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Feeding down the food web?! Trophic cascading reflected in the long-term dietary trends of endangered Indian Ocean humpback dolphins *Sousa plumbea* from KwaZulu-Natal, South Africa

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ABSTRACT

Approximately 60 % of coastal cetacean species globally are at risk of extinction, despite these organisms role as indicators of Ocean Health. Changing food availability due to overfishing and/or climate change has been identified as one stressor among cumulative impacts on cetacean populations. Using a multi-method approach of analysing stomach contents (n = 107), stable isotopes (n = 30) and blubber thickness (n = 87) data (as a proxy for condition), we investigated long-term dietary trends (1972–2017) of incidentally bycaught Indian Ocean humpback dolphin *Sousa plumbea* off the KwaZulu-Natal coast, South Africa. A total of 64 teleost and three cephalopod species were identified. A diet shift was observed in the stomach contents between 2001 and 2020, with new prey species being recorded, which was validated by the significant difference in prey species diversity over time ($p < 0.001$). In addition, significant decreases in $\delta^{13}C$ signatures between time intervals ($p = 0.01$), due to differences between the 2011–2020 decade and the 1971–1980 and 1981–1990 intervals, also indicated a change in prey. A significant decrease was found in the mid-dorsal body condition index (calculated using blubber thickness) between the 1981–1990 and 2001–2010 intervals ($p = 0.02$). Our study provides evidence of a dietary shift in the endangered *S. plumbea* along South Africa's KwaZulu-Natal coastline from 2001 to 2020, likely driven by declining prey availability resulting from overfishing and/or climate change. This highlights the species' role as an indicator of environmental change in the coastal zone of the Indian Ocean and the importance of long-term data for assessing Ocean Health in the region.

1. Introduction

Cetaceans, as marine apex predators, fulfil complex roles as top-down regulators in marine food webs (Baum and Worm, 2009; Heße et al., 2025). However, as cumulative impacts, largely from anthropogenic developments, including man-made climate change, are progressively affecting their populations, they can be considered important indicators of Anthropocene Ocean Health (Plön et al., 2024). As such, their ecology and conservation are of international interest (Burgener et al., 2012; Penniman et al., 2018), but limited historical ecological and/or biological baseline data often prevent the assessment of impact from multiple, cumulative stressors, both anthropogenic and natural (Pasino et al., 2025).

The availability of prey can significantly influence population growth rates (e.g., Horswill et al., 2017), social dynamics (e.g., McHuron et al., 2023), and animal health. Global fisheries data during the second half of the 20th century has illustrated a progressive shift in landings from long-lived, high trophic level, piscivorous bottom fish to short-lived, planktivorous pelagic fish and low trophic level invertebrates due to overfishing, possibly impacting the marine food web (Pauly et al.,

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1998) and undermining the health of entire ecosystems. This disruption to marine food webs can modify predator–prey dynamics, create population imbalances, and may ultimately impact overall nutrition and health conditions of individuals, resulting in the decline or extinction of numerous marine species (Hočevar and Kuparinen, 2021). A notable example is the short-beaked common dolphin (*Delphinus delphis*), once one of the most common species in the Mediterranean Sea, which has undergone a significant population decline since the 1970′s (Bearzi et al., 2003) and is now listed as "endangered" by the International Union for the Conservation of Nature (IUCN; Bearzi, 2012). Competition with fisheries is believed to play a contributing role (Notarbartolo di Sciara et al., 2002; Bearzi et al., 2003), although cause-effect relationships and ecosystem dynamics remain poorly characterized.

The coastal zone possibly experiences the highest accumulation of anthropogenic impacts in marine systems due to the combined effects of terrestrial land-use and Ocean Economy developments (Robledo Ardila et al., 2024; Robledo Ardila et al., 2023). Globally, cetaceans in freshwater and coastal ecosystems are most at risk, with 100 % and 60 % of species, respectively, considered threatened (Braulik et al., 2023b). In the Indian Ocean, the humpback dolphin *Sousa plumbea*, which is distributed in a narrow strip of coastal waters along the Indian Ocean coastline from False Bay, South Africa, in the west, to approximately the southern tip of India, is one such example (Braulik et al., 2023a). Thus, long-term monitoring of this species allows assessment of anthropogenic impacts on ecosystem health in a region with few long-term data.

Collecting ecological and/or biological baseline data to understand the trophic ecology and health condition of threatened marine mammals is a challenge, as they are logistically difficult to observe due to their fast movements, long distance travel, and tendency to do most of their feeding underwater and/or far out at sea (Browning et al., 2014). A variety of methods have been used to investigate marine mammal trophic ecology, each with its own limitations. Stomach content analysis (SCA) is a common technique employed to obtain dietary information in marine mammals, either through examining the stomach contents of dead animals from strandings or by performing stomach lavage on live animals (e.g., Barros and Wells, 1998; Barros et al., 2000; Gibbs et al., 2011; Dunshea et al., 2013). However, erosion of hard parts during digestion often makes the identification of prey species from stomach contents difficult (Browning et al., 2014). Since stomach lavage on live animals is an invasive procedure that can induce high stress levels, SCA of dead stranded animals is typically preferred (Browning et al., 2014). However, SCA of dead stranded animals may not be representative of the feeding habits of the population as a whole, as these animals may have been unhealthy and SCA only provides a "snapshot" of recently consumed prey species, limiting its use (Browning et al., 2014; Heße et al., 2025). These limitations have led researchers to increasingly use more indirect methods to reveal information about marine mammal trophic ecology, such as stable isotope analysis (SIA; Browning et al., 2014).

Stable isotope analysis (SIA) is based on the principle that the isotopic constitution of tissues reflects the diet of the consumer (i.e., "you are what/where you eat"; Deniro and Epstein, 1978; Deniro and Epstein, 1981). Carbon and nitrogen are the two most common isotopic signatures used in marine ecological studies, with carbon isotope ratios (^{13}C:^{12}C) being indicative of sources of primary production, which varies geographically, with elevated values recorded in productive nearshore environments and lower values observed in less productive offshore regions (Pasino et al., 2025). Nitrogen isotope ratios (^{15}N:^{14}N) reflect trophic level, because $\delta^{15}N$ increases per trophic level within the food web (Fry, 1988; Rau et al., 1983; Walker and Macko, 1999). Cetacean teeth are particularly useful for SIA, as dentine layers are continually deposited with age, providing a permanent dietary record throughout the animal's lifetime (Knoff et al., 2008; Walker and Macko, 1999). Stable isotope studies have been conducted to investigate the feeding ecology of a number of cetacean species (Hobson et al., 2004; Hooker et al., 2001; Jansen et al., 2012; MacAvoy et al., 2017; Mendes et al., 2006; Nino-Torres et al., 2006), but to date, investigations into the temporal changes in the diet of the only endangered resident marine mammal in South Africa, *S. plumbea,* are lacking.

While SCA and SIA provide valuable insights into the trophic ecology of marine mammals, blubber thickness is a commonly used indicator of their health and nutritional status (Das et al., 2004; Wells et al., 2004; Murphy et al., 2010). Blubber is unique to marine mammals, making up between 15 and 55 % of the body weight in cetaceans. It is a complex, dynamic, multifunctional subcutaneous tissue, assisting in providing a hydrodynamic body shape, buoyancy, insulation and locomotion (Koopman et al., 2002). Information on blubber thickness has traditionally been used as an indicator for animal condition and nutrition and in recent years, have increasingly been linked to animal and population health (Torres et al., 2022) and associated changes in the marine environment (Vermeulen et al., 2023).

