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ORIGINAL ARTICLE

Niche partitioning among social clusters of a resident estuarine apex predator

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Abstract

Conspecifics may vary in their space use and diet leading to niche partitioning within populations. In social species, such partitioning may correspond to social structure as closely associated individuals likely encounter the same resources. This study investigated whether space use and diet varied among social clusters of a resident estuarine population of Indo-Pacific bottlenose dolphins. Dolphin photo-identification and behavioral data, as well as tissue samples for stable isotope analysis, were collected during boat-based surveys in the Peel-Harvey Estuary, Western Australia. Potential dolphin prey species were also collected for stable isotope analyses. Six mixing models, one assuming an invariant diet and others allowing for variation in diet according to sex, age class, and/or social cluster, were fitted to the data. The model with social cluster was the best fit and estimated detritivorous fish as the main dietary source for social clusters whose core activity space covered the eastern shores of the estuary and the rivers. These clusters occupied the lowest trophic position in the dolphin population. Benthic omnivores and carnivores contributed most to the diet of clusters whose core activity space included the two estuary entrances. These clusters occupied the highest trophic position. Clusters with core activity space located in the estuary basins reflected the overall mean contributions of fish feeding guilds to dolphin diet in this population. Detritivores, omnivores and herbivores, and benthic omnivores and carnivores each contributed approximately a third and water column species the remainder to the annual fish biomass removed from the estuary by the dolphin population. We conclude that dolphins share resources with fishers and piscivorous birds within the estuary.

Significance statement

This study identified intra-population resource partitioning according to social structure in a resident estuarine dolphin population. The heterogeneity in space use and diet among social clusters may result in individuals being susceptible to different pressures and threats. The dolphins' foraging behavior and trophic interactions identified them as an apex predator in the Peel-Harvey Estuary, with their collective minimum annual food intake (~200,000 kg) exceeding the annual fish biomass removed by commercial fishers. As top predators in the system, dolphins may suppress prey populations through consumption and as agents of intimidation by changing prey distribution and behavior. This study provides scientific basis for recognizing dolphins as an important component of the Peel-Harvey Estuary ecosystem.

Keywords Trophic ecology · Foraging behavior · Diet · Stable Isotopes · Top-down control

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Introduction

Trophic interactions and spatial distribution are prominent dimensions of a species' ecological niche (Grinell 1917; Elton 1927; Hutchinson 1957). Conspecifics, however, may vary in their diet and space use patterns, leading to niche partitioning within populations (Bolnick et al. 2003). In social species, such partitioning may correspond to population social structure as highly associated individuals occupy the same habitat and encounter the same resources (Darimont et al. 2004; Semmens et al. 2009).

Bottlenose dolphins (*Tursiops* spp.) are often organized in social communities (hereafter "populations") comprising males and females of all ages (e.g., Urian et al. 2009; Wiszniewski et al. 2009; Chabanne et al. 2017; Genov et al. 2019). Adults preferentially associate with members of the same sex (Connor et al. 1992; Smolker et al. 1992; although see Lusseau et al. 2003), while juveniles live in more dynamic groups (Gero et al. 2005; Galezo et al. 2020). As a result, social clusters, in which individuals associate more frequently with one another than with members of other clusters, may be identified within populations. Resource partitioning corresponding to social structure has been recorded for dolphins (Chilvers and Corkeron 2001) yet has received less attention than partitioning by habitat (Sargeant et al. 2007; Barros et al. 2010; Gibbs et al. 2011) or foraging tactic (Mann and Sargeant 2003; Sargeant et al. 2005; Allen et al. 2011; Krützen et al. 2014).

Bottlenose dolphins exhibit diverse foraging behaviors (Shane 1990; Mann and Sargeant 2003) with the tactic employed determined by habitat features (e.g., Sargeant et al. 2007; Torres and Read 2009) or prey characteristics (Patterson and Mann 2011; Smith and Sprogis 2016; Sprogis et al. 2017). Prey selection is driven by maximizing net energy gain and depends on prey availability, abundance and distribution, inter- and intraspecific competition, and the consumer's ability to harvest resources (MacArthur and Pianka 1966; Bolnick 2001; Svanbäck and Bolnick 2007). Typically, bottlenose dolphin diet comprises large proportions of a few fish species and numerous less frequently or occasionally consumed prey (Cockcroft and Ross 1990; Mead and Potter 1990; Amir et al. 2005). When dominant dietary items do not correspond to the most abundant or available prey in the environment, they are preferentially chosen by consumers (McCabe et al. 2010) potentially leading to intra-population variability in diet.

As higher-order predators, dolphins may control prey populations and community structure and therefore contribute to consumer (i.e., top-down) control in the system (Leopold 1943; Estes and Duggins 1995; Bowen 1997). They may also influence ecosystem structure by disturbing the benthos, which may impact invertebrate communities (Nerini 1984; Oliver and Slattery 1985; Oliver et al. 1985), and via recycling of nitrogen through defecation (Roman and McCarthy 2010). The presence of predators may also produce a "landscape of fear" (Laundré et al. 2010) by which predation risk influences prey distribution and behavior and thereby their foraging ecology and life history (Lima and Dill 1990; Brown et al. 1999; Heithaus and Dill 2002; Wirsing et al. 2008; Ale and Whelan 2008; Heithaus et al. 2009). The complexity of trophic and behavioral interactions makes it difficult to infer dolphins' role in dynamic systems where both bottom-up and top-down control are likely to act in concert (Schmitz 2010). Nevertheless, characterizing foraging and trophic ecology of predators and quantifying their diet will elucidate the effects they may have on prey populations, community structure, and ecosystem function.

Estuaries are productive ecosystems, where high nutrient availability and primary production support complex trophic interactions (Bianchi 2006) . Consequently, estuaries host high densities of prey for piscivorous top predators such as birds, sharks, and dolphins (e.g., Matich and Heithaus 2014; Rossman et al. 2015; Tweedley et al. 2016). Bottlenose dolphins (*Tursiops* spp.) are commonly found in and show varying levels of site fidelity to different estuaries (e.g., Wilson et al. 1997; Zolman 2002; Fury and Harrison 2008; Urian et al. 2014). The Peel-Harvey Estuary in Western Australia is occupied by a resident population of ~ 90 Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) (KN, unpublished data). This population comprises nine social clusters and two lone individuals and has been identified as socially, spatially, and isotopically distinct from dolphin populations found in adjacent coastal waters (KN, unpublished data). In this study, intra-population partitioning in space use and diet of the Peel-Harvey Estuary dolphin population was investigated. Dolphin behavioral observations were used to identify targeted and consumed prey species, while stable isotope ratios of carbon and nitrogen in both the consumer and prey were used to quantify the proportional contribution of sources (i.e., fish) to social clusters' diet. The annual food intake of the dolphin population was also estimated.

Materials and methods

Study area

The Peel-Harvey Estuary (~ 130 km^2) is a microtidal (tidal range ~ 0.5 m) temperate estuary consisting of two shallow (< 2 m deep) basins (Fig. 1). Three rivers flow into the estuary from a catchment area of approximately 94,000 km^2 (Valesini et al. 2019). The estuary is permanently open,

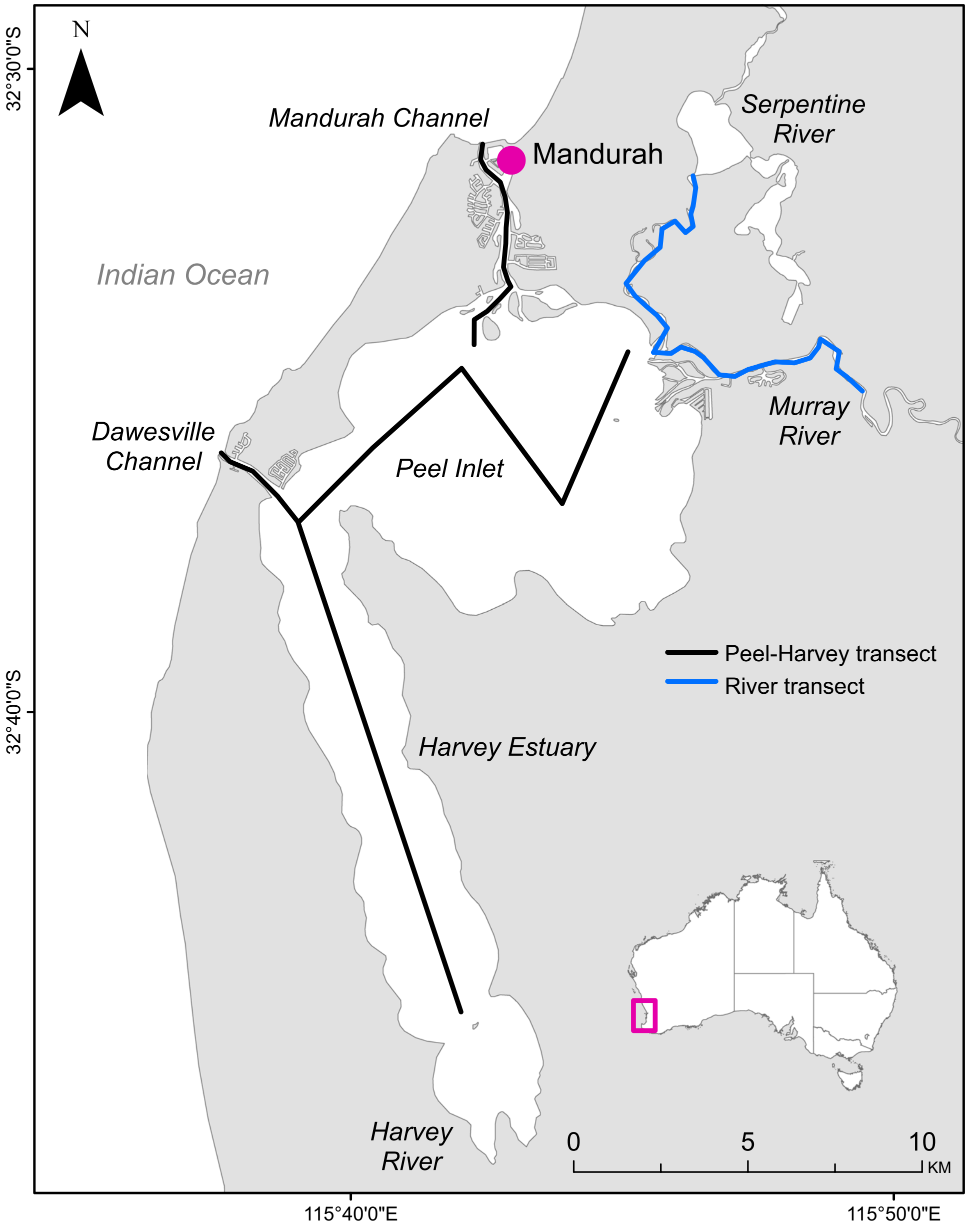

Fig. 1 The Peel-Harvey Estuary (~ 130 km^2) in Western Australia was surveyed for Indo-Pacific bottlenose dolphins (*Tursiops* aduncus). Boat-based transects were run a minimum of three times each season following the same route apart from in the Peel-Inlet where a unique “zigzag” pattern was followed on each sampling occasion between January 2016 and November 2017. The river transect was run opportunistically

connected to the sea by two relatively narrow channels: the Mandurah Channel, a natural opening, and the Dawesville Channel, an artificial opening. The fringing vegetation consists of salt marsh and paperbark communities (Hale and Kobryn 2009), although a proportion of the shoreline has been significantly altered by development (e.g., canal systems, housing, and other infrastructure).

