37 \text{ SD})$ for $\delta^{13}\text{C}$ and $1.57 (\pm 0.52 \text{ SD})$ for $\delta^{15}\text{N}$ (Giménez et al., 2016).

3.10. Statistical analyses of dolphin stomach contents

For dolphin stomach content analyses, the percent frequency of occurrence (%FO) of a particular prey taxa across stomachs was calculated using the following equation (Pusineri et al., 2007):

$$\%FO_i = (n_i / N) \times 100$$

where n_i is the number of stomachs where prey taxon i occurred and N is the total number of stomachs with prey items.

The relative percentage abundance of each taxa (%N) was calculated using:

$$\%N_i = (x_i / X_i) \times 100$$

where x_i is the number of prey i found within a stomach and X_i is the total number of prey in the stomach, then averaged over all stomachs which contained prey items.

Niche breadth (B) was calculated using Levins' index (Mascaro et al., 2007):

$$B = 1 / \sum Pi^2$$

where P_i is the proportion by numbers of each prey group found in the stomach. The index ranges from 0 (representing a specific diet) to 1 (representing a broad diet). Mean niche breadth was calculated for inshore and coastal dolphins as well as an overall population mean.

4. Results

4.1. Dolphin sightings

Over 200 coastal and inshore water surveys were completed between March 2007 and March 2010 (Table 1). The majority of identified dolphins were sighted during 167 coastal and 91 inshore transects. During this time, fourteen dolphins were biopsy sampled, with eleven of these identified from the long-term photo-identification catalogue, and one identified as an offshore type based on morphology. Two dolphins were of unknown identity and distribution. Biopsy samples were collected in February and March 2010 (Table 1). Based on the frequency of sightings data (>60% of sightings in one water body), five dolphins were considered as coastal dolphins and six as inshore dolphins, with an additional unknown dolphin classified as coastal (Table 1, Fig. 2). The dolphin KEY was designated as an inshore dolphin despite the fact that she was sighted 60% of the pre-biopsy surveys in coastal waters. This was due to the fact that when the survey effort was standardized, more weight was placed on the inshore sightings, and the majority of sightings post biopsy date were in inshore waters, leading us to conclude that an inshore designation is most accurate for the dolphin KEY (Table 1). The other two unknown dolphins were not assigned as either coastal or inshore and were included in the population means, but not in the MixSIAR analyses.

Table 1

The sighting's of known individual dolphins in coastal and inshore waters prior to biopsy sampling (from March 2007 to biopsy date). Listed is the percentage of sighting's of each dolphin that was made in the coastal versus inshore waters. In parentheses by each percentage is the proportion of time that each dolphin was sited over the total number of transects during either coastal (163–221 transects) or inshore water surveys (91–118 transects). Coastal waters refer to Back Beach and Buffalo Beach. Inshore waters refer to Koombana Bay and Leschenault Estuary and Inlet (Fig. 1).

Dolphin IDs	Biopsy date	Coastal waters	Inshore waters	Number of coastal transects	Number of inshore water transects
<i>Coastal (n = 5)</i>					
BOB [12]	19/03/10	100% (0.60)	0% (0)	167	91
EIG [6]	19/03/10	100% (0.60)	0% (0)	167	91
MER [10]	19/03/10	100% (0.60)	0% (0)	167	91
SAW [4]	19/03/10	100% (0.60)	0% (0)	167	91
STK [11]	19/03/10	100% (0.60)	0% (0)	167	91
<i>Inshore (n = 6)</i>					
FEN [70]	14/02/10	27% (0.12)	73% (0.62)	221	118
MAS [51]	14/02/10	10% (0.06)	90% (0.99)	163	91
SMI [32]	14/02/10	38% (0.23)	63% (0.69)	163	91
LUN [48]	14/02/10	33.33% (0.20)	66.67% (0.73)	163	91
NIC [67]	14/02/10	16.42% (0.10)	83.58% (0.92)	163	91
KEY [25]	19/03/10	60% (0.36)	40% (0.44)	167	91

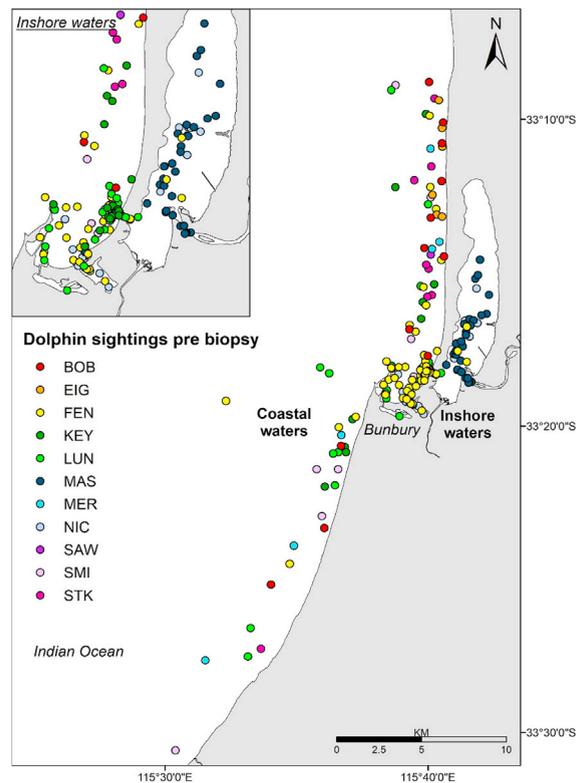


Fig. 2. Pre-biopsy sightings of individual bottlenose dolphins in the Bunbury region, south-western Australia. Colored dots indicate the sighting locations from March 2007 until the date each individual dolphin was biopsied.

5. Stable isotopes

5.1. Dolphins

The mean $\delta^{15}\text{N}$ value of inshore dolphins ($n = 6$) ($13.00\text{‰} \pm 0.78$) was significantly higher than that for dolphins sighted more frequently in coastal waters ($n = 5$) ($11.22\text{‰} \pm 1.07$, $T_9 = 65.91$, $P < 0.001$, Fig. 3). The inshore dolphins also had significantly higher $\delta^{13}\text{C}$ values than the coastal dolphins ($-15.60 \pm 1.19\text{‰}$ and $-17.64 \pm 0.99\text{‰}$, respectively, $T_9 = 7.41$, $P < 0.001$, Fig. 3). Two of the biopsied dolphins were of unknown ID, and therefore were not assigned to either coastal or inshore waters. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of these two dolphins were within the range of values for the dolphins sighted most frequently in coastal waters, but were not included in the statistical analyses (Fig. 3).

The MixSIAR model results indicated a difference in source inputs between coastal and inshore dolphins (Fig. 4). The diet of inshore dolphins was estimated to be composed largely of tailor (*Pomatomus saltatrix*) (approximately 40% of the source signature), followed by Australian herring (*Arripis georgianus*) at approximately 7%, with all other sources contributing less than 5% to the dolphins' isotopic signature. In contrast, coastal dolphins had a much broader diet, with no species estimated to contribute more than 12.5% to the assimilated diet (Fig. 4). Tailor and Australian Herring were the only fish species estimated to contribute more than 5% to coastal dolphin diets.