The Indian Ocean humpback dolphin (*Sousa plumbea* Cuvier, 1829) is a small delphinid found in coastal and estuarine environments in tropical and sub-tropical waters throughout the Indian Ocean (Braulik et al., 2015; Collins et al., 2025. The species occupies various shallow coastal environments, including estuaries and river mouths, and is usually found in water depths of < 25 m (Karczmarski et al., 2000; Atkins et al., 2004; Keith et al., 2013; James et al., 2015); it is an opportunistic feeder, primarily consuming an assortment of nearshore, estuarine and reef fishes (Barros and Cockcroft, 1991; Sekiguchi et al., 1992; Ross et al., 1994). Currently, the Indian Ocean humback dolphin is the only resident marine mammal in South African territorial waters listed as endangered (Plön et al., 2016; Braulik et al., 2015, 2023a), with < 500 individuals remaining (Plön et al., 2015; Vermeulen et al., 2018). Several factors are believed to be causing the decline in the humpback dolphin population in the southern African region (Plön et al., 2016; Plön et al., 2021), one of which is the continued bycatch in bather protection nets (BPNs; Cockcroft, 1990; Atkins et al., 2013; Atkins et al., 2016).

Long-term samples from animals incidentally caught in the BPNs along the KwaZulu-Natal coast offer a unique opportunity to gather critical data on the life history, ecology, and health of these species. Since it is assumed that these animals are accidentally entangled and are otherwise healthy, they can provide important insights into disease, environmental impacts, and overall population dynamics (Plön et al., 2015).

The aim of the current study is to use a multi-method approach, combining stomach content analysis (SCA), stable isotope analysis (SIA), and blubber thickness measurements as a proxy for condition, to understand the long-term dietary changes and health condition of the endangered *S. plumbea* along the east coast of South Africa. This retrospective long-term monitoring approach is crucial for documenting historical changes and establishing ecological and biological baselines essential for the understanding of the variability in the species' diet and condition. The importance of this study lies in its potential to reveal anthropogenic impacts on the population structure, identify variations in food webs, and assess how changes in diet may affect the health and condition of the species, highlighting the reality for coastal cetaceans in the Anthropocene. Collecting such baseline information is vital for future conservation and management strategies to effectively monitor and protect this species as a system-specific indicator of Ocean Health in the coastal zone of the Indian Ocean (Dale and Beyeler, 2001).

2. Materials and methods

2.1. Study area and sampling

Bather protection nets (BPNs) have been in place along the central and south coasts of KwaZulu-Natal since 1952 (Fig. 1), and are maintained and managed by the KwaZulu-Natal Sharks Board (KZNSB), whose associated shark control programme has been described in detail (e.g., Dudley, 1997; Cliff and Dudley, 2011). The nets are checked by KZNSB staff every morning during weekdays (weather permitting) and

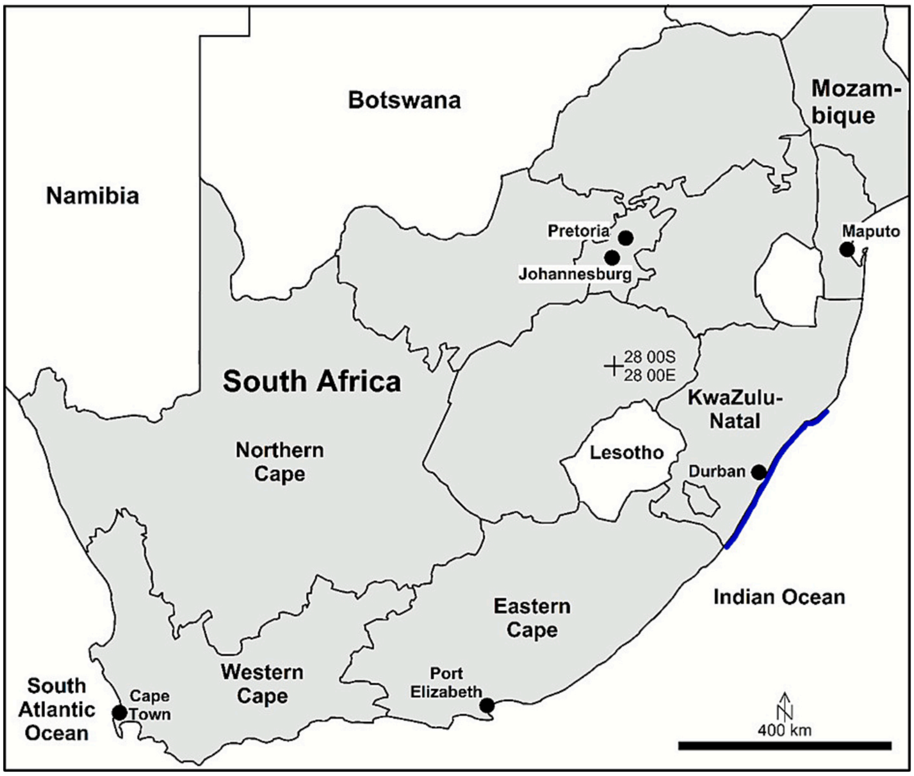

Fig. 1. The bather protection nets (BPNs), shown by the blue line, are located along the south and central KwaZulu-Natal coastline, South Africa. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

individuals found alive are released, while dead animals are removed and taken back to the KZNSB laboratory for research purposes. Under a long-standing agreement between the Port Elizabeth Museum (PEM) and the KZNSB, detailed biological measurements and samples are taken from these animals. Data and samples are accessioned to the Graham Ross Marine Mammal Collection located at the PEM (Cockcroft, 1990; Plön et al., 2012), allowing retrospective long-term monitoring of these populations.

Samples ranged in date from 1972 to 2017 and were grouped into decade-long time intervals for subsequent analysis (see Table 1). For stomach content analysis, stomachs of 107 humpback dolphins (60 males and 47 females) were analysed in relation to age class (Table 1), with individuals being classified as either immature (including calves, neonates and subadults) or adult, following Plön et al. (submitted). After necropsy, whole stomachs (tied at the oesophagus anterior to the forestomach, and at the duodenum posterior to the pylorus) from each animal were stored frozen in sealed and labelled plastic bags until examination. Only stomachs containing prey items were examined and included in the analysis.

For SIA, teeth from 30 humpback dolphins (17 males and 13 females) were analysed (Table 1). Only sexually mature individuals were used for SIA to ensure that the obtained results reflect the diet of adults. Sexual maturity was determined primarily through histological examination of the gonads, and, if these were not available, by estimated age (using growth layer groups (GLGs) in teeth; following Plön et al. (submitted).

2.2. Stomach content analysis (SCA)

Humpback dolphin stomachs were thawed and weighed to the nearest 0.1 g. For those stomachs containing prey items (n = 107), whole prey were removed for identification. photographed and measured. Otoliths and squid beaks were extracted from all intact fish skulls and buccal masses, respectively, as well as removed from the prey remains for further identification of prey items. The PEM reference collections for otoliths and cephalopod beaks as well as Smale et al. (1995) and Clarke (1986) were used for identification to the lowest taxonomic level possible.

For otoliths, the maximum length and for cephalopod beaks the lower rostral length was measured to the nearest 0.02 mm, using either a Zeiss binocular microscope fitted with an eyepiece graticule or digital callipers, with the exception of octopods and sepiids, where the lower crest length was measured (Clarke, 1986; Smale et al., 1995). Using

Table 1
Overview of sample sizes of bycaught humpback dolphins investigated for each category.

