

Using stable-isotope analysis and acoustic telemetry data to infer broad-scale migration patterns of Port Jackson sharks (*Heterodontus portusjacksoni*)

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ABSTRACT

Context. Understanding migratory species' habitat selection is complicated by variation in movement strategies. Stable-isotope analysis provides a powerful tool to investigate such variation. **Aims.** We used acoustic telemetry and stable-isotope analysis to better understand the movement strategies of Port Jackson sharks. **Methods.** We compared the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of fin tissue from acoustically tracked individuals that undertook three distinct movement strategies. Hierarchical cluster analysis was then used to cluster movement strategies of a larger sample of sharks on the basis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. **Key results.** Tracked individuals that remained in Jervis Bay were enriched in ^{13}C , compared with those that migrated south after the breeding season. Individuals were assigned to six clusters and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values indicated that migrating males and females may utilise different geographical areas or niches during the non-breeding season. **Conclusions.** By using stable isotope analysis and acoustic telemetry, we identified distinct groups of Port Jackson sharks with similar broad-scale movement strategies. **Implications.** These variable movement strategies may lead to different reproductive fitness advantages on an individual and population level, having implications for the broader ecosystem, given the important role mesopredators play in southern reef marine ecosystems.

Keywords: acoustic tracking, differential migration, dispersal, ecology, elasmobranchs, isotopes, marine, movement, stable isotopes.

Introduction

The life histories of species that undertake broadscale migrations are influenced by the complex interaction between the abiotic and biotic factors at breeding grounds, non-breeding sites and during migration. The non-breeding phase of the reproductive cycle plays an important role in influencing population dynamics through its relative effect on individual survival, condition and future reproductive success (e.g. Saino *et al.* 2004; Leyrer *et al.* 2013; Goodenough *et al.* 2017). Several physiological, behavioural and life-history-related traits that influence breeding phenology and investment are shaped by the selective pressures operating while individuals are at non-breeding sites. For example, Goodenough *et al.* (2017) found that pied flycatchers (*Ficedula hypoleuca*) that overwintered in more mesic habitats with moderate moisture levels (identified by lower $\delta^{13}\text{C}$ values) had higher levels of breeding success in terms of clutch size, number of young to hatch and number of young to fledge. Studying among-individual variation in non-breeding site selection and its effects on reproductive fitness is essential for a comprehensive understanding of the movement ecology of a species at the population level.

Discerning the non-breeding habitats or locations of marine species that exhibit broadscale migrations can be particularly challenging, given their cryptic nature, vast scales of movement and the medium in which they live. Although electronic tagging, such as acoustic telemetry, archival tags and satellite telemetry can provide detailed insights into animal movement behaviours (Hussey *et al.* 2015), equipment costs can be prohibitive, they can often be expensive to deploy and maintain, are not applicable to

all species or study areas and are often limited by sample size (Sequeira et al. 2019). Further, for acoustic telemetry to generate useful data, tagged individuals must utilise geographical areas and habitats that are monitored by acoustic receivers. Alternatively, methods that allow the retrospective tracking of individuals through the analyses of minor invasive tissue sampling, such as stable isotopes (e.g. Madigan et al. 2018a) and fatty acids (e.g. Cárdenas-Palomo et al. 2018), provide a more economically viable approach that allows investigation of behaviour of large numbers of individuals that may be more reflective of overall population dynamics (Chapman et al. 2015; Madigan et al. 2018b). Analysis of these naturally occurring biochemical markers in tissues can be used to answer questions pertaining to broad-scale movement and migration patterns of individuals (Rubenstein and Hobson 2004; Hussey et al. 2012), discerning residency areas such as overwintering habitat for migratory bird species (Steenweg et al. 2017) and can show population-level variation in past movements (Madigan et al. 2014, 2021).

The application of bulk stable-isotope analysis to investigate movement is based on the premise that variations in biogeochemical processes in spatially distinct areas, i.e. those that have isotopically different baseline $\delta^{13}\text{C}$ values (or in specific cases $\delta^{15}\text{N}$ values; Madigan et al. 2021), are reflected in the tissues of consumers that forage on prey resident in those areas (DeNiro and Epstein 1978, 1981). Isotopic turnover rates differ among tissue types; consequently, tissue selection or the use of multiple tissues is an important consideration for stable-isotope studies of movement–foraging ecology. For example, muscle and cartilage from fin tissue of elasmobranchs has a relatively long estimated isotopic turnover rate and can be used to examine long-term integrated movement patterns, whereas plasma has a relatively shorter isotopic turnover rate, which can be used to investigate seasonal movement patterns (MacNeil et al. 2006; Logan and Lutcavage 2010; Matich et al. 2011; Hussey et al. 2012; Kim et al. 2012). Further, given that only a small tissue sample is needed, it is a minor-invasive and powerful tool to study the movements of cryptic and vulnerable species (Hammerschlag and Sulikowski 2011; Hussey et al. 2012).

