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The impact of wildlife tourism on the foraging ecology and nutritional condition of an apex predator

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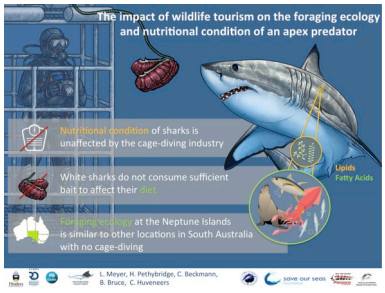
GRAPHICAL ABSTRACT



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ABSTRACT

Shark and ray tourism is growing in popularity and often necessitates attractants like bait and chum to encourage close encounters. Such practices remain contentious amongst stakeholders as they may affect the species they target. We used lipid and fatty acid profiles to investigate the effects of South Australia's cage-diving industry on the diet and nutritional condition of white sharks *Carcharodon carcharias* (n = 75). We found no evidence of dietary shifts or reduced nutritional condition after a > 3 week period of tourism-exposed residency at the Neptune Islands where the cage-diving industry operates. White sharks fed on a variety of prey groups, similar to other populations around Southern Australia that are not exposed to ecotourism provisioning. These findings indicate that current cage-diving operations in South Australia do not alter white shark diet and nutritional condition where prey resources are abundant.

1. Introduction

Wildlife tourism is the fastest growing sector of the tourism industry (Wearing & Neil, 2009), bringing in billions of dollars globally (Huveneers et al., 2017; Vianna, Meeuwig, Pannell, Sykes, & Meekan, 2011; Wunder, 2000) and with it, a myriad of management and conservation challenges (reviewed in Green & Giese, 2004; Newsome, Dowling, & Moore, 2005; Trave, Brunnschweiler, Sheaves, Diedrich, & Barnett, 2017; Macdonald et al., 2017). Owing to their reputation as iconic predators, sharks are particularly popular ecotourism attractions (Apps, Dimmock, Lloyd, & Huveneers, 2016; Gallagher & Hammerschlag, 2011). However their relative rarity encourages provisioning, whereby a range of attractants or direct feeding are used to coax sharks within view of tourists to ensure reliable and consistent encounters (Knight, 2009). Such practices are contentious, with polarized viewpoints from managers, tourism operators, and the public alike

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(Burgin & Hardiman, 2015; Dubois & Fraser, 2013; Lewis & Newsome, 2003; Newsome & Rodger, 2008; Richards et al., 2015; Ziegler et al., 2018).

Elasmobranch (shark and ray) provisioning for ecotourism encompasses numerous activities from directly feeding individuals to using noise attractants (defined in Richards et al., 2015). Such activities can elicit a range of effects on local ecosystems (Shackley, 1998; Topelko & Dearden, 2005) and species, promoting discussion in an abundance of recent reviews (Brena, Mourier, Planes, & Clua, 2015; Gallagher et al., 2015; Patroni, Simpson, & Newsome, 2018; Trave et al., 2017). Behavioural changes include shifts in site occupancy and seasonality (Bruce & Bradford, 2013; Brunnschweiler, Abrantes, & Barnett, 2014; Clarke, Lea, & Ormond, 2011; Rizzari, Semmens, Fox, & Huveneers, 2017) vertical and horizontal space use (Corcoran et al., 2013; Fitzpatrick, Abrantes, Seymour, & Barnett, 2011; Huveneers et al., 2013), abundance (Bruce & Bradford, 2013; Clarke, Lea, & Ormond, 2013; Meyer, Dale, Papastamatiou, Whitney, & Holland, 2009), behaviour (Clarke et al., 2013; Clua, Buray, Legendre, Mourier, & Planes, 2010), activity (Huveneers, Watanabe, Payne, & Semmens, 2018) and health and physiology (Araujo et al., 2014; Barnett, Payne, Semmens, & Fitzpatrick, 2016; Semeniuk, Speers-Roesch, & Rothley, 2007). However, the effects of provisioning on diet and nutritional condition are relatively unexplored. A single paper (Semeniuk, Bourgeon, Smith, & Rothley, 2009) has detailed how provisioning negatively impacts the physiology and body condition of southern stingray *Dasyatis americana*. Changes in "dietary habits" due to provisioning was listed as the least studied of the ten ecological concepts reviewed by Brena et al. (2015), with published work on only two species noted: *D. americana* [Semeniuk et al., 2007] and Caribbean reef shark *Carcharhinus perezi* [Maljković & Côté, 2011]. Coupled with recent work on bull sharks *Carcharhinus leucas* (Abrantes, Brunnschweiler, & Barnett, 2018), these three studies show differing results. The diets of *D. americana* from the Cayman Islands, and larger *C. perezi* in the Bahamas were shown to be effected by tourism provisioning (Maljković & Côté, 2011; Semeniuk et al., 2007). In contrast, there was no detectable change in the diet of *C. leucas* in Fiji (Abrantes et al., 2018). Such disparate findings advocate for context-specific studies.