Categories		Stomach content analysis (n = 107)	Stable isotope analysis (n = 30)	Blubber thickness measurements (n = 87)
Sex	Males	60	17	0
	Females	47	13	0
Age class	Adults	42	30	0
	Juveniles	65	0	0
Time interval	1961–1970	0	1	0
	1971–1980	7	3	0
	1981–1990	47	10	17
	1991–2000	18	5	18
	2001–2010	24	7	37
	2011–2020	11	4	15

regression equations provided in Smale et al. (1995), the length (mm) and mass (g) of each prey item was back calculated. Prey items, where the lowest taxonomic level of identification was to family level, were not included in the analyses for this study (3 % out of all identified prey items). If no regression equation was available for a prey item, it was included in the species list, but excluded from Index of Relative Importance (IRI) calculations (10 % out of all identified prey items). Due to the uncertainties surrounding taxonomic groupings of specific cephalopods (Xavier et al., 2007), cephalopod beaks were identified to genus level, and a representative species from each genus was chosen for the purpose of calculating length and mass using available regression equations. These representative species were *Loligo vulgaris* for *Loligo* sp., *Octopus vulgaris* for *Octopus* sp., and *Sepia officinalis* for *Sepia* sp.

To assess the value of individual prey items in humpback dolphin diet, an Index of Relative Importance (IRI) was calculated for the overall diet for age classes, for sex and for different time intervals (Pinkas et al., 1971). The percentage number (%NA), percentage mass (%MA) and percentage frequency of occurrence (%FO) of the individual species were calculated and incorporated to calculate the IRI as follows:

1. Percentage number of prey species ($\%NA$) $= NA / Nb$ x 100

where Na is the number of prey species a in all stomachs and Nb is the total number of all prey species in all stomachs.

2. Percentage mass of prey species ($\%MA$) $= Ma / Mb$ x 100

where Ma is the estimated mass of prey species a in all stomachs and Mb is the estimated mass of all prey in all stomachs.

3. Percentage frequency of occurrence ($\%FO$) $= Fa / Fb$ x 100

where Fa is the number of stomachs that contain prey item a and Fb is the total number of stomachs containing prey items.

The results from the equations above were used to calculate the IRI as follows:

IRI $= (\%NA + \%MA)$ x $\%FO$

In addition, the Shannon-Weaver diversity index, species evenness and richness (as determined by the number of prey species consumed) were calculated to determine whether the diets of the different sexes and age classes were significantly different as well as to determine significant differences in diet between time intervals. The following equations were used to determine species diversity and evenness:

Shannon-Weaver diversity index $(H) = -\sum[(p_i) \times \log(p_i)]$

where p_i is the proportion of individuals of i-th species.

Species evenness $(E) = H / \ln(k)$

where H is the Shannon-Weaver diversity index and k is the number of prey species consumed.

2.3. Stable isotope analysis (SIA)

2.3.1. Tooth preparation

One tooth per individual, showing the least amount of wear, was selected for SIA analysis. As the teeth in this species are quite large and robust, one tooth provided sufficient material for the analysis. Teeth were sectioned longitudinally, and the innermost part of the tooth was sampled using a dentists' drill by drilling from the centre outwards, ensuring that only the five most recent growth-layer-groups (GLG's; see Plön et al. (submitted) were selected. Based on the date of death of the animal and keeping in mind that the tooth powder represented the most recent five years of the animals' life, the samples were then assigned according to decade for statistical analysis (Table 1), ensuring strong isotope signatures for temporal analysis. The 1961–1970 decade contained only one sample and was therefore excluded from any further analyses. The powder for each tooth was collected in a tinfoil boat and transferred to labelled Eppendorf tubes.

The tooth powder was then decalcified following standard procedures (e.g. Walker and Macko, 1999). Briefly, a 1 M HCL solution was added to individual samples for 24 h to remove carbonates followed by samples being rinsed with distilled water and centrifuged at 12 000 rpm for two minutes, ensuring that decalcified tooth material formed a pellet. After removing the excess distilled water from each tube, the samples were left to dry in a dust-proof container for a minimum of one week. Once dry, the pellet was extracted, ground into powder and weighed. Weighed sample aliquots were combusted in an elemental analyser (Flash EA, 1112 Series, Thermo™, Thermo Fisher Scientific). The $\delta^{13}C$ and $\delta^{15}N$ isotopes were determined using a continuous-flow isotope ratio mass spectrometer (Delta V Plus, Thermo Finnigan) at the Stable Isotope Laboratory of the Mammal Research Institute, University of Pretoria, South Africa. Results were presented using standard delta notation in parts per thousand (‰) relative to Vienna PeeDee Belemnite, the international standard for $\delta^{13}C$, and to atmospheric N_2 (air) for $\delta^{15}N$.

2.4. Blubber thickness data

Biological measurements obtained from carcasses and accessioned to the Graham Ross Marine Mammal Collection at the PEM included measurements of ventral, lateral and dorsal blubber thickness. A body condition index (BCI; expressed as blubber thickness (cm)/total body length (cm); Ambrose et al., 2013) was calculated for animals incidentally caught between 1981 and 2017 for all three blubber measurements with the aim to eliminate effects of age and to standardise results. The results were then binned into four decades for further analysis (Table 1).

2.5. Statistical analysis

To assess whether the diets of the different sexes, age classes and time intervals differed, Shapiro–Wilk's normality tests were conducted on the species diversity index (H), as calculated from humpback dolphin stomach contents. The results indicated that the data was not normally distributed ($p < 0.05$), and thus a non-parametric Kruskal-Wallis Rank Sum Test and appropriate *post-hoc* test were used to determine whether species diversity differed between the different groups.

To test whether $\delta^{13}C$ and $\delta^{15}N$ ratios differed between sexes or temporally between different decades (Table 1), normality assessments were conducted using the Shapiro–Wilk's test. The $\delta^{13}C$ and $\delta^{15}N$ values met the assumptions of these tests ($p > 0.05$) and thus, a standard parametric one-way ANOVA was used. If a given test result showed an overall significant difference, a Tukey's HSD *post hoc* test was performed to determine which variables were driving the overall difference. The oldest time interval, 1961–1970, was included for comparative purposes; however, this interval was not included in any statistical analyses as it only contained a single isotope sample.

Similarly, to compare the BCI between decades, normality tests using the Shapiro–Wilk's test were conducted, with BCI values meeting the assumptions of the test ($p > 0.05$), and as such, a standard parametric one-way ANOVA with a Tukey's HSD *post hoc* test was performed.

All statistical analyses were performed in R v. 2024.09.0 "Cranberry Hibiscus" Release (c8fc7aee, 2024-09-16) for windows (R Core Team, 2024) using a *priori* significance level of $\alpha = 0.05$.

3. Results

3.1. Stomach content analysis (SCA)

3.1.1. Overall diet composition

A total of 64 teleost (28 families) and three cephalopod (three families) species were identified from the 107 stomachs analysed (Table 2). The majority of the teleost species belonged to the Sparidae (13 species), Sciaenidae (8 species) and Mugilidae (7 species) families, while the cephalopod species were represented by Loliginidae, Octopodidae and Sepiidae families. Only 14 stomachs of individuals caught between 2004 and 2013 contained cephalopod remains.

IRI values were calculated for 39 prey items (36 teleosts and three cephalopods) for which regression equations were available. According to the IRI (Table 2), the five most important species in the humpback dolphin diet, in descending order of importance, were orange mouth

Table 2

Teleost and cephalopod prey items of all incidentally bycaught *S. plumbea* along KwaZulu-Natal coastline between 1972 and 2016, and their calculated Index of Relative Importance (IRI) values (n = 107). Asterisk (*) denotes prey items for which no regression equations were available.

