



Multidimensional trace metals and nutritional niche differ between sexually immature and mature common dolphins (*Delphinus delphis*)

Karen A. Stockin^{a,b,*}, Gabriel E. Machovsky-Capuska^{a,c,1}, Emily I. Palmer^a,
Christophe Amiot^{d,e,2}

^a Cetacean Ecology Research Group, School of Natural Sciences, Massey University, Auckland, 0745, New Zealand

^b Animal Welfare Science and Bioethics Centre, School of Veterinary Science, Massey University, Private Bag 11-222, Palmerston North, 4442, New Zealand

^c Nutri Lens, East Ryde, NSW, 2113, Australia

^d UFR Science et Technologie, Nantes Université, 44000, Nantes, France

^e BiodivAG, Angers Université, Angers, 49000, France

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ABSTRACT

There is a need to understand the links between metals and nutrition for apex marine predators, which may be subject to different ecotoxicological effects at different life stages. We combined stomach content analyses (SCA), prey composition analysis (PCA), the Multidimensional Niche Framework (MNMF) with Bayesian multivariate ellipses, trace metal analysis and nicheROVER to investigate nutrition and trace metals across sex, age, and sexual maturity status in common dolphins (*Delphinus delphis*) from New Zealand. A broader prey composition niche breadth (SEAc) was estimated for immature compared to mature conspecifics, showing a higher degree of prey and nutrient generalism driven by protein (P) intake. Cd and Zn niche similarities suggests these metals were incorporated through similar prey in both immature and mature dolphins, whereas Hg and Se niche divergence indicates uptake occurred via different prey. Our multidisciplinary assessment demonstrated how nutrients and metal interactions differ in common dolphins depending upon sexual maturity. This approach has relevance when considering how marine pollution, environmental fluctuations and climate change may affect nutritional and trace metal interactions during different reproductive stages within marine predators.

1. Introduction

Marine mammals have evolved in response to a myriad of life history challenges relevant to their aquatic existence (Evans and Stirling, 2001). Specifically, they must breathe oxygen, while simultaneously developing subsurface foraging strategies to capture and digest prey underwater, to meet nutrient and energy demands necessary for growth and reproduction (Peddemors et al., 1992; Meynier et al., 2008a; Hindell & Walters, 2015). Environmental factors may also compromise the ability of young individuals to reach maturity (Bronson, 1985). For example, environmental fluctuations (e.g., El Niño and La Niña events, changes in sea surface temperatures) in particular, can affect both the availability and quality of prey, influencing foraging strategies and the ability of an individual to meet their energy and nutritional requirements (Costa, 2007; Machovsky-Capuska et al., 2018). An additional challenge to

foragers is the ubiquitous presence of anthropogenic contaminants (e.g., plastics, non-essential trace metals, persistent organochlorine compounds, per- and polyfluorinated substances –PFAS–, among others) in their environment (Santos et al., 2021; Stockin et al., 2021a). Such contaminants may biomagnify through the food chain to bioaccumulate within the tissues of apex predators, leading to potentially chronic physiological health effects that may hamper growth and/or reproduction (Stockin et al., 2007; Machovsky-Capuska et al., 2019; Machovsky-Capuska et al., 2020b; Stockin et al., 2021b).

While progress has been made to understand the different prey pathways for the ingestion of these metals and their physiological effects on individuals (e.g., O'Shea, 1999; Ramos and González-Solís, 2012; Harley and O'Hara, 2015; Fossi et al., 2018), our current understanding of prey nutritional and chemical linkages remains unknown (Bignert et al., 1993). This knowledge gap has hampered our insights to how

* Corresponding author. Cetacean Ecology Research Group, School of Natural Sciences, Massey University, Auckland, 0745, New Zealand.

E-mail address: k.a.stockin@massey.ac.nz (K.A. Stockin).

¹ Both authors contributed equally to the manuscript.

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marine mammals fulfil their nutritional and energetic needs, while consuming various concentrations of contaminants during different life stages (Malinowski and Herzing, 2015; Machovsky-Capuska and Raubenheimer, 2020). While ecological tools have advanced our understanding of the diet and trophodynamics of marine mammals, there remains considerable uncertainty around such estimations (Ramos and González-Solís, 2012; Majdi et al., 2018; Trites and Spitz, 2018; Würsig et al., 2018). Energy-centred models have been broadly accepted to provide budgetary quantifications of foraging behaviour and prey choice (Costa and Maresh, 2018), whereas stable isotopes have been applied to interpret foraging between different trophic levels (McHuron et al., 2018). However, while dietary insights allow understanding of potential trace element sources, the assumption that carbon and nitrogen stable isotopic values serve as a proxy for P and L variability in prey species is inaccurate (Doucett et al., 1999; Raubenheimer et al., 2009).

To assess the complex behavioural, nutritional, and ecological variables that influence dietary breadth in wildlife, a multidimensional nutritional niche framework was developed (MNNF, Machovsky-Capuska et al., 2016). By applying the MNNF, the nutritional compositions of prey lead to the characterization of the prey composition niche (i.e., the combined nutritional content of multiple prey defines the nutritional composition of a diet). Further, the nutritional compositions of those diets (i.e., collective prey consumed) form a realized nutritional niche. Indeed, the MNNF has previously been applied to marine mammals (Denuncio et al., 2017; Machovsky-Capuska and Raubenheimer, 2020; Machovsky-Capuska et al., 2020b; Denuncio et al., 2021; Stockin et al., 2022) to answer nutritional and anthropogenic contaminant questions within an ecological niche context (Machovsky-Capuska et al., 2019; Machovsky-Capuska et al., 2020a; Machovsky-Capuska et al., 2020b).

