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**Not all sawsharks are equal: species of co-existing
sawsharks show plasticity in trophic consumption both
within and between species**

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1 **Not all sawsharks are equal: species of co-existing sawsharks**
2 **show plasticity in trophic consumption both within and between**
3 **species**

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8

9 **Abstract**

10 Despite the global distribution of sawsharks, little is known about their diets or their role in the marine
11 biosphere. As species in higher trophic positions are generally considered to be more at risk to
12 perturbations such as fishing, understanding their role in the food chain will enable better
13 conservation and management strategies for these species. Two sawshark species (*Pristiophorus*
14 *cirratus*, *P. nudipinnis*) co-occur in waters off east Tasmania, Australia. This study determined the
15 trophic positions of these sawsharks, and whether they avoided competing with each other through
16 resource partitioning. Isotopic analysis of muscle tissue revealed that *P. cirratus* and *P. nudipinnis*
17 had significantly different trophic levels, with *P. cirratus* likely to have a diet of primary consumers
18 and *P. nudipinnis* likely to have a piscivorous diet. Due to their different isotopic signatures, it is also
19 likely that the sawshark rostrum has multiple functions. Both species shifted to higher trophic levels
20 during ontogeny. Maternal isotopic signatures were detectable in *P. cirratus* juveniles.

21 **Keywords:** *Pristiophoridae*, isotopes, diet, resource partitioning, niche divergence, *Pristidae*

22

23 Introduction

24 Species living in close proximity will tend to reduce competition through niche divergence or
25 resource partitioning when faced with limited resources (Ross 1986; Schoener 1974). While terrestrial
26 animals generally tend toward spatial niche separation (MacArthur 1965), trophic separation is
27 commonly observed amongst organisms in the marine environment (Sale 1979). Research conducted
28 in the area of resource partitioning often produces wide-ranging results, which range from competitive
29 exclusion of one species through the development of diverging sub-optimal resource use by that
30 species (Schoener 1989), to competing species continuing to exist on a similar resource (Gabler and
31 Amundsen 2010). Such conflicting results on diet partitioning may be a product of the difficulty of
32 accurately quantifying species' diets through short-term snapshots of stomach contents (Baker et al.
33 2014), or inappropriate levels of taxonomic resolution in identification of prey (Barnes et al. 2011).

34 Stable isotopes are one marker that allows researchers to determine trophic level (Vander Zanden et
35 al. 1997), migratory patterns (Hansson et al. 1997), and short, medium and long term diet shifts
36 (Estrada et al. 2006; Hussey et al. 2011; Shiffman et al. 2012). Predators at high trophic levels enrich
37 bioaccumulable markers present at lower trophic levels, enabling researchers to identify distinct
38 chemical signatures present at each trophic level (Hobson et al. 2002). Unlike traditional gut-content
39 analyses, stable isotopes can provide average dietary information assimilated over time (Dalerum and
40 Angerbjörn 2005), and are not affected by the digestibility of prey items, food expulsion during
41 capture, or opportunistic feeding. Thus stable isotopes are a more reliable indicator of trophic level
42 and long-term diet patterns than other more traditional methods, which are still necessary to correctly
43 identify prey species.

44 Interspecific competition between closely related species sharing a common resource can be
45 symmetric, where either species can fill a particular trophic level or niche (Munday 2004), or
46 asymmetric, where one competitor is superior and a trade-off occurs in relation to the resource
47 (Munday et al. 2001; Schoener 1983; Young 2004). Body and mouth size often play important roles
48 in such competition because larger individuals with wider mouths can potentially feed on a greater

range of prey sizes (Cohen et al. 1993). It is thus commonly assumed that closely-related species that are of similar size will have similar resource requirements. Where they co-occur, however, such species may have coevolved to use the divergent aspects of that resource over time (Connell 1980). In this case, we would hypothesise that the species that utilize prey from a higher trophic level would be gaining an advantage and would thus act as the superior competitor.

Sawsharks (*Pristiophoridae*) are elasmobranchs characterised by elongate bodies, ventral barbels, and saw-like rostrum (Last and Stevens 2009). To date, nine sawshark species have been identified, two of whom were classified in the last few years (Ebert and Cailliet 2011; Ebert and Wilms 2013). Two species co-occur in south-eastern Australian waters: *P. nudipinnis* and *P. cirratus*: the entire range of *P. nudipinnis* is within the wider range of *P. cirratus* (Last and Stevens 2009). Both species grow to similar lengths and weights, and can only be visually differentiated by slight changes in their rostral/body length ratios (higher for *P. cirratus*), the position of their rostral barbels (closer to the mouth for *P. nudipinnis*), and their colouration (spotted yellow/brown *P. cirratus*, uniform brown *P. nudipinnis*) (Last and Stevens 2009). Both species occur on the continental shelf at depths between 50 and 500 meters, and predominantly inhabit sandy benthic environments (Raoult et al., unpublished data).