	Family	Species	Number	%NA	Mass (g)	%MA (g)	Frequency	%FO	IRI	Rank
Teleosts	Alosidae	*Sardinops ocellatus**	7	0.23	–	–	1	0.93	–	–
	Apogonidae	*Apogon apogonides**	1	0.03	–	–	1	0.93	–	–
		*Apogon aureus**	2	0.06	–	–	1	0.93	–	–
	Atherinidae	*Atherinomorus lacunosus**	1	0.03	–	–	1	0.93	–	–
	Cheilodactylidae	*Cheilodactylus fasciatus*	2	0.06	584.95	0.46	1	0.93	0.49	27
	Clupeidae	*Hilsa kelee**	90	2.90	–	–	11	10.28	–	–
		*Sardinella aurita**	1	0.03	–	–	1	0.93	–	–
		*Sardinella gibbosa**	24	0.77	–	–	2	1.87	–	–
	Dichistiidae	*Coracinus multifasciatus**	11	0.35	–	–	3	2.80	–	–
	Dinopercidae	*Dinoperca petersi*	3	0.10	247.09	0.19	1	0.93	0.27	32
	Engraulidae	*Thryssa setirostris*	4	0.13	52.65	0.04	2	1.87	0.32	30
		Thryssa vitrirostris	1078	34.71	19992.63	15.66	32	29.91	1506.44	1
	Exocoetidae	*Cheilopogon pinnatibarbatus**	3	0.10	–	–	1	0.93	–	–
	Gerreidae	*Gerres rappi**	2	0.06	–	–	1	0.93	–	–
	Haemulidae	*Pomadasys commersonnii*	47	1.51	11871.52	9.30	19	17.76	192.04	8
		Pomadasys furcatum	7	0.23	2941.31	2.30	6	5.61	14.19	16
		*Pomadasys multimaculatum**	1	0.03	–	–	1	0.93	–	–
		Pomadasys olivaceum	377	12.14	7542.55	5.91	30	28.04	506.01	4
		Pomadasys striatum	200	6.44	5848.28	4.58	24	22.43	247.21	5
		*Pomadasys stridens**	38	1.22	–	–	4	3.74	–	–
	Kyphosidae	*Neoscorpis lithophilus**	1	0.03	–	–	1	0.93	–	–
	Leiognathidae	*Gazza minuta**	9	0.29	–	–	2	1.87	–	–
		Secutor insidiator	52	1.67	135.96	0.11	7	6.54	11.65	17
	Lutjanidae	*Lutjanus fulviflamma**	6	0.19	–	–	2	1.87	–	–
	Mugilidae	*Liza alata**	2	0.06	–	–	2	1.87	–	–
		Liza dumerilii	12	0.39	1104.42	0.87	7	6.54	8.19	18
		Liza richardsonii	1	0.03	212.99	0.17	1	0.93	0.19	35
		Liza tricuspidens	41	1.32	4096.18	3.21	7	6.54	29.63	13
		Mugil cephalus	24	0.77	6629.15	5.19	8	7.48	44.61	11
		*Valamugil buchanani**	2	0.06	–	–	2	1.87	–	–
		*Valamugil robustus**	35	1.13	–	–	6	5.61	–	–
		*Valamugil seheli**	27	0.87	–	–	9	8.41	–	–
	Muraenesocidae	*Muraenesox bagio**	2	0.06	–	–	2	1.87	–	–
	Ophidiidae	*Brotula multibarbata**	1	0.03	–	–	1	0.93	–	–
	Pempheridae	*Pempheris adusta**	2	0.06	–	–	1	0.93	–	–
	Pleuronectidae	*Poecilopsetta natalensis**	1	0.03	–	–	1	0.93	–	–
	Polynemidae	*Polydactylus sextarius**	2	0.06	–	–	1	0.93	–	–
	Pomatomidae	*Pomatomus saltatrix*	18	0.58	1819.77	1.43	10	9.35	18.74	14
	Pseudochromidae	*Pseudochromis dutoiti**	1	0.03	–	–	1	0.93	–	–
	Sciaenidae	*Argyrosomus hololepidotus*	4	0.13	112.25	0.09	3	2.80	0.61	26
		Argyrosomus thorpei	103	3.32	2709.29	2.12	18	16.82	91.50	9
		Atrobucca nibe	58	1.87	729.69	0.57	14	13.08	31.91	12
		Johnius amblycephalus	173	5.57	7520.88	5.89	19	17.76	203.54	7
		Johnius dussumieri	24	0.77	359.85	0.28	5	4.67	4.93	20
		Otolithes ruber	268	8.63	6678.52	5.23	48	44.86	621.81	2
		Umbrina canariensis	29	0.93	1059.03	0.83	10	9.35	16.48	15
	Serranidae	*Epinephelus andersoni*	3	0.10	1698.24	1.33	3	2.80	4.00	21
	Sillaginidae	*Sillago chondropus**	1	0.03	–	–	1	0.93	–	–
		Sillago sihama	9	0.29	908.74	0.71	7	6.54	6.55	19
	Sparidae	*Acanthopagrus berda*	3	0.10	329.47	0.26	2	1.87	0.66	25
		Chrysoblephus laticeps	1	0.03	322.40	0.25	1	0.93	0.27	33
		Diplodus cervinus	1	0.03	479.12	0.38	1	0.93	0.38	29
		Diplodus sargus capensis	49	1.58	3345.77	2.62	16	14.95	62.79	10
		Pachymetopon aeneum	1	0.03	123.54	0.10	1	0.93	0.12	37
		Pagellus bellottii natalensis	1	0.03	61.09	0.05	1	0.93	0.07	38
		*Polyamblyodon germanium**	1	0.03	–	–	1	0.93	–	–
		Polysteganus praeorbitalis	2	0.06	297.09	0.23	1	0.93	0.28	31
		Porcostoma dentata	6	0.19	804.41	0.63	1	0.93	0.77	24
		Rhabdosargus globiceps	4	0.13	492.51	0.39	2	1.87	0.96	23
		Rhabdosargus sarba	1	0.03	157.06	0.12	1	0.93	0.15	36
		*Rhabdosargus thorpei**	26	0.84	–	–	4	3.74	–	–
		Sarpa salpa	2	0.06	212.76	0.17	2	1.87	0.43	28
	Synodontidae	*Saurida undosquamis*	4	0.13	90.79	0.07	1	0.93	0.19	34
	Trichiuridae	*Trichiurus lepturus*	133	4.28	14370.89	11.26	35	32.71	508.38	3
Cephalopods	Loliginidae	*Loligo* sp.	58	1.87	20782.36	16.28	13	12.15	220.52	6
	Octopodidae	*Octopus* sp.	2	0.06	852.03	0.67	2	1.87	1.37	22
	Sepiidae	*Sepia* sp.	1	0.03	52.35	0.04	1	0.93	0.07	39

anchovy (*Thryssa vitrirostris*), tigertooth croaker (*Otolithes ruber*), large-head hairtail (*Trichiurus lepturus*), olive grunt or "piggy/pinky" (*Pomadasys olivaceum*), and striped grunter (*Pomadasys striatum*). Collectively, by numerical abundance, these five species constituted 66 % of the prey consumed by humpback dolphins over the study period.

In terms of percentage number, *T. vitrirostris* (34.71 %), *P. olivaceum* (12.14 %), and *O. ruber* (8.63 %), made up the majority of the prey items consumed (55 %; Table 2). *Loligo* sp. (16.28 %), *T. vitrirostris* (15.66 %), *T. lepturus* (11.26 %) had the highest percentage by mass (g), while *O. ruber* (44.86 %), *T. lepturus* (32.71 %), and *T. vitrirostris* (29.91 %) had the highest percentage frequency of the prey items (Table 2).

3.1.2. Diet composition by sex, age class and time intervals

Dominant prey items were similar for both sexes, with the majority of male and female diets comprising *T. vitrirostris* (41 % and 23 %, respectively), and *P. olivaceum* (11 % and 15 %, respectively; Fig. 2). However, *P. striatum* was more prevalent in male diets (8 % versus 3 % in female diets), while *O. ruber* featured more dominantly in female diets (15 % versus 5 % in male diets; Fig. 2). Some prey species, like *V. robustus*, were found only in female diets (3 %), while *Loligo* sp. and *A. nibe* were only present in male diets (2 % and 2 %, respectively; Fig. 2).