Via food webs, cetaceans both bioaccumulate and biomagnify contaminants (Fossi and Panti, 2018). Trace metals may be non-essential for biological functions (e.g., Hg, Cd) or essential (e.g. Se, Zn), with the former potentially toxic even at low concentrations (Das et al., 2000). Marine mammals typically consume fish and cephalopods, that are the primary source of Hg, Se, Zn and Cd concentrations, and macronutrients proteins (P) and lipids (L), the source of energy for basic metabolic processes (Machovsky-Capuska and Raubenheimer, 2020). The ecological niche in which cetaceans inhabit (Hinton et al., 2022; Peters et al., 2022) can affect their susceptibility to contaminants. For example, common dolphins (*Delphinus delphis*) are widely distributed and accordingly, span diverse ecological habitats, foraging strategies, food preferences (Young & Cockcroft, 1994; Silva, 1999; Stockin et al., 2007; Meynier et al., 2008a; Machovsky-Capuska et al., 2020b; Peters et al., 2020; Peters et al., 2022), which subsequently affect their accumulate of non-essential metals (Stockin et al., 2007; Lavery et al., 2008; Stockin et al., 2021b). Morphological variation during growth and sexual maturity likely imposes different physiological demands that could lead to different nutritional strategies among life history stages, as reported in striped dolphins (*Stenella coeruleoalba*; Gómez-Campos et al., 2011) and Atlantic spotted dolphins (*S. frontalis*; Malinowski and Herzing, 2015). Age-related bioaccumulation trends for Cd and Hg have further been described in common dolphins (Lavery et al., 2008; Machovsky-Capuska et al., 2020b; Stockin et al., 2021b).

Here, we combine dietary analysis (i.e., stomach content analyses), nutritional composition of prey, the MNNF with Bayesian multivariate ellipses, trace metal analysis and nicheROVER to investigate the nutritional and trace metal niche dynamics across sex, age, and sexual maturity status in common dolphins in New Zealand. Specifically, we: i) assess whether sexual maturity influences the prey consumption, diet, and the nutritional niche breadth; ii) establish whether trace metal accumulation (Hg, Cd, Se, and Zn) is related to age, sex, and sexual maturity status; iii) understand the role of Se and Zn as detoxification mechanisms of Hg and Cd; and iv) assess the links between P and L intake with metal accumulation within a multidimensional niche.

2. Materials and methods

2.1. Samples

Common dolphins ($n = 20$) which either live stranded and subsequently died or were found beachcast along the New Zealand coast between 2011 and 2013, were examined and sampled post-mortem following Stockin et al. (2009). Sex, age, sexual maturity, body condition, decomposition state, stomach contents and trace element burden were determined for each animal (Table 1).

2.2. Age, sexual maturity and body condition

Growth layer groups (GLGs) within teeth were assessed following Palmer et al. (2022). Age estimates were initially made 'blind' (i.e., in the absence of biological information), following Westgate and Read (2007). Body condition (Table 1) was defined as per Stockin et al. (2007). Sexual maturity was assessed by gross and histological examination of testes and ovaries for males and females, respectively following Palmer et al. (2023) and Palmer et al. (2022). Sexual maturity in females was indicated by at least one *corpus albicans* (CA) or *corpus luteum* (CL) and/or evidence of pregnancy or lactation (Murphy et al., 2009). Males were classified as immature or mature based on the presence and proportion of cell types (Murphy et al., 2005; Kemper et al., 2014). No pubescent individuals (i.e., presence of both spermatogonia and spermatocytes) were included. Body condition was assessed based on three (dorsal, lateral and ventral) blubber depth measures, following Stockin et al. (2021b). Only carcasses classified as fresh or mild decomposition, as defined by Stockin et al. (2009) were included in the study.

2.3. Stomach content analysis -SCA

Stomach contents analysis (SCA) methods followed Stockin et al. (2022). Briefly, diagnostic hard parts were identified using published guides (Clarke, 1986; Smale et al., 1995). The mass of each prey species was used to estimate the percentage of total wet mass that the species contributed to the overall diet (M%, wet weight), as detailed in Meynier et al. (2008a, 2008b).

2.4. Proximate composition analysis

A total of 31 individual prey samples originating from seven species were selected for proximate composition analyses (PCA). All selected prey species contributed >1% wet mass to the diets of both immature and mature dolphins. We measured the proximate composition of protein (P), lipid (L) and water (W) and used $P = 17 \text{ kJ g}^{-1}$ and $L = 37 \text{ kJ g}^{-1}$ to convert wet mass values to energy (E) content (N.R.C, 1989; Supplementary Table S1). Carbohydrates were excluded based on their negligible component within squid and marine fish species (Craig et al., 1978). Additionally, we measured total L (ether extract), whereas Kjeldahl analysis was used to measure total nitrogen (N) and then converted to P ($N \times 6.25$, AOAC 981.10, AOAC, 2005), following Blich and Dyer (1959). Refer to Stockin et al. (2022) for full laboratory details.

2.5. Hg, Cd, Se and Zn analysis

Zinc (Zn), selenium (Se), mercury (Hg) and cadmium (Cd) were quantified in hepatic and renal tissues of sampled dolphins. Trace element concentrations were quantified atASUREQuality Laboratories, New Zealand (Supplementary Table S2) following Stockin et al. (2022). Inductively-coupled plasma mass spectrometry was applied to elements typically present at relatively low concentrations (e.g., Sn), whereas inductively-coupled plasma optical emission spectrometry quantified elements that occur at higher concentrations (e.g., Zn). Following Stockin et al. (2007), approximately 1 g (wet weight, ww) of hepatic and

Table 1

Specimen details of common dolphins (*Delphinus delphis*) examined between 2011 and 2013, North Island, New Zealand. Note: Age (years) and sexually maturity is based on GLGs and reproductive parameters as detailed in Palmer et al. (2022) and Palmer et al. (2023).