Ecological studies from a wide range of taxa typically use the conservative fractionation of carbon isotopes (i.e. $\delta^{13}\text{C}$; $\sim 1\%$) to examine where an individual forages (e.g. Couturier et al. 2013) because ^{13}C can vary between benthic and pelagic habitats (France 1995) and is influenced by marine, freshwater and terrestrial inputs (Fry and Sherr 1989), whereas the marked fractionation of nitrogen isotopes (i.e. $\delta^{15}\text{N}$; 3.4‰) is typically used to estimate trophic position and to examine food-web structure (Hobson 1999; Hussey et al. 2012, 2014; but see Madigan et al. 2018b for system-specific applications of $\delta^{15}\text{N}$). In the marine environment, stable-isotope analysis has been successfully employed to reconstruct the movement ecology of seabirds (e.g. Votier et al. 2010),

fishes (e.g. Matley et al. 2017), mammals (e.g. Aurioles et al. 2006) and elasmobranchs (e.g. Abrantes and Barnett 2011; Hussey et al. 2011a; French et al. 2018). Specifically, variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of shark tissues has allowed inference on broad-scale movement patterns (Hussey et al. 2011a), movements of individuals among distinct habitats (Abrantes and Barnett 2011; Hussey et al. 2011a), as well as sexual (Abrantes and Barnett 2011; French et al. 2018) or ontogenetic segregation (Nielsen et al. 2019; Di Lorenzo et al. 2020). However, the majority of these studies have focused on large, apex-predator species, identifying a need for more focused effort to understand smaller, benthic elasmobranch species (Simpfendorfer and Heupel 2012). These smaller, benthic species, which often occupy mesopredator roles in marine ecosystems, play an important role in linking lower and upper trophic levels as both predators and prey (Ritchie and Johnson 2009). Studying the movement ecology of these species can have important implications not only at the species level, but also for the communities in which they live (Ritchie and Johnson 2009).

Port Jackson shark (*Heterodontus portusjacksoni*) is a benthic shark species that acts as a tertiary consumer in temperate ecosystems confined to the southern coast of the Australian continent (Powter et al. 2010). Given the assumed important ecological role of adult Port Jackson sharks, as well as their high abundance and high levels of site fidelity, coupled with broad-scale migrations along the Australian coastline (Bass et al. 2017), they represent a useful model species to develop a greater understanding of the role of mesopredators in linking spatially distinct temperate marine ecosystems. Stomach content and fatty acid analyses have been used to quantify the diets of Port Jackson sharks throughout their distribution (Powter et al. 2010; Sommerville et al. 2011; Beckmann 2014), showing significant differences in foraging among regions and by size class. Sommerville et al. (2011) and Powter et al. (2010) noted an ontogenetic shift in the diet of Port Jackson sharks, which Powter et al. (2010) attributed to a shift in ecological role from secondary consumers as juveniles and subadults to tertiary consumers as adults. There have been no *in situ* studies using stable-isotope analysis to examine the foraging behaviour or movements of Port Jackson sharks. Combining acoustic-telemetry tracking of individuals (Speed et al. 2012; Matich and Heithaus 2014) with stable-isotope analysis of tagged and non-tagged individuals by using analytical approaches such as cluster analysis (Hobson 1999) has the potential to further our understanding of the movement ecology of mesopredatory elasmobranch species.

Here, we used stable-isotope analysis of fin tissue of a large sample of Port Jackson sharks in conjunction with an extensive acoustic telemetry array to monitor the large-scale movements of a subset of individuals to infer the non-breeding habitat for this species. Specifically, we aimed to (1) determine whether variation in stable-isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) among tracked individuals was correlated

with known discrete movement strategies derived through long-term acoustic-telemetry tracking, and then (2) define clusters within a larger sample size of individuals on the basis of only $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to examine size-based and sex-specific variation in non-breeding movements at the population level. These data advance our understanding of Port Jackson shark movement ecology in temperate ecosystems, showing complex movement behaviours similar to those of larger-bodied species.

Materials and methods

Capture and tagging procedures

Port Jackson sharks were opportunistically hand-caught on snorkel between July and September 2012 at Dent Rock ($n = 19$) and Plantation Point ($n = 109$), two subtidal rocky reef habitats located in Jervis Bay, Australia. All Port Jackson sharks were measured (total length, cm), sexed based on the presence or absence of claspers, a fin clip was taken from the trailing edge of the first dorsal fin for stable-isotope and genetic analyses and individuals were tagged with passive integrated transponder (PIT) tags to allow for individual identification. Fin tissue was used for this study to allow for a longer-term assessment of movement and foraging behaviour (Matich *et al.* 2011) and was obtained using a standardised sampling location to minimise composition variability among samples and to allow for a more accurate comparison among individuals (Hussey *et al.* 2011b). A subset of the sampled individuals ($n = 13$) were also fitted with V16-x acoustic transmitters (Innovasea, Halifax, NS, Canada; nominal delay 90 s; expected battery life 7.5 years; frequency 69 kHz). Within Jervis Bay, New South Wales Department of Primary Industries installed an acoustic receiver array ($n = 27$ receivers; Innovasea VR2-W receivers) to monitor the movements and residency of a number of fish species on rocky reefs within the bay and across the bay entrance. The receivers were estimated to have a detection range of ~ 250 m (50% probability of detection; Swadling *et al.* 2020). Additional receivers were deployed around the Australian coastline ($n = 112$ between Jervis Bay and Tasmania), as a part of the Integrated Marine Observing System (IMOS) animal-tracking database, a national collaborative research initiative of various universities, government and private research institutions. Details on residency, local movements and migration patterns of Port Jackson sharks based on these data have previously been described by Bass *et al.* 2017, 2021a, 2021b). The migration data from Bass *et al.* (2017) are used here to validate the application of isotopes to understand population-level movement behaviour.