The region experiences a Mediterranean climate with cool, wet winters and hot, dry summers. Approximately 90% of the mean annual rainfall (~ 800 mm) and 95% of the river flow occur between May and October (Valesini et al. 2019). Mean salinities in the basins remain close to marine salinity (34–37 ppt), while the rivers are brackish with high variability between 5 (winter) and up to 71 ppt (summer) in the Serpentine River (Thomson 2019). Mean water temperature varies from 10 to 12 °C in the winter to high 20 s in the summer (annual averages 18.5–20.4 °C) (Thomson 2019). Phytoplankton is co-dominated by diatoms and cryptophytes in the basins, by diatoms and dinophytes in the Murray River and by cyanobacteria in the Serpentine River (Thomson 2019). Macrophyte communities are dominated by seagrass species *Ruppia megacarpa* (Krumholz 2019). The high estuarine productivity supports a diversity of hyperbenthic and infaunal communities (Valesini et al. 2009; Wildsmith et al. 2009), > 80 species of fish (Valesini et al. 2009; Potter et al. 2016) and > 100 species of wetland-dependent birds (Hale and Butcher 2007). The Peel-Harvey Estuary is part of the Ramsar-listed Peel-Yalgorup wetland system.

Data collection

Dolphin photo-identification surveys were conducted throughout the estuary and in adjacent coastal waters on board a 5.6 m research vessel between January 2016 and November 2017. Predetermined transects were run every season ($\geq$three in each season) in the estuary ($n=37$) and coastal waters ($n=28$). Data collected in coastal waters were not included in this study apart from locational records of identified estuarine resident dolphins encountered outside the estuary. In the Peel-Harvey Estuary, transects followed a similar route apart from in the Peel Inlet where a unique "zigzag" pattern was followed on each sampling occasion (Fig. 1). The Serpentine and Murray Rivers were not part of the dedicated study area but were surveyed every season to ~ 7.5 km upstream (Fig. 1). Additional search effort was conducted to collect dolphin tissue samples and laser photogrammetry data for aging individuals (van Aswegen et al. 2019).

A group of dolphins was defined using a "10-m chain rule" where individuals are part of the same group if they are within 10 m of any other group member (Smolker et al. 1992). Individual/group location was recorded, and dorsal fin photographs were taken for individual identification (Würsig and Würsig 1977). Predominant behavior (i.e., > 50% of group members engaged [Mann 1999]) of foraging, travelling, socializing, resting, or unknown was recorded for the first 5 min and thereafter opportunistically. Previously described foraging tactics of peduncle dive foraging, bottom grubbing, snacking (Mann and Sargeant 2003; Sargeant et al. 2007), tossing (Sprogis et al. 2017), tail-whacking (Scott et al. 1990; Shane 1990), foraging along/against structures (described in this study), and begging (Finn et al. 2008; Senigaglia et al. 2019) were recorded (Table 1). Behavioral events (e.g., fish chases, handling, or capture of prey) were recorded opportunistically. Prey items were identified from photographs by two independent, experienced fish ecologists. It was not possible to record data blind (i.e., methods that may reduce observer bias or prevent changes in behavior of the observed subject) as this study involved observation of animals in the field.

Space use by social clusters

Seven social clusters and a lone adult female (LF) in the resident Peel-Harvey dolphin population, identified using an average linkage hierarchical cluster analysis, were included in this study (KN, unpublished data). Two clusters (AM1 and AM2) comprised adult males, two clusters (AF1 and AF2) adult females, one (JM) juvenile males, and two clusters (M1 and M2) had a mixture of adult females and juveniles of both sexes. One lone male and two additional social clusters, collectively comprising five individuals, were not sampled for stable isotope analyses and were therefore excluded from analyses.

A non-parametric fixed kernel method (Silverman 1986; Worton 1989) was used to estimate the utilization distribution (UD) for each dolphin social cluster. Locational records of individuals within clusters were combined to represent clusters' spatial distribution. The UD for each cluster was estimated using the Epanechnikov kernel function (Epanechnikov 1969) over a grid (cell size 100 m × 100 m) created over the study area. The ad hoc (h_{ref}) smoothing parameter (Silverman 1986; Worton 1989) was used to determine the shape of the kernels as visual inspections may be subjective and least-squares cross-validation method was not considered appropriate for the data structure in this study (Silverman 1986). Both 50% and 95% kernels were estimated to reflect the core and full UDs, respectively, for each cluster.

Ideally, UDs would be estimated considering boundaries that animals cannot cross (Barry and McIntyre 2011; Sprogis et al. 2016). The R package adehabitatHR version 0.4.18 (Calenge 2015) used for UD analyses, however, does not support highly irregular shapes, like the Peel-Harvey Estuary, as boundaries. Therefore, land was removed from UDs post hoc using a Boolean land mask followed by renormalizing the kernel density estimates. The UD overlaps between social clusters were calculated as the probability of a member of one cluster being found in the UD of another cluster and vice versa (Ostfeld 1986).

Stable isotope analyses

Dolphin skin samples ($n=38$) were collected for stable isotope analyses using a remote biopsy system (PAXARMS modified 0.22 caliber biopsy rifle) developed for small cetaceans (Krützen et al. 2002). Samples were collected from adult and juvenile dolphins, placed in an empty vial, and stored on ice for transport to storage in − 80 °C freezer.

Fish samples were collected from the shallow nearshore and deeper offshore waters of both estuary basins (i.e., northern and southern Harvey Estuary, eastern and western Peel Inlet) and two of the rivers (Murray and Serpentine Rivers) between February and September 2017. Fish were collected using seine and gill nets as part of a separate study documenting the fish community structure of the estuary (Hallett et al. 2019). Fish retained for stable isotope analysis ($n=141$) ranged in length from 19 to 357 mm and belonged to 24 potential prey species (including ten species not observed being consumed by dolphins) and to a variety of feeding guilds (i.e., benthic detritivore, herbivore, omnivore, benthic carnivore, benthic omnivore, or water column feeder, as assigned via reference to FishBase: Froese and Pauly 2019; Table 2). Whole fish were transferred on ice and stored in − 20 °C freezer until processing for stable isotope analyses.

Table 1 Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) foraging tactics, and associated prey species, observed consistently in the Peel-Harvey Estuary, Western Australia. Surveys refer to a minimum of 5-min behavioral observation of a group or an individual. Foraging/feeding was observed in a total of 236 surveys

Foraging strategy	Description	Prey species identified	Number of surveys observed in
Bottom grubbing	Dolphin is oriented vertically in the water column, probing into the substrate, or weed patch with its rostrum. A turbid sediment plume is often observed at the water's surface, and dolphin may surface with mud on rostrum and head	*Cnidoglanis macrocephalus* (*n* = 5) *Pelates octolineatus* (*n* = 3) *Sillago schomburgkii* (*n* = 2) *Nematalosa vlaminghi* (*n* = 1) *Pseudorhombus jenynsii* (*n* = 1) *Gerres subfasciatus* (*n* = 1)	49
Peduncle dive foraging (> 1 individual)	Dolphins are often widespread (> 10 m) changing directions with respect to each other at each surfacing with peduncle dive (peduncle raised out of the water as dolphin descends) the main surfacing type. Birds are often associated with this feeding strategy	*Pelates octolineatus* (*n* = 3) *Sillago* sp. (*n* = 3) *Gerres subfasciatus* (*n* = 1) *Rhabdosargus sarba* (*n* = 1)	47
Tossing	Dolphin tosses prey out of the water. Often preceded by bottom grub or chase in open water	*Cnidoglanis macrocephalus* (*n* = 12) *Rhabdosargus sarba* (*n* = 2) *Arripis truttacea* (*n* = 1) *Octopus cf. O. tetricus* (*n* = 1) *Platycephalus laevigatus* (*n* = 1) *Pseudorhombus jenynsii* (*n* = 1) *Sillago schomburgkii* (*n* = 1) *Mugil cephalus* (*n* = 1)	30
Foraging along/against structures	Dolphin swims along a structure changing direction or stopping in response to fish movement. If fish is hiding between rocks or structures beyond reach, dolphin may engage in stalking (i.e., stay stationary in front of where the prey is hiding)	*Mugil cephalus* (*n* = 2) *Aldrichetta forsteri* (*n* = 1) *Aldrichetta forsteri*/*Mugil cephalus* (*n* = 2) *Arripis truttacea* (*n* = 1)	26
Tail-whacking	Dolphin stops abruptly turning and swinging its flukes sharply, often producing a big fanlike splash. Fish are often flown up in the air. Tail-whacks are frequently preceded by a rooster-tail (i.e., a fast swim with a sheet of water trailing off the dorsal fin)	*Mugil cephalus* (*n* = 4) *Aldrichetta forsteri* (*n* = 1) *Rhabdosargus sarba* (*n* = 1)	25
Snacking	Dolphin swims inverted close to the water surface chasing and capturing fish	*Hyporhamphus* sp. (*n* = 4) *Rhabdosargus sarba* (*n* = 2) *Aldrichetta forsteri* (*n* = 2) *Pelates octolineatus* (*n* = 1)	17
Begging	Dolphin approaches a stationary or slow-moving vessel, most often to the side or stern and remains close to it. Dolphin may also lift head out of the water and open its mouth	n/a	0

Dolphin skin samples were divided into two aliquots, one for δ^{15}N measurements from bulk (i.e., untreated) samples and the other for δ^{13}C measurements from lipid-extracted samples (de Lecea and Charmoy 2015; Giménez et al. 2016). The bulk samples were oven-dried at 60 °C for 24 h and powdered with a mortar and pestle. The other aliquot underwent lipid extraction with three consecutive 24 h soaks in 2:1 chloroform/methanol solvent solution (Newsome et al. 2006). Samples were then rinsed in deionized water, oven dried, and powdered as per bulk samples.

Fish dorsal muscle samples were oven-dried to constant weight at 60 °C for 24 h and powdered using a TissueLyser. Two aliquots were prepared from the homogenized tissue. One aliquot underwent lipid extraction following methods described in Logan et al. (2008). Samples were immersed in 2:1 chloroform/methanol solvent solution, mixed for 30 s, and left for at least 30 min. Samples were then centrifuged for 10 min at 2500 rpm. The supernatant, containing solvent and lipids, was discarded. The process was repeated until the supernatant was clear following centrifugation. Samples

Table 2 Mean carbon (δ^{13}C) and nitrogen (δ^{15}N) values in the muscle tissue of fish species included as sources in a mixing model to estimate feeding guild contributions to Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) diet in the Peel-Harvey Estuary. Notations**:** *SD* standard deviation,—= no sample