Little is known about the diets or ecology of sawsharks. Research on the critically endangered sawfish (*Pristis microdon*) found that the saw-like rostrum is used to disable schools of fish in the water column (Wueringer et al. 2012). Sawfish rostral teeth are permanent and much thicker and smoother than the finer, more jagged sawshark teeth that are frequently replaced (Slaughter and Springer 1968). While the two taxa have evolved rostral saws independently (Aschliman et al. 2012), it is highly probable that the rostrum may serve a different use between sawfish and sawsharks. Alternate uses for the rostrum could include defence from predators, or foraging through sediment.

Three-hundred tons of *P. cirratus* and *P. nudipinnis* valued at over \$2 million AUD are caught annually in south-eastern Australian commercial fisheries. The majority of this catch is bycatch via

75 gill nets and fish trawling, and few other commercial fishing methods (i.e. demersal longlining)
76 capture these fish reliably (Raoult *et al.*, unpublished data). Australian government authorities (e.g.
77 the New South Wales Department of Primary Industries) have flagged *P. nudipinnis* and *P. cirratus*
78 for target research due to the large number of sharks caught yearly and the dearth of information on
79 their life-history traits.

80 We hypothesised that where *P. cirratus* and *P. nudipinnis* co-occurred, the two species would have
81 divergent prey resources at different trophic levels to reduce dietary overlap and thus competition
82 despite their similar morphology. Moreover, we hypothesised that if trophic separation occurred, such
83 dietary divergence would occur between the two species throughout ontogeny. This study used
84 muscle-tissue isotope analysis to determine the trophic levels of juvenile and adult *P. cirratus* and *P.*
85 *nudipinnus* from the north-eastern coast of Tasmania, Australia, to ascertain their average trophic
86 level. Using this trophic data, it may be possible to infer diet composition and therefore the use of the
87 sawshark rostrum during feeding. The ontogenetic profiles of these species were compared against
88 those from other ontogenetic studies worldwide to document whether patterns of isotopic plasticity
89 were prevalent in sharks. A greater understanding of the trophic levels of *P. cirratus* and *P.*
90 *nudipinnus* will increase our knowledge of the ecology of the community, and thus reduce uncertainty
91 in management and conservation efforts for these understudied species.

92

93 **Materials and Methods**

94 *P. cirratus* and *P. nudipinnis* were collected as bycatch from repeated research trawls on board the
95 Australian Maritime College vessel *FTV Bluefin* in July, August and December 2011-2012 along the
96 north-eastern coastline of Tasmania, Australia (40°18.101 S, 148°33.596 E; figure 1). These trawls
97 were aimed at catching the majority of the benthic community. Two trawl methods were used: one at
98 a depth of ~30m while using a 35mm mesh prawn net and another at a depth of ~80m when using a
99 70mm mesh demersal fish net. All trawls were conducted for 30 minutes at a speed of ~3.1kts.

100 *Pristiophorus nudipinnis* and *P. cirratus* caught in trawls were measured (total length, rostral length,
101 mouth width, fins dimensions, in mm) and weighed (g). Each animal was then dissected immediately.
102 The muscle in marine elasmobranchs represents, on average, a reliable isotopic signature for diet over
103 the past months to years (Kim et al. 2012a; MacNeil et al. 2006; Madigan et al. 2012). Muscle tissue
104 samples (~3cm³) were therefore taken from the area dorsal of the cervical vertebra for isotope
105 analyses. (Hussey et al. 2012b; Post et al. 2007) Care was taken to ensure samples were taken from the
106 same position on each animal. Muscle samples were stored in 5ml screw-cap tubes and frozen at -
107 20°C for storage until analysis as recommended by Kim and Koch (2012). Twenty-one *P. cirratus*
108 muscle samples were collected from different individuals, and 24 *P. nudipinnis* samples.