All tagging and sampling procedures were conducted in accordance with a New South Wales fisheries permit (P08/0010-3.1) and an Animal Research Authority permit

(2012/009) granted by the Macquarie University Animal Ethics Committee.

Tissue collection and processing

Tissue samples for stable-isotope analysis were taken from the trailing edge of the first dorsal fin of each individual and stored at -20°C on returning to the laboratory. Tissue samples were then freeze-dried and transported to the Great Lakes Institute for Environmental Research, University of Windsor, Canada, for stable-isotope analysis. Fin tissue samples were first homogenised and ground into a fine powder and then lipids were extracted to remove their potential bias on $\delta^{13}\text{C}$ values (Post *et al.* 2007). In brief, lipid extraction involved agitating samples in a 2:1 chloroform–methanol solution for 24 h, decanting of the solution at the end of this period and drying the resulting tissue pellet for 48 h in a fume cupboard to remove any remaining solvent following standard procedures (Hussey *et al.* 2012). Urea, a tissue solute known to influence $\delta^{15}\text{N}$ values in elasmobranchs, was not extracted given expected low concentrations in fin tissue and previous experimental work demonstrating minimal effect of this processing step on derived fin isotope values (Shipley *et al.* 2017). Processed tissues sampled were weighed into tin capsules (between 400 and 600 μg) and carbon and nitrogen stable-isotope ratios were analysed using a continuous flow isotope-ratio mass spectrometer (Finnigan MAT Deltaplus, Thermo Finnigan, San Jose, CA, USA) interfaced with an elemental analyser (Costech 4010). Stable isotope abundances are expressed in delta notation (δ) because the ratio of a sample to recognised standards in parts per thousand (‰), using the following equation:

$$\delta_X = [(R_{\text{sample}} \div R_{\text{standard}}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N , R_{sample} is the corresponding ratio of $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$ and R_{standard} represents the isotopic ratios of the respective standards (Pee Dee Belemnite carbonate for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$). The analytical precision for $\delta^{15}\text{N}$ was $<0.20\text{‰}$ and for $\delta^{13}\text{C}$ it was $<0.12\text{‰}$ on the basis of more than 100 analyses of NIST standard 8414 and tilapia muscle. Instrument accuracy, on the basis of the analysis of certified NIST standards 8542 and 8547, was 0.08‰ for $\delta^{15}\text{N}$ and 0.02‰ for $\delta^{13}\text{C}$.

Data analysis

Statistical analyses were conducted in RStudio (ver. 1.0.136, RStudio PBC, Boston, MA, USA, see <https://rstudio.com/>) using the packages ‘stats’ (ver. 4.3.0, see <https://stat.ethz.ch/R-manual/R-devel/library/stats/html/00Index.html>), ‘Rfit’ (ver. 0.24.2, see <https://CRAN.R-project.org/package=Rfit>; Kloke and McKean 2012), ‘dplyr’ (ver. 1.0.10, see <https://CRAN.R-project.org/package=dplyr>), ‘factoextra’ (ver. 1.0.7, see <https://CRAN.R-project.org/package=factoextra>) and

'ggplot2' (ver. 3.4.0, see <https://CRAN.R-project.org/package=ggplot2>; Wickham 2016).

Detection trends of acoustically tagged individuals based on previous work (see Bass *et al.* 2017 for further details) showed that the majority of Port Jackson sharks departed Jervis Bay after the breeding season and exhibited southward migrations, with individuals being detected up to 645 km south of Jervis Bay (Fig. 1). However, some individuals were not detected outside of the breeding season and at least two individuals remained in Jervis Bay year-round. For the current study, these tagged individuals were categorised into the following three movement strategies on the basis of their behaviour observed in Bass *et al.* (2017): those detected within Jervis Bay throughout the year (i.e. resident; $n = 2$), individuals detected by the IMOS Narooma Line (i.e. southern migrators; $n = 6$) and those not detected outside of the breeding season (i.e. unknown movements after present in Jervis Bay for the breeding season; $n = 5$). Owing to the sparse distribution of acoustic receivers along the southern part of the eastern coast of Australia, it is possible that individuals that were not detected outside of the breeding season may have moved southward to or past

the IMOS Narooma Line. A Kruskal–Wallis test was used to examine whether variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values correlated with these three known discrete movement strategies. A Dunn test was used to examine pairwise differences between $\delta^{13}\text{C}$ values and migration strategy, with P -values adjusted using the Benjamini–Hochberg method.