5.2. Stable isotopes values in the food web

The range of $\delta^{15}\text{N}$ values for all dolphins (7.68–13.53‰) overlapped with the range observed for fish and cephalopods in the coastal and inshore waters (Figs. 5 and 6, Table 2). The lowest $\delta^{15}\text{N}$ values were recorded for algae and plankton (3.72–6.20‰, $x = 4.80$) and did not appear to differ between coastal and inshore waters (Figs. 2 and 5, Table 2). Fish from the estuary had the largest range of $\delta^{15}\text{N}$ values, representing the highest diversity of trophic levels within a habitat, with one sample (*P. saltatrix*) having a higher mean $\delta^{15}\text{N}$ value (13.53‰) than the highest mean of any prey species from the ocean environment (Fig. 5).

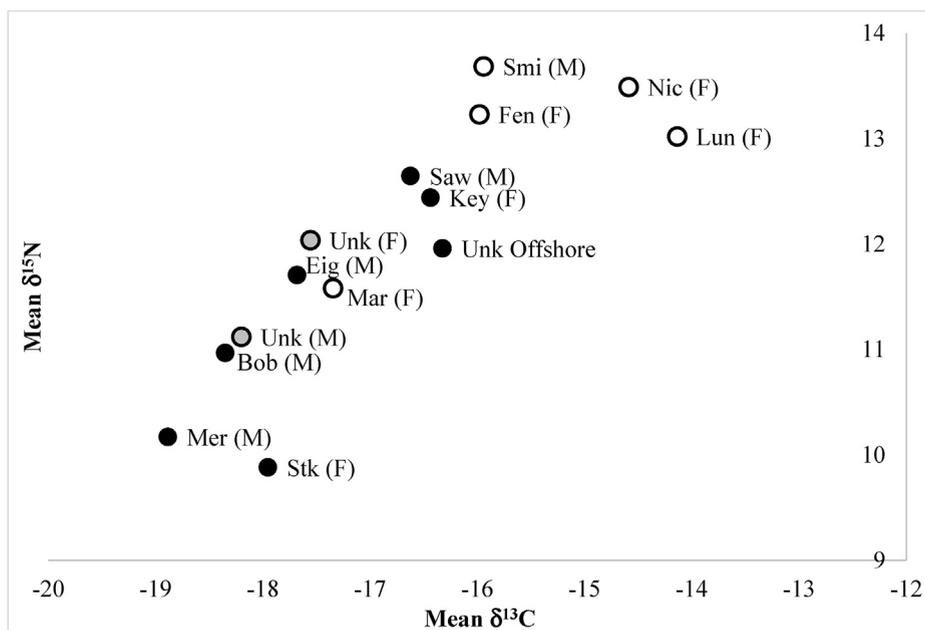


Fig. 3. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope ratios of coastal and inshore bottlenose dolphins from the Bunbury region in south-western Australia. Black markers indicate the isotopic ratios of dolphins who were sighted over 60% of line transect surveys in coastal waters. White markers indicate dolphins who were sighted over 60% of surveys in inshore waters. Grey markers indicate dolphins of unknown (unk) distribution. Sex of dolphins is indicated in parentheses: (F) = female and (M) = male.

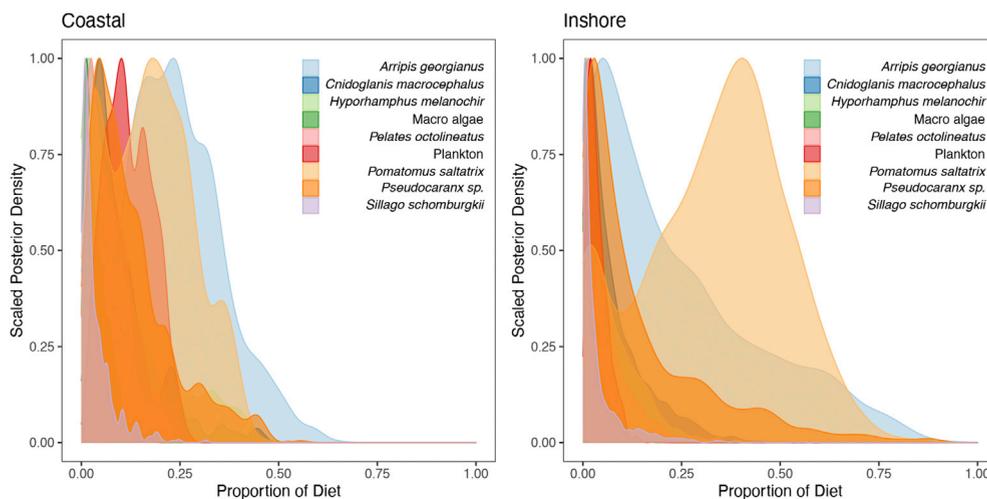


Fig. 4. MixSIAR model output showing scaled posterior density plots depicting the proportion of source input for diet of coastal dolphins and inshore dolphins from the Bunbury region, south-western Australia.

The prey species that had nitrogen isotope ratios one trophic level below that of the coastal dolphins included squid (*Cephalopoda* spp.), blue swimmer crab (*Portunus armatus*), Estuary cobbler (*Cnidoglanis macrocephalus*), Southern garfish (*Hyporhamphus melanochir*), Western gobbleguts (*Ostorhinchus rueppellii*), and blue sprat (*Spratelloides robustus*). Prey species with $\delta^{15}\text{N}$ values one trophic level below those of inshore dolphins included Australian herring (*Arripis georgianus*), gummy shark (*Mustelus antarcticus*), marbled flathead (*Platycephalus marmoratus*), southern blue-spotted flathead (*Platycephalus speculator*), and trevally (*Pseudocaranx* spp.). Prey species that were a trophic level below both coastal and inshore dolphins included western striped grunter (*Pelates octolineatus*), yellowfin whiting (*Sillago schomburgkii*), southern school whiting (*Sillago bassensis*), Perth herring (*Nematolosa vlaminghi*), and yellow eye mullet (*Aldrichetta forsteri*) (Table 2, Fig. 6). The $\delta^{15}\text{N}$ values of coastal dolphins were lower than those of the inshore dolphins, which may reflect a more offshore oceanic diet that is not as enriched as prey found in estuaries.