109 Muscle samples were dried at 60°C for 36 hours, ground to a fine powder using a mortar and pestle
110 and 1-2 mg was transferred into tin capsules, as per Bessey and Vanderklift (2014). Samples were
111 then analysed for carbon (¹³C: ¹²C) and nitrogen (¹⁵N: ¹⁴N) stable isotopes using a Europa EA GSL
112 elemental analyser coupled to a Hydra 2022 mass spectrometer (Sercon Ltd, UK) at Griffith
113 University (Queensland, Australia). Precision for this spectrometer is expected to be within 0.2 for
114 both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios. The ratios of ¹³C/¹²C ($\delta^{13}\text{C}$) and ¹⁵N/¹⁴N ($\delta^{15}\text{N}$) were expressed as the
115 relative per thousand (‰) difference between the sample and standard (Pee Dee belemnite for carbon
116 and atmospheric nitrogen for nitrogen).

117 To assess whether the isotope ratios (and thus diet) differed significantly between *P. nudipinnis* and *P.*
118 *cirratus*, mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values were analysed with a two sample T-test. Linear
119 regressions were then used to determine the relationship between length and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for both
120 species. Individuals were further split into juvenile and adults (*P. nudipinnis* > 800mm TL were adults
121 (n = 10); *P. cirratus* > 600mm TL were adults (n = 14)) and the relationship between length (and thus
122 maturity) and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ determined. Mouth width is known to be related to prey choice (Karpouzi
123 and Stergiou 2003; Kwak et al. 2004), consequently mouth width was compared to $\delta^{15}\text{N}$ to determine
124 whether the mouth size difference of the two species may have an effect on prey choice using a
125 generalized linear model (GLM). Studies that compared juvenile and adult shark isotopic ratios were

compiled and contrasted from this study: only studies that examined sharks from juvenile to adulthood were used.

Results

Different trophic levels were observed for *P. cirratus* and *P. nudipinnis*. Mean isotope ratios were significantly different between the two species for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($df=44$, $t=2.02$, $p<0.01$ in both cases, Fig. 2). Trophic shifts occurred during ontogeny in both *P. cirratus* and *P. nudipinnis*: $\delta^{15}\text{N}$ was significantly positively correlated with length (*P. cirratus*: $df=1$, $F=16.39$, $p<0.01$, $R^2=0.46$; *P. nudipinnis*: $df=1$, $F=7.76$, $p=0.01$, $R^2=0.25$, respectively, Fig. 3). *P. cirratus* $\delta^{13}\text{C}$ was significantly correlated with length ($df=1$, $R^2=0.43$, $F=14.37$, $p<0.01$, Fig. 4). This change in $\delta^{13}\text{C}$ during ontogeny was not detectable in *P. nudipinnis* ($df=1$, $R^2=0.03$, $F=0.95$, $p>0.05$, Fig. 4). There was no significant interaction between species and mouth width on $\delta^{15}\text{N}$ values (GLM, $F=0.04$, $p>0.05$, Fig. 5).

$\delta^{15}\text{N}$ values were negatively correlated with length in juvenile *P. cirratus* ($df=1$, $R^2=0.73$, $F=11.31$, $p<0.05$). $\delta^{15}\text{N}$ values of juvenile *P. nudipinnis* and adult stages of *P. cirratus* and *P. nudipinnis* did not change during ontogeny, as they were not correlated with length ($df=1$, $R^2=0.19$, $F=2.56$, $p>0.05$; $df=1$, $R^2=0.10$, $F=1.52$, $p>0.05$; $df=1$, $R^2=0.39$, $F=3.9$, $p>0.05$, respectively). While some studies suggest that lipid extraction from muscle tissue is necessary for some elasmobranch species (Hussey et al. 2012b), C:N ratios in these sharks had a mean of 2.65, indicating low lipid levels below the recommended threshold where lipid extractions or corrections are necessary (C:N > 3.5; (Post et al. 2007)).

It is unclear whether sharks always exhibit maternal isotopic signatures irrespective of the style of embryonic development, and whether size is always related to prey choice. Furthermore, to determine likely prey items and trophic level, the results from this study were compared with those of Davenport and Bax (2002), which were also obtained in south-eastern Australia: *P. cirratus* $\delta^{15}\text{N}$ values were in the upper range of tertiary consumers in the area, while *P. nudipinnis* $\delta^{15}\text{N}$ values were above tertiary

consumers (Table 1). Twelve studies documented shark $\delta^{15}\text{N}$ isotope ratios from juveniles to adults (Table 2). Only two studies found maternal $\delta^{15}\text{N}$ signatures (only one *Carcharodon carcharias* study detected such signatures). Not all studies found significant $\delta^{15}\text{N}$ /size ratios, and some populations/individuals within the same species had different $\delta^{15}\text{N}$ /size slopes.