Feeding guild	Common name	Peel Inlet, Harvey Estuary, Serpentine River			Murray River		
Species		δ^{13}C ‰ (SD)	δ^{15}N ‰ (SD)	n	δ^{13}C ‰ (SD)	δ^{15}N ‰ (SD)	*n*
Benthic detritivore		**−14.20 (1.41)**	**6.98 (1.15)**	**8**	**−16.21 (1.97)**	**6.60 (0.61)**	**7**
*Mugil cephalus**	Sea mullet	−12.69 (0.47)	5.49 (0.21)	2	−16.19 (2.47)	6.34 (0.38)	4
*Nematalosa vlaminghi**	Perth herring	−14.70 (1.23)	7.47 (0.81)	6	−16.23 (1.60)	6.96 (0.76)	3
Herbivore		**−15.36 (0.93)**	**7.90 (0.23)**	**6**	**−20.28 (2.63)**	**9.35 (0.69)**	**3**
*Pelates octolineatus**	Western striped grunter	−15.36 (0.93)	7.90 (0.23)	6	−20.28 (2.63)	9.35 (0.69)	3
Omnivore		**−16.38 (1.87)**	**8.68 (0.71)**	**4**	**−19.32 (2.07)**	**9.00 (0.26)**	**3**
*Rhabdosargus sarba**	Tarwhine	−16.38 (1.87)	8.68 (0.71)	4	−19.32 (2.07)	9.00 (0.26)	3
Benthic carnivore/water column		**−15.84 (1.33)**	**8.89 (0.91)**	**21**	-	-	-
Atherinosoma elongata	Elongate hardyhead	−15.50 (1.40)	8.60 (0.73)	9	-	-	-
Favonigobius lateralis	Southern longfin goby	−15.05 (1.09)	8.49 (0.55)	3	-	-	-
Gymnapistes marmoratus	Soldier	−15.75 (1.24)	8.41 (1.60)	3	-	-	-
Leptatherina presbyteroides	Silverfish	−16.72 (1.78)	9.78 (0.09)	6	-	-	-
Benthic carnivore		**−16.38 (1.29)**	**9.01 (0.85)**	**25**	**−21.52 (1.13)**	**9.93 (0.72)**	**3**
*Cnidoglanis macrocephalus**	Estuary catfish	−16.96 (0.64)	8.80 (0.42)	2	-	-	-
Ostorhinchus rueppellii	Western gobbleguts	−16.24 (1.34)	9.18 (0.30)	6	-	-	-
*Pseudorhombus jenynsii**	Small toothed flounder	−17.69 (0.00)	9.20 (0.00)	1	−20.32 (0.00)	9.10 (0.00)	1
*Sillaginodes punctatus**	King George whiting	−15.76 (1.20)	8.29 (0.88)	8	-	-	-
*Sillago burrus**	Trumpeter whiting	−18.12 (2.64)	9.56 (1.45)	2	−22.12 (0.61)	10.34 (0.01)	2
*Sillago schomburgkii**	Yellowfin whiting	−15.93 (0.68)	9.18 (0.43)	3	-	-	-
*Sillago vittata**	Western school whiting	−16.75 (0.09)	10.11 (0.30)	3	-	-	-
Benthic omnivore		**−16.55 (1.11)**	**9.27 (0.79)**	**17**	**−24.16 (5.02)**	**10.07 (0.77)**	**10**
Acanthopagrus butcheri	Black bream	-	-	-	−28.68 (2.45)	10.92 (0.37)	4
*Aldrichetta forsteri**	Yelloweye mullet	−16.59 (1.17)	9.12 (0.90)	9	−22.96 (3.49)	9.54 (0.16)	3
*Gerres subfasciatus**	Common siver biddy	−16.33 (1.07)	9.64 (0.35)	7	−19.33 (3.70)	9.47 (0.16)	3
Haletta semifasciata	Blue weed whiting	−17.79 (0.00)	8.04 (0.00)	1	-	-	-
Water column		**−17.73 (1.71)**	**10.95 (1.41)**	**29**	**−21.64 (2.78)**	**10.70 (0.81)**	**5**
*Arripis georgianus**	Australian herring	−18.78 (0.98)	11.04 (1.18)	12	-	-	-
*Arripis truttacea**	Western Australian salmon	−16.09 (0.46)	11.11 (0.15)	6	-	-	-
Atherinomorus vaigiensis	Common hardyhead	−17.72 (0.11)	9.88 (0.11)	3	−20.99 (2.86)	10.51 (0.25)	3
Engraulis australis	Australian anchovy	-	-	-	−20.21 (0.00)	9.95 (0.00)	1
Pomatomus saltatrix	Tailor	−17.40 (2.40)	11.10 (2.28)	8	−25.00 (0.00)	12.04 (0.00)	1

*Identified as dolphin prey from behavioral observations

were then rinsed in 2:1 chloroform/methanol solvent solution and dried at 50 °C. All samples were weighed to the nearest 0.01 mg, packed into tin capsules, and sent to the West Australian Biogeochemistry Centre at the University of Western Australia for δ^{15}N and δ^{13}C measurements using a continuous flow system (Delta V Plus mass spectrometer, with a Thermo Flush 1112 via ConFlo IV (Thermo Finnigan/Germany)). Details of the analytical technique can be found in Skrzypek and Paul (2006). The δ^{13}C and δ^{15}N values are given in per mil (‰) difference between the sample and the international standards of Vienna Pee Dee belemnite carbonate and atmospheric nitrogen, respectively.

Isotopic partitioning among social clusters

Six social clusters were included in testing the null hypothesis of no difference in isotopic values among social clusters: LF and cluster AF2 ($n = 2$) were excluded due to low sample sizes. More than 50% of individuals in each of the other social clusters were sampled (Table 3). Data exploration was performed by visual inspection of box plots and QQ-plots. The Shapiro–Wilk test was used to test the null hypothesis that δ^{13}C and δ^{15}N values within clusters were normally distributed. If they were, the Bartlett test was used to test for homogeneous variance among groups, if not, the

Table 3 Mean carbon (δ^{13}C) and nitrogen (δ^{15}N) values in the skin of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) of seven social clusters identified as resident in the Peel-Harvey Estuary, Western Australia. Notations: *SD* standard deviation, *Su* summer, *At* autumn, *W* winter, *Sp* spring, *n/a* not applicable

Social cluster	*n* Sampled/members	Mean sighting frequency (SD)	Sampled (Su/At/W/Sp)	Mean δ^{13}C (SD) ‰	Mean δ^{15}N (SD) ‰
Adult male 1 (AM1)	3/6	48.00 (5.57)	0/3/0/0	– 15.41 (0.23)	10.61 (0.30)
Adult male 2 (AM2)	5/6	33.20 (6.42)	0/4/0/1	– 15.63 (0.45)	10.00 (0.16)
Adult female 1 (AF1)	5/7	41.8 (5.36)	1/3/1/1	– 15.28 (0.58)	10.30 (0.34)
Adult female 2 (AF2)	2/2	9.5 (0.70)	0/1/0/1	– 14.62 (0.66)	8.65 (0.34)
Juvenile male (JM)	4/5	36.25 (5.06)	0/2/1/1	– 15.08 (0.23)	10.24 (0.14)
Mixed sex/age 1 (M1)	11/21	22.27 (4.61)	1/3/0/7	– 15.28 (0.52)	9.90 (0.35)
Mixed sex/age 2 (M2)	7/10	19.14 (7.13)	0/7/0/0	– 15.61 (1.00)	9.10 (0.70)
Lone female (LF)	1/1	41	0/0/1/0	– 15.82 (n/a)	10.52 (n/a)
Adults	25/39	29.51 (12.85)	6/16/1/6	– 15.24 (0.55)	9.95 (0.57)
Juveniles	13/25	25.90 (8.46)	0/7/1/5	– 15.54 (0.72)	9.68 (0.78)
Males	16/29	36.17 (8.14)	0/12/1/3	– 15.46 (0.48)	10.02 (0.59)
Females	22/35	25.29 (10.48)	2/11/1/8	– 15.26 (0.71)	9.73 (0.68)
Overall	**38/6**	**30.04 (10.90)**	**2/23/2/11**	**– 15.34 (0.62)**	**9.85 (0.65)**

Levene's test was used. One-way ANOVA was used to test whether mean stable isotope values differed significantly among clusters for normally distributed and homogeneous data, whereas Welch's ANOVA, followed by Games-Howell post hoc test, was used when data were normally distributed but heterogeneous. The *t*-test and the Mann–Whitney *U* test were used to test whether δ^{13}C and δ^{15}N values differed significantly between juveniles and adults, males and females, and seasons (spring and autumn). Based on δ^{13}C and δ^{15}N turnover rates in bottlenose dolphin (*Tursiops truncatus*) skin (Giménez et al. 2016), sampling seasons of spring and autumn likely reflect isotopic composition of individuals in winter and summer, respectively.

Dietary sources

Seven social clusters and LF were included in the analysis to investigate the contribution of prey taxa, based on carbon and nitrogen assimilation, to their diet. A set of six Bayesian mixing models with different covariate structures were applied using the MixSIAR package (Stock and Semmens 2016; Stock et al. 2018) in R (R Core Team 2019). The null model considered all individuals in the population to share the same diet, while other fitted models allowed variation in diet according to sex, age (i.e., adult/juvenile), and social cluster membership (Table 4). The covariates of sex and age were modeled as fixed effects and social cluster membership as a random effect. Models with hierarchical structure, where variability according to sex, age, and/or individual within social clusters was allowed, were also considered. These models, however, had convergence issues and are therefore not discussed further.

Table 4 Mixing models fit with MixSIAR on Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) data with 38 consumers (i.e., adult and juvenile dolphins of both sexes) belonging to eight social clusters within an estuarine dolphin population. Covariates "sex," "age," and "sex:age" (i.e., covariate created by combining sex and age) were included as fixed effects and "social cluster" as a random effect. The deviance information criterion (DIC) was used to evaluate relative model fit

Model covariate	DIC
Social cluster	594.49
Sex + age	612.79
Age	613.04
Null	617.86
Sex	618.07
Sex:age	619.28

Dolphin prey species caught in the two basins and rivers within the estuary were pooled by region (i.e., Peel Inlet, Harvey Estuary, Serpentine, and Murray Rivers) to test whether δ^{13}C values varied among regions. Fish muscle δ^{13}C values of fish caught in the Murray River were significantly lower than those from the other regions (Welch's ANOVA, $F_{3,25}$= 9.44, $P<0.01$; Games-Howell post hoc, Murray River – Harvey Estuary T_{32}= 5.08, $P<0.001$; Murray River – Peel Inlet $T_{32}=4.45$, $P<0.001$; Murray River – Serpentine River $T_{27}=3.80$, $P<0.05$). Therefore, for the mixing model, fish caught in the Murray River were considered separate to fish caught in other regions.

To further simplify the mixing space, the blue swimmer crab (*Portunus armatus*) and banded toadfish (*Torquigener pleurogramma*) were removed from source data as they were assumed not to be regularly consumed by dolphins (Barros and Odell 1990; Corkeron et al. 1990; Huisman and Twomey 2008). Sources were aggregated by feeding guild with δ^{13}C and δ^{15}N values of each sample included in the mixing model. Trophic discrimination factor (i.e., difference in the isotopic ratio between consumer and its diet) was set to 1.01

(SD = 0.37) for δ^{13}C and 1.57 (SD = 0.52) for δ^{15}N (Giménez et al. 2016). All mixing models were fitted with generalist (i.e., uninformative) priors with a Dirichlet distribution (i.e., all combinations of the proportions are equally likely) and a multiplicative error term (i.e., process*residual). Markov Chain Monte Carlo simulations were used to estimate the probability, "posterior," distribution of dietary contribution for each source (i.e., the proportional contribution of each fish feeding guild to a social cluster's diet). Three chains were run with their length set to 1,000,000 with a burn-in of 500,000 and thinning of 500. The Gelman-Rubin and Geweke diagnostics, together with visual inspection of the Markov chains, were used to confirm convergence of the models (Gelman et al. 2013). The deviance information criterion (Spiegelhalter et al. 2002) was used to evaluate relative model fit.

Total food intake by the dolphin population

An approximation of annual food intake of the dolphin population was made based on 64 independent individuals (inclusive of two calves orphaned in 2016) being present in the population in 2016 and 2017 (KN, unpublished data). Adults ($n = 39$) were assigned a weight of 200 kg, based on a length–weight curve for coastal *Tursiops truncatus* in North America (Mead and Potter 1990) and the respective asymptotic total lengths of 246 cm and 244 cm estimated for males and females in the Peel-Harvey population (van Aswegen et al. 2019). Sexually immature individuals separated from their mother were considered juveniles ($n = 25$). Based on the estimated length of 187.1 cm (95% CI = 186.5–187.7 cm) for individuals reaching the end of their third year of life (van Aswegen et al. 2019), juveniles in this study would weigh between ~ 90 and 200 kg and were each assigned an average weight of 145 kg. The annual food intake estimation for the population is based on dolphins consuming 5.2–6.3% of their body mass per day (Cheal and Gales 1992).