Prior to assessing population-level movements beyond the breeding season on the basis of isotope values, we first examined whether tagging location ($n = 2$; Dent Rock and Plantation Point) influenced overall $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of all individuals sampled ($n = 128$) by using a Kruskal–Wallis test. Given that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values did not differ between tagging locations ($\delta^{13}\text{C}$: KW = 1.774, d.f. = 2, $P = 0.412$; $\delta^{15}\text{N}$: KW = 2.324, d.f. = 2, $P = 0.313$), all individuals were combined into a single data set. Because of a non-normal distribution of the data, Kruskal–Wallis test was used to examine potential sex-based effects on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values separately. Rank-based estimation regression was then used to identify any size-based effects on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ fin-tissue values. Given sexual dimorphism, whereby female Port Jackson sharks are larger than males, we mean-centred the total length data for each sex independently (ranging from zero for the smallest individual to one for the largest individual) prior to undertaking the regression analysis.

To examine size-based and sex-specific variation in non-breeding movements at the population level, K-means clustering was then used to assign individuals into groups on the basis of similarity of their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values as a proxy for different movement strategies. The 'fviz_nbclust()' function in the 'factoextra' package in R was used to determine the optimal number of clusters by using the silhouette method. Following this, an ANOVA was used to test whether $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values differed among derived clusters. Given our low sample size of acoustically tagged individuals ($n = 13$) relative to our total sample size ($n = 128$), a Fisher's exact test was used to compare the movement strategies of individuals to their cluster assignment, to validate the clusters and to allow assignment of preliminary movement strategies to the derived clusters for the larger non-tagged population sample size.

The derived clusters based on the larger population size were then re-examined to determine whether demographic factors (sex and body size) differed (1) among clusters and (2) among individuals within each cluster, indicative of differential foraging or movement habits. For Point 1, a chi-squared test of association was used to examine whether there was a significant level of association between sex and cluster assignment and a Kruskal–Wallis test was employed to determine whether the mean-centred total lengths (TLs) of individuals differed among derived clusters. To determine whether males and females within each cluster differed in their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (i.e. for Point 2), Kruskal–Wallis tests were used. For size effects, linear regression was used

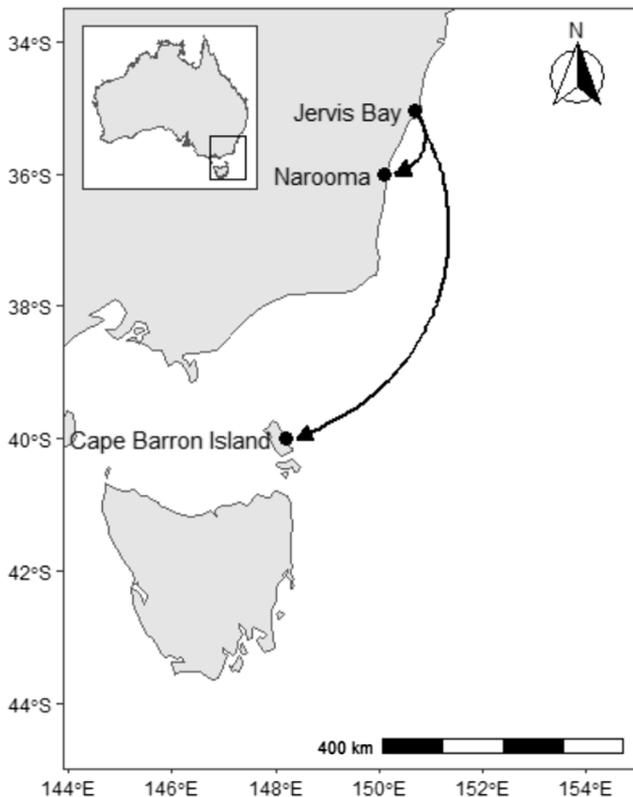


Fig. 1. Movement strategies of acoustically tagged Port Jackson sharks along the south-eastern coast of Australia. The location of the receiver arrays that detected tagged individuals are represented by filled circles and the arrows connecting locations represent movements between those sites (movement data from Bass *et al.* 2017).

to examine the influence of mean-centred TL on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values within each cluster.

Results

General results

In total, 99 male and 29 female Port Jackson sharks were captured, sampled and PIT-tagged at Dent Rock and Plantation Point. Females ranged in body size from 107 cm to 132 cm TL and males from 74 cm to 115 cm TL. There was considerable variation in both $\delta^{13}\text{C}$ values (mean \pm s.e. = -15.4 ± 0.1 ; range = -12.4 to -20.3) and $\delta^{15}\text{N}$ (mean \pm s.e. = 14.0 ± 0.1 ; range = 11.9 – 17.0) of fin tissue among individuals. Although there was no significant difference between the $\delta^{13}\text{C}$ values of all sampled males and females (KW = 1.6258, d.f. = 1, $P = 0.202$; Fig. 2), males exhibited higher $\delta^{15}\text{N}$ values than did females (KW = 4.460, d.f. = 1, $P = 0.035$; Fig. 2). Additionally, there was no significant relationship between mean-centred TL and $\delta^{13}\text{C}$ ($t = 1.030$, $P = 0.3051$) or $\delta^{15}\text{N}$ ($t = 0.411$, $P = 0.682$) for all sampled sharks.