Over 50 % of the diet of juvenile and adult animals were comprised of the same species: *T. vitrirostris* (42 % and 23 %, respectively), *P. olivaceum* (8 % and 19 %, respectively), *O. ruber* (9 % and 8 %, respectively), and *P. striatum* (4 % and 10 %, respectively; Fig. 3). However, adults fed on a wider variety of prey items compared to juveniles (12 and 9 dominant species, respectively). In addition, *H. kelee* (5 %), *L. tricuspidens* (3 %), *V. robustus* (2 %), *P. commersonnii* (2 %), *S. insidiator* (2 %), and *V. seheli* (2 %) featured as dominant prey items in adult diets, but were not present in juvenile diets. Similarly, *A. thorpei* (4 %), *A. nibe* (3 %), and *Loligo* sp. (3 %) were dominant prey items in juvenile diets, but not present in adult diets (Fig. 3).

With the exception of the 1991–2000 decade, where *P. olivaceum* was the dominant prey item, *T. vitrirostris* was the dominant prey item consumed in all decades (Fig. 4). The 1971–1980 time interval had the lowest number of dominant prey items making up the diet (3 prey species; n = 7). By contrast, the 2001–2010 interval had the highest number of dominant prey items (7 species; Fig. 4). During the 1981–1990 interval, *A. thorpei* was the dominant prey species (7 %), while *Loligo* sp. Identified as a dominant prey item (7 %) in the 2001–2010 interval (Fig. 4). The 2011–2020 decade shows three prey items not present as a dominant prey item in previous decades: *V. robustus* (9 %), *S. gibbosa* (8 %) and *V. seheli* (5 %; Fig. 4).

The differences in the number of the dominant prey items are reflected by the Shannon-Weaver Diversity Index (Table 3). Females and adults had higher species evenness and diversity compared to the males and juveniles. Differences in species diversity were not significant in both cases ($p > 0.05$; Fig. 2; 3; Table 3). Temporally, the 1981–1990 and 2001–2010 decades displayed the highest species richness, evenness and diversity, while the 1971–1980 decade displayed the lowest compared to the other decades (Fig. 4; Table 3). Species diversity differed significantly between the time intervals ($p < 0.001$), mainly driven by differences between the 1971–1980, 1981–1990 and 2001–2010 decades with the other intervals.

3.2. Stable isotope analysis (SIA)

The relative δ^{13}C and δ^{15}N signatures for males ranged from –14.01 to –10.89 ‰ (mean: –12.48 ± 0.81) and from 13.43 to 15.53 ‰ (mean: 14.40 ± 0.52), respectively (Fig. 5). The relative δ^{13}C and δ^{15}N signature for females ranged from –13.68 to –11.15 ‰ (mean: –12.13 ± 0.71) and from 13.61 to 15.25 ‰ (mean: 14.36 ± 0.57), respectively (Fig. 5). There was no significant difference in the mean δ^{13}C and δ^{15}N signatures of the adult males and females (ANOVA; $p > 0.05$; Fig. 5). As a result, isotope data for males and females were pooled to investigate any temporal changes in isotopic signatures.

The temporal analysis of isotopic signatures from 1961 to 2020 showed varying trends for δ^{13}C and δ^{15}N signatures (Fig. 6). The average δ^{13}C signatures steadily decreased each decade from 1971 (–11.71.‰ ± 0.17) to 1981 (–11.96 ‰ ± 0.46). The following two decades were characterised by a further decrease in δ^{13}C signatures, 1991–2000 time interval (–12.13 ‰ ± 1.16), and 2001–2010 (–12.79 ‰ ± 0.59) to 2011–2020 (–13.26 ‰ ± 0.34; Fig. 6). ANOVA indicated that the observed decrease was statistically significant (df = 5; $p = 0.01$), mainly due to differences between the 2011–2020 decade and the 1971–1980 and 1981–1990 intervals (Fig. 6). The mean δ^{15}N signatures remained within a narrow range from 1971 (14.53 ‰ ± 0.54) to 1990 (14.59 ‰ ± 0.59). Thereafter, the values decreased over the next two decades (14.48 ‰ ± 0.69 from 1991 to 2000 and 14.04 ‰ ± 0.25 from 2001 to 2010), ending with a minor increase in the last decade of 2011–2020 (14.11 ‰ ± 0.34; Fig. 6). There were, however, no significant temporal differences in the δ^{15}N signatures over the period of investigation ($p > 0.05$).

3.3. Blubber thickness data

Mid-dorsal blubber measurements were consistently the highest (ranging from 7 mm to 37 mm), while the mid-lateral measurements were consistently the lowest out of the three body locations (ranging from 4 mm to 33 mm). The BCI for mid-dorsal blubber thickness showed a consistent decrease over the first three decades (0.12 for 1981–1990, 0.10 for 1991–2000, and 0.09 for 2001–2010), remaining constant in the last decade (0.09 for 2011–2017; Fig. 7a). This was supported by a

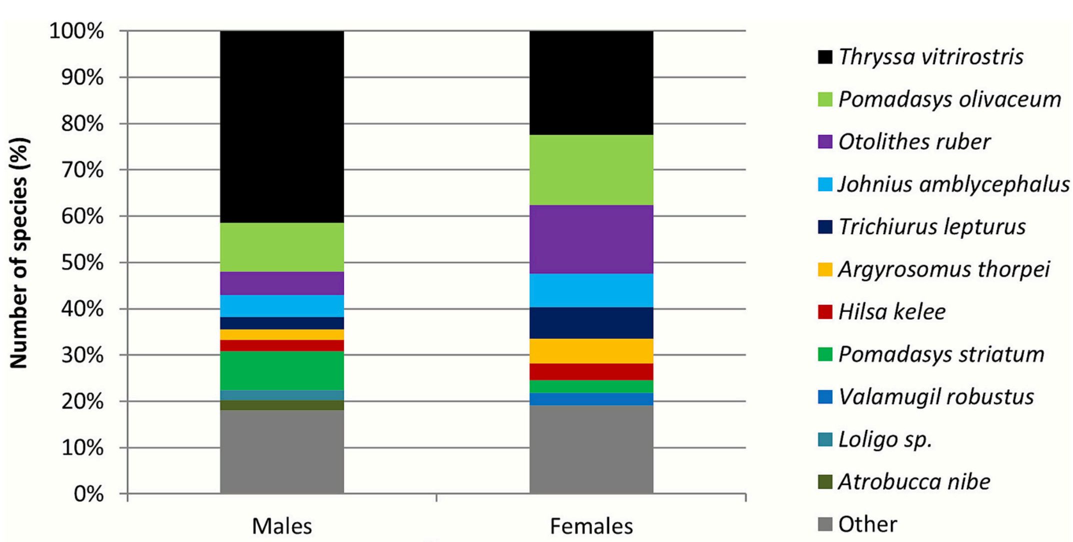

Fig. 2. Dominant prey species (≥2 % number) in the diet of male and female *S. plumbea* incidentally caught in BPNs off the KwaZulu-Natal coastline between 1972 and 2016.