Results

Behavioral observations

Behavioral surveys were conducted on 483 dolphin groups encountered in the estuary between January 2016 and November 2017. Foraging was identified as the predominant activity in 206 surveys with feeding events observed in a further 30 surveys. These surveys resulted in seventeen species being identified as dolphin prey (Table 1, Online Resource Fig. S1). The most observed species caught by dolphins was the estuary catfish (*Cnidoglanis macrocephalus*, 23%), followed by sea mullet (*Mugil cephalus*, 13%), tarwhine (*Rhabdosargus sarba*, 11%), and western striped grunter (*Pelates octolineatus*, 9%). Garfish (*Hyporhampus* spp.) was observed as prey on four occasions and rock flathead (*Platycephalus laevigatus*) and octopus (*Octopus tetricus*) on one occasion each. These three species were not caught during fish sampling and therefore were not included as sources in the stable isotope mixing model. Of all the prey species identified, 14% were benthic detritivores, 20% herbivores and omnivores, 53% benthic omnivores and carnivores, and 13% water column feeders (Table 2).

The most often observed dolphin foraging tactics were bottom grubbing and peduncle dive foraging, both of which targeted mainly benthic species (Table 1, Online Resource Fig. S2). Dolphins tossing prey primarily involved adult estuary catfish (60%), foraging along or against structures either sea or yelloweye mullet (*Aldrichetta forsteri*), while tail-whacking was mostly associated with sea mullet. Although dolphins were observed to "snack" (i.e., swimming inverted close to the water's surface chasing/capturing fish) on multiple species, garfish was the only species observed to be targeted solely by this tactic (Table 1). Leap and porpoise foraging, where dolphins within a group are moving multi-directionally and continuously leaping or porpoising within an area (Mann and Sargeant 2003), was observed during two surveys. Based on behavioral observations, a combination of benthic omnivores and carnivores and the herbivorous western striped grunter were targeted in 61% of surveys, sea mullet in 16%, (a detritivore) either of the mullet species in 17%, and water column species in 11%. These exceed 100% as during some surveys multiple tactics were used to target different prey species. Birds (*Hydroprogne caspia*, *Thalasseus bergii*, *Croicocephalus novaehollandiae*, and *Pelecanus conspicillatus*) were associated with foraging dolphins in 19% of the surveys.

Space use by social clusters

Overall, the 95% utilization distributions (UDs) of social clusters extended over the basins, entrance channels to the estuary, and into the Serpentine and Murray Rivers (Fig. 2). The 50% UDs, reflecting the core activity space for each cluster, differed among clusters. The core activity space of cluster AF1 comprised Mandurah Channel, while for clusters AM1, JM, and LF, the core activity space was bimodal over both Mandurah and Dawesville channels (Fig. 2). The core activity space for AM2 was primarily in the Peel Inlet and Harvey Estuary, while that for M1 covered nearly the entire Harvey Estuary. The core activity space of AF2 and M2 extended into the rivers (Fig. 2). The probability of individuals of one social cluster being in another social cluster's activity space varied among clusters and was asymmetric (Table 5). For the 95% UDs, probability ranged from 0.27 to 0.92 for different cluster combinations. For the 50% UDs, the probabilities were lower, between 0 and 0.49.

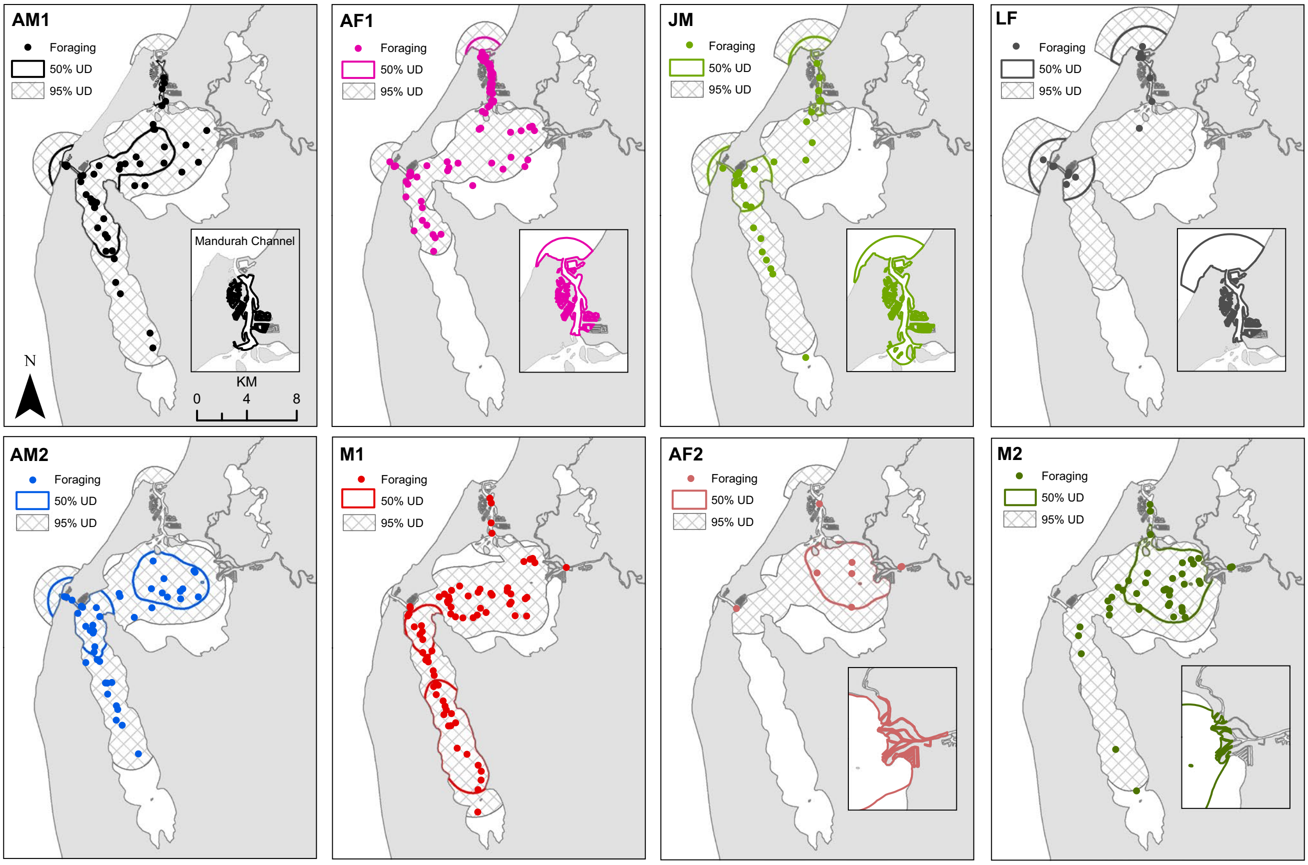

Fig. 2 Core (i.e., 50%) and full (i.e., 95%) utilization distributions (UD) for Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) social clusters, and a lone adult female, resident to the Peel-Harvey Estuary in Western Australia. Points show locations of observed foraging/feeding behavior. Social Clusters: AM1, adult males cluster 1; AM2, adult males cluster 2; AF1, adult females cluster 1; AF2, adult females cluster 2; JM, juvenile males; M1, mixed sex/age cluster 1; M2, mixed sex/age cluster 2; LF, lone adult female

Table 5 Probability of overlap in utilization distribution (UD) of social clusters ($n = 8$) of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) within the Peel-Harvey Estuary, Western Australia. The full UD is a 95% kernel density estimate and the core UD (probability of overlap inside brackets) a 50% kernel density estimate

Social cluster	AM1	AM2	AF1	AF2	JM	M1	M2	LF
Adult male 1 (AM1)	-	0.93 (0.33)	0.87 (0.21)	0.78 (0.02)	0.88 (0.35)	0.90 (0.04)	0.84 (0.09)	0.70 (0.23)
Adult male 2 (AM2)	0.89 (0.33)	-	0.86 (0.00)	0.82 (0.24)	0.84 (0.29)	0.77 (0.03)	0.86 (0.34)	0.67 (0.19)
Adult female 1 (AF1)	0.67 (0.02)	0.70 (0.00)	-	0.77 (0.00)	0.70 (0.13)	0.34 (0.00)	0.70 (0.00)	0.58 (0.13)
Adult female 2 (AF2)	0.54 (0.01)	0.65 (0.14)	0.87 (0.00)	-	0.60 (0.01)	0.27 (0.00)	0.79 (0.33)	0.51 (0.00)
Juvenile male (JM)	0.86 (0.27)	0.81 (0.23)	0.89 (0.49)	0.54 (0.02)	-	0.79 (0.03)	0.59 (0.00)	0.81 (0.36)
Mixed sex/age 1 (M1)	0.82 (0.06)	0.80 (0.05)	0.59 (0.00)	0.64 (0.00)	0.68 (0.06)	-	0.79 (0.00)	0.45 (0.00)
Mixed sex/age 2 (M2)	0.74 (0.06)	0.77 (0.22)	0.65 (0.00)	0.90 (0.41)	0.64 (0.00)	0.79 (0.00)	-	0.42 (0.03)
Lone female (LF)	0.81 (0.21)	0.81 (0.18)	0.92 (0.48)	0.65 (0.00)	0.88 (0.38)	0.47 (0.02)	0.63 (0.00)	-

Isotopic partitioning among social clusters

The δ^{13}C values for dolphin skin tissue ranged from − 16.98 to − 14.15‰ and the δ^{15}N values from 8.09 to 10.88‰ (Fig. 3, Table 3). Mean δ^{13}C values did not differ significantly among social clusters ($F_{5,30} = 0.64$, $P = 0.67$), males and females ($T_{36} = 0.95$, $P > 0.35$), juveniles and adults ($T_{36} = -1.41$, $P = 0.17$), or seasons ($T_{32} = -0.04$, $P = 0.97$). The mean δ^{15}N values were normally distributed within groups ($P > 0.05$) but heteroscedastic (Bartlett's $K\text{-}squared_5 = 13.34$, $P < 0.05$) with statistically significant difference detected in δ^{15}N values among social clusters