Determining whether known movement strategies correlate with discrete stable-isotope values

When considering the three movement strategies of Port Jackson sharks derived from acoustic-telemetry tracking, namely, continuously detected in Jervis Bay throughout the year ($n = 2$), detected at Narooma (200 km south of Jervis Bay) outside of the breeding season ($n = 6$) and not detected outside of the breeding season ($n = 5$), there was a significant difference between $\delta^{13}\text{C}$ values of fin tissue of

tagged individuals (KW = 7.640, d.f. = 2, $P = 0.022$; Fig. 3a). Pairwise comparisons showed that tagged individuals detected in Jervis Bay year-round had significantly lower $\delta^{13}\text{C}$ values than did those detected at Narooma during the non-breeding season ($z = 2.621$, $P = 0.026$), but were not different from tagged individuals that were only seasonally detected in Jervis Bay (i.e. not detected during the migration period; $z = 1.710$, $P = 0.131$). The $\delta^{13}\text{C}$ values of tagged individuals that were only seasonally detected in Jervis Bay and those of tagged individuals that were detected at Narooma were similar ($z = -1.320$, $P = 0.187$, Fig. 3a). The $\delta^{15}\text{N}$ values of tagged individuals across the three different movement strategies did not differ (KW = 0.976, d.f. = 2, $P = 0.614$, Fig. 3b). Accepting the small sample size, the standard error of isotope values for individuals detected within Jervis Bay throughout the year was lower than that of the two other groups. This suggests that further research may be needed to investigate whether individuals from the Narooma group and the group that were not detected outside of the breeding season fed over a broader range of habitats and geographical areas than did the two individuals that remained in Jervis Bay.

Cluster analysis to assign the population-level sample to movement strategies on the basis of stable-isotope data alone

Cluster analysis on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the larger population sample size of non-tagged Port Jackson sharks combined with tagged animals found six distinct clusters with a silhouette measure of cohesion and separation of 0.7 (Fig. 4). An ANOVA showed significant differences in fin-tissue $\delta^{13}\text{C}$ values among clusters ($F = 225.2$, d.f. = 5, 122, $P < 0.001$), with Tukey's *post hoc* tests identifying all clusters being different, with the exception of Clusters 3 and 5 (diff = 0.315, $P = 0.052$). There were also significant differences in $\delta^{15}\text{N}$ values among clusters ($F = 41.42$, d.f. = 5, 122, $P < 0.001$), but Tukey's HSD *post hoc* tests found that the majority (Clusters 1, 2, 3 and 4) were similar ($P > 0.05$). A significant association between movement strategy defined from acoustic-telemetry data and cluster assignment based on stable-isotope data was not apparent (Fisher's exact test; $P = 0.180$), likely being a result of our small sample size. Nevertheless, Cluster 2, which was the most enriched in ^{13}C , contained both acoustically tagged individuals that were detected in Jervis Bay year-round and no acoustically tagged individuals that were detected at Narooma.

Effect of demographic factors among and within assigned clusters

There was a significant association between sex and cluster assignment ($\chi^2 = 16.498$, d.f. = 5, P -value = 0.006), but this was most likely to be a result of male bias in sampling

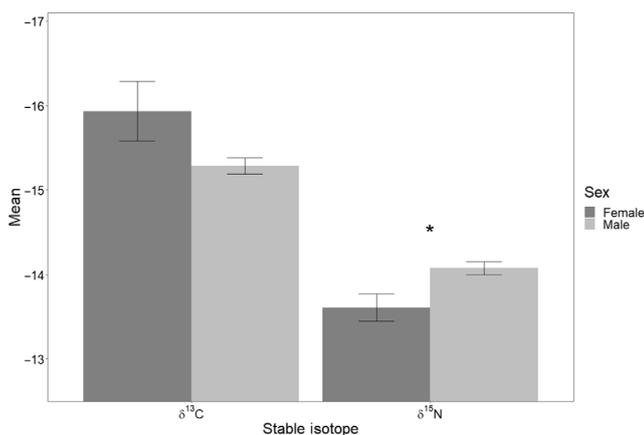


Fig. 2. Mean (\pm s.e.) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of male and female Port Jackson shark-fin tissue split by sex. The asterisk (*) represents a significant difference (i.e. $P < 0.05$) between males and females for that stable isotope.