Sample	Date	Location	Sex	TBL (cm)	Age (yr)	Sexual Maturity	Body Condition
KS11-08Dd	13/2/2011	Torbay, Auckland	M	176.5	6	Immature	Good
KS11-12Dd	2/5/2011	Te Pupu Beach, Thames	M	171.0	6	Immature	Good
KS11-14Dd	12/5/2011	Mairangi Bay, Auckland	F	195.0	12	Mature	Moderate
KS11-39Dd	18/8/2011	Waiheke Island, Auckland	F	152.0	2	Immature	Moderate
KS11-40Dd	13/5/2011	Devonport, Auckland	F	149.0	2	Immature	Moderate
KS11-50Dd	16/11/2011	Warkworth, Auckland	F	195.0	≥14	Mature	Moderate
KS11-52Dd	4/12/2011	Waitemata Harbour, Auckland	M	186.0	8	Immature	Moderate
KS12-05Dd	11/3/2012	Tauranga Harbour, Bay of Plenty	M	207.0	13	Mature	Moderate
KS12-10Dd	23/4/2012	Waiwera, Auckland	M	>200	10	Mature	Poor
KS12-13Dd	17/7/2012	Thornton Bay, Thames	F	189.0	8	Mature	Good
KS12-14Dd	21/7/2012	Whangaparaoa, Auckland	M	185.0	11	Immature	Good
KS12-15Dd	4/8/2012	Browns Bay, Auckland	F	190.0	≥20	Mature	Good
KS12-17Dd	25/8/2012	Te Pupu Beach, Thames	M	156.0	1.5	Immature	Good
KS12-23Dd	5/12/2012	Kawau Island, Auckland	M	146.0	2.5	Immature	Good
KS13-08Dd	27/7/2013	Howick, Auckland	F	155.0	2.5	Immature	Good
KS13-09Dd	3/8/2013	Weiti River, Auckland	M	172.0	5.5	Immature	Good
KS13-10Dd	6/9/2013	Whangaparaoa, Auckland	F	199.5	18	Mature	Good
KS13-11Dd	7/8/2013	Firth of Thames, Thames	F	160.0	6.5	Immature	Moderate
KS13-12Dd	16/8/2013	Matakatia Bay, Auckland	M	172.0	3	Immature	Good
KS13-18Dd	6/11/2013	Maratai, Auckland	F	131.0	1.5	Immature	Good

renal tissue for each dolphin was digested in concentrated nitric acid with a trace of hydrofluoric acid. All metals were analysed within the laboratory's International Accreditation New Zealand (IANZ) accreditation (No. 175) under standard quality control protocols.

2.6. Data analysis

Following Machovsky-Capuska et al. (2018), we estimated the prey composition and realized nutritional niche breadths of both immature and sexually mature dolphins by combining Proportions-based Nutritional Geometry (PNG, Raubenheimer, 2011) with the MNNF (Machovsky-Capuska et al., 2016). Bayesian multivariate ellipses were further applied to account for small sample sizes (SEAc, Jackson et al., 2011; Syväranta et al., 2013). Our approach enabled us to quantify the multidimensional dynamics between the wet mass proportions of P, L and W from prey species, diets, and niches of both immature and mature dolphins. Three-dimensional nutritional niche space was also estimated using a Bayesian approach (to reduce underestimation of volumes due to convex surface approximation on a planar surface), to investigate any potential intraspecific divergence in resource utilization (Rossman et al., 2016; Skinner et al., 2019).

Posterior estimates (SEAb), product of Bayesian inference and Markov chain Monte Carlo simulations (2×10^4 iterations with 2 chains, a burning of 1×10^3 and thinning of 10, Grainger et al. (2020)), enabled SEAc comparisons between immature and mature dolphins at different scales. Prey composition niches and realized nutritional niches were compared at a nutritional level, whereas Cd–Zn and Hg–Se relationships within hepatic and renal tissues were investigated as contaminant source and detoxification mechanisms, respectively. To estimate the proportional overlap area between two ellipses (overlapping ellipses are equal to 1 whereas distinctive ellipses are equal to 0), and to further understand whether trace metal intake occurred from different sources, we applied the maxLikOverlap function (SIBER package, Jackson et al., 2011).

Following Stockin et al. (2022), the nutritional niche ellipses (prey and diet) ≤ 0.30 represented low overlap, moderate overlap equalled > 0.31 – 0.59 and significant overlap was represented by ≥ 0.60 . Data were assessed for homoscedasticity and normality using Levene's and Shapiro-Wilk's tests, respectively (Levene, 1960; Shapiro and Wilk, 1965). Linear models (LMs) were implemented using the lm function (Bates et al., 2014), to establish potential differences in the nutritional composition (logit transformed wet mass proportions of P, L, W, the

protein to lipid ratio -P:L- and energy (E)) of prey and diets between sex, age (years) and sexual maturity against the nutritional composition from prey and diets as the response. LMs were further applied to establish potential differences in the concentrations of Hg, Se, Cd and Zn in renal and hepatic tissues between immature and mature dolphins. Where appropriate, LSD tests were applied to estimate marginal means and assess the significance between treatments using the 'emmean' package (Lenth et al., 2018). Linear regressions were used to investigate the concentrations of Hg, Se, Cd and Zn in liver and kidney tissue in relation to age and dorsal blubber for each animal, using Pearson correlations.

We also quantified the multidimensional niche relationships between P, L, and trace metals (Hg, Se, Cd, Zn) using 'nicheROVER' function (Lysy et al., 2014). The niche region was defined as the joint probability density function of the proposed multidimensional niche indicators ran over 1000 replicates with a 95% probability (Swanson et al., 2015). Statistical significance was implied at $p < 0.05$. Data are reported as mean \pm standard deviation (SD), unless otherwise stated, with all analyses performed in R4.1.2 (R Development Core Team, 2021).

3. Results

We examined the stomach contents of sexually immature ($n = 13$) and mature ($n = 7$) dolphins between February 2011 and September 2013, from the northeast coast of North Island, New Zealand (Table 1). The sample comprised 10 females and 10 males, ranging from 131 to 207 cm in body length and 1.5 and > 20 years in age (see Table 1).

3.1. Diet composition and nutritional niche breadths of immature and mature dolphins

Common dolphin consumed seven prey species including grey mullet (*Mugil cephalus*), pilchard (*Sardinops sagax*), jack mackerel (*Trachurus novaezelandiae*), arrow squid (*Nototodarus* spp.), snapper (*Pagrus auratus*), garfish (*Hyporhamphus ihi*) and anchovy (*Engraulis australis*). Six species including grey mullet (41.75 %M), pilchard (30.51 %M), jack mackerel (16.67 %M), arrow squid (5.16 %M), snapper (3.56 %M) and garfish (1.62 %M) all contributed $> 1\%$ wet mass towards the diet of immature dolphins. Comparatively, mature dolphins predominantly consumed five prey species including jack mackerel (42.82 %M), grey mullet (28.53 %M), pilchard (22.18 %M), arrow squid (3.33 %M), anchovy (1.00 %M).