Cage-diving with white sharks (*Carcharodon carcharias*) is particularly popular, due to their rarity, threatened conservation status, size, role as a top predator, and notoriety in popular media (Apps et al., 2016; Huveneers et al., 2017). White shark cage-diving occurs in Australia, Mexico, USA, South Africa, and New Zealand, often with multiple operators visiting one site simultaneously, sometimes offering multiple expeditions per day. The white-shark cage-diving industry began in the late 1970s in South Australia, where it uses tethered baits (southern bluefin tuna *Thunnus maccoyii* heads and gills), berley (minced tuna creating an inedible oil slick) and acoustics to attract sharks to the dive cages. Unlike other elasmobranch provisioning sites (e.g. Stingray City in the Cayman Islands [Semeniuk et al., 2007] and the Bahamas [Maljković & Côté, 2011]), government regulations prohibit operators from intentionally feeding white sharks (DEWNR, 2016) thus mandating that baits are retracted prior to being consumed. However, sharks do occasionally consume the bait when operators cannot retrieve it quickly enough (Huveneers et al., 2015). This can result in the incidental consumption of a few baits, but new management regulations enacted in July 2017 (DEWNR, 2016) limit the amount of attractant operators can use, which have further reduced bait consumption (Huveneers & Lloyd, 2017). Although directly feeding sharks can alter elasmobranch's diet at wildlife tourism sites (Maljković & Côté, 2011; Semeniuk et al., 2007), the dietary effects of incidental bait consumption during cage-diving activities are currently unknown (Bruce, 2015).

The time spent around cage-diving vessels changes fine-scale habitat use of white sharks (Huveneers et al., 2013) and may disrupt their natural foraging behaviour and their ability to feed on pinnipeds. Such effects have been documented in orcas (*Orcinus orca*), whereby whale watching vessels disrupted foraging activities, decreasing energy intake by 18% from lost feeding opportunities (Williams, Lusseau, & Hammond, 2006). Furthermore, these direct (bait consumption) and indirect (altered foraging) changes to diet may put increased pressure on shark's nutritional condition and fitness, as interacting with cage-diving increases the daily activity of white sharks (Huveneers et al., 2018). Such effects have been explored on whitetip reef sharks (*Triaenodon obesus*), whereby ecotourism activities increased energy expenditure and metabolic rate (Barnett et al., 2016), prompting inquiries about the extent and collective influence of similar effects on other species. Consumption of bait instead of natural prey can result in decreased foraging on pinnipeds with high energy yields, which could have detrimental effects on white sharks that can have high feeding requirements (Semmens, Payne, Huveneers, Sims, & Bruce, 2013). These concerns have been articulated in recent studies (Gallagher & Huveneers, 2018; Huveneers et al., 2018; Richards et al., 2015; Bruce, 2015) and white shark cage-diving has been identified as a potential threat to the recovery of white sharks in Australia (DSEWPaC, 2013).

The use of lipids and fatty acids (FA) as dietary tracers in elasmobranchs is growing in popularity (Munroe, Meyer, & Heithaus, 2018; Semeniuk et al., 2007; Meyer, Pethybridge, Nichols, Beckmann, & Huveneers, 2019). Lipid content and the ratio of lipid classes (triacylglycerols, wax esters, phospholipids, sterols, free fatty acids) quantifies energy availability and nutritional state (Fraser, 1989; Orešič, 2009; Tocher, 2003). When energy demand exceeds intake, due to lack of 'fatty' prey items or increased activity, organisms mobilise fat stores, decreasing lipid content within tissues (Song, Lin, & Xu, 2012) and changing the ratio of storage:structural lipid classes (Fraser, 1989; Zammit & Newsholme, 1979). Lipids can be further broken down into fatty acids (FAs), with distinct chemical structures retained from different basal food-chain production (e.g. bacteria, diatoms, dinoflagellates) (Ackman, 1994; Sargent, Bell, McEvoy, Tocher, & Estevez, 1999; Tocher, 2003). As these compounds are passed from prey to predator with minimal modification, they can trace feeding ecology across different habitats with distinct food sources (Meyer et al., 2019). Furthermore, certain FAs are preferentially assimilated into distinct taxa-specific tissues (i.e. teleost muscle vs. marine mammal blubber vs. cephalopod mantle), providing additional insight into key prey items (Budge, Iverson, & Koopman, 2006; McMeans et al., 2013; Pethybridge et al., 2010; Pethybridge, Nichols, Virtue, & Jackson, 2013). Fatty acids have been used in elasmobranch studies to investigate dietary shifts due to ontogeny (Belicka, Matich, Jaffé, & Heithaus, 2012), spatial-temporal variability (Every, Fulton, Pethybridge, Kyne, & Crook, 2018; Steeves et al., 2016), and notably, provisioning during wildlife tourism operations (Semeniuk et al., 2007). As lipids are more metabolically active than bulk protein, they reflect changes in diet and nutrition at shorter time scales than stable isotopes (weeks *vs*. months-years (Beckmann, Mitchell, Stone, & Huveneers, 2013), making lipid and FA analysis an ideal tool to explore changes in feeding ecology across a short time period (Pethybridge, Choy, Polovina, & Fulton, 2018).

Here, we assessed the effects of South Australia's cage-diving industry on the foraging ecology of white sharks residing at the Neptune Islands. The integration period for lipids and fatty acids (Beckmann, Mitchell, Seuront, Stone, & Huveneers, 2013) allowed for the newly arrived sharks (< 3 weeks at the Neptune Islands) to serve as a control group for comparison with individuals exposed to the white shark cage-diving industry (> 3 weeks of tourism-exposed residency at the Neptune Islands). Specifically, we aim to investigate changes in 1) shark diet from incidental bait consumption (using FA profiles and individual FAs as biomarkers for bluefin tuna consumption); 2) altered foraging (FA profiles and markers for blubber consumption and habitat use); and 3) changes in nutritional condition (lipid content and lipid class profiles) from decreased or shifting foraging opportunities as sharks may be impacted by ongoing exposure to and interactions with provisioning-based cage-diving operations.