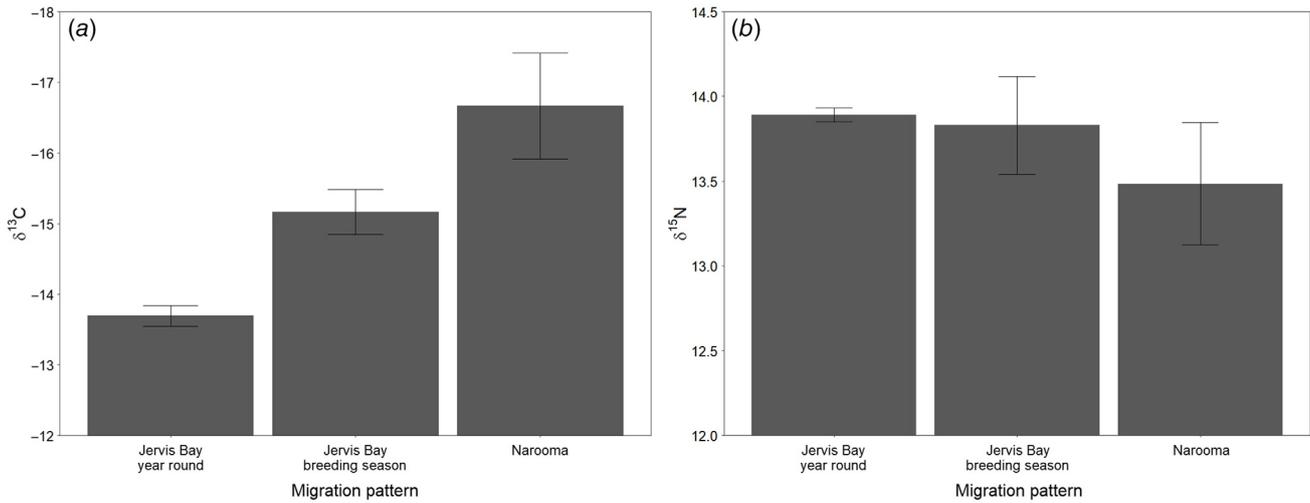


Fig. 3. Mean (\pm s.e.) values of (a) $\delta^{13}\text{C}$ and (b) $\delta^{15}\text{N}$ in lipid-extracted fin tissue sampled from Port Jackson sharks that were grouped on the basis of distinct movement strategies outside the breeding season, based on acoustic telemetry data.

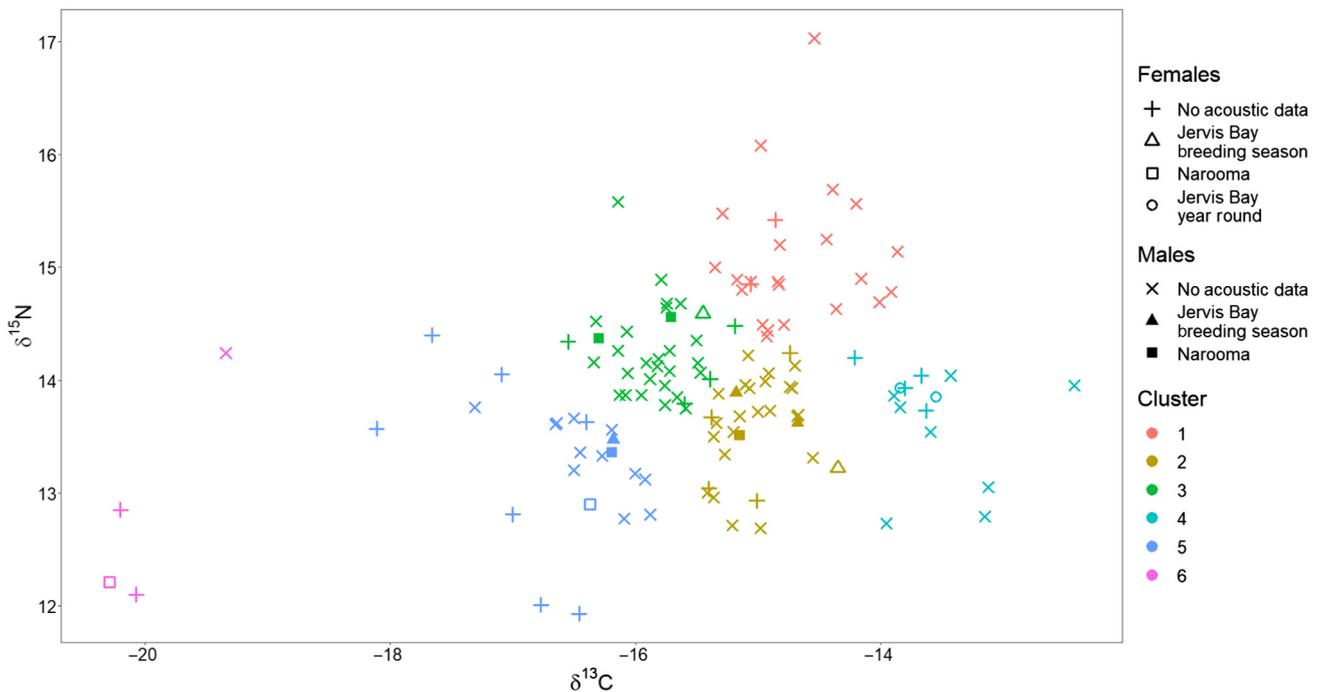


Fig. 4. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of lipid-extracted fin tissue of individual Port Jackson sharks ($n = 128$) assigned to groups by K-means clustering (identified by colour) and according to sex and movement strategy outside of the breeding season determined from acoustic-telemetry data (identified by shape of the symbol).