The nutritional composition of prey consumed by dolphins ranged from wet mass P:L = 2.6:1.0 to 14.6:1.0, with an energy content that ranged from 3.5 to 5.4 KJ g⁻¹ (Supplementary Table S1, Fig. 1a). A comparison of the prey composition niche breadths (SEAC) between different stages of sexual maturity, revealed that immature dolphins (11.9) had a broader niche breadth compared to mature (10.3) individuals (Probability SEAB mature < SEAB immature, $p = 0.64$, <0.05), showing a 0.78 degree of overlap between niches (Fig. 1b).

Dolphin diet revealed a nutritional composition that ranged from P:L = 2.8:1.0 to 14.6:1.0 (Fig. 2a). Comparing estimated wet mass diet composition between immature and mature dolphins revealed no difference in P ($18.72 \pm 1.84\%$ and $18.84 \pm 1.49\%$, respectively, LM, $p = 0.93$), L ($2.92 \pm 1.44\%$ and $3.15 \pm 1.43\%$, respectively, LM, $p = 0.92$) and W ($74.20 \pm 4.36\%$ and $74.06 \pm 2.64\%$, respectively, LM, $p = 0.86$). The realized nutritional niche breadth (SEAC) of immature dolphins (10.3) was broader than mature conspecifics (7.2) (Probability SEAB mature < SEAB immature, $p = 0.65$, <0.05), with a 0.57 overlap between niches reported (Fig. 2b). No sex or age differences were evident in the wet mass proportion of P (LM, $p = 0.78$ and $p = 0.03$, respectively; T.ratio, 2011/12 T = -0.441, $p = 0.899$, 2011/13 T = -2.586, $p = 0.08$, 2012/13 T = -2.144, $p = 0.114$), L (LM, $p = 0.16$ and $p = 0.65$) and W (LM, $p = 0.22$ and $p = 0.041$; T.ratio, 2011/12 T = 1.200, $p = 0.471$, 2011/13 T = 3.819, $p = 0.51$, 2012/13 T = 2.619, $p = 0.84$).

3.2. Trace metal accumulation and detoxification mechanisms

Hg concentrations in kidney and liver ranged between 0.64 and 21 mg kg⁻¹ (5.58 ± 5.47 mg kg⁻¹, ww) and 2.10 and 210 mg kg⁻¹ (34.49 ± 50.28 mg kg⁻¹, ww), respectively. Se concentrations in kidney and liver varied between 2.50 and 51 mg kg⁻¹ (12.78 ± 13.25 mg kg⁻¹, ww) and 2.10 and 15 mg kg⁻¹ (5.21 ± 2.95 mg kg⁻¹, ww), respectively. Cd concentrations in kidney and liver ranged from 0.51 to 31.80 mg kg⁻¹ (3.61 ± 6.93 mg kg⁻¹, ww) and 0.14 and 3.23 mg kg⁻¹ (0.65 ± 0.73 mg kg⁻¹, ww), respectively. Meanwhile, Zn concentrations in kidney and liver varied between 24 and 73 mg kg⁻¹ (43.68 ± 14.69 mg kg⁻¹, ww), and 20 and 43 mg kg⁻¹, (26.79 ± 6.12 mg kg⁻¹, ww), respectively. No renal or hepatic differences were observed in the trace metal concentrations between sexes (Supplementary Table S2) or with age (Supplementary Table S3).

Strong positive correlations were observed between Hg and Se concentrations in kidney and liver with age ($p < 0.0001$, Fig. 3), whereas no age trends were noted for Cd and Zn in kidney (Pearson, $p = 0.13$ and $p =$

0.85 , respectively, Supplementary Figure S1) or liver (Pearson, $p = 0.49$ and $p = 0.53$, respectively, Supplementary Figure S1). Dorsal blubber thickness was significantly correlated with Hg (Pearson $r = 0.56$, $p < 0.01$) and Se (Pearson, $r = 0.69$, $p < 0.001$) in kidney and Cd (Pearson, $r = 0.54$, $p < 0.01$) in liver, whereas no trends were apparent for Cd (Pearson, $p = 0.47$) and Zn (Pearson, $p = 0.40$) in kidney and Hg (Pearson, $p = 0.15$), Zn (Pearson, $p = 0.13$) and Se (Pearson, $p = 0.12$) in liver.

Concentrations of Hg and Se in renal and hepatic tissues significantly differed between immature and mature dolphins (Table 2). Range of Hg and Se concentrations in the kidneys of immature (black ellipse, SEAC = 6.22 (mg kg⁻¹)²) and mature dolphins (grey ellipse, SEAC = 19.35 (mg kg⁻¹)²) revealed a low overlap probability (27.36%) between niches, with an estimated mathematical non-overlap of 0.18 and a mean Bayesian overlap of 0.17 (Fig. 4a). Increasing disparities were observed in the livers of immature (black ellipse, SEAC = 16.35 (mg kg⁻¹)²) and mature dolphins (grey ellipse, SEAC = 867.94 (mg kg⁻¹)²), where the concentrations of both metals showed a lower overlap niche probability (18.57%), with an estimated mathematical non-overlap of 0.02 and a mean Bayesian overlap of 0.05 (Fig. 4b).

No differences were observed in renal or hepatic Cd and Zn concentrations with sexual maturity (Table 2). In kidneys, mature dolphins showed a broader ellipse (grey ellipse, SEAC = 101.37 (mg kg⁻¹)²) compared to immature conspecifics (black ellipse, SEAC = 16.16 (mg/kg⁻¹)²), with a high probability of overlap (70.32%) between niches and an estimated mathematical non-overlap of 0.09, and a mean Bayesian overlap of 0.10 (Fig. 5a). A similar overlap was noted between the hepatic tissues of immature (black ellipse, SEAC = 14.03 (mg Kg⁻¹)²) and mature dolphins (grey ellipse, SEAC = 72.87 (mg Kg⁻¹)²), with a high overlap probability (69.29%) noted between niches and an estimated mathematical non-overlap and a mean Bayesian overlap of 0.19 and 0.21, respectively (Fig. 5b).

3.3. Niche relationships of nutrients and trace metals

Density plots revealed similar L values across immature and mature groups (Figs. 6 and 7). The estimated P values were broad in immature compared to the very narrow and high values recorded in mature dolphins (Figs. 6 and 7). Mature individuals reported higher corrected values for Hg (Fig. 6) and Se (Fig. 7) in kidney and liver compared to their immature conspecifics (Table 2).