2. Methods

2.1. Sample collection

White shark muscle samples were collected from May 2012 to April 2017 at the Neptune Islands Group Marine Park, South Australia (including both North and South Neptune Islands), where free-swimming sharks were targeted opportunistically throughout the year during standard cage-diving operations. Sharks were attracted to the cage-diving vessels using a combination of attractants (bait and chum [mixture of minced bluefin tuna head, tails, gills and guts]) (DEWNR, 2016; Huveneers & Lloyd, 2017). Biopsies were taken from diving cages or from above the water's surface using a single 20 mm rubber speargun, with the end of the 1.3 m spear modified into a hollow 1 cm diameter stainless steel biopsy probe (Meyer, Fox, & Huveneers, 2018), targeting the dorsal or upper flank musculature directly below the dorsal fin. Biopsies were immediately frozen (−4 °C) and transported to the laboratory where white muscle tissue was dissected from the subdermal tissue and skin. Tissue samples were weighed and freeze dried prior to lipid extraction and analysis.

Individual sharks were identified (Nazimi, Robbins, Schilds, & Huveneers, 2018), sexed (based on clasper presence/absence), and sized to the nearest 10 cm using visual size estimates (May, Meyer, Whitmarsh, & Huveneers, 2019). White sharks frequenting the Neptune Islands are identified daily by cage-diving operators, enabling to record the date each shark was first sighted, thus marking the start of their tourism-exposed residency period. Telemetry was not appropriate to determine residency in this context as relatively few (n = 7) biopsied sharks were tagged and tags might have not been deployed at the beginning of the period of tourist-exposed residency. The amount of interaction between sharks and operators or number of days sighted by cage-diving operators could not be reliably quantified due to the logistical challenges of operators accurately recording this level of detail. We instead conservatively used residency at the Neptune Islands, defined as the period between first day sighted and day biopsied, acknowledging the limitation of using residency as a proxy for exposure to cage-diving operations. Where possible, sharks that had spent several weeks or more residing at the Neptune Islands, and those for which a biopsy was previously collected, were preferentially targeted. Additionally, biochemical data from eight white sharks caught at other locations throughout South Australia were also obtained (Pethybridge, Parrish, Bruce, Young, & Nichols, 2014). These were included in the control group and considered not to have recently visited the Neptune Islands. *Residency* was grouped into two categories (< 3 weeks [control] and > 3 weeks [tourism-exposed] at the Neptune Islands) as shifts in FA profiles were noted within 3 weeks of a diet switch in captive Port Jackson sharks *Heterodontus portjacksoni* (Beckmann, Mitchell, Seuront et al., 2013).

2.2. Biochemical analysis

Total lipid was extracted from freeze dried muscle samples (minimum 12 mg dry weight [DW]) using the modified Bligh and Dyer method (Bligh & Dyer, 1959; described in detail in (Meyer et al., 2017)). Briefly, the lipids were separated from proteins and carbohydrates using a solvent solution of dichloromethane, methanol, MilliQ water. The total lipid extract (TLE) was then dried under nitrogen and weighed prior to lipid class and FA analysis. Lipid classes [phospholipid (PL), triacylglycerol (TAG), sterols (ST), wax esters (WE) and free fatty acids (FFA)] were determined from an aliquot of the TLE using thin layer chromatography coupled with a flame ionisation detector (TLC-FID). Lipid class results were expressed as a relative proportion (percent area) of the total lipid class compounds.

Individual FAs were separated from the glycerol backbones of the polar and non-polar lipids in the TLE (not individual lipid classes) with a heated methanol, hexane, and hydrochloric acid solvent scheme. Subsequently, the FAs were identified and quantified using gas chromatography analysis using the Agilent Technologies 6890N GC (Palo Alto, California, USA) with a HP-5 cross-linked methyl silicone fused silica capillary column (50 × 0.32 mm i.d.), an FID, a splitless injector and an Agilent Technologies 7683 Series auto-sampler. Quality checks, including the addition of internal FA standard (C23 in each sample), blank samples (each batch of 50), replicates (weekly) and gas chromatography - mas spectrophotometry checks on FAs (twice throughout the analysis) were run to ensure accurate results and appropriate laboratory protocols. FA results were expressed as a proportion of the total identified compounds. Out of the 61 fatty acids identified, only those with means > 0.1% (24) were included in the subsequent statistical analyses.

2.3. Statistical analysis

We tested the influence of tourism-exposed residency (*residency* hereafter) at the Neptune Islands on white shark muscle lipid content, lipid class, and FA profiles using multivariate statistical analyses undertaken in PRIMER7 +PERMANOVA (Plymouth Routines in Multivariate Ecological Research, Clarke & Gorley, 2015). Permutational analysis of variance (PERMANOVA) main tests with Monte Carlo simulations (denoted as p(MC)) were run on Bray-Curtis similarity matrices calculated from the square-root transformed profile data to determine if *residency* significantly influenced the overall lipid content, lipid class, and FA profiles. The lipid and FA profiles of the eight sharks sampled outside of the Neptune Islands were compared (using PERMANOVAs) to the control sharks (< 3 weeks at the Neptune Isalnds). Following non-significant (lipid content p(MC) = 0.847, lipid class p(MC) = 0.617, FA p(MC) = 0.712) differences, these two groups were combined. PERMANOVA models testing for differences between the control (< 3 weeks and sharks from outside the Neptune Islands) and tourism-exposed sharks (> 3 weeks at the Neptune Islands) included sampling *season* to account for temporal variation in prey availability and FA production (Steeves et al., 2016) and *size* (total length) as a continuous covariate to account for ontogenetic diet shifts (Hussey et al., 2012). Additionally, permutational analysis of multidimensional dispersion (PERMDISP denoted at p(perm)) was used to determine the relative amount and statistical significance of the dispersion within *residency* groups. The influence of *residency* (accounting for sampling *season* and shark *size)* was also investigated for select individual FAs (reflecting either marine mammal or teleost consumption, or pelagic foraging, Table 2) using Generalized Linear Mixed Effect Models (GLMMs) fitted with gamma distribution and log link using the *glm* function and restricted maximum likelihood approach in the R statistical environment (R Core Team, 2016). Significance for all statistical tests was declared at p(MC) or p(perm) < 0.05.