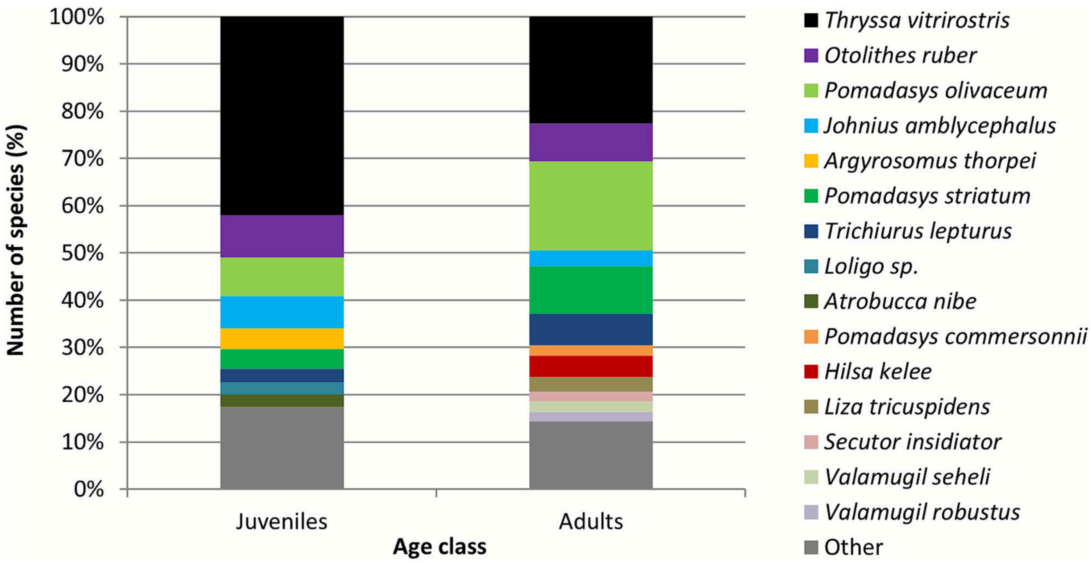

Fig. 3. Dominant prey species (≥2 % number) in the diet of juvenile and adult *S. plumbea* incidentally caught in BPNs off the KwaZulu-Natal coastline between 1972 and 2016.

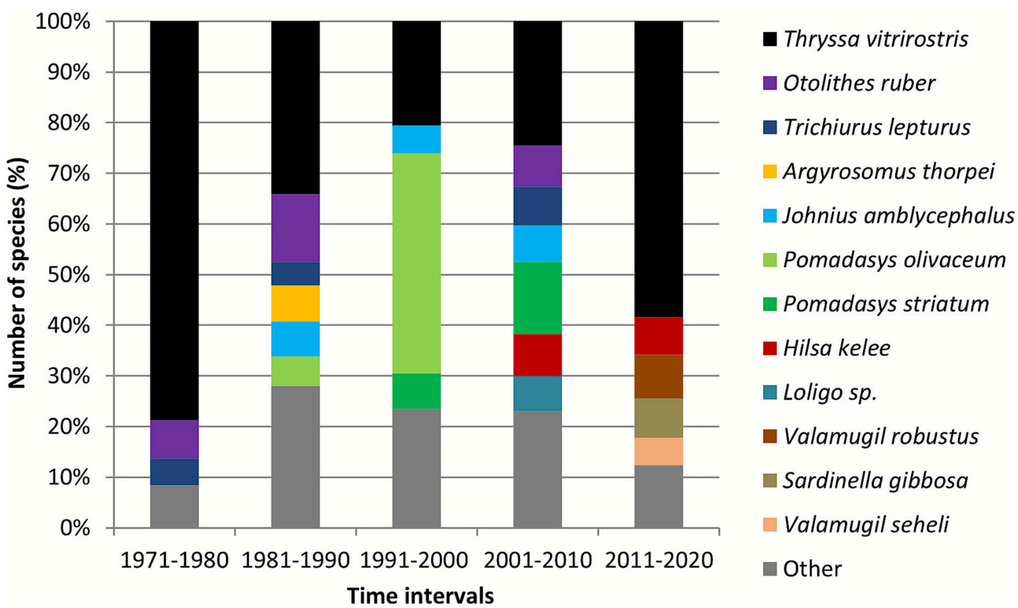

Fig. 4. Dominant prey species (≥5% number) in the diet of *S. plumbea* incidentally caught in BPNs off the KwaZulu-Natal coastline over five decades.

Table 3
Species richness, evenness and diversity (represented by the Shannon-Weaver Diversity Index) calculated for the different sexes, age classes and time intervals. The Kruskal-Wallis rank sum test compared differences in species diversity and only the $p -$ values that represent significant differences ($\alpha = 0.05$) are shown *in post hoc* comparisons.

Factor		Richness	Even-ness	Diversity	Rank sum test			*Post hoc* test	
					df	Chi^2	P	Groups	P
Sex	Males	52	0.61	2.40	1	0.0001	0.9		
	Females	47	0.69	2.66					
Age class	Juveniles	52	0.60	2.36	1	0.21	0.6		
	Adults	42	0.71	2.65					
Time interval	1971–1980	12	0.37	0.91	4	34.54	< 0.001	1971–1980; 1981–2010	0.0003
	1981–1990	34	0.69	2.42				1971–1980; 1991–2000	0.03
	1991–2000	24	0.61	1.93				1971–1980; 2001–2010	0.01
	2001–2010	49	0.69	2.68				1981–1990; 2011–2020	0.03
	2011–2020	19	0.55	1.63				1991–2000; 2001–2020	0.001
								2001–2010; 2011–2020	0.0001

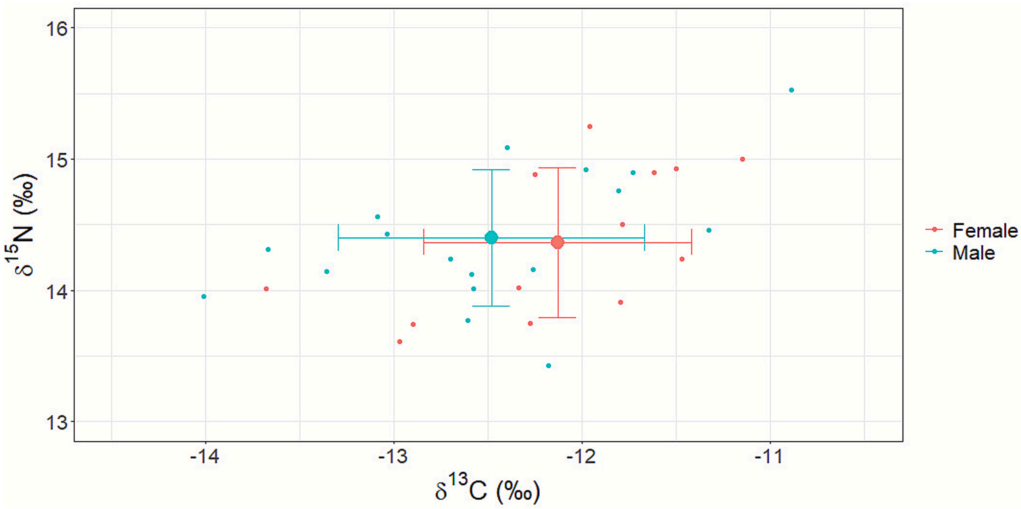

Fig. 5. Biplot of $\delta^{13}C$ and $\delta^{15}N$ ratios with mean values for *S. plumbea* sexes. Error bars represent standard deviation (SD).