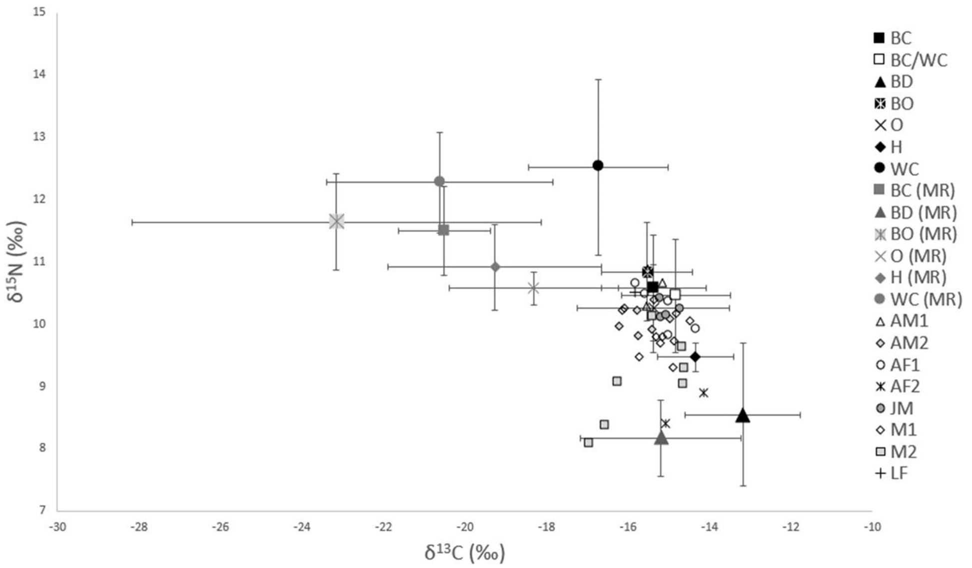

Fig. 3 Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios (mean ± SD, ‰) measured in the skin of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) resident to the Peel-Harvey Estuary in Western Australia and in the muscle of their potential prey species (fish) aggregated by feeding guild. Feeding guilds: BD, benthic detritivore; H, herbivore; O, omnivore; BO, benthic omnivore; BC, benthic carnivore; WC, water column feeder; MR, Murray River (i.e., fish caught in MR). Social clusters: AM1, adult males cluster 1; AM2, adult males cluster 2; AF1, adult females cluster 1; AF2, adult females cluster 2; JM, juvenile males; M1, mixed sex/age cluster 1; M2, mixed sex/age cluster 2; LF, lone adult female

($F_{5,11} = 5.66$, $P < 0.01$). Cluster M2 had significantly lower $\delta^{15}N$ values than clusters AM1, AF1, and JM (post hoc Games-Howell test $P < 0.05$). Individuals in cluster AF2 had the lowest $\delta^{15}N$ values (mean ± SD = 8.65 ± 0.34) for adults. The mean $\delta^{15}N$ values did not significantly differ between males and females ($T_{36} = -1.37$, $P = 0.18$), juveniles and adults ($W = 140$, $P = 0.50$), or between individuals sampled in spring and autumn ($W = 155$, $P = 0.31$).

Dietary sources

The model most supported by the stable isotope data for dolphin and fish prey allowed variation in diet among social clusters (Table 4). Prey feeding guild contributions to dolphin diet were heterogeneous among social clusters (Table 6). The dietary sources of clusters AM1, AF1, JM, and LF consisted mostly of benthic omnivores and carnivores (55.0%, 47.6%, 45.3%, and 45.8%, respectively), while the diet of M2 and AF2 was largely dominated by benthic detritivores (60.9% and 65.4%, respectively). Herbivores and omnivores contributed the second largest proportion to the diet of clusters AM1, AF1, JM, and LF (23.4%, 30.1%, 32.3%, and 28.1%, respectively) while contributing equally with benthic omnivores and carnivores to the diet of clusters M2 and AF2 (herbivores and omnivores, 18.2% and 16.9%; benthic omnivores and carnivores, 16.3% and 14.5%, respectively). Dietary sources of AM2 and M1 consisted of approximately equal proportions of herbivores and omnivores (36.4% and 32.6%, respectively) and benthic omnivores and carnivores (33.9% and 35.5%, respectively) with slightly lower contribution by benthic detritivores (22.5% and 26.0%, respectively). Water column species contributed < 11% to the diet of all social clusters (Table 6). The largest contributors to the diet of social clusters AM2, AF2, M1, and M2 were benthic detritivores caught in the Murray River.

Total food intake by the dolphin population

Considering the proportion of adults ($n = 39$) and juveniles ($n = 25$) in this dolphin population, an average individual was estimated to weigh 179 kg and consume between 3,395 and 4,125 kg annually, with a daily intake of between 9.3 and 11.3 kg. The dolphin population ($n = 64$) was estimated to consume between 217,248 and 263,968 kg of fish annually. Taking into account the number of individuals and their age class, and the proportional contribution of each feeding guild to the diet of each social cluster, the total annual food intake for the population was estimated to comprise 29% benthic detritivores, 29% herbivores and omnivores, 36% benthic omnivores and carnivores, and 6% water column feeders, mostly piscivores.

Table 6 Proportional contribution (largest in bold) of different fish feeding guilds to the diet of eight social clusters of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) resident to the Peel-Harvey Estuary, Western Australia. Notations: Global = the overall dolphin population, *SD* standard deviation, *BD* benthic detritivore, *H* herbivore, *O* omnivore, *BC* benthic carnivore, *BO* benthic omnivore, *WC* water column feeder, *AM* adult males, *AF* adult females, *JM* juvenile males, *M* mix of adult females and Juveniles, *LF* lone female

Feeding guild	Global Mean % (SD)	Dolphin social cluster							
		AM1 Mean % (SD)	AM2 Mean % (SD)	AF1 Mean % (SD)	AF2 Mean % (SD)	JM Mean % (SD)	M1 Mean % (SD)	M2 Mean % (SD)	LF Mean % (SD)
BD	7.9 (6.4)	5.1 (6.9)	6.8 (7.9)	7.4 (9.5)	11.2 (16.7)	7.9 (9.2)	8.4 (10.4)	3.6 (6.5)	6 (8.1)
BD (MR)	17.7 (8.6)	6.4 (6)	**15.7 (10.6)**	7.7 (7.3)	**54.2 (24.6)**	7.7 (7.2)	**17.6 (11.6)**	**57.3 (21.5)**	9.6 (9.5)
H	10.4 (8)	8.3 (10.5)	16 (17.8)	9.8 (12.6)	7.6 (13.1)	15 (15.9)	14.5 (18.8)	5.8 (12.7)	8.4 (11)
H (MR)	3.8 (4.1)	2.4 (4.6)	3.9 (6)	2.5 (4.7)	2 (4.9)	2.2 (3.4)	2.8 (4.4)	3.2 (7.6)	3.8 (7.5)
O	9.4 (7.6)	9.5 (14.5)	10.7 (14.3)	14.4 (21.1)	5.2 (9.8)	12 (16.3)	11.7 (16.8)	6.4 (14.3)	10.9 (16.5)
O (MR)	4.6 (4.9)	3.2 (5.6)	5.8 (8.6)	3.4 (6.9)	2.1 (4.4)	3.1 (5.7)	3.6 (6.3)	2.8 (6.2)	5 (9.5)
BC/WC	11.9 (8.6)	17.2 (20.2)	9.7 (10.7)	**21.7 (23.2)**	5 (7.2)	**17.9 (18.8)**	12.7 (15)	4.5 (5.7)	**13.9 (17.5)**
BC	10.3 (7.9)	16.3 (21.2)	10 (12)	14.6 (20.1)	4.1 (5.7)	12.9 (15.6)	11.7 (15.4)	4.4 (5.9)	13.8 (18.6)
BC (MR)	2.9 (3.3)	1.7 (2.6)	2.6 (3.7)	1.4 (2.2)	1.1 (2.1)	1.5 (2.1)	1.8 (2.7)	1.9 (3.6)	2.6 (4.5)
BO	9.6 (7.4)	**18.7 (22.6)**	9.6 (11.6)	8.8 (11.8)	3.4 (4.4)	12 (13.2)	8 (10.3)	4.2 (5.6)	13.5 (18)
BO (MR)	2.3 (2.9)	1.1 (1.7)	2 (2.9)	1.1 (1.6)	0.9 (1.6)	1 (1.4)	1.3 (2)	1.3 (2.3)	2 (3.7)
WC	5.9 (5)	7.9 (9.8)	4.2 (4.9)	5.1 (6.8)	2 (2.8)	5.1 (6.2)	3.9 (5.2)	2.8 (3.8)	7.2 (9.8)
WC (MR)	3.2 (3.5)	2.2 (3.4)	3.0 (4.2)	2.0 (3.5)	1.2 (2.0)	1.8 (2.6)	2.0 (3.0)	1.8 (3.0)	3.4 (5.6)

Discussion

This study demonstrated spatial and isotopic niche partitioning among social clusters of a population of Indo-Pacific bottlenose dolphins residing in an estuary. Dolphins foraged throughout the Peel-Harvey Estuary using different foraging tactics depending on the prey species they targeted. Both behavioral observations and stable isotope analyses identified demersal fish species as the most important food source for dolphins. Dolphin social clusters varied in their space use within the estuary. Similarity in clusters' core habitat reflected similarity in their diet. Overall, the annual food intake of the dolphin population was estimated to be > 200,000 kg, with detritivores, omnivores and herbivores, and benthic omnivores and carnivores each contributing approximately a third and water column species the remainder of the biomass.

Intra-population partitioning in space use and dietary sources

Detritivores were proportionately the largest (~ 60%) dietary sources for social clusters AF2 (consisting of adult females) and M2 (consisting of adult females and juveniles of both sexes). Detritivores, particularly the cosmopolitan sea mullet (Whitfield et al. 2012), are commonly reported as bottlenose dolphin prey (Gunter 1942; Barros and Odell 1990; Barros and Wells 1998; Simões-Lopes et al. 1998; Fury and Harrison 2011). In this study, sea mullet and Perth herring (*Nematalosa vlaminghi*) represented detritivores in the stable isotope analyses, with sea mullet being targeted more often based on behavioral observations. In the Peel-Harvey Estuary, these species travel up the rivers during the dry season and return to the lower reaches during the wet season (Potter et al. 1983; Loneragan et al., 1986, 1987; Valesini et al. 2009; Gibbs 2011). Both species are found in lower numbers in the estuary basins (Potter et al. 2016). The core activity space of social clusters AF2 and M2 extended from the eastern Peel Inlet into the rivers (Fig. 2, Online Resource Fig. S3) suggesting that overlap in habitat use, and the relative abundance of sea mullet in the rivers, resulted in high proportional contribution of detritivores to the diet of these two clusters.

Mandurah Channel was part of the core activity space for social clusters AF1, AM1, JM, and LF (Fig. 2). The core activity space of clusters AM1, JM, and LF also included the Dawesville Channel. Results from the stable isotope mixing model showed that benthic omnivores and carnivores contributed the most to the diet of these four clusters, which had significantly higher δ^{15}N values than AF2 and M2. Estuary mouths and entrance channels are commonly used by dolphins (e.g., Wilson et al. 1997; Harzen 1998; Stockin et al. 2006; Chabanne et al. 2012) and often host a high diversity and abundance of fish (Loneragan et al. 1986, 1989; Valesini et al. 2009; Potter et al. 2016). The channel habitats in the Peel-Harvey Estuary are highly modified by structures (e.g., jetties, canals, and breakwalls) that function as barriers against which dolphins herd fish, mainly yelloweye and sea mullet (Table 1, Online Resource Fig. S2). Such barriers likely improve foraging efficiency by aiding in prey detection, herding, and manipulation (Heimlich-Boran 1988; Hastie et al. 2003). Given the core activity space of these four clusters also extended slightly to coastal areas, it is likely that their diet is supplemented by prey from the marine food web.

Dietary sources for social clusters AM2 and M1 consisted of approximately equal proportions of herbivores and omnivores, and benthic omnivores and carnivores with slightly lower contribution by detritivores. The core activity spaces of these clusters were in the estuary basins with the activity space of AM2 extending to Dawesville Channel. Unlike clusters AM1, JM, and LF, which also occupied Dawesville Channel, AM2 did not have significantly higher δ^{15}N values than the river-going social clusters. Both AM2 and M1 had a low probability of occupying the core space of AF1, which is effectively the Mandurah Channel (Fig. 2). As such, dietary source partitioning in this population corresponds to the degree to which individuals use the Mandurah Channel or the eastern shores of the estuary including the Serpentine and Murray Rivers. Individuals frequenting the rivers feed at the lowest trophic position for the dolphins, indicating a shorter detritus-based food chain in these regions (i.e., detritus, sea mullet, dolphins). In contrast, individuals using the Mandurah Channel feed at the highest trophic position with several consumer trophic interactions having taken place prior to prey being consumed by dolphins. Individuals that primarily use the estuary basins (i.e., AM2 and M1) fall in between these two opposing trophic positions and reflect the estimated "global" mean dietary source proportions in this population (i.e., an average individual's dietary proportions).