As the 3-week threshold determined by Beckmann et al. (2013a) used captive Port Jackson sharks, it is uncertain whether this threshold is directly applicable to white sharks in a natural setting. Furthermore, Port Jackson sharks were not sampled prior to 3 weeks, so the turnover rate may in fact be quicker. As such, all PERMANOVA and GLMM analyses were repeated with *residency* groups < 1, 1–2, 2–3, and < 3 weeks; and < 2 weeks (control) and < 2 weeks (tourism-exposed); and CAPs were run on these categorical *residency* groups along with the CAPs of *residency* (days) as a continuous factor as reported below. Similarly, all GLMMs were run with *residency* as a continuous (days) or categorical (grouped by week, and 2 week threshold as above). None of the alternative groupings altered our findings and results from the < 3 week and < 3 week *residency* groupings are presented (Fig. 1). To visualize and quantify shifts in lipid class and FA profiles across *residency*, a Canonical Analysis of Principal Coordinates (CAP) (Anderson & Willis, 2003) was run against *residency* (in days) as a continuous covariate.

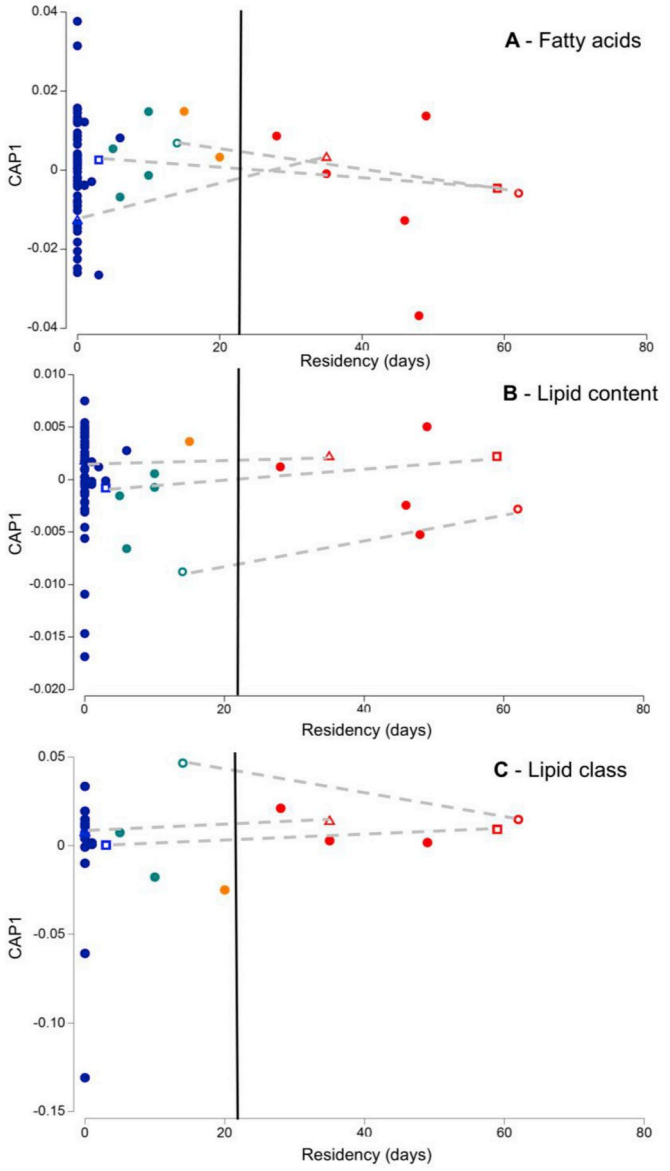

Fig. 1. Canonical Analysis of Principal Coordinates (CAP) of white shark *Carcharodon carcharias* muscle. A – Fatty acid profile, B – Lipid content, and C – Lipid class profile plotted against *residency* (days) at the Neptune Islands. Dark blue symbols indicate individual sharks which have spent < 1 week at the Neptune Islands, green 1–2 weeks, orange 2–3 weeks and red > 3 weeks. The black vertical line demarcates the 3 week biochemical integration period for lipids and fatty acids (Beckmann et al., 2013a), such that data on the left represents control sharks and data on the right, tourism-exposed sharks. Open circles indicate results from S-63, open squares from S-66, and open triangles from S-72. The dashed grey line shows the magnitude and direction of shift between two samples taken from three individual sharks. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3. Results

Seventy-five white sharks (26 females, 46 males and 3 unknown) ranging 1.8–5.5 m total length (mean ± standard deviation, SD: 3.5 ± 0.7 m) were sampled in South Australia, 67 of which were biopsied at the Neptune Islands and eight sampled as bycatch from various locations in South Australia. Most (34%) were sampled in spring, followed by autumn (27%), summer (23%), and least in winter (16%). These sharks were sighted and identified by the cage-diving operators at the Neptune Islands from 0 to 62 days prior to sampling (mean +/- SD: 5.0 ± 12.2 days), the majority (n = 61) of which had spent less than one week interacting with the cage-diving vessels. Of those that remained at the Neptune Islands for more than a week, five sharks were sampled between 1 and 2 weeks of arriving, two between 2 and 3 weeks, and the remaining eight sharks were sampled after more than three weeks of interacting with the cage-diving vessels. Three sharks (two females; S-66, S-63, and one male; S-72) were sampled twice throughout their residency (in any one sampling year). S-63, a 4.1 m female was initially biopsied 14 days after being first sighted, and again after 62 days (the longest period of time after which a shark was sampled). S-66 (4.7 m) was biopsied after three days and 56 days later, while S-72 (3.8 m) was sampled on the first day he was sighted and 35 days later.