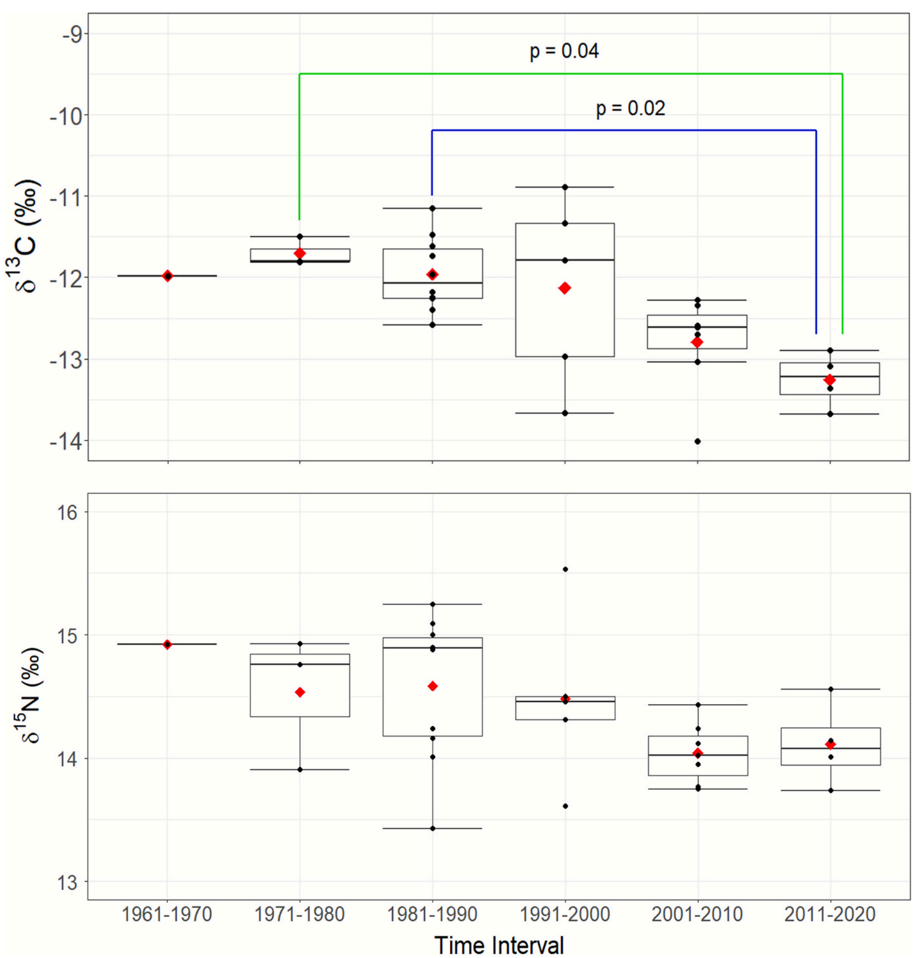

Fig. 6. Boxplots of $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures during different 10-year time intervals for *S. plumbea*. Red points indicate the mean values and error bars are represented by standard deviation (SD). Significant differences ($p < 0.05$) of $\delta^{13}C$ values between time intervals are denoted as follows: green line = 1971–1980 and 2011–2020 decades and blue line = 1981–1990 and 2011–2020 decades. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

statistical significance between time intervals (df = 3; $p = 0.04$), mainly driven by differences between the 1981–1990 decade with the 2001–2010 interval ($p = 0.02$; Fig. 7a). By contrast, the mid-lateral BCI and mid-ventral BCI remained constant from 1981 to 2010 (mid-lateral BCI: 0.07 and mid-ventral-BCI: 0.09), but decreased in the 2011–2020 decade (mid-lateral: 0.06 and mid-ventral: 0.07; Figs. 7b and 7c). There were no significant temporal differences evident in BCI ($p > 0.05$).

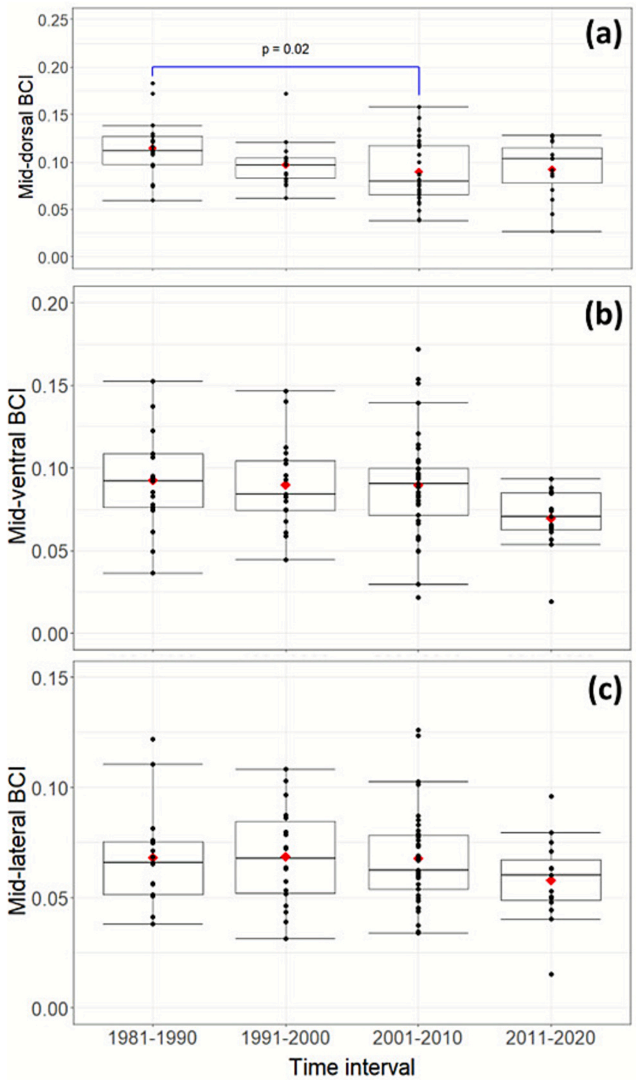

Fig. 7. Boxplots of blubber condition index (BCI) for a) mid-dorsal, b) mid-lateral and c) mid-ventral locations during three 10-year time intervals for *S. plumbea*. Red points indicate the mean values and error bars are represented by standard deviation (SD). The significant difference ($p < 0.05$) between the 1981–1990 and 2001–2010 decades for the mid-dorsal BCI is denoted by the blue line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

The aim of this study was to employ a multi-method approach to retrospectively examine temporal trends in the diet and body condition of the endangered costal Indian Ocean humpback dolphin, *S. plumbea*, along the east coast of South Africa using a long-term dataset (1972 – 2016) to assist in the establishment of ecological and/or biological baselines.

4.1. Prey diversity

A total of 67 prey species comprising 64 teleost and three cephalopod species were identified over the period of investigation (Table 2). Prey items where the lowest taxonomic level of identification was to family level (3 % out of all identified prey items) were omitted from the analysis. IRI values were calculated for 36 teleosts and three cephalopods, with results indicating that *T. vitrirostris*, *O. ruber*, *T. lepturus*, P. *olivaceum*, and *P. striatum* were the five most important prey species in *S. plumbea* diet (Table 2). This result is broadly in agreement with the findings of Cockcroft and Ross (1983) who analysed the diet of 17 *S. plumbea* using stomach contents from the same geographic location. Investigations of the diet of two *S. plumbea* stranded in the Eastern Cape, South Africa (Barros and Cockcroft, 1991), found a single *P. commersonnii* in a male dolphin stomach, which was also recorded as being in the top 10 important prey species consumed in this study. It is unclear whether the low representation of cephalopods in the diet of *S. plumbea* during this study reflects the small sample size or a sampling error. The absence of cephalopods in the diet between the 1980s and 2000s would have affected the SIA values. Cetaceans who feed primarily on cephalopods, such as the Risso's dolphin (*Grampus griseus*), typically have lower δ^{13}C (mean values of –17 to –16 ‰) and δ^{15}N (mean values of 12 to 13 ‰) isotopic signatures than those reported in this study (e.g., Borrell et al., 2021; Plint et al., 2023). With the exception of *V. robustus*, which was well represented in female diets, but absent from male diets, the dominant prey items were similar between the sexes (Fig. 2). *S. plumbea* are considered to be generalist feeders that occupy a narrow niche along coasts throughout their distribution range (Barros and Cockcroft, 1991; Ross et al., 1994). The absence of any differences in the diet composition of adult males and females is therefore, not unexpected. This is confirmed by the isotope analyses, which found no significant differences in the δ^{13}C and δ^{15}N signatures of males and females (Fig. 5). Adults were found to feed on a wider variety of prey items, including *H. kelee* (5 %), *L. tricuspidens* (3 %), *V. robustus* (2 %), *P. commersonnii* (2 %), *S. insidiator* (2 %), and *V. seheli* (2 %), which were not present in juvenile diets (Fig. 3). No significant differences in species diversity were recorded between age classes (Table 3), indicating that the difference in diet between juvenile and adult dolphins was negligible.