The observed spatial partitioning may lead to individuals being exposed to different pressures and threats which may affect their fitness and consequently population viability. For example, through trophic interactions, dolphins that frequent the riverine habitat (i.e., 19% of the population and 27% of the mature females) may be exposed to algal toxins based on potentially harmful algae recorded in the Serpentine and Murray Rivers (Thomson 2019). Biotoxins may cause immunomodulation in dolphins (Twiner et al. 2011) with harmful algal blooms linked to unusual mortality events (Lefebvre et al. 1999; Flewelling et al. 2005; Fire et al. 2011). In contrast, individuals showing high site fidelity to areas with greater human use (e.g., boating and fishing) such as the Mandurah and Dawesville channels (i.e., 30% of the population and 30% of the mature females) may be more susceptible to disturbance and fishing line entanglements. These individuals also face higher predation risk as they visit coastal waters (KN, unpublished data).

This study did not detect differences in mean isotopic values in dolphin skin tissue between seasons, sexes, or age classes nor did it find support for these factors driving diet variability in this population. Fish abundance and species richness in the Peel-Harvey Estuary change spatially and temporally in response to water quality parameters (e.g., salinity, temperature, and dissolved oxygen: Loneragan et al. 1986, 1987; Valesini et al. 2009), shifts in macroalgal habitat, and external influences from the marine environment (Potter et al. 2016; Valesini et al. 2019). Consequently, dolphin space use and diet may also vary spatially and temporally (e.g., Heithaus and Dill 2002; Zanardo et al. 2017). Given the complexity of trophic interactions and unquantified variation in each individual's resource use over time, the data collected (i.e., individuals were sampled only once) may not detect seasonal variation, even if it existed. Similarly, although δ^{15}N values between juveniles and adults did not differ statistically, ontogenetic shifts in diet and foraging strategies/tactics occur, at least to a degree: juveniles were not observed feeding on adult estuary catfish or Western Australian salmon (*Arripis truttacea*) and did not engage in tail-whacking behavior (KN, unpublished data).

Resource sharing with fishers

The estimated minimum annual food intake of the resident Peel-Harvey Estuary dolphin population (~200,000 kg) exceeds the mean annual finfish biomass removed by commercial fishers in the estuary (Gaughan et al. 2019; Fisher et al. 2020). Commercial fishers target sea mullet (~50–70% of catch), yellowfin whiting (*Sillago schomburgkii*), yelloweye mullet, and to a lesser extent Australian herring (*Arripis georgianus*), Perth herring, tailor (*Pomatomus saltatrix*), and estuary catfish, while recreational fishers, whose total catch is less than commercial landings, mainly target Australian herring, tailor, tarwhine (*Rhabdosargus sarba*), black bream (*Acanthopagrus butcheri*), King George (*Sillago punctatus*), and other whiting species (Gaughan et al. 2019; Government of Western Australia 2015; Fisher et al. 2020). Of these species, sea mullet, yelloweye mullet, estuary catfish, and whiting species (*Sillago* spp.) were identified as common dolphin prey, with sea mullet (and potentially Perth herring) contributing ~30% to the overall dolphin diet. Western striped grunter was a commonly foraged species by dolphins; however, it is not targeted by either commercial or recreational fishers. As such, dolphins target some species that are not taken by fishers while sharing resources to a greater extent with commercial rather than recreational fishers given < 11% of dolphin dietary sources comprised water column species.

Competition between fishers and dolphins may exist only if they overlap spatially and temporally and take the same species at the same life cycle stage. Approximately 14% of the estuary, including Mandurah Channel and the rivers, are closed to commercial fisheries (Government of Western Australia 2015). This reduces potential competition between fishers and dolphins occupying mainly these areas (49% of the population). Although the size of fish taken by dolphins and fishers vary, the overall take of sea mullet, yelloweye mullet, and whiting species, based on observations and life history of the species (Potter et al. 2016), consists largely of immature fish or maturing fish migrating to sea. In contrast, given the legal catch size limits (Fish Resources Management Regulations 1995) for estuary catfish and as all individuals caught by dolphins were > 40 cm (size estimated from photographs against approximate size of dolphin's features such as rostrum or dorsal fin), both fishers and dolphins are primarily removing mature individuals of this species (Nel et al. 1985). Thus, it can be concluded that dolphins and fishers target prey species at the same life cycle stage.

Most fish species targeted by dolphins in the Peel-Harvey Estuary are part of defined stocks that extend outside the estuary and are considered stable and sustainably harvested (Gaughan et al. 2019). An exception may be the estuary catfish for which the Peel-Harvey Estuary is considered a discrete stock from coastal and other estuarine stocks (Nel et al. 1985; Potter et al. 1983; Ayvazian et al. 1994; Gaughan et al. 2019). Given that this species was most commonly observed being caught by dolphins, dolphins and fishers targeting similarly sized individuals and dolphins being the only known predator of adult individuals in the estuary, incorporating mortality due to predation by dolphins in fish population models should be considered to improve fisheries management for this species (Tyrrell et al. 2011; Smith and Lenanton 2021).

The estimated amount of food intake by the dolphin population, and the proportional feeding guild contributions to it, should be treated as an approximate minimum as not all sources of variability or uncertainty were accounted for. For example, it was not considered that food intake may vary seasonally and among individuals (Cheal and Gales 1992). Energetic demands of lactating females are higher than that of non-lactating females (Cheal and Gales 1991; Bejarano et al. 2017), and males may feed on wider variety of species (Hernandez-Milian et al. 2015) and have consistently higher food intakes (Cheal and Gales 1992) and bioenergetic requirements than females (Bejarano et al. 2017). Prey species also vary in their caloric content (McCluskey et al. 2016) with prey selection influencing the amount of fish individuals need to consume to meet their energy demands. Future work should consider applying a bioenergetic model (e.g., Bejarano et al. 2017; Reed et al. 2020) that incorporates uncertainty and variability in individuals' energy demands as well as energy content of prey to refine the estimated annual fish biomass removed by dolphins from the estuary. The prey species and heterogeneity in diet among social clusters identified in the current study can be used to inform such a model.

Ecological role of dolphins in the estuary

Dolphins occupy the role of an apex predator (as defined by Sergio et al. 2014) within the Peel-Harvey Estuary as they feed on fish at all consumer levels while being free from predation risk effects themselves (large sharks are thought to be mostly absent from the estuary). As such, they have the potential to exert top-down pressure on prey populations through both consumption (Leopold 1943; Estes and Duggins 1995; Estes et al. 1998; Ripple and Beschta, 2012; Ripple et al. 2014; Williams et al. 2004) and as agents of intimidation (Lima 1998; Abrams 2000; Brown and Kotler 2004; Morosinotto et al. 2010). Any decline or increase in dolphin abundance or changes in their foraging behavior and diet may influence the trophic structure in the estuary. It is unlikely that dolphins can, through consumption, deplete fish species from this permanently open estuary as the presence and abundance of the main dolphin prey species is directly linked to recruitment from the marine environment (Potter et al. 2016). Exceptions are the estuary catfish and black bream which complete their lifecycle in the estuary (Potter et al. 2016), although the latter was not considered an important dietary source for dolphins. Declines in dolphin abundance may lead to greater food availability for open and deeper water (> 1 m) avian piscivores, which at least partially occupy the same foraging niche to dolphins (Trayler et al. 1989; Stockwell et al. 2021), and consequently their increased abundance. Bottom grubbing, by which dolphins mechanically disturb sediments, was the most observed foraging tactic. Through this behavior, dolphins may influence the benthic microbial and faunal communities (Findlay et al. 1990a, b; Cross and Curran 2000, 2004) and release nutrients into the water column further promoting anoxic conditions (Almroth et al. 2009). However, in comparison to re-suspension of sediments caused by abiotic (e.g., river flow, tidal currents, wind, and waves) and anthropogenic (e.g., dredging) factors (Tweedley et al. 2016), bioturbation by dolphins is likely to be negligible.

Conclusions

This study confirmed spatial and isotopic niche partitioning according to social structure within a resident estuarine bottlenose dolphin population. The heterogeneity in social clusters' space use and diet indicates that individuals may be exposed differently to threats and extrinsic pressures. This has implications for conservation management as maintaining the collective niche of individuals requires consideration of impacts on individuals across social clusters. The annual food intake across consumer trophic levels and the year-round presence of dolphins throughout the estuary has the potential to suppress prey populations and affect community structure through consumptive and non-consumptive pressures. As apex predators, dolphins collectively remove a substantial amount of demersal fish from the system and should be recognized as an important component of the estuarine ecosystem.

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Data availability The datasets and R code used for analyses in this study are available in the GitHub repository GitHub-KristaNicholson/Niche-partitioning-among-social-clusters-of-a-resident-estuarine-apex-predator.

Declarations

Ethics approval All applicable international, national, and institutional guidelines for the use of animals were followed. Dolphin research was carried out under research permit from the Government of Western Australia Department of Biodiversity, Conservation and Attractions (08–000880-2, 08–000880-3, SF010738) and the Commonwealth of Australia Department of Environment (2015–0004, AU-COM2015-293) with an animal ethics permit from Murdoch University, Western Australia (R2649/14, R2945/17). Fish collection was carried out as part of Australian Research Council Linkage project LP150100451, under WA Department of Fisheries exemption permit 2753.

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Conflict of interest The authors declare no competing interests.

References

Abrams PA (2000) The evolution of predator-prey interactions: theory and evidence. Annu Rev Ecol Syst 31:79–105

Ale SB, Whelan CJ (2008) Reappraisal of the role of big, fierce predators! Biodivers Conserv 17:685–690

Allen SJ, Bejder L, Krützen M (2011) Why do Indo-Pacific bottlenose dolphins (*Tursiops* sp.) carry conch shells (*Turbinella* sp.) in Shark Bay, Western Australia? Mar Mamm Sci 27:449–454

Almroth E, Tengberg A, Andersson JH, Pakhomova S, Hall PO (2009) Effects of resuspension on benthic fluxes of oxygen, nutrients, dissolved inorganic carbon, iron and manganese in the Gulf of Finland, Baltic Sea. Cont Shelf Res 29:807–818

Amir OA, Berggren P, Ndaro SG, Jiddawi NS (2005) Feeding ecology of the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) incidentally caught in the gillnet fisheries off Zanzibar, Tanzania. Estuar Coast Shelf Sci 63:429–437

Ayvazian S, Johnson M, McGlashan D (1994) High levels of genetic subdivision of marine and estuarine populations of the estuarine catfish Cnidoglanis macrocephalus (Plotosidae) in southwestern Australia. Mar Biol 118:25–31

Barros N, Odell D (1990) Food habits of bottlenose dolphins in the southeastern United States. In: Leatherwood S, Randall RR (eds) The bottlenose dolphin. Academic Press, San Diego, pp 309–328

Barros NB, Ostrom PH, Stricker CA, Wells RS (2010) Stable isotopes differentiate bottlenose dolphins off west-central Florida. Mar Mamm Sci 26:324–336

Barros NB, Wells RS (1998) Prey and feeding patterns of resident bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. J Mammal 79:1045–1059

Barry RP, McIntyre J (2011) Estimating animal densities and home range in regions with irregular boundaries and holes: a lattice-based alternative to the kernel density estimator. Ecol Model 222:1666–1672