Table 1
Total lipid content (n = 65) and relative proportions of lipid classes (n = 27) and fatty acids (n = 78) (as mean precent ± standard deviation of total lipid or FA) of muscle from *Carcharodon carcharias*.

Lipid content	28.0 ± 7.4
Lipid class	
TAG	1.01 ± 2.45
FFA	2.49 ± 6.89
ST	6.79 ± 3.11
PL	89.63 ± 7.93
Fatty Acid	
14:0	0.48 ± 0.35
16:0	17.96 ± 4.54
17:0	0.53 ± 0.23
18:0	14.38 ± 6.64
22:0	0.16 ± 0.25
ΣSFA	33.53 ± 7.23
16:1ω7	1.44 ± 1.27
17:1ω8˚	0.59 ± 0.27
18:1ω9	18.67 ± 5.16
20:1ω9	1.44 ± 0.61
20:1ω7	0.19 ± 0.12
22:1ω9	0.37 ± 0.27
22:1ω7	0.18 ± 0.23
24:1ω9	1.01 ± 1.70
ΣMUFA	23.89 ± 6.62
18:4ω3	0.20 ± 0.24
18:2ω6	0.31 ± 0.30
20:4ω6	10.75 ± 3.11
20:5ω3	1.09 ± 1.01
20:3ω6	0.24 ± 0.41
20:4ω3	0.15 ± 0.10
20:2ω6	0.21 ± 0.10
22:5ω6	0.92 ± 0.37
22:6ω3	16.88 ± 7.84
22:4ω6	3.53 ± 1.50
22:5ω3	2.37 ± 0.97
ΣPUFA	36.66 ± 12.78

TAG - triacylglycerols; FFA – free fatty acids; ST – sterols; PL – phospholipids; SFA - saturated fatty acids; MUFA - monounsaturated fatty acids; PUFA - polyunsaturated fatty acids. ˚ coellute with a17:0.

3.1. Fatty acids

The FA profiles (composed of 21 FAs, not grouped into PUFA, SFA, and MUFAs, Table 1) showed no discernible shift with *residency* (CAP p = 0.639, p(MC) = 0.834, Fig. 1A); accounting for sampling *season* (p (MC) = 0.06), and shark *size* p(MC) = 0.082). There was also no

change in FA profile dispersion between the two *residency* categories (control vs. tourism-exposed PERMDISP p = 0.356, Fig. 1A). Similarly, none of the three FA groups or seven individual FAs indicative of bluefin tuna (bait) consumption (16:0, 18:0, 22:6ω3, PUFAs [Nichols, Virtue, Mooney, Elliott, & Yearsley, 1998; Meyer unpub. data]), blubber consumption (18:1ω9, 20:1ω9, 20:4ω6, MUFAs [Bradshaw et al., 2003; Budge et al., 2006; Waugh, Nichols, Schlabach, Noad, & Bengtson, 2014]) or pelagic foraging (16:0, 22:6w3, PUFAs [Gladyshev, Sushchik, Tolomeev, & Dgebuadze, 2017; Meyer et al., 2019; Parrish, Pethybridge, Young, & Nichols, 2014; Pethybridge et al., 2010]) were influenced by *residency* (Table 2). The three repeat sampled individual sharks had variable changes in FA profiles, as S-66 and S-63's profiles shifted from positive to negative along the Y-axis (CAP1), while S-72 shifted in the opposing direction. Individual indicator FAs and FA groups (PUFAs, MUFAs, and SFAs) also showed no change in relation to *residency* (Table 2). Similarly, individual FAs indicative of pelagic foraging, blubber, or bluefin tuna (bait) consumption shifted inconsistently between the three resampled individuals (Table 3), further suggesting a lack of industry-induced shifts in foraging, diet, and habitat use.

3.2. Lipid content

White shark muscle lipid content was highly variable, ranging from 12.5 to 50.1 mg/g dry muscle (mean +/- SD: 28.0 ± 7.4) (Fig. 1B) and was not influenced by *residency* (CAP p = 0.452, PERMANOVA p (MC) = 0.895, Fig. 1B), accounting for *season* (p(MC) = 0.756) and *size* (p(MC) = 0.744). All three resampled sharks increased in lipid content between sampling (Table 3, Fig. 1B).

3.3. Lipid class

White shark muscle was dominated by phospholipids (89.63 ± 7.93), with little relative contribution from sterols, free fatty acids, or triacylglycerols (Table 1). *residency,* accounting for *season* (p (MC) = 0.575), and *size* (p(MC) = 0.644), had no effect on the lipid

Table 2
The influence of *residency* (< 3 weeks [control] vs. < 3 weeks [tourism-exposed]) at the Neptune Islands, sampling *season,* and shark *size* on individual fatty acids and fatty acid groups, determined by linear mixed effect models fitted with a gamma distribution and log link. **Bold** indicates statistical significance determined as P < 0.05.