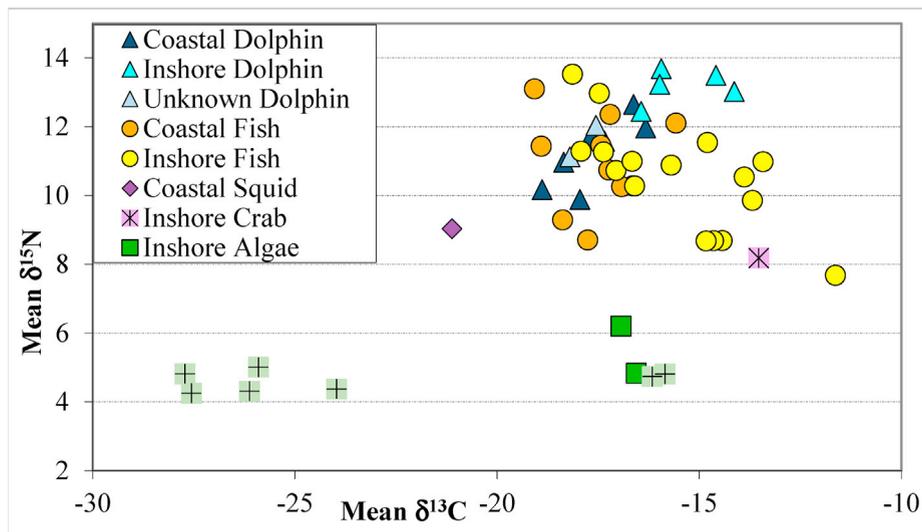


Fig. 5. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of plankton, macroalgae, crab, squid, finfish, and dolphins collected from inshore and coastal habitats of the Bunbury region, south-western Australia. Dolphin habitat was determined by the region where the individual dolphin was sighted over 60% of the effort during surveys.

5.3. Dolphin stomach contents

A total of 13 dolphin stomachs were collected from stranding's between 2007 and 2010, and 10 of these contained prey parts (Table 3). Of these 10, six were from known dolphins in Bunbury, two were retrieved less than 10 km north of Bunbury, one was retrieved less than 60 km north of Bunbury, and one animal was retrieved approximately 130 km north of Bunbury. The remaining three stomachs contained parasites only. Seven stomachs contained fish otoliths and four of these contained cephalopod remains. One stomach contained only cephalopod remains (adult female, F1). Two stomachs contained cephalopod and other remains, but no fish hard parts. Two stomachs contained fish, cephalopod, and other non-cephalopod mollusk remains. The stomach with the highest diversity of prey remains (21 families) was also filled with compacted mud and seagrass (juvenile male, M3). Compacted mud and seagrass has been observed in the stomachs of other stranded *T. aduncus* in Western Australia (Krzyszczuk et al., 2013).

A total of 2,594 individual prey were identified from the 10 stomachs with items, belonging to a minimum of 54 prey taxa (Table 3). Dolphin stomachs contained predominately the otoliths of teleost fishes (proportion of teleost fish per stomach $65 \pm 14.7\%$), followed by cephalopod remains ($28 \pm 12.2\%$), then other taxa, such as gastropods ($7.3 \pm 0.84\%$) (Table 3). Individual prey items across stomachs primarily belonged to Perciforme fishes (93%), followed by cephalopods (2%). All other identified orders made up the remaining 5% ($n = 11$, plus 1 unknown category). These prey were represented by 24 families: 20 of finfish, two of cephalopods, and two of gastropods (Supplementary information 1). Nine groups of otoliths, one cephalopod beak, and one gastropod could not be identified to family. The minimum number of individuals (MNI) in each stomach varied from 1 to 1,884 (Table 3). The number of families represented per stomach ranged from 1 to 21, and the number of species per stomach ranged from 1 to 32 (Table 3). The three stomachs that contained the highest number of prey parts were dominated by fish otoliths (94–99% of MNI). The three stomachs with the least number of prey (<5), were dominated by cephalopod remains. No stomach had a higher proportion of 'other' invertebrate prey than cephalopod or fish prey (Table 3). The fish families with the highest percentage frequency of occurrence (%FO) in the dolphin stomachs were Apogonidae (60%), unknown cephalopoda (60%), Gobiidae (50%), Cynoglossidae (40%), Sillaginidae (40%) and Hemiramphidae (30%). All other families had a %FO below 30% (Supplementary information 1). The families present in the highest total number of individuals included Gobiidae (82% of individual prey items identified across all stomachs), followed by Apogonidae (8%), cephalopoda (3%), and Sillaginidae (2%). All other taxa made up 1% or less of the total identified prey items (Fig. 7). Each dissected stomach contained a unique assemblage of prey families and total number of prey (Fig. 7). The Levins' Index value for all dolphins was 0.031. When calculated separately for coastal and inshore dolphins, the Levins' Index values for these groups were 0.086 and 0.008, respectively.

6. Discussion

We used complementary techniques to investigate the diet of a population of Indo-Pacific bottlenose dolphins off the south-west coast of Australia. Carbon and nitrogen stable isotope signatures from tissue samples collected from free-ranging dolphins and species across the food chain were analyzed and compared to stomach contents of deceased stranded dolphins. Findings indicated that: i) there were differences in the foraging habitats, reflected from stable isotope analysis, between

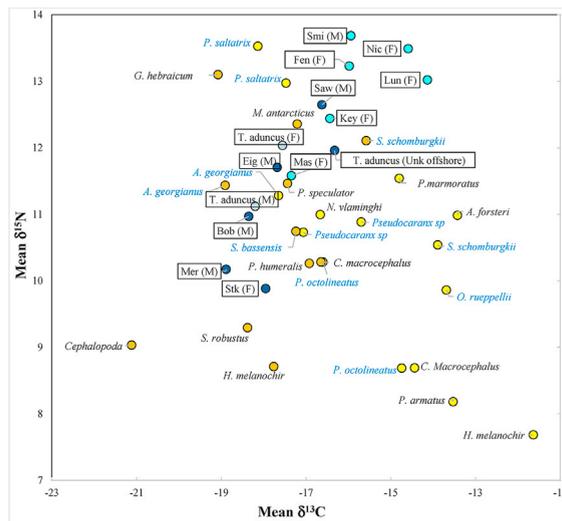


Fig. 6. Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios of dolphins and potential prey species in the Bunbury region, south-western Australia. Individual dolphin labels are boxed. Dark blue markers indicate the isotopic ratios of dolphins who were sighted over 60% of line transect surveys in coastal waters. Turquoise markers indicate dolphins who were sighted over 60% of surveys in inshore waters, and dolphins of unknown distribution have light blue markers. Sex of dolphins are indicated as (F) = female and (M) = male. Finfish and invertebrate species sampled from the inshore waters are depicted with yellow markers, and those from coastal waters are depicted with orange markers. Blue data labels indicate fish species belonging to the order perciforme. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

dolphins sighted predominately in inshore waters versus those seen mainly in coastal regions; and ii) dolphins were selective foragers as the diet reflected in stomach contents was not proportional to the relative abundance of the species recorded in the marine environment (McCluskey et al., 2016), with the prey identified by hard parts remaining in the stomach contents dominated by the teleost family Gobiidae (Gobies).

6.1. Stable isotopes

Estuaries are often enriched with terrestrial sourced nitrogen (McClelland et al., 1997; Deegan et al., 2002), which is reflected up the food chain to predator species (Martinetto et al., 2006). This phenomenon is consistent with our findings which reflected higher $\delta^{15}\text{N}$ signatures of the dolphins sighted most frequently in the inshore waters off Bunbury. Nitrogen is enriched with each step of the food chain. An enrichment of 2–5‰ for endothermic organisms has been used as a general guideline when assigning trophic status (Best and Schell, 1996; Cherel et al., 2008; Beltran et al., 2016). However, in a long-term controlled feeding study, Giménez et al. (2016) found that the skin of bottlenose dolphins (*T. truncatus*) reflected a nitrogen enrichment from prey of $1.74\text{‰} \pm 0.55 \text{ SD}$, which is substantially less than the assumed enrichment of 2–5‰. Using the dolphin specific enrichment rate as a guideline for trophic step, in the current study the sampled prey species fell into three categories; one a trophic step below the inshore dolphins, one a trophic step below the coastal dolphins, and one with overlapping values of both coastal and inshore dolphins (Fig. 6). It may be that some of the species that occupied a trophic niche below the coastal dolphins, and therefore might be assumed prey of those dolphins, are species that are distributed inshore. The Bunbury dolphins do move between habitats, and may have very different diets in the warmer months versus the colder months, when the coastal dolphins are not sighted as frequently in the area (Smith et al., 2016; Sprogis et al., 2018).