Discussion

P. cirratus and *P. nudipinnis* caught in Tasmania exhibited significant inter and intra-specific trophic plasticity. A comparison between isotope levels of *P. nudipinnis* and previous research suggests that their diet was predominantly piscivorous and were potentially quaternary consumers. Isotope values of *P. cirratus* are consistent with those of secondary/tertiary consumers. Ontogenetic shifts in diet were apparent between juveniles and adults in both species, and in all but three of the ontogeny studies from other species of sharks. This is the first study to determine the trophic level of sawsharks.

The difference in isotope levels between *P. cirratus* and *P. nudipinnis* suggests that, when co-occurring, they appear to avoid direct competition through resource partitioning at different trophic levels. Mean $\delta^{13}\text{C}$ values were significantly different between *P. cirratus* and *P. nudipinnis*, but this it is unlikely to be indicative of separate diet sources and more likely a consequence of the higher trophic diet of *P. nudipinnis* (difference of 1‰), which causes higher carbon/nitrogen fractionation at higher trophic levels (Zanden and Rasmussen 2001). A study by Kinney et al. (2011) detected resource partitioning in various juvenile shark species in shark nursery areas at comparable trophic levels, therefore this may be a widespread occurrence with co-occurring elasmobranchs.

In competitive environments larger animals have access to a greater size range of prey, and *P. nudipinnis* grows to lengths 200mm longer than *P. cirratus*. The maximum size of each species size is unlikely to have a significant effect on prey choice; however, as there was no significant interaction between species and mouth width on isotope ratios. The main morphological differences between these two species, aside from total length and colour patterns, are the width and thickness of the

rostrum (Last and Stevens 2009). The driver for resource partitioning between these two species of sawshark is therefore more likely to be behaviourally-driven rather than morphological.

The function of the rostral saw in sawsharks is unknown, although they are routinely hypothesised to be used in a similar fashion as sawfish (*Pristid* spp.) for prey capture (Slaughter and Springer 1968, Wueringer et al. 2009). This study suggests that the trophic level of *P. cirratus* is similar to species that prey on benthic primary consumers; consequently *P. cirratus* may use their rostrums to sift through substrate in the search of prey. The isotope levels of *P. nudipinnis* suggest a more piscivorous diet, and raise the possibility that they feed in a similar manner as some *Pristidae* species (Wueringer et al. 2012). Further research into diet, feeding modes, and rostrum use is necessary to elucidate the specifics of feeding in these species.

Both species of sawshark were hypothesised to show similar traits because they share the same development pattern (aplacental viviparity), and the few studies on sawshark phylogeny suggest they are a highly related monophyletic group (Dosay-Akbulut 2006). The negative isotopic correlation of juvenile *P. cirratus* was indicative of maternal isotope signatures. This pattern was not visible in *P. nudipinnis* samples, possibly due to the lack of very young individuals in this data set. Other shark species have similar maternal isotopic signatures or fractionation in juveniles (Campana et al. 2010, Vaudo et al. 2010), however only two studies that analysed isotopic signatures throughout development detected such patterns (Campana et al. 2010; Estrada et al. 2006). Maternal signatures are lost quickly after birth (Olin et al. 2011) and that the lack of newborns in data sets under-estimates the number of shark species with maternal isotopic signatures. Future research should examine the drivers and diversity of maternal isotopic signatures in elasmobranchs.

Adult isotope levels that were not correlated with length suggest that a dietary shift occurs quickly during the sub-adult phase in *P. cirratus* and *P. nudipinnis*. As similar ontogenetic patterns have been observed in other species of sharks (Kim et al. 2012b), it is possible that different sawshark trophic ecotypes exist in other areas, or that in areas where the two species do not co-occur it is possible that the remaining species will fill the available trophic niche. The majority of studies that examined

isotope ratios during ontogeny found similar length-correlated ratios (Fig. 2), though the degree of variation during ontogeny varied inter and intra-specifically. This suggests that ontogenic shift in diet may be partially linked to species-specific traits. Geographically distinct populations of certain species also have different patterns of trophic shift (Abrantes and Barnett 2011), suggesting that an ontogenetic shift in diet may also be related to prey availability and/or environmental conditions. The spread of isotopic deltas per length (in this study as well as others listed above) suggests a high degree of individual feeding preference within species (Kim et al. 2012b). Studies that examine trophic plasticity through ontogeny must therefore do so on small scales and at high resolutions, otherwise results will be diluted due to noise from inter and intra-specific variability. Furthermore, these conclusions suggest that changes in temporal and geographical variables greatly affect trophic studies that use stable isotopes, and further research should aim to quantify the level of these effects.