Fatty acid		Effect	Standard error	t-value	P-value	Diet indicator
16:0	**Intercept**	**3.00**	**0.15**	**19.64**	**< 0.001**	Mesopelagic fish[1]
	Residency	0.14	0.08	1.72	0.09	Pelagic foraging[2]
	Spring	0.03	0.07	0.49	0.62	Tuna[8]
	Summer	0.11	0.08	1.48	0.14	Bait[9]
	Winter	−0.02	0.08	−0.25	0.80	
	Size	−0.02	0.04	−0.62	0.54	
18:0	**Intercept**	**2.46**	**0.33**	**7.46**	**< 0.001**	Reef foraging[2]
	Residency	−0.05	0.18	−0.27	0.79	Tuna[8]
	Spring	−0.16	0.14	−1.11	0.27	
	Summer	−0.31	0.16	−1.90	0.06	
	Winter	−0.32	0.18	−1.81	0.08	
	Size	0.12	0.09	1.42	0.16	
18:1ω9	**Intercept**	**2.63**	**0.19**	**13.70**	**< 0.001**	Blubber consumption[3]
	Residency	0.02	0.11	0.20	0.84	
	Spring	0.04	0.08	0.49	0.63	
	Summer	0.04	0.09	0.39	0.70	
	Winter	−0.07	0.10	−0.73	0.47	
	Size	0.10	0.05	1.97	0.05	
20:1ω9	Intercept	0.33	0.30	1.08	0.28	Blubber consumption[4]
	Residency	0.07	0.17	0.42	0.68	
	Spring	−0.05	0.13	−0.42	0.68	
	Summer	−0.17	0.15	−1.12	0.27	
	Winter	−0.32	0.16	−1.97	0.05	
	Size	0.05	0.08	0.60	0.55	
20:4ω6	**Intercept**	**2.60**	**0.20**	**13.30**	**< 0.001**	Reef foraging[2]
	Residency	−0.01	0.11	−0.11	0.92	Blubber consumption[3]
	Spring	−0.02	0.08	−0.28	0.78	
	Summer	−0.09	0.10	−0.89	0.38	
	Winter	0.18	0.10	1.70	0.10	
	Size	−0.05	0.05	−0.95	0.35	
20:5ω3	Intercept	0.22	0.42	0.52	0.61	Demersal foraging[2]
	Residency	−0.15	0.23	−0.64	0.52	
	Spring	0.10	0.18	0.52	0.60	
	Summer	0.13	0.21	0.63	0.53	
	Winter	0.34	0.22	1.52	0.13	
	Size	−0.08	0.11	−0.72	0.46	
22:6ω3	**Intercept**	**3.44**	**0.32**	**10.91**	**< 0.001**	Offshore migrations[5]
	Residency	−0.06	0.17	−0.34	0.73	Deep sea foraging[2]
	Spring	0.01	0.14	0.05	0.96	Tuna[8]
	Summer	0.04	0.16	0.29	0.78	
	Winter	0.24	0.17	0.43	0.16	
	Size	**−0.18**	**0.08**	**−2.16**	**0.03**	

(*continued on next page*)

Table 2 (*continued*)

Fatty acid		Effect	Standard error	t-value	P-value	Diet indicator
SFA	**Intercept**	**3.46**	**0.15**	**23.47**	**< 0.001**	Preferentially metabolised during migrations[7]
	Residency	0.07	0.08	0.82	0.41	
	Spring	−0.08	0.06	−1.32	0.19	
	Summer	−0.09	0.07	−1.24	0.22	
	Winter	−0.15	0.08	−1.92	0.06	
	Size	0.03	0.04	0.89	0.38	
MUFA	**Intercept**	**2.82**	**0.19**	**14.91**	**< 0.001**	Preferentially metabolised during migrations[7]
	Residency	0.01	0.10	0.14	0.89	Blubber consumption[3,4]
	Spring	0.03	0.08	0.37	0.71	
	Summer	0.07	0.09	0.77	0.44	
	Winter	−0.09	0.10	−0.93	0.36	
	Size	0.10	0.05	1.96	0.05	
PUFA	**Intercept**	**3.97**	**0.25**	**16.36**	**< 0.001**	Preferentially retained during migrations[7]
	Residency	−0.03	0.13	−0.20	0.84	Tuna[8]
	Spring	−0.01	0.11	−0.09	0.93	
	Summer	−0.02	0.12	−0.14	0.89	
	Winter	0.19	0.13	1.47	0.15	
	Size	−0.11	0.06	−1.80	0.08	

[1]Pethybridge et al., 2010.
[2]Meyer et al., 2019.
[3]Waugh, Nichols, Schlabach, Noad, & Bengtson, 2014.
[4]Bradshaw et al., 2003.
[5]Colombo, Wacker, Parrish, Kainz, & Arts, 2016.
[6]Alfaro, Thomas, Sergent, & Duxbury, 2006.
[7]Osako, Saito, Hossain, Kuwahara, & Okamoto, 2006.
[8]Nichols, Virtue, Mooney, Elliott, & Yearsley, 1998.
[9]Meyer et al., unpub. data.
[10]Gladyshev, Sushchik, Tolomeev, & Dgebuadze, 2017.

Table 3
Mean relative (%) changes in muscle lipid content and lipid class components for three resampled white sharks at the Neptune Islands.

Shark ID	Days within residency individuals were biopsied	Lipid content	Lipid class (change in % of total profile)		Fatty acids (change in % of total profile)	
S-63	14–63	+55%	TAG	- 0.03	16:0	+0.42
			FFA	+0.11	18:1w9	+0.23
			ST	+5.23	20:4w6	+0.50
			PL	- 5.33	22:6w3	+0.31
					PUFA	+5.62
S-66	3–59	+25%	TAG	- 0.21	16:0	+0.09
			FFA	- 0.60	18:1w9	+0.27
			ST	+4.40	20:4w6	- 0.10
			PL	- 3.11	22:6w3	- 0.66
					PUFA	- 7.48
S-72	0–34	+3%	TAG	+0.02	16:0	- 0.57
			FFA	- 0.05	18:1w9	- 0.77
			ST	- 7.35	20:4w6	+0.76
			PL	+7.21	22:6w3	+1.23
					PUFA	+16.8

class profiles (CAP p = 0.731, p(MC) = 0.573, Fig. 1C). The three resampled individuals did not show any trends in lipid class throughout *residency,* as minimal and inconsistent shifts were detected in TAG and FFA (Table 3). ST and PL showed greater shifts across *residency* (difference > 7% each), however, these changes were similarly inconsistent (Table 3).