The $\delta^{13}\text{C}$ values are also often higher in benthic, near-shore environments than those further offshore (Matley et al., 2015), and we therefore expected that the $\delta^{13}\text{C}$ values from the inshore water dolphins to be relatively high compared to the coastal dolphins, reflecting a closer association with benthic production (Rossman et al., 2016). With the exception of the offshore squid and the garfish from the estuary, all prey sampled for stable isotopes were within range of the carbon isotope values of the dolphins. The coastal dolphins did generally reflect lower carbon signatures than the inshore dolphins, which is consistent with the lower carbon signatures of the more pelagic prey items sampled in the coastal habitat. However it should also be noted that the $\delta^{13}\text{C}$ signature of the plankton sampled from the inshore waters was the most negative, indicating potential input from mangroves into the food web (Loneragan et al., 1997). The diet of the coastal dolphins appears to differ, at least seasonally, to that of the inshore resident dolphins, which was further illustrated by the results of the MixSIAR model. The proportion of diet from each source input in the model indicated that the coastal dolphins were more generalist in their diet than the inshore dolphins, who appeared to obtain the largest proportion of their diet from tailor (*P. saltatrix*). Sampled tailor had overlapping nitrogen values to those of the inshore dolphins, indicating that the dolphins were not a trophic step above the tailor. This discrepancy might be explained by the fact that the sampled tailor were sub-adults from the inshore habitats (mean length of 221 mm while sexual maturity is reached at 300 mm and common adult length is 600 mm (Collette and

Table 2

Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (± 1 Standard Error) values for each fish species, algae, plankton, and dolphins. N = number of samples analyzed for each species. Trophic step below dolphins indicates prey species with a mean $\delta^{15}\text{N}$ value 1.74 ± 0.55 below the mean value for coastal (C) and inshore (I) dolphins.

Species	Common Name	Mean 13C	Mean N15	Trophic step below dolphins
Plankton		-23.26 \pm 4.88	4.65 \pm 0.39	
Macro Algae	<i>Hormophysa triquetra</i> , <i>Laurencia</i> sp, <i>Enteromorpha</i> sp, and <i>Heterozostera</i> sp	-15.58 \pm 3.28	4.80 \pm 0.92	
Invertebrates	<i>Cephalopoda</i>			
	Squid	-21.12 \pm 2.05	9.03 \pm 0.84	C
	Blue Swimmer Crab	-13.53 \pm 0.08	8.18 \pm 0.17	C
Fish	<i>Aldrichetta forsteri</i>	-13.43 \pm 0.12	10.99 \pm 0.15	C, I
	<i>Arripis georgianus</i>	-18.42 \pm 0.54	11.36 \pm 0.10	I
	<i>Cnidogobius macrocephalus</i>	-15.54 \pm 1.22	9.49 \pm 0.89	C
	<i>Glaucosoma hebraicum</i>	-19.08 \pm 0.03	13.10 \pm 0.25	
	<i>Hyporhamphus melanochir</i>	-14.70 \pm 3.36	8.20 \pm 0.58	C
	<i>Mustelus antarcticus</i>	-17.21 \pm 0.10	12.36 \pm 0.12	I
	<i>Nematolosa vlaminghi</i>	-16.66 \pm 0.42	11.00 \pm 0.07	C, I
	<i>Ostorhinchus rueppellii</i>	-13.69 \pm 0.07	9.86 \pm 0.07	C
	<i>Pelates octolineatus</i>	-15.62 \pm 1.07	9.49 \pm 0.89	C, I
	<i>Pelsartia humeralis</i>	-16.92 \pm 0.04	10.26 \pm 0.13	C, I
	<i>Platycephalus marmoratus</i>	-14.80 \pm 0.04	11.54 \pm 0.11	I
	<i>Platycephalus speculator</i>	-17.44 \pm 0.05	11.46 \pm 0.06	I
	<i>Pomatomus saltatrix</i>	-17.89 \pm 1.23	13.29 \pm 0.37	
	<i>Pseudocaranx</i> spp	-16.38 \pm 0.75	10.81 \pm 0.12	I
	<i>Sillago bassensis</i>	-17.24 \pm 0.31	10.74 \pm 0.70	C, I
	<i>Sillago schomburgkii</i>	-15.02 \pm 0.96	11.58 \pm 1.06	C, I
	<i>Spratelloides robustus</i>	-18.38 \pm 0.07	9.29 \pm 0.07	C
Dolphin	<i>Turciops aduncus</i>	-16.71 \pm 1.47	12.05 \pm 1.24	

Smith, 1984), and therefore reflected estuary enrichment while the dolphins, though designated as inshore animals, do spend time in coastal areas and may be feeding on larger, pelagic feeding tailor while in those habitats. The MixSIAR may also be associating the isotope signatures of tailor as being important in the diet of inshore dolphins due to the differences in carbon signature between the two organisms.

This separation of nutrients assimilated by coastal and inshore dolphins is similar to the segregation observed at a finer scale between different social groups of dolphins using the Peel-Harvey Estuary, ~80 km north of Bunbury. In this study, detritivorous fish were the largest contributors to diet in dolphin social clusters with high site fidelity to the eastern shores of the Estuary and rivers (Nicholson, pers comm¹). Dolphin clusters with a home range around the estuary openings (i.e. nearest the ocean) had a greater contribution from benthic omnivores and carnivores and were at a higher trophic level than the "riverine" dolphins, with the dolphin cluster showing fidelity to the estuary basins having an intermediate trophic level (Nicholson, pers comm¹).

6.2. Biases and benefits of stable isotope analyses

Stable isotopes are a useful means of ascertaining trophic level of a predator as well as general feeding location (Newsome et al., 2010). However, using stable isotope analyses (SIA) are not without biases. When the trophic levels of prey species overlap with the predator, or come from a range of trophic levels, it can be difficult to estimate their relative contribution to the consumers' diet (Gibbs et al., 2011; Polito et al., 2011). In this study, the sampled prey species represented a range of piscivorous and plankton feeders, however their relative contribution to isotopic signatures of the dolphins is unknown without information from stomach content analyses. Prior knowledge of the stable isotope signatures of a large number of possible prey species helps to resolve this issue for any mixing models, which in most cases, like this study, is not feasible (Polito et al., 2011). Although stable isotope analyses do not have the same limitations of temporal sampling or differential digestion rates that affect stomach content analyses, they are not as prey specific as the latter technique. However, when used with complementary methods to study diet, such as stomach contents (Polito et al., 2011; Nielsen et al., 2019) and relative prey availability (McCluskey et al., 2016), stable isotope analyses can be a useful tool in exploring feeding habits across temporal scales, and are often the only means of studying the foraging behavior of cryptic animals that have large ranges and are difficult to observe, such as marine mammals (Rossman et al., 2015a, 2016).