within the study population (male: $n = 99$; female: $n = 29$). When comparing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of males and females within clusters, no significant differences were observed, with the exception of Cluster 1 ($P > 0.05$ for all tests). Males in Cluster 1 ($n = 14$) were significantly enriched in ^{13}C compared with females ($n = 8$; $\text{KW} = 6.044$, $\text{d.f.} = 1$, $P = 0.014$). There were no significant differences between

the mean-centred TL of individuals among clusters ($\text{KW} = 10.328$, $\text{d.f.} = 5$, $P = 0.066$). When considering within-cluster variation, only individuals in Cluster 6 showed a significant positive relationship between mean-centred TL and $\delta^{13}\text{C}$ ($F = 8.039$, $\text{d.f.} = 1, 31$, $P = 0.008$). There was no significant relationship between mean-centred TL and $\delta^{15}\text{N}$ values among individuals within any of the clusters ($P > 0.05$).

Discussion

The combined application of acoustic telemetry and stable-isotope analysis of fin tissue of Port Jackson sharks provides evidence for potential differences in broad-scale movement patterns of male and female Port Jackson sharks outside of the breeding season. Individuals showed considerable variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ within fin tissue and isotopic variation among acoustically tagged sharks was broadly associated with known movement behaviours. Individuals from our larger non-tagged population sample size were assigned to six clusters on the basis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, with some clusters matching known movements of acoustically tagged individuals. These clusters suggest that individuals of a mesopredator shark species show marked variation in movement strategies (denoted by $\delta^{13}\text{C}$) and potentially foraging behaviour (denoted by $\delta^{15}\text{N}$) while not at their breeding grounds. Furthermore, males and females differed in $\delta^{15}\text{N}$ values, suggesting potential sexual segregation or niche specialisation with respect to geographical area, habitat selection or foraging behaviour beyond the breeding season. While accepting limitations related to sample size (number of individuals tracked and male bias in our population sample) and using fin tissues for stable-isotope analysis (variable composition of fin tissue and unknown fin-tissue incorporation rates for Port Jackson sharks), these data demonstrated the power of combined isotope and telemetry data for cost-effective inference of the movement dynamics of a mesopredator shark. Moreover, differential movement behaviours observed at the population level indicated that managing smaller-bodied shark species is potentially more complex than was previously thought (Shaw 2020).

Variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among the assigned clusters suggests that Port Jackson sharks within each cluster feed in different habitats or geographical zones beyond the breeding season. For example, the observed variation in $\delta^{13}\text{C}$ values among clusters could indicate that groups of Port Jackson sharks feed over a latitudinal or inshore-offshore gradient. Given the distribution of acoustically tagged individuals within clusters and accepting our sample size of tagged individuals, it is possible to infer the migration behaviour of several clusters. Clusters 1, 3, 4 and 6 all contained individuals that were detected at Narooma and those that were not detected outside of the breeding season, indicating a southward migration. Because of the sparse spatial distribution of receivers along the New South Wales coast, it is possible that undetected individuals still migrated south using deeper waters, bypassing the receivers at Narooma (Bass *et al.* 2017). However, variation among these clusters (i.e. the degree of ^{13}C depletion) could indicate that individuals migrate varying latitudinal distances to habitats along this stretch of coastline (Bass *et al.* 2017) or that they may preferentially migrate to different inshore

or offshore environments (Hobson 1999). Several studies have suggested that intraspecific variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of shark tissue may be indicative of intraspecific variation in movement or foraging behaviour (Abrantes and Barnett 2011; Borrell *et al.* 2011; Marcus *et al.* 2019). For example, Marcus *et al.* (2019) suggested that high variability in the $\delta^{15}\text{N}$ values of whale sharks sampled on Ningaloo reef was indicative of different foraging patterns among individuals characterised by movements between Ningaloo reef and along the Western Australian coastline. Additionally, Li *et al.* (2016) found that eight species of pelagic shark that are commonly caught in the north-eastern central Pacific Ocean exhibited a reasonably wide range of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, which the authors suggested indicates that each species may forage in distinct habitats or feed on more than one trophic level. Similarly, variation in the $\delta^{15}\text{N}$ values between clusters of Port Jackson sharks, namely individuals in Cluster 5 and Cluster 6, may indicate feeding on prey at different trophic levels or in habitats that are enriched in ^{15}N during the non-breeding season.