4.2. Temporal changes

The main focus of this study was to evaluate temporal changes in *S. plumbea* diet using a multi-method approach. Stomach content analysis indicated that the highest number of dominant prey items was recorded in the 2001–2010 decade (7 dominant species; Fig. 4), which is reflected by the significant difference in species diversity, driven by differences between the 2001–2010 decade and the 1971–1980, 1991–2000 and 2011–2020 time intervals (Table 3). Despite the dominance of *T. vitrirostris* in every decade (with the exception of the 1991–2000 decade, Fig. 4), *S. plumbea* diet appeared to shift from 2001 onwards, as indicated by new prey items in the diet. This included two new prey species in the 2001–2010 decade (*H. kelee* and *Loligo* sp.) and three new prey species in the 2011–2020 decade (*V. robustus*, *S. gibbosa* *V. seheli*; Fig. 4). The change in diet was also reflected in the δ^{13}C stable isotope results, where significant differences were found between time intervals (Fig. 6), indicative of either an offshore movement or, alternatively, a loss of productivity nearshore due to an absence of the prey previously found in inshore waters (Pasino et al., 2025). Although the δ^{15}N signatures also showed a decreasing trend over the decades, indicative of a change in trophic level feeding, these differences were not statistically significant (Fig. 6). Over the corresponding period, the dorsal blubber thickness significantly decreased (Fig. 7a), although the blubber thickness measurements at the other locations stayed more or less the same (Figs. 7b and c). Of the three body locations, the dorsal blubber measurement is considered the most important indicator of body condition (Koopman, 1998; Koopman et al., 2002; Mclellan et al., 2002). The statistically significant decrease in dorsal blubber thickness not observed at other locations is suggestive of a decline in body condition, possibly as a result of a change in prey base and subsequent feeding at a lower trophic level. However, more recent studies have found that histological examinations of adipocytes in the blubber may provide a better insight into the condition of cetaceans (Castrillón et al., 2017; Roussouw et al., 2022).

Diet shifts have previously been recorded for delphinids from the same geographic location (KwaZulu-Natal, South Africa) over the same time period (Ambrose et al., 2013). Examining datasets from 1972 to 1992 and 2000–2009, the primary prey of the common dolphin (*Delphinus delphis*), sardines, accounted for as much as 49 % of the total mass of stomach contents from 1972 to 1992. By contrast, chub mackerel (*Scomber japonicus*) emerged as the predominant prey between 2000 and 2009, constituting 66 % of the stomach contents (Ambrose et al., 2013). Although *D. delphis* is considered an offshore species with a wide geographic distribution in the Atlantic and Pacific Ocean (Best, 2007), the Mediterranean subpopulation was declared "endangered" in 2003 due to multifactorial and increasing anthropogenic threats, including a decline in prey availability accredited to overfishing and habitat degradation (Bearzi, 2003).

The combined results from our study of long-term data on stomach content analysis, stable isotope analysis and examination of blubber thickness are indicative of a diet shift in *S. plumbea*. The species has over the last decade also been classified as "endangered" in South African waters (Braulik et al., 2015; Braulik et al., 2023a; Plön et al., 2016), and our results highlight not only possible impacts from changes in trophic level feeding, but also likely knock-on effects in body condition, which may affect survival, reproductive rates (van den Hoff et al., 2014) and overall fitness.

Boat-based near-shore line fishery represents the most significant segment of the commercial fishery in KZN waters (Fennessy et al., 2014; Penney et al., 1999). Species captured through hook-and-line methods along a substantial portion of the KZN coastline contribute ≈ 40 % of the total mass of fish landed annually by both commercial and recreational fishing activities (Penney et al., 1999). Investigations of long-term trends (1910–1995) of the catch and effort of this fishery found that despite increased fishing efforts, the overall catch had decreased, with a corresponding reduction in the catch per unit effort (CPUE; Penney et al., 1999). Additionally, significant changes in catch composition have been recorded over this period, resulting in the targeting of smaller sparids and migratory shoaling species rather than the original larger endemic reef fishes (Penney et al., 1999). The line fish resources off the coast of KZN have historically been unable to support the fishing pressure in the area, resulting in the overexploitation of most resident fish species. A gradual shift in fish landings from long-lived, high trophic-level piscivorous species towards shorter-lived, lower trophic-level species was documented from the 1990s to 2010s, reflecting the unsustainable exploitation of slow-growing, long-lived fish species (Dunlop and Mann, 2012). The observed diet shift in *S. plumbea* in our study may therefore reflect the effects of the overexploitation of shallow water coastal fish species (Plön et al., 2012; Plön et al., 2015).

Dietary shifts have also been reported in the Indo-Pacific humpback dolphin *S. chinensis* for populations in the Pearl River estuary, China (Ning et al., 2020; Lin et al., 2021). Lin et al. (2021) examined stomach contents of 54 stranded *S. chinensis* individuals from 2003 to 2017 in the Pearl River Delta (PRD) region, China, with results suggesting a shift in diet from mostly demersal fish species to more neritic and pelagic prey species. This study also found that the size and quantity of prey items recovered from dolphin stomachs had declined in recent years similar to the size of dolphin foraging groups (Lin et al., 2021). These results were corroborated by blubber fatty acid signatures over the same time period, showing that the proportion of larger fish in the diet had demonstrated a notable downward trend, while the percentage of smaller fish in the diet climbed gradually (Ning et al., 2020). The observed dietary shifts were mainly attributed to fishing pressure in the PRD, but also other impacts on large fishes in estuarine waters, such as climate change, pollution, land reclamation, and sand mining (Ning et al., 2020; Lin et al., 2021).

4.3. Conclusion

The present study provided evidence of a shift in the diet of the endangered *S. plumbea* found along the KZN coastline, South Africa, from 2001 to 2020. This dietary shift suggests changes in both trophic level feeding and foraging location with potential knock-on effects on animal condition and health. The observed changes in diet could be indicative of declining prey availability as a result of numerous factors, one of which includes overfishing off the KZN coast by near-shore line fisheries. The diet shift observed here for *S. plumbea* and previously for *D. delphis* are the first warning signs of a potential disruption in the balance of marine food webs along the South African east coast, with the potential to harm the health of the entire ecosystem. Combining both the historical and contemporary dietary data of *S. plumbea* revealed variations within the population not previously recorded, emphasizing the value of long-term data collection. The analysis of data from bycaught individuals, as opposed to stranded individuals, which are often sick and not representative of the wild population, strengthens the results presented here.

Our findings underscore the role of marine mammals as indicators of ecosystem integrity in the Anthropocene and highlight the importance of establishing baselines upon which impact can be measured. Using *S. plumbea* as a globally relevant example from the Indian Ocean showcases the current demise of particularly coastal dolphins that integrate multiple, cumulative stressors, which also impact other taxa. Considering the drive for Ocean Economy developments in the Indian Ocean, which presents one of the least developed regions globally, such data is imperative to measure the continued health and well-being of the ocean system.

CRediT authorship contribution statement

Natasha Roussouw: Writing – review & editing, Writing – original draft, Formal analysis, Data curation. **William P. Froneman:** Writing – review & editing, Visualization, Supervision, Methodology, Formal analysis. **Kay Weltz:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Kirsty Venter:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Danielle Conry:** Writing – review & editing, Data curation. **Malcolm J. Smale:** Writing – review & editing, Validation, Supervision, Data curation. **Stephanie Plön:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Stephanie Ploen reports financial support was provided by Exxon Mobil Corporation. Stephanie Ploen reports article publishing charges was provided by International Union for the Conservation of Nature (IUCN). Natasha Roussouw reports financial support was provided by BioConsult SH Research and Conservation gGmbH. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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