¹ Nicholson, Krista, Murdoch University, unpublished data

Table 3

Summary of the number of prey types and proportion of prey types from each individual dolphin stomach from dolphins stranded in the Bunbury region of south-western Australia ($n = 10$). Dolphins are grouped by female (F1–F3), male (M1–M3). MNI = minimum number of individuals for fish otoliths and cephalopod beaks.

Year of death	Dolphin Sex	Age Class	MNI	Number of Families	Number of Species	Number of Fish	Number of Cephalopods	Number Other	Proportion Fish	Proportion Cephalopod	Proportion Other	
2008	F1	Female Adult	1	1	1	0	1	0	0%	100%	0%	
2008	F2	Female Juvenile	107	6	7	63	38	0	59%	36%	0%	
2009	F3	Female Juvenile	1884	10	16	1884	0	0	100%	0%	0%	
2010	F4	Female Juvenile	4	2	2	0	3	1	0%	75%	25%	
2007	F5	Female Calf	26	4	5	26	0	2	100%	0%	8%	
2008	M1	Male Adult	254	12	17	235	13	2	93%	5%	1%	
2009	M2	Male Juvenile	43	3	3	43	0	0	100%	0%	0%	
2009	M3	Male Juvenile	233	21	32	229	3	0	98%	1%	0%	
2009	M4	Male Juvenile	41	5	7	41	0	0	100%	0%	0%	
2009	M5	Male Juvenile	3	2	2	0	2	1	0%	67%	33%	
TOTAL UNIQUE				2596	26	54			Mean \pm 1 SE	65% \pm 14.7	28% \pm 12.2	7.3% \pm 0.8

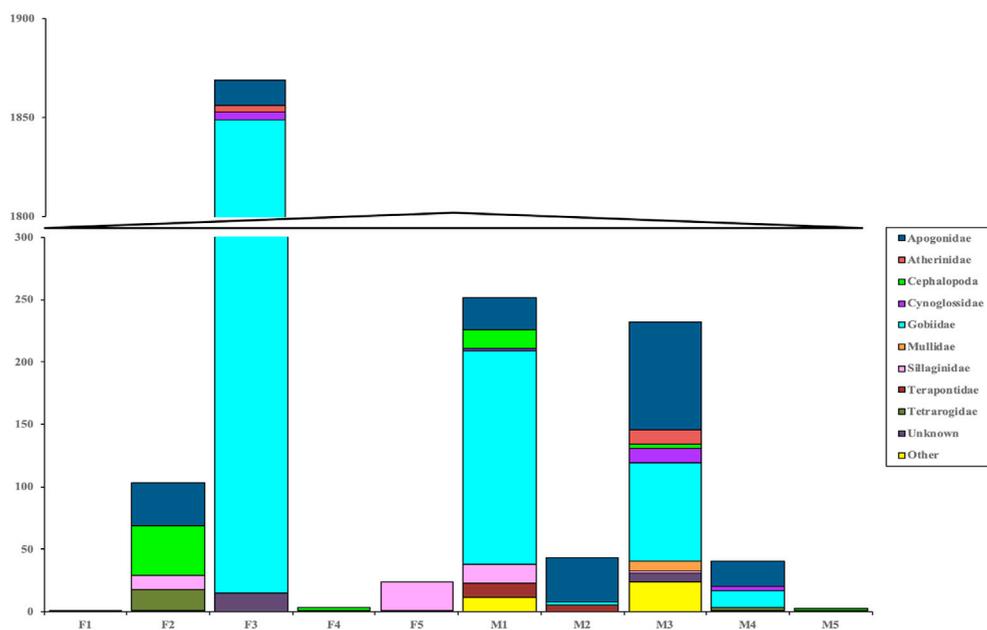


Fig. 7. Minimum number of individuals identified in the stomachs of deceased stranded dolphins grouped by family. Dolphins are grouped by female (F1–F5) and male (M1–M5). Note break in Y-axis denoted by black triangle.

6.3. The relative frequency of prey in dolphin stomachs and caloric value of prey

Stomach contents were evaluated from thirteen stranded dolphins and compared to 'potential dolphin prey species' captured during a previous prey sampling study in Bunbury from 2008 to 2010 (McCluskey et al., 2016). Since six of the 10 stomachs with contents came from known inshore dolphins, and four from coastal animals, it is assumed that the combined stomachs reflect general prey choice for both habitats. However, only two of the stomachs were from adult dolphins, while seven stomachs were from juvenile animals, and one stomach from a calf. Therefore, our findings likely reflect the diet of juvenile dolphins more so than adults and cannot be considered representative of adult diet. The stomach contents of the stranded dolphins had some overlap with the assemblage of prey captured during prey sampling by McCluskey et al. (2016). Of the 36 families captured (McCluskey et al., 2016), 17 were found in the stomachs of dolphins that stranded during the same years, represented in the current study. An additional seven prey families found in the dolphin stomachs (Belontiidae (flat needlefish), Cynoglossidae (MacCulloch's sole and tongue sole), Diodontidae (slender-spined porcupine fish), Myctophidae (southern lanternfish), Scomberesocidae (king gar), Cranchiidae (glass squid), and Ctenopterygidae (tooth finned squid)), were not found during prey sampling in McCluskey et al. (2016). Of the 20 families of finfish identified in the dolphin stomachs, 15 were caught during prey sampling (75%). Thirteen of those 15 families were considered to be potential dolphin prey (McCluskey et al., 2016). There were two additional finfish families that were represented in dolphin stomachs in the current

study that can be included on the list of Bunbury dolphin prey developed by McCluskey et al. (2016): Mullidae (Goatfish) and Tetragoridae (Waspfishes).

Perciforme fishes (perch-like fishes) made up 30% of the species caught during prey sampling and 96% of the otoliths identified in the stomach contents. The prey identified in the stomachs were dominated by the Gobiidae (Gobies), with 82% of the total individual prey identified, found in 50% of the dissected stomachs. The second most numerous prey family in the dolphin stomachs was the Apogonidae (cardinalfish) (8%), followed by Sillaginidae (smelt-whitings) (2%). This contrasted with the most frequently captured family of prey during prey sampling, which was the Clupeidae (herrings, sardines), representing 35% of the total catch, followed by the Atherinidae (silversides) (22%) and Gobiidae (13%). The proportions of both Apogonidae (8%), and Sillaginidae (2.5%) species captured during prey sampling were very similar to the proportions found in the dolphin stomachs (McCluskey et al., 2016). Spitz et al. (2010a) found the energy content of a Gobiidae species (*Lesueurigobius friesii*) in the Bay of Biscay was 5.6 KJ.g⁻¹, which is slightly higher than that of the most common species of Apogonidae captured in the Bunbury region (*Ostorhinchus rueppellii*) (4.14 KJ.g⁻¹, McCluskey et al., 2016). Both families represent 'medium value' prey as described by Spitz et al. (2010a). However, the Gobiidae appears to have higher energy content than the Atherinidae (4.23 KJ.g⁻¹) and therefore would be a more energetically profitable prey (McCluskey et al., 2016). This may explain why the Bunbury dolphins appear to be selectively foraging for Gobiidae species.