Compliance with ethical standards

Trawling for research purposes was permitted in accordance with ethical guidelines number A0011023, UTAS ACEC. All procedures performed were in accordance with the ethical standards of the University of Tasmania.

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Figure 1. Map of Tasmania and research trawl sites (marked with grey stars)

Figure 2. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for individual *P. cirratus* and *P. nudipinnis*.

Figure 3. $\delta^{15}\text{N}$ in relation to total length for *P. cirratus* and *P. nudipinnis*. Trend line to show significant correlations between length and isotopic delta for each species.

Figure 4. $\delta^{13}\text{C}$ in relation to total length for *P. cirratus* and *P. nudipinnis*. Trend line to show significant correlations.

Figure 5. Mouth width/ $\delta^{15}\text{N}$ relationship for *P. cirratus* and *P. nudipinnis*.

Table 1: Comparison of soft tissue $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges from species caught in south-eastern Australia (taken from Davenport and Bax (2002)), and the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of *P. nudipinnis* and *P. cirratus* from this study.

Consumer	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)
Tertiary consumers (e.g. Pink Ling, <i>Genypterus blacodes</i>)	12.2 – 13.8	(-14.6) - (-17.2)
Secondary consumers (e.g. Elephant Fish, <i>Callorhynchus milii</i>)	10.3 – 13.1	(-16.8) - (-19.1)
Primary consumers (e.g. Ophiuroids)	5.3 – 9.4	(-16.7) - (-18.1)
<i>P. cirratus</i> (Common Sawshark/Longnose Sawshark)	12.9 – 14.1	(-17.1) – (-17.9)
<i>P. nudipinnis</i> (Southern Sawshark)	13.5 – 15.5	(-15.8) – (-17.1)

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Table 2: Comparison of tissue $\delta^{15}\text{N}$ (‰) for studies that recorded isotopic levels through ontogeny.

Study	Species	$\delta^{15}\text{N}$ (‰) maternal signature yes/no	Significant $\delta^{15}\text{N}$ (‰)/size relationship yes/no	Slope of $\delta^{15}\text{N}$ (‰)/size relationship
Current study	<i>P. nudipinnis</i> (southern sawshark), <i>P. cirratus</i> (common sawshark)	No/Yes	Yes	Linear/linear
Borrell et al. (2011)	<i>Rhincodon typus</i> (whale shark)	No	Yes	logarithmic
Borrell et al. (2010)	<i>Rhincodon typus</i> (whale shark), <i>Shpyrna lewini</i> (scalloped hammerhead)	No/No	Yes/Yes	Logarithmic/logarithmic
Abrantes and Barnett (2011)	<i>Notorynchus cepedianus</i> (broadnose sevengill)	No	Yes/No (depending on site)	Linear
Estrada et al. (2006)	<i>Carcharodon carcharias</i> (white shark)	Yes	Yes	Three step
Fisk et al. (2002)	<i>Somniosus microcephalus</i> (Greenland shark)	No (only 2 juveniles)	Yes	Linear
Speed et al. (2012)	<i>Carcharhinus melonapterus</i> (blacktip reef shark), <i>C. amblyrhynchos</i> (grey reef shark)	No	No	N/A
Malpica-Cruz et al. (2013)	<i>Isurus oxyrinchus</i> (shortfin mako), <i>Carcharodon carcharias</i> (white shark)	No	Yes	Sigmoid/Logarithmic
Kim et al. (2012b)	<i>Carcharodon carcharias</i> (white shark)	No	Yes/No (depending on individuals)	Logarithmic/linear (depending on individuals)
Campana et al. (2010)	<i>Carcharhinus leucas</i> (bull shark), <i>Galeocerdo cuvier</i> (tiger shark)	Yes	Yes/Maybe	Inversed parabolic/Possibly inversed parabolic
Hussey et al. (2012)	<i>Carcharodon carcharias</i> (white shark)	No	Yes	Sigmoid or logarithmic
Werry et al. (2011)	<i>Carcharhinus leucas</i> (bull shark)	No (perhaps in $\delta^{13}\text{C}$?)	Yes	Logarithmic
Papastamatiou et al. (2010)	<i>Carcharhinus melanopterus</i> (blacktip reef shark)	No	No/Yes (dependent on region)	Linear