Bejarano AC, Wells RS, Costa DP (2017) Development of a bioenergetic model for estimating energy requirements and prey biomass consumption of the bottlenose dolphin *Tursiops truncatus*. Ecol Model 356:162–172

Bianchi TS (2006) Biochemistry of Estuaries. Oxford University Press, Oxford

Bolnick DI (2001) Intraspecific competition favours niche width expansion in *Drosophila melanogaster*. Nature 410:463–466

Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. Am Nat 161:1–28

Bowen W (1997) Role of marine mammals in aquatic ecosystems. Mar Ecol Prog Ser 158:267–274

Brown JS, Kotler BP (2004) Hazardous duty pay and the foraging cost of predation. Ecol Lett 7:999–1014

Brown JS, Laundré JW, Gurung M (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. J Mammal 80:385–399

Calenge C (2015) Home range estimation in R: the adehabitatHR package, https://mran.microsoft.com/snapshot/2017-12-11/web/packages/adehabitatHR/vignettes/adehabitatHR.pdf

Chabanne D, Finn H, Salgado-Kent C, Bedjer L (2012) Identification of a resident community of bottlenose dolphins (*Tursiops aduncus*) in the Swan Canning Riverpark, Western Australia, using behavioural information. Pac Conserv Biol 18:247–262

Chabanne DB, Finn H, Bejder L (2017) Identifying the relevant local population for Environmental Impact Assessments of mobile marine fauna. Front Mar Sci 4:148

Cheal AJ, Gales NJ (1991) Body mass and food intake in captive, breeding bottlenose dolphins, *Tursiops truncatus*. Zoo Biol 10:451–456

Cheal AJ, Gales NJ (1992) Growth, sexual maturity and food-intake of Australian Indian-Ocean bottle-nosed dolphins, *Tursiops truncatus*, in captivity. Aust J Zool 40:215–223

Chilvers LB, Corkeron PJ (2001) Trawling and bottlenose dolphins' social structure. Proc R Soc Lond B 268:1901–1905

Cockcroft V, Ross G (1990) Food and feeding of the Indian Ocean bottlenose dolphin off southern Natal, South Africa. In: Leatherwood S, Randall RR (eds) The bottlenose dolphin. Academic Press, San Diego, pp 295–308

Connor RC, Smolker RA, Richards AF (1992) Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). P Natl Acad Sci USA 89:987–990

Corkeron PJ, Bryden M, Hedstrom K (1990) Feeding by bottlenose dolphins in association with trawling operations in Moreton Bay, Australia. In: Leatherwood S, Randall RR (eds) The bottlenose dolphin. Academic Press, San Diego, pp 329–336

Cross R, Curran M (2000) Effects of feeding pit formation by rays on an intertidal meiobenthic community. Estuar Coast Shelf Sci 51:293–298

Cross RE, Curran MC (2004) Recovery of meiofauna in intertidal feeding pits created by rays. Southeast Nat 3:219–230

Darimont C, Price M, Winchester N, Gordon-Walker J, Paquet P (2004) Predators in natural fragments: foraging ecology of wolves in British Columbia's central and north coast archipelago. J Biogeogr 31:1867–1877

de Lecea AM, de Charmoy L (2015) Chemical lipid extraction or mathematical isotope correction models: should mathematical models be widely applied to marine species? Rapid Commun Mass Sp 29:2013–2025

Elton C (1927) Animal ecology. Sidgwick and Jackson Ltd, London

Epanechnikov VA (1969) Non-parametric estimation of a multivariate probability density. Theory Probab Appl 14:153–158

Estes JA, Duggins DO (1995) Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. Ecol Monogr 65:75–100

Estes JA, Tinker MT, Williams TM, Doak DF (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282:473–476

Findlay RH, Trexler MB, Guckert JB, White DC (1990a) Laboratory study of disturbance in marine sediments: response of a microbial community. Mar Ecol Prog Ser 62:121–133

Findlay RH, Trexler MB, White DC (1990b) Response of a benthic microbial community to biotic disturbance. Mar Ecol Prog Ser 62:135–148

Finn H, Donaldson R, Calver M (2008) Feeding flipper: a case study of a human-dolphin interaction. Pac Conserv Biol 14:215–225

Fire SE, Wang Z, Byrd M, Whitehead HR, Paternoster J, Morton SL (2011) Co-occurrence of multiple classes of harmful algal toxins in bottlenose dolphins (*Tursiops truncatus*) stranding during an unusual mortality event in Texas, USA. Harmful Algae 10:330–336

Fish Resources Management Regulations (1995) (WA) https://www.legislation.wa.gov.au/legislation/statutes.nsf/law_s4447_currencies.html#:~:text=%20%20%20%20Consolidated%20Versions%20%20,%20%2014-e0-02%20%2017%20more%20rows%20

Fisher EA, Evans SN, Desfosses CJ, Johnston DJ, Duffy R, Smith KA (2020) Ecological risk assessment for the Peel-Harvey Estuarine Fishery. Fisheries Research Report No. 311. Department of Primary Industries and Regional Development, Perth, WA

Flewelling LJ, Naar JP, Abbott JP et al (2005) Red tides and marine mammal mortalities. Nature 435:755–756

Froese R, Pauly D (2019) Fishbase, www.fishbase.in

Fury CA, Harrison PL (2008) Abundance, site fidelity and range patterns of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in two Australian subtropical estuaries. Mar Freshw Res 59:1015–1027

Fury CA, Harrison PL (2011) Seasonal variation and tidal influences on estuarine use by bottlenose dolphins (*Tursiops aduncus*). Estuar Coast Shelf Sci 93:389–395

Galezo AA, Foroughirad V, Krzyszczyk E, Frère CH, Mann J (2020) Juvenile social dynamics reflect adult reproductive strategies in bottlenose dolphins. Behav Ecol 31:1159–1171

Gaughan D, Molony B, Santoro K (2019) Status reports of the Fisheries and Aquatic Resources of Western Australia 2017/18: The State of the Fisheries. Department of Primary Industries and Regional Development, Western Australia

Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin DB (2013) Bayesian data analysis. Chapman and Hall/CRC Press, Boca Raton

Genov T, Centrih T, Kotnjek P, Hace A (2019) Behavioural and temporal partitioning of dolphin social groups in the northern Adriatic Sea. Mar Biol 166:11

Gero S, Bejder L, Whitehead H, Mann J, Connor RC (2005) Behaviourally specific preferred associations in bottlenose dolphins, Tursiops spp. Can J Zool 83:1566–1573

Gibbs M (2011) An Aboriginal fish trap on the Swan Coastal Plain: the Barragup mungah. Rec West Aust Mus Suppl 79:4–15

Gibbs SE, Harcourt RG, Kemper CM (2011) Niche differentiation of bottlenose dolphin species in South Australia revealed by stable isotopes and stomach contents. Wildlife Res 38:261–270

Giménez J, Ramírez F, Almunia J, Forero MG, de Stephanis R (2016) From the pool to the sea: applicable isotope turnover rates and diet to skin discrimination factors for bottlenose dolphins (*Tursiops truncatus*). J Exp Mar Biol Ecol 475:54–61

Government of Western Australia (2015) Finfish resources of the Peel-Harvey Estuary, Harvest strategy 2015-2020. Fisheries management paper 274. Department of Fisheries, Perth

Grinell J (1917) The niche relationship of California thrasher. Auk 1:64–82

Gunter G (1942) Contributions to the natural history of the bottlenose dolphin, *Tursiops truncatus* (Montague), on the Texas coast, with particular reference to food habits. J Mammal 23:267–276

Hale J, Butcher R (2007) Ecological character description of the Peel-Yalgorup Ramsar site. A report to the Department of Environment and Conservation and the Peel-Harvey Catchment Council, Perth, WA

Hale J, Kobryn H (2009) Peel-Yalgorup Ramsar wetlands monitoring: littoral & fringing vegetation mapping. A report to Department of Environment and Conservation, Perth

Hallett C, Valesini F, Yeoh D (2019) Assessing the health of the Peel-Harvey Estuary through its fish communities. ARC Linkage Project LP150100451. Unpublished report, Murdoch University, Murdoch, WA

Harzen S (1998) Habitat use by the bottlenosed dolphin (*Tursiops truncatus*) in the Sado Estuary, Portugal. Aquat Mamm 24:117–128

Hastie GD, Wilson B, Thompson PM (2003) Fine-scale habitat selection by coastal bottlenose dolphins: application of a new land-based video-montage technique. Can J Zool 81:469–478

Heimlich-Boran JR (1988) Behavioral ecology of killer whales (*Orcinus orca*) in the Pacific Northwest. Can J Zool 66:565–578

Heithaus MR, Dill LM (2002) Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83:480–491

Heithaus MR, Wirsing AJ, Burkholder D, Thomson J, Dill LM (2009) Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. J Anim Ecol 78:556–562

Hernandez-Milian G, Berrow S, Santos MB, Reid D, Rogan E (2015) Insights into the trophic ecology of bottlenose dolphins (*Tursiops truncatus*) in Irish waters. Aquat Mamm 41:226–239

Huisman J, Twomey L (2008) The black Swan: investigating the estuary after dark. Landscope 23:46–51

Hutchinson GE (1957) Concluding remarks. Cold Spring Harb Symp Quant Biol 22:415–427

Krumholz O (2019) Macrophyte communities in the Peel-Harvey Estuary: historical trends and current patterns in biomass and distribution. Dissertation, Murdoch University

Krützen M, Barré LM, Möller LM, Heithaus MR, Simms C, Sherwin WB (2002) A biopsy system for small cetaceans: darting success and wound healing in *Tursiops* spp. Mar Mamm Sci 18:863–878

Krützen M, Kreicker S, MacLeod CD, Learmonth J, Kopps AM, Walsham P, Allen SJ (2014) Cultural transmission of tool use by Indo-Pacific bottlenose dolphins (Tursiops sp.) provides access to a novel foraging niche. Proc R Soc B 281:20140374

Laundré JW, Hernández L, Ripple WJ (2010) The landscape of fear: ecological implications of being afraid. Open Ecol J 3:1–7

Lefebvre KA, Powell CL, Busman M et al (1999) Detection of domoic acid in northern anchovies and California sea lions associated with an unusual mortality event. Nat Toxins 7:85–92

Leopold A (1943) Deer irruptions. Trans Wis Acad Sci Arts Lett 35:351–366

Lima SL (1998) Nonlethal effects in the ecology of predator-prey interactions. Bioscience 48:25–34

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Logan JM, Jardine TD, Miller TJ, Bunn SE, Cunjak RA, Lutcavage ME (2008) Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. J Anim Ecol 77:838–846

Loneragan N, Potter I, Lenanton R, Caputi N (1986) Spatial and seasonal differences in the fish fauna in the shallows of a large Australian estuary. Mar Biol 92:575–586

Loneragan N, Potter I, Lenanton R, Caputi N (1987) Influence of environmental variables on the fish fauna of the deeper waters of a large Australian estuary. Mar Biol 94:631–641

Lusseau D, Schneider K, Boisseau OJ, Haase P, Slooten E, Dawson SM (2003) The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations. Behav Ecol Sociobiol 54:396–405

MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. Am Nat 100:603–609

Mann J (1999) Behavioral sampling methods for cetaceans: a review and critique. Mar Mamm Sci 15:102–122

Mann J, Sargeant B (2003) Like mother, like calf: the ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (*Tursiops* sp.). In: Fragaszy DM, Perry S (eds) The biology of traditions: models and evidence. Cambridge University Press, Cambridge, pp 236–266

Matich P, Heithaus MR (2014) Multi-tissue stable isotope analysis and acoustic telemetry reveal seasonal variability in the trophic interactions of juvenile bull sharks in a coastal estuary. J Anim Ecol 83:199–213