The three-dimensional niche size was consistently larger in the liver

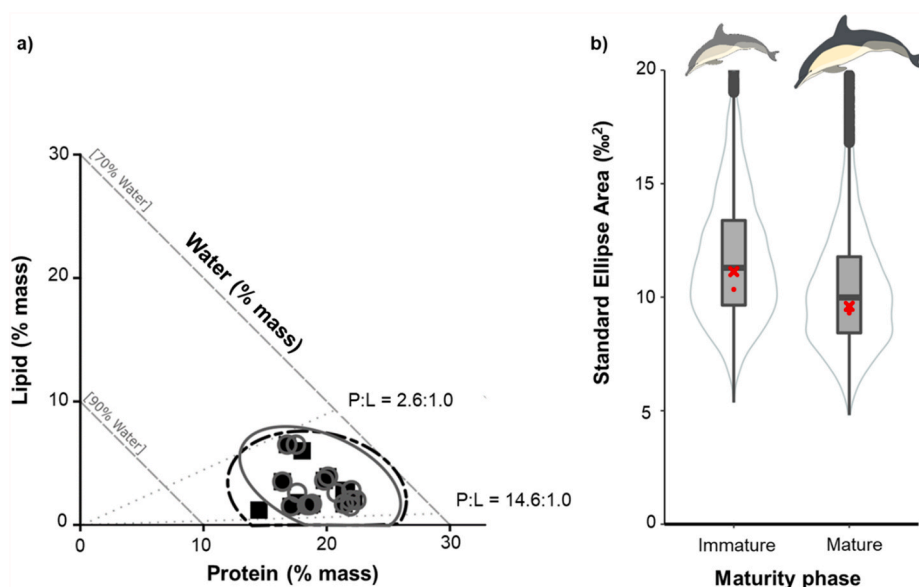


Fig. 1. Consumed prey range (prey composition niches, sensu Machovsky-Capuska et al., 2016) for immature and mature common dolphins (*Delphinus delphis*) in New Zealand. a) Proportions Nutritional Geometry (PNG) showing the nutritional composition of prey consumed and the niche breadths measured as the small corrected standard ellipse areas (SEAC) for immature (black squares, SEAC: 11.9, black ellipse) and mature (grey hollow circles, SEAC: 10.3, grey ellipse) dolphins. b) Box plots combined with mirrored kernel densities in the form of violins are used for comparing the Bayesian estimates (SEAB) for the realized nutritional niches of each maturity phases. Note: Red crosses indicate the Maximum-likelihood estimated SEAC and red dots represent SEAB. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

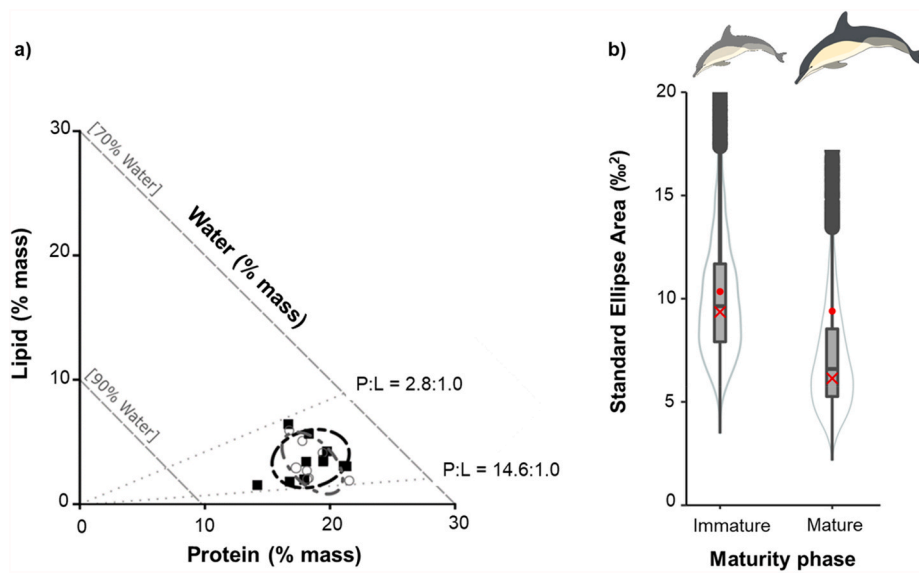


Fig. 2. Diet range (i.e., product of consumed diverse prey; realized nutritional niches, sensu Machovsky-Capuska et al., 2016) for immature and mature common dolphins (*Delphinus delphis*) in New Zealand. a) Proportions Nutritional Geometry (PNG) showing the nutritional composition of individual diets and the niche breadths estimated as the small sample corrected standard ellipse areas (SEAc) for immature dolphins (black squares and SEAc: 10.3, black ellipse) and mature dolphins (grey hollow circles, SEAc: 7.2, grey ellipse). b) Box plots combined with mirrored kernel densities in the form of violins are used for comparing the Bayesian estimates (SEAb) for the realized nutritional niches of each maturity phases. Note: Red crosses indicate the Maximum-likelihood estimated SEAc and red dots indicate SEAb. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