None of the four prey families representing the highest biomass captured during prey sampling (McCluskey et al., 2016) were present in the dolphin stomachs of the current study: Arripidae (Australian salmon), Carangidae (jackfish), Tetraodontidae (pufferfish) and Portunidae (swimming crabs). The Tetraodontidae was not expected to be entirely consumed by dolphins due to the spines and toxic flesh (Huisman and Twomey, 2008), however Bunbury dolphins have been observed chasing and catching pufferfish in their mouths in estuarine waters (Sprogis pers. obs.). It is possible that Portunidae (crabs) were consumed, but the exoskeletons were too crushed to be identified in the post-mortem examinations. The Arripidae and Carangidae both had relatively high biomasses in the study area, and have high caloric values (McCluskey et al., 2016), which makes it surprising that they were not better represented in the dolphin stomach contents. This may be due to the seasonality of occurrence of these families and the "spot" nature of stomach content analyses. Significantly higher biomass of carangids were caught in the winter months than in the summer in the Bunbury region (McCluskey et al., 2016), which could explain an absence of these species in the stomachs of dolphins stranded during the summer. However, the 13 stomachs analyzed came from dolphins that stranded in every season, including five from dolphins that stranded in winter.

The limited data from stranded dolphin stomach contents suggests that generally, the bottlenose dolphins in the Bunbury region are not selecting prey in proportion to the relative availability in the environment, as would be expected of an opportunistic forager. This is supported by the low value of the overall Levins' Index (0.03), indicating a specialized foraging niche. The Levins' Index is measured on a scale between 0 and 1, one representing a very broad diet and zero representing a very specific diet, and values below 0.4 considered to show a low niche breadth (Novakowski et al., 2008; Dias et al., 2017). The Bunbury dolphins therefore appear to be selecting prey based on factors other than prey abundance, such as catchability and energetic gain.

Cephalopods were the highest contributor to the contents of four of the ten stomachs, with three of these stomachs containing only cephalopod remains. The sample size was too small for any statistical comparisons between age class or sex of dolphins, however, we found that cephalopods made up an average of 45% of the proportion of female stomach contents, while cephalopods accounted for only an average of 2% of male stomach contents (Table 3). This finding is consistent with the dolphin behaviors observed by Sprogis et al. (2017a), who found that predominantly female dolphins tossed and shook octopus before consuming them in the inshore and coastal waters around Bunbury. Furthermore, mainly female dolphins were observed breaking cuttlefish apart before consuming them in the coastal waters of Bunbury during the cooler months (Smith and Sprogis, 2016). Thus, cephalopods appear to be important prey items for individual dolphins in the Bunbury region, especially as cephalopods are high in energy value (Clarke et al., 1985) and are also a common prey source among bottlenose dolphins in other regions of the world such as the Gulf of Mexico, Southern Africa, and the Mediterranean (Barros and Odell, 1990; Cockcroft and Ross, 1990; Blanco et al., 2001; Gannon and Waples, 2004; Amir et al., 2005).

Like this study, other diet studies of bottlenose dolphins have found a high diversity of species consumed, yet a few select prey species appear to be the most important contributors to energy consumption (Amir et al., 2005). For example, stomach contents of Indo-Pacific bottlenose dolphins ($n = 26$) off Zanzibar contained 1,403 prey items from 50 species of fish and three species of squid but only eight species accounted for 64.8% of the consumed mass (Amir et al., 2005). Out of the 91 stomachs of *Tursiops* spp. from South Australia (of which 64 had prey parts), Gibbs et al. (2011) recorded 2,569 prey items from 28 species of fish and six cephalopod species. Five out of 25 families (Carangidae, Clupeidae, Gerreidae, Terapontidae and Apogonidae) accounted for the highest abundance and frequency of occurrence of fish prey across all stomachs in that study (Gibbs et al., 2011). The current study examined fewer numbers of stomachs ($n = 13$, including three empty), yet had far greater numbers of prey items, from fewer unique identified species than those in dolphins off Zanzibar, and a comparable number of species found in the stomachs of dolphins off South Australia: 2,596 prey items from 45 species of fish (including unique otoliths of unknown identity) and two species of squid (Supplementary information 1). The eight most abundant species in our study accounted for 82% of the consumed prey (Fig. 7).

The Apogonidae (cardinalfish) ranked second in both caloric value (4.1 KJ.g⁻¹) captured in prey sampling and presence in dolphin stomachs, indicating that Apogonidae species, particularly *Ostorhinchus (=Apogon) rueppellii*, are likely important prey species for the dolphins of this region. This species is particularly abundant in the summer and autumn months in the shallows of the estuaries of south-western Australia. Similarly, the Apogonidae was one of the three families recorded in the

highest abundance in bottlenose dolphin (*T. truncatus*) stomachs in the Sea of Oman (Ponnampalam et al., 2012). And off Zanzibar, *Apogon apogonides* was one of the five most important prey species of fish identified in stomachs of *T. aduncus* (Amir et al., 2005). In South Australia Apogonidae was one of the top four most frequently occurring prey families identified in the stomachs of *Tursiops* sp. (Gibbs et al., 2011). Species in the Apogonidae family may be important prey items for bottlenose dolphins on a broader geographic scale.

Although the Atherinidae (silversides) species had a relatively high calorific content (4.23 KJ.g⁻¹) (McCluskey et al., 2016), they represented only 1% of stomach contents. This may be due to the small size of Atherinidae species and subsequent rapid deterioration of the very small otoliths, making identification of such species more difficult. Fifty-three (2.1%) of the otoliths in the stomachs were unable to be identified due to their small size, cracking, and lack of identifiable features due to digestive processes. It is possible that many of these otoliths were Atherinidae species and our results under-represent their presence in dolphin diet. Gobiidae species are also small in size and have very small otoliths. However, the highest number of the otoliths from dolphin stomachs were identified as members of the Gobiidae family. Due to their small size, it is also possible that at least some proportion of the Gobiidae otoliths represented secondary consumption, rather than direct consumption by dolphins i.e., they are contained in the stomachs of other fish species consumed by the dolphins. However, this would involve the otoliths being exposed to the digestive processes of multiple stomachs, further reducing the chances of maintaining identifying characteristics. It is therefore likely that these results reflect an accurate representation of direct consumption rates of the Bunbury dolphins.