McCabe EJB, Gannon DP, Barros NB, Wells RS (2010) Prey selection by resident common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. Mar Biol 157:931–942

McCluskey SM, Bejder L, Loneragan N (2016) Dolphin prey availability and calorific value in an estuarine and coastal environment. Front Mar Sci 3:30

Mead J, Potter C (1990) Natural history of bottle nose dolphins along the central Atlantic coast of the United States. In: Leatherwood S, Randall RR (eds) The bottlenose dolphin. Academic Press, San Diego, pp 165–195

Morosinotto C, Thomson RL, Korpimäki E (2010) Habitat selection as an antipredator behaviour in a multi-predator landscape: all enemies are not equal. J Anim Ecol 79:327–333

Nel S, Potter I, Loneragan N (1985) The biology of the catfish Cnidoglanis macrocephalus (Plotosidae) in an Australian estuary. Estuar Coast Shelf Sci 21:895–909

Nerini M (1984) A review of gray whale feeding ecology. In: Jones ML, Swartz SL, Leatherwood S (eds) The gray whale, *Eschrichtius robustus*. Academic Press, London, pp 423–450

Newsome SD, Koch PL, Etnier MA, Aurioles-Gamboa D (2006) Using carbon and nitrogen isotope values to investigate maternal strategies in northeast Pacific otariids. Mar Mamm Sci 22:556–572

Oliver JS, Kvitek RG, Slattery PN (1985) Walrus feeding disturbance: scavenging habits and recolonization of the Bering Sea benthos. J Exp Mar Biol Ecol 91:233–246

Oliver JS, Slattery PN (1985) Destruction and opportunity on the sea floor: effects of gray whale feeding. Ecology 66:1965–1975

Ostfeld RS (1986) Territoriality and mating system of California voles. J Anim Ecol 55:691–706

Patterson EM, Mann J (2011) The ecological conditions that favor tool use and innovation in wild bottlenose dolphins (Tursiops sp.). PLoS One 6:e22243

Potter IC, Loneragan NR, Lenanton RCJ, Chrystal PJ, Grant CJ (1983) Abundance, distribution and age structure of fish populations in a Western Australian estuary. J Zool 200:21–50

Potter IC, Veale L, Tweedley JR, Clarke KR (2016) Decadal changes in the ichthyofauna of a eutrophic estuary following a remedial engineering modification and subsequent environmental shifts. Estuar Coast Shelf Sci 181:345–363

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, https://www.R-project.org/

Reed J, Harcourt R, New L, Bilgmann K (2020) Extreme effects of extreme disturbances: a simulation approach to assess population specific responses. Front Mar Sci 7:519845

Ripple WJ, Beschta RL (2012) Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. Biol Conserv 145:205–213

Ripple WJ, Estes JA, Beschta RL et al (2014) Status and ecological effects of the world's largest carnivores. Science 343:1241484

Roman J, McCarthy JJ (2010) The whale pump: marine mammals enhance primary productivity in a coastal basin. PLoS One 5:e13255

Rossman S, Ostrom PH, Stolen M, Barros NB, Gandhi H, Stricker CA, Wells RS (2015) Individual specialization in the foraging habits of female bottlenose dolphins living in a trophically diverse and habitat rich estuary. Oecologia 178:415–425

Sargeant BL, Mann J, Berggren P, Krützen M (2005) Specialization and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (*Tursiops* sp.). Can J Zool 83:1400–1410

Sargeant BL, Wirsing AJ, Heithaus MR, Mann J (2007) Can environmental heterogeneity explain individual foraging variation in wild bottlenose dolphins (*Tursiops* sp.)? Behav Ecol Sociobiol 61:679–688

Schmitz OJ (2010) Resolving ecosystem complexity (MPB-47). Princeton University Press, UK

Scott MD, Wells RS, Irvine AB (1990) A long-term study of bottlenose dolphins on the west coast of Florida. In: Leatherwood S, Randall RR (eds) The bottlenose dolphin. Academic Press, San Diego, pp 235–244

Semmens BX, Ward EJ, Moore JW, Darimont CT (2009) Quantifying inter-and intra-population niche variability using hierarchical Bayesian stable isotope mixing models. PLoS One 4:e6187

Senigaglia V, Christiansen F, Sprogis KR, Symons J, Bejder L (2019) Food-provisioning negatively affects calf survival and female reproductive success in bottlenose dolphins. Sci Rep 9:8981

Sergio F, Schmitz OJ, Krebs CJ, Holt RD, Heithaus MR, Wirsing AJ, Ripple WJ, Ritchie E, Ainley D, Oro D (2014) Towards a cohesive, holistic view of top predation: a definition, synthesis and perspective. Oikos 123:1234–1243

Shane SH (1990) Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. In: Leatherwood S, Randall RR (eds) The bottlenose dolphin. Academic Press, San Diego, pp 267–283

Silverman BW (1986) Density estimation for statistics and data analysis. Chapman and Hall, London

Simões-Lopes PC, Fabián ME, Menegheti JO (1998) Dolphin interactions with the mullet artisanal fishing on southern Brazil: a qualitative and quantitative approach. Rev Bras Zool 15:709–726

Skrzypek G, Paul D (2006) δ13C analyses of calcium carbonate: comparison between the GasBench and elemental analyzer techniques. Rapid Commun Mass Sp 20:2915–2920

Smith H, Sprogis K (2016) Seasonal feeding on giant cuttlefish (*Sepia apama*) by Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in south-western Australia. Aust J Zool 64:8–13

Smith KA, Lenanton RCJ (2021) Almost forgotten: historical abundance of eel-tail catfish populations in south-western Australian estuaries and their decline due to habitat loss and historical overfishing. Reg Stud Mar Sci 41:101605

Smolker RA, Richards AF, Connor RC, Pepper JW (1992) Sex differences in patterns of association among Indian Ocean bottlenose dolphins. Behaviour 123:38–69

Spiegelhalter DJ, Best NG, Carlin BR, van der Linde A (2002) Bayesian measures of model complexity and fit. J Roy Stat Soc B Met 64:583–616

Sprogis KR, Raudino HC, Hocking D, Bejder L (2017) Complex prey handling of octopus by bottlenose dolphins (*Tursiops aduncus*). Mar Mamm Sci 33:934–945

Sprogis KR, Raudino HC, Rankin R, MacLeod CD, Bejder L (2016) Home range size of adult Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in a coastal and estuarine system is habitat and sex-specific. Mar Mamm Sci 32:287–308

Stock BC, Semmens BX (2016) MixSIAR GUI User Manual, Version 3.1, https://github.com/brianstock/MixSIAR

Stock BC, Jackson AL, Ward EJ, Parnell AC, Phillips DL, Semmens BX (2018) Analyzing mixing systems using a new generation of Bayesian tracer mixing models. PeerJ 6:e5096

Stockin KA, Weir CR, Pierce GJ (2006) Examining the importance of Aberdeenshire (UK) coastal waters for North Sea bottlenose dolphins (*Tursiops truncatus*). J Mar Biol Ass UK 86:201–207

Stockwell S, Greenwell CJ, Dunlop JN, Loneragan NR (2021) Distribution and foraging by non-breeding Caspian Terns on a large temperate estuary of south-western Australia - preliminary investigations. Pac Conserv Biol (published online, https://doi.org/10.1071/PC20082)

Svanbäck R, Bolnick DI (2007) Intraspecific competition drives increased resource use diversity within a natural population. Proc R Soc Lond B 274:839–844

Thomson C (2019) Regional Estuaries Initiative, Estuary Condition Report: Peel-Harvey 2016/17. Department of Water and Enviromental Regulation, Perth

Torres LG, Read AJ (2009) Where to catch a fish? The influence of foraging tactics on the ecology of bottlenose dolphins (*Tursiops truncatus*) in Florida Bay, Florida. Mar Mamm Sci 25:797–815

Trayler K, Brothers D, Wooller R, Potter I (1989) Opportunistic foraging by three species of cormorants in an Australian estuary. J Zool 218:87–98

Tweedley JR, Warwick RM, Potter IC (2016) The contrasting ecology of temperate macrotidal and microtidal estuaries. Oceanogr Mar Biol 54:73–79

Twiner MJ, Fire S, Schwacke L, Davidson L, Wang Z, Morton S, Roth S, Balmer B, Rowles TK, Wells RS (2011) Concurrent exposure of bottlenose dolphins (*Tursiops truncatus*) to multiple algal toxins in Sarasota Bay, Florida, USA. PLoS One 6:e17394

Tyrrell M, Link J, Moustahfid H (2011) The importance of including predation in fish population models: implications for biological reference points. Fish Res 108:1–8

Urian KW, Hofmann S, Wells RS, Read AJ (2009) Fine-scale population structure of bottlenose dolphins (*Tursiops truncatus*) in Tampa Bay, Florida. Mar Mamm Sci 25:619–638

Urian KW, Waples DM, Tyson RB, Hodge LE, Read AJ (2014) Abundance of bottlenose dolphins (*Tursiops truncatus*) in estuarine and near-shore waters of North Carolina, USA. J North Carolina Acad Sci 129:165–171

Valesini FJ, Coen NJ, Wildsmith MD, Hourston M, Tweedley JR, Hallett CS, Linke TE, Potter IC (2009) Relationships between fish faunas and habitat type in south-western Australian estuaries. Fisheries Research and Development Corporation Final Report, Perth

Valesini FJ, Hallett CS, Hipsey MR, Kilminster KL, Huang P, Hennig K (2019) Peel-Harvey Estuary, Western Australia. In: Wolanski E, Day JW, Elliott M, Ramachandran R (eds) Coasts and Estuaries. Elsevier, Burlington, pp 103–120

van Aswegen M, Christiansen F, Symons J, Mann J, Nicholson K, Sprogis K, Bejder L (2019) Morphological differences between coastal bottlenose dolphin (*Tursiops aduncus*) populations identified using non-invasive stereo-laser photogrammetry. Sci Rep 9:12235

Whitfield A, Panfili J, Durand J-D (2012) A global review of the cosmopolitan flathead mullet *Mugil cephalus* Linnaeus 1758 (Teleostei: Mugilidae), with emphasis on the biology, genetics, ecology and fisheries aspects of this apparent species complex. Rev Fish Biol Fish 22:641–681

Wildsmith M, Rose T, Potter I, Warwick R, Clarke K, Valesini F (2009) Changes in the benthic macroinvertebrate fauna of a large microtidal estuary following extreme modifications aimed at reducing eutrophication. Mar Pollut Bull 58:1250–1262

Williams TM, Estes JA, Doak DF, Springer AM (2004) Killer appetites: assessing the role of predators in ecological communities. Ecology 85:3373–3384

Wilson B, Thompson P, Hammond P (1997) Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. J Appl Ecol 34:1365–1374

Wirsing AJ, Heithaus MR, Frid A, Dill LM (2008) Seascapes of fear: evaluating sublethal predator effects experienced and generated by marine mammals. Mar Mamm Sci 24:1–15

Wiszniewski J, Allen SJ, Möller LM (2009) Social cohesion in a hierarchically structured embayment population of Indo-Pacific bottlenose dolphins. Anim Behav 77:1449–1457

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168

Würsig B, Würsig M (1977) The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). Science 198:755–756

Zanardo N, Parra GJ, Passadore C, Möller LM (2017) Ensemble modelling of southern Australian bottlenose dolphin *Tursiops* sp. distribution reveals important habitats and their potential ecological function. Mar Ecol Prog Ser 569:253–266

Zolman ES (2002) Residence patterns of bottlenose dolphins (*Tursiops truncatus*) in the Stono River estuary, Charleston County, South Carolina, USA. Mar Mamm Sci 18:879–892