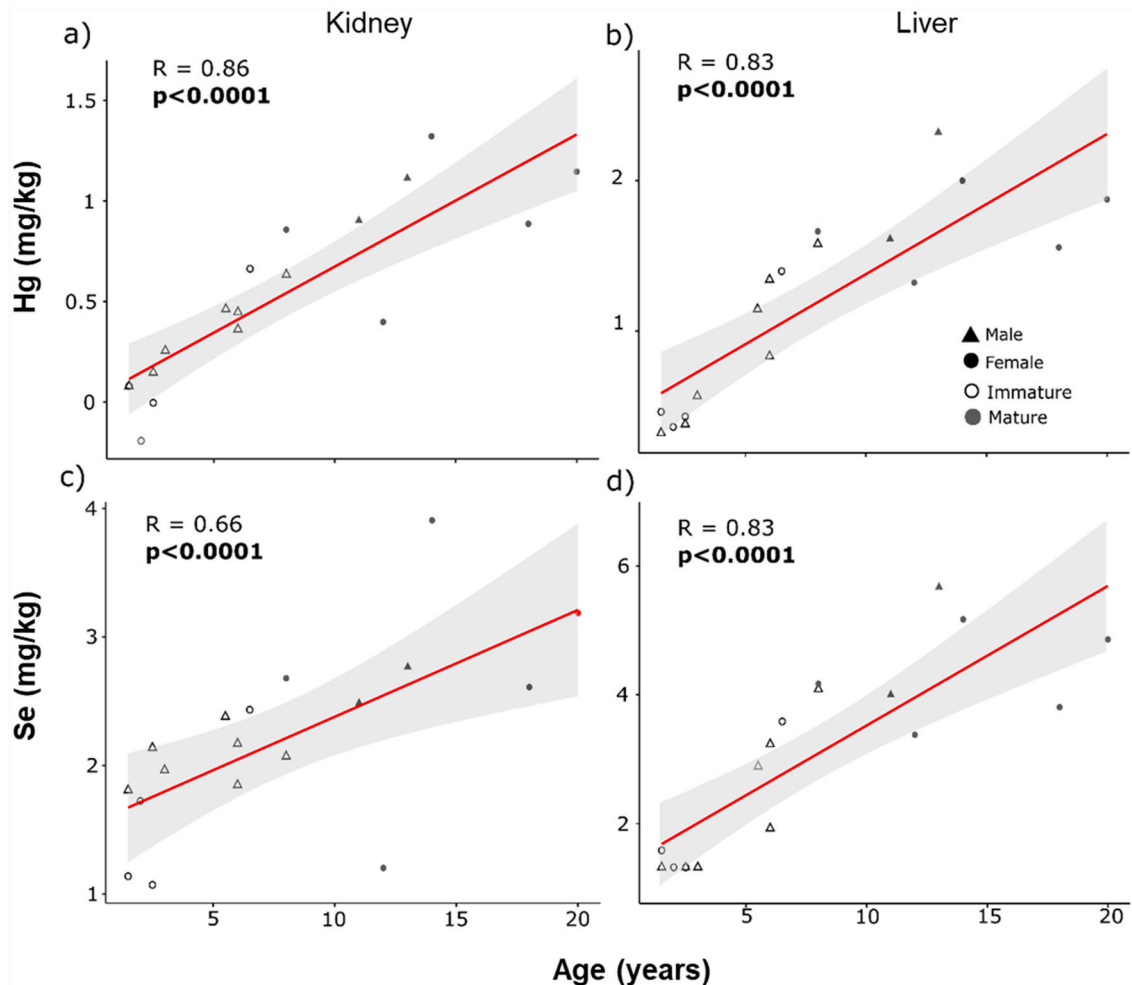


Fig. 3. Linear regressions of Hg concentrations (a, b) and Se (c, d) in kidney and liver in relation to age (years) in common dolphins (*Delphinus delphis*). Grey shading represents regression confidence interval. Note: Only chemicals which demonstrated statistically significant correlations ($p < 0.05$) with age are shown.

Table 2

Comparisons between the trace metal concentrations in liver and kidney tissue of immature and mature common dolphins (*Delphinus delphis*) using linear models (LM). Data presented as mean \pm standard error ($M \pm SE$ in mg kg^{-1} , wet weight). Significant differences marked in bold.

Parameter	Immature	Mature	LM	P
Kidney				
Hg	2.19 \pm 1.33	10.24 \pm 5.62	$F=28.6$	<0.0001
Cd	1.78 \pm 1.05	6.13 \pm 10.47	$F=3.05$	0.10
Se	3.85 \pm 1.07	7.09 \pm 3.71	$F=7.79$	<0.01
Zn	25.27 \pm 4.00	28.88 \pm 8.06	$F=1.46$	0.24
Liver				
Hg	10.53 \pm 11.79	75.57 \pm 64.91	$F=24.1$	<0.0001
Cd	0.58 \pm 0.47	0.76 \pm 1.10	$F=0.00$	0.98
Se	5.70 \pm 4.78	24.91 \pm 14.59	$F=25.6$	<0.0001
Zn	41.58 \pm 13.06	47.29 \pm 17.64	$F=0.53$	0.48

of mature compared to immature dolphins, with the highest values for Se observed (280.85%³ and 44.95%³, respectively; Fig. 7 and Table 3), followed by Hg (100.91%³ and 29.58%³, respectively; Fig. 6 and Table 3), Cd (84.30%³ and 27.73%³, respectively) and finally Zn (25.86%³, 11.34%³, respectively; Table 3). While a similar pattern was observed in kidney, general values were comparatively lower to those reported for liver (Table 3, Figs. 6 and 7).

4. Discussion

Sexual maturation is a significant evolutionary transition in the life history of vertebrates, reflecting their ability to reproduce and influence

the expansion and survival of their populations (Bernardo, 1993). As apex predators, marine mammals face considerable challenges on reaching sexual maturity, including feeding at trophic levels necessary to sustain life history processes, while simultaneously being subject to anthropogenic pollutants that accumulate in prey (Stockin et al., 2021b; Fossi and Panti, 2018; Polizzi et al., 2013). Given our knowledge of common dolphin life history (Young and Cockcroft, 1994; Westgate and Read, 2007; Murphy et al., 2013; Grandi et al., 2022; Palmer et al., 2022; Palmer et al., 2023) and their role as environmental sentinel species (Stockin et al., 2007; Machovsky-Capuska et al., 2020b; Stockin et al., 2021a; Stockin et al., 2022), our study provides unique first insights to how delphinids detoxify multiple non-essential trace metals, while achieving their nutritional requirements.