One potential driver for the observed variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among Port Jackson sharks may relate to partial migration to and from Jervis Bay during the non-breeding season. Individuals within Cluster 2 ($n = 14$) were less depleted in ^{13}C than were those in all other clusters, indicating that these individuals were feeding in more northerly or inshore waters. Further, two individuals in Cluster 2 were acoustically tagged and were detected within Jervis Bay throughout the year, suggesting that the rest of the individuals within this cluster may have also remained in Jervis Bay throughout the non-breeding season. Anecdotal observations of large aggregations of Port Jackson sharks on deep rocky reefs just outside of Jervis Bay (Paul Daniels, pers. comm.) provides further evidence that not all Port Jackson sharks exhibit long-distance migratory behaviours outside of the breeding season. McLaughlin and O'Gower (1971) also speculated that some individuals may move to deeper waters offshore, whereas others migrate in a southward direction. Partial migration has been identified in a few shark species (Chapman *et al.* 2012; Papastamatiou *et al.* 2013) and adds further complexity to understanding the impact of mesopredators in temperate marine ecosystems.

Male and female Port Jackson sharks showed differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, suggesting a degree of sexual segregation or niche specialisation with respect to foraging behaviour outside of the breeding season. Previous research at breeding aggregation sites has indicated that males and females show different habitat preferences (Powter and Gladstone 2008, 2009). The association between sex and cluster provides further support of sexual segregation of Port Jackson sharks outside of the breeding season. For example, the tissues of individuals in Cluster 4, which contained a reasonably high proportion of females (female: male = 3:1), were significantly more depleted in ^{13}C , indicating that these individuals were feeding in more

southerly or offshore waters. In agreement, Christie (2015) noted female-only aggregations in the Point Cooke Marine Sanctuary (~30 km south of Melbourne). Female Port Jackson sharks may, similarly to other elasmobranch species (Carrier et al. 1994; Sims et al. 2001; Wearmouth and Sims 2008), utilise different geographical areas from males to avoid harassment, to prepare for the energetically expensive processes of reproduction, egg production and laying or because of their considerably larger size than that of males. Alternatively, Powter et al. (2010) suggested that dietary variation among individual Port Jackson sharks may be a result of variable dentition and structure or morphology of the head and jaw rather than of competition for resources, which could explain the highly variable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ observed. Understanding the mechanism of sexual segregation has important biological and ecological implications for the reproductive fitness of individuals within populations, as well as broader implications for understanding the movement ecology (i.e. space use) of shark and ray species (Wearmouth and Sims 2008).

There is a growing body of evidence that elasmobranchs of the same sex and age class exhibit intraspecific variation in residency, movement and habitat use within a season or on an annual cycle (Vaudo et al. 2014; Bass et al. 2021a; Espinoza et al. 2021). Intraspecific variation in migration behaviour in other taxa, in particular overwintering or non-breeding locations of birds (Saino et al. 2004; Leyrer et al. 2013; Goodenough et al. 2017; Steenweg et al. 2017), can influence the fitness and reproductive success of individuals, with consequences for their survival and resilience. Further, for species that are susceptible to anthropogenic disturbance, variability in movement ecology may have important implications for their effective management and their adaptability to disturbances. To further explore individual variation in the movement ecology and foraging behaviour of elasmobranchs by using stable-isotope analysis, future studies should sample multiple tissue types (e.g. plasma, red blood cells and muscle tissues) with known incorporation rates (i.e. established through captive-feeding experiments) from the same individual and establish baseline isotope values within ecosystems (i.e. endpoints) throughout the year (Hussey et al. 2012; Matich and Heithaus 2014; Munroe et al. 2015). The compilation of ecosystem baseline isotope values at multiple locations within Jervis Bay and along the eastern coast of Australia combined with shark isotope data would allow the use of isotopic clocks to further investigate population-level movement behaviour (Madigan et al. 2021; Shipley et al. 2021).

Conclusions

The current study represents the first application of stable-isotope analyses to examine population-level variation in

the movement patterns of Port Jackson sharks beyond the breeding season and provides evidence for differences in movement strategies among individuals and potentially between sexes. Combined tracking data from acoustic telemetry provided a degree of validation for variation observed in stable-isotope data (e.g. Madigan et al. 2021) and provided further detail into the inter-individual variability observed in this and other studies (Doherty et al. 2010; Matich and Heithaus 2014; Harrison et al. 2017). Moreover, combining the two methodologies provided a reasonable approach to scale up sample sizes, to address limitations of some methods (e.g. sparse acoustic receiver coverage) and to optimise data collected from each individual to better understand the prevalence and complexities of variable movement strategies (Matley et al. 2022). The seasonal immigration of Port Jackson sharks into Jervis Bay from a diverse range of habitats and geographical areas may represent an important influx of nutrients into the ecosystem through egestion (e.g. Williams et al. 2018) or through the deposition of eggs (e.g. Bouchard and Bjorndal 2000; Gende et al. 2002; Fritz and Whiles 2018). Elucidating the behaviour of sharks at these non-breeding locations and the fitness advantages of differential migration strategies has important ecological and management implications for the seasonal communities in which they migrate to (Heithaus et al. 2008) and highlights the important role that coastal and benthic sharks play in connecting distant and diverse ecosystems on both an individual and species level.

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Conflicts of interest. The authors declare that they have no conflicts of interest.

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