We found a large number of otoliths from small fish species in the stomachs, indicating that high density compensates for smaller size for the foraging dolphins. Prey size differs among age classes of dolphins, with adult animals generally consuming larger prey than younger animals (Cockcroft and Ross, 1990). As juvenile free-ranging dolphins, up to 1.70 m in length, have been observed with milk in their stomachs (Barros and Odell, 1990), it is likely that milk supplementation, as well as inferior physical speed and agility compared to adult dolphins, may influence the size of prey eaten by younger individuals. For example, calves may feed more frequently on prey that are easier to catch, rather than those of the highest caloric content, or present in the highest concentrations (Fury et al., 2013). The findings from the current study support this hypothesis as the dolphin with the highest number of prey items in her stomach ($n = 1,884$) was a juvenile, with the majority of prey represented by the otoliths of southern longfin (*Favonigobius lateralis*) or bridled gobies (*Arenigobius bifrenatus*), both of are small fish with a maximum total length of <120 mm (McCluskey et al., 2016).

The families of fish in Bunbury with the highest energy value per fish and the highest KJ density per gram included the Arripidae, Carangidae, Platycephalidae (Flatheads), Plotosidae (Eel-tail catfishes), and Tetrarogidae (McCluskey et al., 2016). Based on abundance and the energy value of the prey sampled, atherinids accounted for 23% of the KJs caught. Apogonid species accounted for 17% and the Mugilidae (Mulletts) accounted for 10% of the KJ captured during prey sampling (McCluskey et al., 2016). However, otoliths of these families were either not identified in the stomach contents or represented less than 1% of identified prey parts. According to Spitz et al. (2010b), common dolphins (*Delphinus delphis*) in the Bay of Biscay appear to select prey of medium caloric value (4–6 KJ.g⁻¹). In the current study, all of the identified prey from dolphin stomachs of known caloric value were classified as medium or high energy value prey (five and four families, respectively). Additionally, caloric values of similar species to those found in the Bunbury dolphin stomachs were also of medium or high energy value (three and two families, respectively) (Spitz et al., 2010a). Nine of the finfish and invertebrate families identified in stomachs were of unknown energy value, either by direct measurement or by proxy of similar species. Evaluating these prey families for energy content would be important to assessing selectivity based on caloric intake. However, the species of unknown energy value make up only 2.4% of the identified individuals in the stomachs, and therefore do not influence the findings that the Bunbury dolphins are consuming prey of medium and high caloric value.

6.4. Biases and benefits of stomach contents

Relying on opportunistic acquisition of stomachs from stranded individuals makes it difficult to test differences in stomach contents among locations, age class, or sexes of dolphins (Spitz et al., 2006). Stomachs of sick or injured animals may not represent typical diet (Santos et al., 2013; Dede et al., 2015), yet in this study there seemed to be no relationship between body condition and presence of prey parts. In fact, some of the individuals with the highest number of prey parts in their stomachs were also those with the most compromised body condition, such as the juvenile male M3, who was severely emaciated when he died and had a stomach full of mud and seagrass along with over 400 fish otoliths and 3 cephalopods (Krzyższyk et al., 2013) (Table 3). Gadiform fishes may be over-represented compared to other teleost fishes as their otoliths are more resistant to gastric erosion (Kemp et al., 2011). However, this is not relevant for the present study as no gadiformes were identified in the dissected stomachs and none were sampled in the prey sampling program (McCluskey et al., 2016). Fish species with larger otoliths may also be over-represented in the stomachs, as the smallest otoliths degrade at a faster rate. However, in this study, the vast majority of otoliths were small (<3 mm), indicating that the stomach content analysis was not biased toward larger prey items.

Based on the occurrence of octopus beaks in the stomachs of other populations of dolphins (*Lagenorhynchus acutus* in *T. truncatus*, *T. aduncus*) (Blanco et al., 2001; Gibbs et al., 2011; Hernandez-Milian et al., 2016), the relatively high protein value of cephalopods (Santos et al., 2001), and the observations of octopus and cuttlefish handling in the region (Smith and Sprogis, 2016; Sprogis et al., 2017a), octopus and cuttlefish were expected to be significant prey of dolphins in Bunbury. While squid beaks were identified in the dolphin stomachs ($n = 6$ of 10 that had prey parts), no octopus or cuttlefish beaks were found. The

whole heads of octopus have been observed to be consumed by dolphins off Bunbury (Stephens et al., 2017), and in other cases the head of octopus and cuttlefish is removed by tossing and shaking and may not be ingested, thus evading the retention of beaks by the dolphins (Smith and Sprogis, 2016; Sprogis et al., 2017a). Therefore, we cannot conclude that the lack of octopus and cuttlefish beaks detected in the limited number of dolphin stomachs from this study represented an absence of cephalopods from the Bunbury dolphins' diet.

Another prey species likely to be more prevalent in the diet of the dolphins than is detected by stomach content analysis is the estuary cobbler (*Cnidoglanis macrocephalus*). Dolphins have been observed tossing cobbler in the estuary to remove the head, which contains venomous spines, and therefore the dolphins are not likely to always ingest the cobbler otoliths (Sprogis pers. obs.). Only one cobbler otolith was identified in the stomachs from the ten dolphins, yet cobbler was relatively abundant during prey sampling (ranking 6th in biomass of the species caught using a gillnet) and has a medium caloric value (5.31 KJ.g⁻¹), making it a likely prey item for the dolphins (McCluskey et al., 2016). While most odontocetes tend to consume their prey whole, dolphins in other parts of the world have been observed adapting strategies for dealing with spiny prey. For example, some individuals in the Eastern Gulf of Mexico have developed a method for decapitating various species of catfish (Ariidae), which possess barbed spines that have been related to dolphin deaths when ingested (Ronje et al., 2017). The authors conclude that catfish may be greatly underestimated in stomach content analyses due to the lack of ingested otoliths (Ronje et al., 2017).

Despite these limiting factors, stomach content analyses remain a direct and important method for obtaining information on the diet of marine predators (Barros and Wells, 1998; Berens McCabe et al., 2010; Dunshea et al., 2013). Because of stomach content analyses, this study found two families of fish (Mullidae and Tetraogidae) to add to the list of dolphin prey for the Bunbury dolphins, and therefore two more families of fish to prioritize for sustainable population management. Stomach contents remain the most specific method of identifying cetacean diet, as fecal matter is difficult to collect from aquatic mammals and close, direct observations of surface feeding dolphins during daylight hours can be extremely limited. In an important review of the validity of stomach content analyses, Dunshea et al. (2013) compared molecular detection of prey in gastric and fecal samples from a population of *T. truncatus* in the United States, whose stomach contents have been studied for decades. The authors found a remarkable agreement between the molecular results and those from the opportunistic stomach content identification.