4.1. Nutrients: prey, diet and niche breadth

While prey taxonomic classification has been the focus of studies to understand the resources required to maintain different life history phases in wild populations (i.e., ecological niche) (Pulliam, 2000), the MNNF demonstrates the importance of characterising the nutritional niche space that species and populations exploit (Machovsky-Capuska et al., 2016; Machovsky-Capuska et al., 2018). Here, we demonstrated that prey composition niche breadths (SEAc) differ. Specifically, immature dolphins demonstrate a broader niche breadth (11.9) compared to mature counterparts (10.3). Such differences in niche breadth may be attributable to the physiology and nutritional needs of specific reproductive phases, for example, gestation and lactation in sexually mature females. From a foraging perspective, immature and

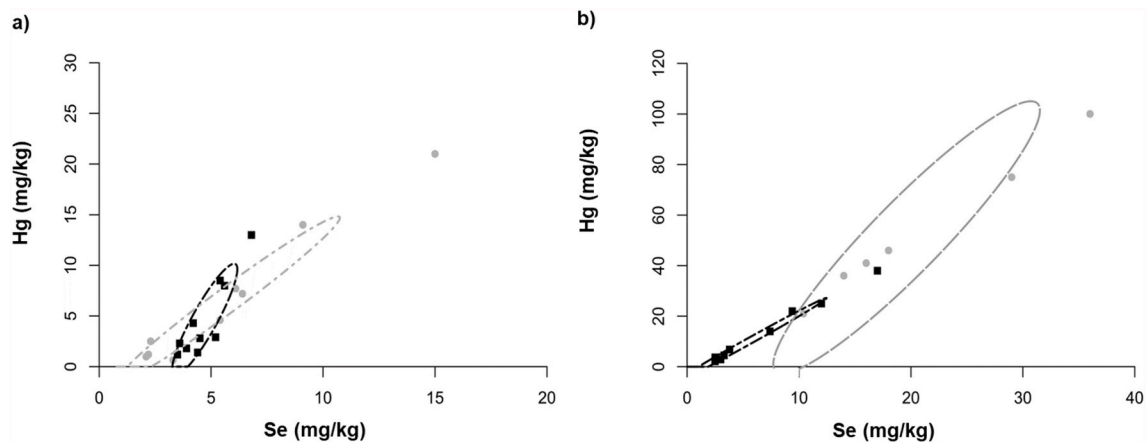


Fig. 4. Bayesian ellipse analysis showing the range of Hg and Se concentrations in the kidney of (a) immature (black ellipse, $SEAc = 6.22 (\text{mg Kg}^{-1})^2$) and mature dolphins (grey ellipse, $SEAc = 19.35 (\text{mg Kg}^{-1})^2$); and in the livers of (b) immature (black ellipse, $SEAc = 16.35 (\text{mg Kg}^{-1})^2$) and mature dolphins (grey ellipse, $SEAc = 867.94 (\text{mg Kg}^{-1})^2$).

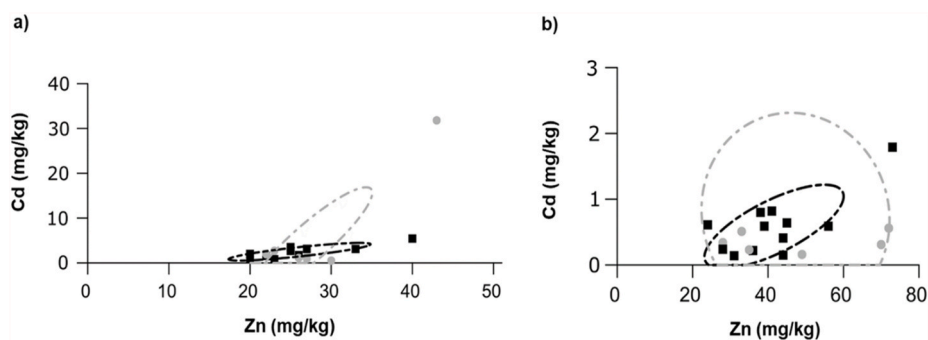


Fig. 5. Bayesian ellipse analysis showing the range of Cd and Zn concentrations in the kidneys of (a) immature (black ellipse, $SEAc = 16.16 (\text{mg Kg}^{-1})^2$) and mature dolphins (grey ellipse, $SEAc = 101.37 (\text{mg Kg}^{-1})^2$); and in the livers of (b) immature (black ellipse, $SEAc = 14.03 (\text{mg Kg}^{-1})^2$) and mature dolphins (grey ellipse, $SEAc = 72.87 (\text{mg Kg}^{-1})^2$).

Table 3

Posterior distribution of ellipsoid volume size estimated for immature and mature common dolphins (*Delphinus delphis*) based on L, P as constants, and the metal parameter for each tissue (%³). Data presented as mean overlap ± standard deviation (M ± SD).

Parameter	Immature	Mature
Kidney		
Hg	22.13 ± 9.62	59.13 ± 22.13
Cd	23.03 ± 13.27	57.69 ± 29.03
Se	40.94 ± 21.59	102.62 ± 44.99
Zn	3.79 ± 1.83	16.14 ± 6.38
Liver		
Hg	29.58 ± 13.26	100.91 ± 39.74
Cd	27.73 ± 12.52	84.30 ± 24.26
Se	44.95 ± 18.65	280.85 ± 104.86
Zn	11.34 ± 6.41	25.86 ± 11.54

with similar wet mass P:L ratios (ranging from 2.6:1.0 to 14.6:1.0), resulting in highly similar niches (0.78), with prey consumption occurring within a similar nutritional space. These findings further confirm the ability of cetaceans to consume prey of different nutritional and energetic values (Spitz et al., 2010; Machovsky-Capuska and Raubenheimer, 2020; Stockin et al., 2022).

The realized nutritional niche breadth (SEAc) of immature dolphins (10.3) was broader than their mature conspecifics (7.2), suggesting that both maturity groups have a moderate overlap (0.57) in their nutritional space. Under the MNNF, marine predators characterized as nutritional niche generalists, are known for their ability to successfully exploit a diversity of nutritional combinations while foraging in complex environments (Machovsky-Capuska et al., 2016; Machovsky-Capuska et al., 2018; Denuncio et al., 2021; Stockin et al., 2022). Thus, survival pressures evident in these heterogeneous marine environments may have influenced the ability of immature individuals to develop a higher degree of nutritional generalism in their diets (i.e., realized nutritional niche) when compared to their mature conspecifics. Indeed, similar observations were reported in western Mediterranean for striped dolphins (Gómez-Campos et al., 2011).