4. Discussion

Shark- and ray-based tourism is growing in popularity worldwide (Gallagher & Hammerschlag, 2011), but provisioning remains contentious amongst scientists, managers, and tourists (Burgin & Hardiman, 2015; Newsome & Rodger, 2008). Using lipid content, class, and FA profiles, we found no evidence of nutritional or dietary shifts as sharks reside around cage-diving operators at the Neptune Islands Group Marine Park. Many of the biochemical markers were highly variable among individuals, but showed no consistent increase or decrease with tourism-exposed residency. The lack of shift in FAs indicative of marine mammal, tuna consumption or pelagic foraging, suggest that white sharks have a similar diet at the Neptune Islands than in other areas, foraging on a variety of preys and not solely on pinnipeds.

The lack of dietary shifts towards a bluefin tuna (bait) based diet may be attributed to industry management strategies (DEWNR, 2016), prohibiting intentional feeding sharks and limiting the amount of bait that can be used by operators. The small number of baits consumed by sharks were not sufficient to elicit a measurable shift in overall diet or increase in tuna markers FAs 16:0, 18:0, 22:6ω3 and ΣPUFAs. Unlike findings from directly provisioned stingrays in the Cayman Islands (Semeniuk et al., 2007) and reef sharks in the Bahamas (Maljković & Côté, 2011), we found no shift in diet at the community or individual level using comparable biochemical approaches, similar to a study on bull sharks in Fiji (Abrantes et al., 2018). Furthermore, our sampling strategy (detailed in Meyer et al., 2018) inherently targeted the boldest individuals that came within a few meters of the cages, and interacted with the industry most regularly, as they provided us with greater opportunity to obtain a biopsy. Our sampling was, therefore, well-suited to detect changes in bold individuals, if the effects of the industry was limited to bold sharks, as observed in reef sharks (Maljković & Côté, 2011) and noted at other white shark cage-diving locals, e.g. South Africa (Johnson & Kock, 2006; Laroche, Kock, Dill, & Oosthuizen, 2007). However, as no changes were detected, even in a shark that visited the Neptune Islands over a period of 63 days, the use of bait at the Neptune Islands, does not appear to measurably effect the sharks' diet.

The provisioning attracts a number of animals, including birds, teleosts and other chondrichthyans, some of which are potential white shark prey items (Hussey et al., 2012; Malcolm, Bruce, & Stevens, 2001; Pethybridge et al., 2014) (e.g. yellowtail kingfish *Seriola lalandi*, bronze whalers *Carcharhinus brachyurus*, and rays). However, the shark's unaltered diet negates concerns that large groups of teleosts, encouraged by the presence of bait and chum, create additional feeding opportunities around the cage-diving operators. For example, a switch from pinnipeds to teleosts would manifest as altered FA profiles, and be particularly apparent with increased teleost indicators (FA 22:6ω3) and decreased marine mammal indicators (i.e. 18:1ω9, 20:1ω9, 20:4ω6), which was not seen here. Additionally, dive operators and scientists have yet to witness attempted predation on any of the species attracted by the bait and chum, despite close proximity and apparent ease of capture (pers. com. A. Fox and A. Wright). This combination of observation and dietary biomarkers negates the hypotheses that provisioning creates additional or unnatural foraging opportunities for white sharks around cage-diving operations.

Despite the lack of direct provisioning, a number of studies have found that interacting with the cage-diving industry elicits changes in white shark swimming behaviour (Bruce & Bradford, 2013; Huveneers et al., 2013; Laroche et al., 2007) and increases daily activity (Huveneers et al., 2018), prompting concerns about the indirect effects on white shark nutrition. Lipid content and lipid class profiles (revealing nutritional condition), however, remained unchanged with residency, suggesting no detectable effect on nutrition, despite increased activity from interacting with cage-diving vessels and in light of the species' notoriously high feeding requirements (Semmems et al., 2013). As white sharks are highly mobile, high-energy ambush predators, the increase in daily activity associated with interacting with the industry may not be costly enough to deplete the lipid stores of these naturally active sharks. Instead, all three resampled sharks showed an increase in lipid content through residency (+3%, +25% and +55%), despite the group comparison (Lipid content PERMANVOAs comparing control and tourism-exposed sharks, n = 65) showing no difference. This disparity in results could be a reflection of the high variability in lipid content (mean ± SD 28.0 ± 7.4 mg/g), which may be masking an underlying increase not detectable in the grouped analysis of 65 individuals. Such an increase in lipid content corroborates that white sharks at the Neptune Islands forage on locally abundant prey items, such as energy-rich pinnipeds (Fig. 2) and teleosts (including tunas), and are unperturbed by exposure to the cage-diving industry. Alternatively, the increase in lipid content in three individuals is a product of chance in a small sample size, and lipid content is unchanged with residency. This still supports that cage-diving does not negatively affect the nutritional condition of white sharks through extended exposure to ecotourism. However, as we were unable to quantify the level of interaction with dive operators, instead using residency at the Neptune Islands as a proxy, further investigations comparing lipid content, lipid class, and other markers with clearly quantified levels of interaction with the industry warrants investigation and may reveal different results.