6.5. Combining stable isotope and stomach content analyses

Stable isotopes have been used as a complimentary tool to stomach content analyses in other diet studies (Dehn et al., 2007; Rossman et al., 2015a; Giménez et al., 2017), however information on isotope signatures for both predator and prey as well as stomach contents is rare. Because stomach contents reflect short term diet, and stable isotopes reflect longer time periods, using both techniques can combine findings of seasonal or ontogenetic changes in diet for individuals or populations (Jansen et al., 2013; Nielsen et al., 2019). Because of this, results from stable isotope and stomach contents do not always align. In a study of terapontid fish in the upper Burdekin catchment of north-eastern Australia, Davis et al. (2012) found that $\delta^{13}\text{C}$ isotope data reflected the shifts in ontogenetic diet change seen in the stomachs. However, the $\delta^{15}\text{N}$ results and stomach content analyses did not agree on trophic position. The stomach content analyses indicated no significant diet change with growth of two freshwater fish species, whereas the stable isotope analysis indicated an increase in trophic level as the fish increased in body size. The authors speculated that this may be due to errors in assumed trophic fractionation rates for species that undergo a diet change from insectivore to herbivore (Davis et al., 2012). Jansen et al. (2013) investigated the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures and stomach contents of the same individuals of harbor porpoises (*Phocoena phocoena*) along the Dutch coastline and found that the stomach contents reflected a diet of benthic and demersal species inhabiting the near-shore, where the porpoises were foraging prior to stranding, whereas the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures reflected a more offshore diet, consisting of pelagic, schooling fishes. Their finding is similar to those from the current study, which found demersal, near-shore species in the stomachs of both inshore and coastal dolphins, yet detected significant differences in their carbon and nitrogen signatures. In both regions, this finding likely represents seasonal differences in diet, as well as movement between habitats.

The MixSIAR model indicated that tailor was the most significant prey source for inshore dolphins, yet tailor was not present in the stomach contents of any of the dolphins. Tailor was captured in all seasons in the inshore waters during prey sampling and had a high caloric value (6.57 KJ.g⁻¹ and mean of 852.38 KJ/fish) (McCluskey et al., 2016). It is therefore reasonable to assume that despite the lack of tailor otoliths in the stomachs of stranded dolphins, tailor is a utilized prey source for the inshore dolphins. Tailor was not captured in coastal waters during prey sampling, which aligns with the results of the scaled posterior density plot for coastal dolphins, which did not indicate tailor as a selected prey over other prey sources (Fig. 4). The discrepancy between the stomach contents and the stable isotope data further indicates the importance of using complementary approaches to decipher diet, as each method contributes different insights into the foraging habits of predators.

Other studies have reported alignment between stable isotope and stomach content results. For example, in South Australia, Gibbs et al. (2011) concluded that two species of bottlenose dolphins with overlapping distributions showed niche partitioning in their diet; the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of one species (*Tursiops* sp.) indicated a diet of mixed demersal and pelagic species, which was also reflected in their stomach contents. The other species (*T. truncatus*) had $\delta^{13}\text{C}$ values representing a more offshore diet, and $\delta^{15}\text{N}$ signatures representing a higher trophic level than the *Tursiops* sp., which was corroborated with

the stomach contents from those individuals. Dolphins in both Bunbury and South Australia appear to show niche differentiation between groups of dolphins. Other studies have used stable isotopes and scat analyses in combination to assess the diet of marine mammals such as California sea lions (*Zalophus californianus*), and have found that results of both scat analysis and stable isotope signatures align (i.e. Zeppelin and Orr 2010). Looking at diet using multiple tools is therefore useful in developing a more complete picture of foraging ecology for marine top predators (Mahfouz et al., 2017; Secchi et al., 2017).

Because stable isotope samples and stomach content data were not obtained from the same individuals in this study, a direct comparison of results from these two methods is not possible. Our stable isotope results indicate that the coastal dolphins feed on a more pelagic diet than the inshore dolphins, which are sighted mostly in the study region year-round. However, the stomach contents from all the dolphins analyzed in this study, including those associated with a more coastal distribution, contained mostly prey associated with shallow bays and estuaries. Yet this would not preclude these animals from having a more coastal distribution, as the marine waters of south-western Australia remain relatively shallow (<40–50 m) until the continental shelf, which is approximately 92 nm from the coast in the Bunbury region. The carbon and nitrogen signatures of sampled prey that were within the range of possible diet of the dolphins were also present in the stomachs. The one exception to this was the single squid that was analysed for stable isotopes, which had a carbon value that was lower than any of the dolphin carbon values (mean $\delta^{13}\text{C}$ of squid = -21.12 ± 0.84 , mean $\delta^{13}\text{C}$ of dolphins = -16.71 ± 0.26 ; Table 2). This is likely due to either the small sample size, or because the sampled dolphins were inshore at the time of biopsy and feeding predominately on inshore species which would have had higher carbon signatures than the squid. It is likely that if coastal dolphins were sampled when they first arrived in the inshore waters in the late spring, their carbon signatures would be lower and closer to those of the sampled squid.

7. Conclusions

The dolphins inhabiting the waters around Bunbury appear to be selective foragers, as the diet reflected in stomach contents was not proportional to the relative abundance of the species recorded in the marine environment. For example, 96% of the dolphin stomachs contained perciformes, whereas perciformes made up 30% of the catch during prey sampling in the same habitats (McCluskey et al., 2016). The Bunbury dolphins had an overall niche breadth of 0.031 (Levins' Index), indicating a specialized diet. The inshore dolphins had a lower niche breadth than the offshore dolphins (0.008 vs 0.086 respectively), however both groups can be categorized as selective foragers. The carbon and nitrogen stable isotopes of the dolphins also reflected niche differences between the coastal and inshore dolphins with the coastal dolphins having a carbon signature in line with more pelagic prey species and a lower nitrogen signature than the inshore dolphins, whose higher nitrogen values were likely due to greater nutrient enrichment of the inshore habitats and the surrounding urban development of Bunbury.

Information on diet composition is important for managing resources for the conservation of this population of dolphins, as well as for managing potential interactions or competition between commercial and recreational fisheries and dolphin foraging habits (Secchi et al., 2017). Knowledge of dolphin diet and prey preferences aids in the sustainable management of commercial and recreational fisheries by incorporating dolphin consumption into stock assessment models (Tyrrell et al., 2011). Goby (Gobiidae) and tailor (*P. saltatrix*) appear to be particularly significant in the diets of inshore dolphins, therefore changes in their populations may directly affect dolphin condition. Continued monitoring of the dolphins' diet is necessary, as changes in fishing and climactic pressures could alter the selective prey preferences found in this study.

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Ethics approval

The fish capture work of this study was conducted under the approval of the Murdoch University Animal Ethics Committee (W2114/07), and licensed as scientific research by the Western Australian Department of Fisheries (2007–20), and Western Australian Department of Environment and Conservation (SF6538). Biopsy work was conducted under the Murdoch University Animal Ethics Committee permits (W2009/06 and W2342/10) and licensed by the Western Australian Department of Environment and Conservation (SF005811 and SF008624).

Consent to participate

N/A.

Consent for publication

N/A.

Availability of data and material

The datasets generated during this study are available at the Zenodo repository, <http://doi.org/10.5281/zenodo.3660673>. R code used in the stable isotope analysis is available on GitHub at https://github.com/jmlondon/dolphin_isotopes and has been archived in a Zenodo repository (10.5281/zenodo.4408514).

Authors' contributions

SMM conducted field work associated with this study, as well as preformed all laboratory work. SMM composed the manuscript, including most of the figures and tables. KRS conducted field work associated with dolphin sightings and created Figs. 1 and 2 as well as Table 1. JML navigated R code to run the MixSIAR model and created Fig. 4. LB aided in funding procurement and led the biopsy sampling efforts. NRL assisted with the development of the methods and the analyses. All authors contributed to refining the manuscript and read and approved the final manuscript.

Declaration of competing interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

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