4.2. Trace elements: concentrations and detoxification mechanisms

Age played a vital role in both renal and hepatic bioaccumulation of Hg and Se, with higher concentrations observed in older dolphins due to longer exposure periods. These trends are consistent with previous findings of Hg levels in common dolphins (Cecilio et al., 2006; Lahaye et al., 2007; Machovsky-Capuska et al., 2020b; Stockin et al., 2021b), and among cetaceans worldwide (reviewed in Kershaw and Hall, 2019). As a metabolically active tissue, liver is known for its ability to accumulate high concentrations of metals, particularly Hg (Kershaw and Hall, 2019). However, the highest concentrations of Hg in the liver of immature (41 mg kg⁻¹, ww) and mature (210 mg kg⁻¹, ww) individuals were low in comparison to harbour porpoises (*Phocoena phocoena*) in the North and Baltic Seas (up to 449 mg kg⁻¹, ww without evidence of hepatic lesions; Siebert et al., 1999). Accordingly, it is likely that the tolerance for Hg concentrations without hepatic damage may be species specific in cetaceans (Kershaw and Hall, 2019). To bioaccumulate a highly toxic metal known to have a half-life of 10 years (Wagemann et al., 1998), cetaceans have developed the ability to combine Se with demethylated Hg to form mercury-selenium (HgSe) inert crystals in both liver and kidney tissue (Kershaw and Hall, 2019; Koeman et al., 1975).

The concentrations of Cd and Zn in the kidney and liver of both sexual maturity groups were similar. With a half-life of 10–30 years, Cd concentrations measured for kidneys reached up to 31.8 mg kg⁻¹ww (i.e., lower than the proposed range of 40–200 mg kg⁻¹ww considered to induce renal disfunction in mammals; reviewed in Bowles, 1999). Cetaceans mitigate toxicity by binding Cd with metallothioneins (Das et al., 2000) and via the formation of cadmium and zinc (Cd:Zn)

granules in the kidneys (Gallien et al., 2001). Several issues may affect the timing of sexual maturity of common dolphins, including but not limited to, density dependant factors (Westgate and Read, 2007; Murphy et al., 2009; Palmer et al., 2022). While the average age (ASM) and length (LSM) that common dolphins reach sexual maturity differs between populations (Würsig et al., 2018), the ASM and LSM at sexual maturity for New Zealand *Delphinus* is 8.8 and 7.5 years and 198.3 and 183.5 cm, for males and females, respectively (Palmer et al., 2022; Palmer et al., 2023).

4.3. Nutritional nexus: diet-trace metals relationship

Multiple questions have arisen on the ability of the ecological niche concept to capture the different variables that shape wild populations. The MNNF enabled the characterizations of prey composition niche and the realized nutritional niches, showing that both immature and mature dolphins consumed prey and assimilated diets within a comparable nutritional space. Immature dolphins showed the ability to exploit diverse prey (i.e. “prey composition generalist”) and a wider nutritional range of diets (i.e. “nutrient generalist”) compared to their sexually mature conspecifics. The NicheROVER models confirmed that this nutritional variation was driven by P intake, while L intake remained consistent across immature and mature groups.

The degree of niche overlap between maturity groups estimated by SIBER models provides new insights to the pathways and resources (prey and habitat) from which metals were incorporated (Lyons et al., 2019). A high degree of overlap was observed between Cd and Zn niches within liver and kidney tissue across both sexual maturity groups. Pilchard, anchovy and arrow squid are recognised sources of Cd (Bustamante et al., 1998; Gerpe, 2006; Okyere et al., 2015; Lischka et al., 2020), which were consumed in different proportions by immature and mature dolphins. Broader Hg and Se niches were estimated for mature dolphins and characterized by the higher contaminant concentrations in liver and kidney tissues, resulting in low niche overlap with their immature conspecifics. This difference in trace metal niche estimation suggest that the sources of Hg and Se differ between immature and sexually mature animals.

Both maturity groups consumed six prey species known for different Hg and Se accumulation in the muscle and liver and kidney, and gonads, respectively (Geng et al., 2015). Nutritional variability in the composition of fish has been detected relative to prey distribution within the water column (Denuncio et al., 2021). Accordingly, this may also lead to differential accumulation of Hg and Se across prey species (Le Croizier et al., 2019). Thus, most coastal and pelagic prey consumed by dolphins not only provide nutrients important for metabolism but further result in elevated Hg and Se ingestion (Geng et al., 2015; Machovsky-Capuska and Raubenheimer, 2020). An alternative, plausible explanation for the observed difference in concentrations could be linked to prey size. While this variable was not directly measured in the present study, body size is positively correlated with metal concentrations (Leonzio et al., 1982; Authman et al., 2015; Geng et al., 2015). While prey size is suggested to increase with the TBL of marine predators, no distinct trend has yet been reported for common dolphins (Young and Cockcroft, 1994; Meynier et al., 2008a; Santos et al., 2013).

Our study applied a multidisciplinary approach to overcome individual methodological shortfalls (Majdi et al., 2018), to understand the nutritional and trace metal interactions with the ecological niche that common dolphins inhabit. In alignment with the United Nations Sustainable Development Goal 14 – Life Below Water, our findings have particular relevance when addressing how marine pollution and climate change may influence the nutritional and trace metal pathways, and thus the nutritional requirements and potential fitness of marine predators in the wild (Machovsky-Capuska et al., 2020b).

5. Conclusions

Our findings revealed how nutritional and trace metal dynamics were influenced by sexual maturity. The characterizations of prey composition niche and the realized nutritional niche showed that both immature and sexually mature dolphins consumed prey and amassed collective diets within the same nutritional space. Immature dolphins showed a higher degree of prey and nutrient generalism driven by P intake compared to mature individuals. Cd and Zn niche similarities suggests these metals are incorporated through similar prey in both immature and mature dolphins, whereas Hg and Se niche divergence indicates that uptake is from different prey species. This multidisciplinary approach will be invaluable to further investigate these dynamics across specific reproductive stages including pregnancy, lactation, and reproductive senescence.

Author statement

KAS and GEMC contributed to the conception, design of the study and manuscript preparation. KAS and GEMC collected the field data, EIP completed the literature review, aged and classified sexual maturity of individuals and compiled citations and referencing for the manuscript. CA with the assistance from GEMC and KS, analysed the data and designed the figures and tables. KAS and GEMC created the supplementary material. All authors discussed the contents of the manuscript and contributed to manuscript editing and revision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data included in Supplementary Materials

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.envpol.2023.121935>.

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