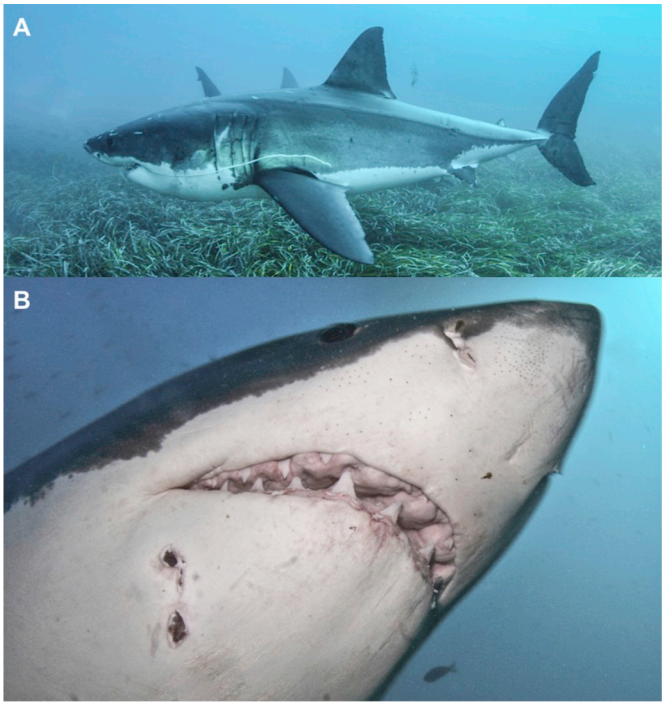

Fig. 2. White sharks *Carcharodon carcharias* at the Neptune Islands, South Australia. A - White shark with pinniped entrials trailing from the mouth. B – Shark with fresh wounds under the bottom jaw, presumably from fur seal, *Arctocephalus forsteria*, teeth. Photographs by Andrew Fox.

As white sharks linger around cage-diving sites, with increased local residency (Bruce & Bradford, 2013) and altered fine-scale swimming patterns (Huveneers et al., 2013), the need to investigate industry-induced disruptions to natural foraging patterns have been highlighted (Dubois & Fraser, 2013; Gallagher & Huveneers, 2018). As the FA profiles and levels of individual FA tracers were not detectably different, it indicates that the diet of white sharks at the Neptune Islands includes prey in similar proportions to other regions frequented by white sharks prior to visiting the Neptune Islands. Specifically, the unchanged proportions of marine mammal indicators (FAs 20:5ω3, 18:1ω9, 20:1ω9, 20:4ω6 and 22:5ω3) highlight that despite the cage-diving industry operating at the Neptune Islands, sharks are consuming pinnipeds in similar quantities as elsewhere. This is corroborated by the observation of sharks with visable pinniped remains in their mouths and coming out of their gills (Fig. 2A), and fresh wounds from predation attempts on pinnipeds (Fig. 2B, pers. com. A. Fox and A. Wright), highlighting that they remain a key food source for sharks around the Neptune Islands. In South Africa, cage-diving operations elicited changes in white shark swimming behaviour (Laroche, 2006), similar to those documented in South Australia (Bruce & Bradford, 2013), yet predation pressure on the seals remained unaffected (Laroche, 2006; Laroche et al., 2007). This was attributed to relatively few sharks showing interest in the cage-diving vessels, while the majority continue to forage unaffected. The effects of South Australia industry may be similar and limited to a few individuals, with most sharks being transient (Nazimi et al., 2018) and having short interactions with operators.

These findings provide the first insights into the nutritional effects of white shark cage-diving, a need highlighted in scientific literature (Gallagher & Huveneers, 2018; Huveneers et al., 2018; Bruce, 2015) and in management strategies (DEWNR, 2012). Australia's white shark recovery plan (DSEWPaC, 2013) and the Neptune Islands Marine Park management plan (DEWNR, 2012) specifically states the importance of investigating the impacts of wildlife tourism, as regional managers need to balance ecology, protected species conservation, industry, economics, and the ecosystem functionality and conservation capacity of the Neptune Islands as a marine park. The lack of dietary effects from tourism operations indicates that current management strategies are adequately protecting the nutritional health of the industry's focal species, a key factor in Dubois and Fraser (2013) framework for assessing wildlife provisioning acceptability. This helps ensure the long-term sustainability of white shark-cage diving, while contributing towards a socially acceptable license for the industry to operate.

Furthermore, as the diet and nutrition of white sharks at the Neptune Islands does not differ from elsewhere in southern Australia, this marine park is likely one of many regionally-important foraging grounds. Hypotheses that white sharks aggregate around this marine park solely to predate upon pinnipeds may overestimate the significance of this group of long-nosed fur seals (*Arctocephalus forsteri*), understating the value of other pinniped-rich foraging grounds, which warrant investigation (DSEWPaC, 2013; objective 7 – identify and

protect critical white shark habitat, with an emphasis on key foraging areas). Additionally, the dietary importance of pinnipeds may be overstated, driven by the relative ease of observing breaching predation attempts (Hammerschlag, Martin, & Fallows, 2006; Martin, Hammerschlag, Collier, & Fallows, 2005) and that most known white shark aggregations are in the vicinity of pinniped colonies, despite the abundance of cetaceans and teleosts in white shark gut content (Hussey et al., 2012). Understanding the relative importance of different prey items, in the context of key foraging grounds, requires further research extending outside cage-diving locations. Such insight informs species-specific and regional management strategies, ensuring the protection of one of Australia's most iconic marine species.

Declarations of interest

None.

Author contributions

All authors designed the study. LM, CB and CH collected research material and LM, HP and CB performed the laboratory analyses. LM and CH performed the statistical analyses, and all authors contributed to drafting and revising the manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.tourman.2019.04.025.

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