Relationship between morphometrics and trophic levels in deep-sea fishes

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ABSTRACT: Marine food webs are structured, in part, by predator gape size. Species found in deep-sea environments may have evolved such that they can consume prey of a wide range of sizes, to maximise resource intake in a low-productivity ecosystem. Estimates of gape size are central to some types of ecosystem model that determine which prey are available to predators, but cannot always be measured directly. Deep-sea species are hypothesized to have larger gape sizes than shallower-water species relative to their body size and, because of pronounced adaptive foraging behaviour, show only a weak relationship between gape size and trophic level. Here we present new data describing selective morphological measurements and gape sizes of 134 osteichthyan and chondrichthyan species from the deep sea (200–1300 m) off New Zealand. We describe how gape size (height, width and area) varied with factors including fish size, taxonomy (class and order within a class) and trophic level estimated from stable isotopes. For deep-sea species, there was a strong relationship between gape size and fish size, better predicted by body mass than total length, which varied by taxonomic group. Results show that predictions of gape size can be made from commonly measured morphological variables. No relationship between gape size and trophic level was found, likely a reflection of using trophic level estimates from stable isotopes as opposed to the commonly used estimates from FishBase. These results support the hypothesis that deep-sea fish are generalists within their environment, including suspected scavenging, even at the highest trophic levels.

KEY WORDS: Trophic level · Isotopic ecology · Gape limitation · Deep-sea fish · Ecosystem modelling · Generalists

1. INTRODUCTION

Body size and the relationships between the sizes of predators and prey play major roles in the formation and operations of food webs (Cohen et al. 2003). Gape size can dictate the roles of predators and prey, as it is a limiting factor for predation (Heupel et al. 2014). Features of the gape, including height, width and position (terminal, projecting, etc.), inform us about how fishes select, approach and capture their prey, and in which habitat they are likely to be feeding (Karpouzi

& Stergiou 2003, Villéger et al. 2017a). Understanding what traits may predict the gape, and gape-limitations, of a given species, is fundamentally important to understand connections between ecosystem structure and dynamics. One relationship proposed by Ware (1978) described the number of prey encounters as a function of gape size and visual radius. By extension, in relatively impoverished environments, such as much of the deep sea, fishes may be expected to have increased sensory range, and increased relative gape size, to maximise their chances of encountering

and being physically able to consume all available prey (Ebeling & Cailliet 1974, Rex et al. 2006, De Leo et al. 2010). Indeed, some deep-sea fishes are renowned for having large gapes and/or teeth, while for example, the Anoplogastridae ('fang-tooths') have shown impressive sensory ability, and the orange roughy *Hoplostethus atlanticus* possesses notable sensory systems (Collett 1889, Koslow et al. 1995).

Many ecosystem models are size-structured or use size-based metrics to determine predator–prey linkages (e.g. Fulton et al. 2004a, Blanchard et al. 2009, Smith et al. 2015). In these models, gape size plays a key role in prey availability and selection, as it is assumed that the predator is limited to eating prey which it can capture and handle (Wainwright & Richard 1995). However, measurements of gape size for all ecologically significant species in an ecosystem are time consuming and expensive to obtain, and are usually missing. Instead, ecosystem modelling studies use common morphological measurements taken from routine biological sampling, such as fish length and weight, to predict gape limitations of predators (Fulton et al. 2004b, Audzijonyte et al. 2017).

Fish length is a good predictor of gape size in many species of Osteichthyes (bony fishes) (Karpouzi & Stergiou 2003, Slaughter & Jacobson 2008). Less understood is how this relationship evolves in chondrichthyans (cartilaginous fishes). Cartilaginous fishes are generally thought of as large, apex predators (Heupel et al. 2014), although this status is limited to a few species, typically sharks, and many have body sizes that overlap those of bony fishes. Despite having far fewer species than bony fishes (<5%), cartilaginous fishes tend to show many of the same feeding habits as bony fishes (Motta & Wilga 2001, Gardiner & Motta 2012). Some cartilaginous fishes do, however, have relatively well-developed teeth compared to most bony fishes (whose teeth are often small and/or conical), allowing cartilaginous fishes to both consume entire organisms, and also take bites out of larger prey (Motta & Wilga 2001, King et al. 2007). Sharks evolved to have a shorter lower jaw, which provides a higher biting force per muscle mass but decreases its maximum gape size (Moss 1977), suggesting a different gape–length relationship compared to bony fishes. Therefore, cartilaginous fishes may show some differences in gape–length relationships compared to bony fishes.

The relationship between adjusted gape measurements (area corrected for body length) and feeding habits (predicted by trophic level) has been reported in upper midwater (<100 m depth) fishes (Karpouzi & Stergiou 2003, Karachle & Stergiou 2011). A positive relationship between body size (length) and trophic levels was also found for both sharks (Cortés 1999) and rays (Ebert & Bizzaro 2007). However, no relationship between body size and trophic level was found for northeast Atlantic fishes until fishes were grouped into size classes (Jennings et al. 2001). In the deep sea, relationships between trophic level, body size and gape size may be weaker than in the shallow sea, as species that spend significant amounts of time searching for food and occur in large, unproductive environments, should evolve to be adaptive generalists (MacArthur & Pianka 1966, Pearcy & Ambler 1974).

Trophic levels can be estimated by examining stable isotopes in fish tissues (Fry 2006), and isotopic values can also be used to estimate the trophic diversification (niche width) of a population through isotope variability between individuals (Jack & Wing 2011). Carbon and nitrogen isotopes, $\delta^{13}C$ and $\delta^{15}N$, are the most used for tracking organic matter sources and estimating trophic levels and trophic niches of animals (Ramos & González-Solís 2012). Estimating trophic levels relies on isotopic fractionation of nitrogen between trophic positions: $\delta^{15}N$ in bulk muscle tissue increases substantially when organic matter is transferred between consumers, allowing trophic level to be estimated when baseline values are known (Vander Zanden & Rasmussen 2001, Post 2002).

Here we present new data on body size and gape size, and collate data on trophic position, for deep-sea fishes that occur off New Zealand. We use these data to (1) describe the relationship between gape characteristics and body mass/morphology (total body length and head width), separately for cartilaginous fishes and bony fishes, and (2) test relationships between gape characteristics and trophic level. For deep-sea fishes, we hypothesized that significant correlations exist between fish size and gape size, because of physical limitations. However, we hypothesized that such correlations between gape size and trophic level in deep-sea fishes would be weak, because of the advantages of generalist foraging in the deep sea.

2. MATERIALS AND METHODS

2.1. Fish samples

Sampling of fishes for morphological measurements was conducted during a standardized research survey on Chatham Rise (175° E to 175° W, 43° to
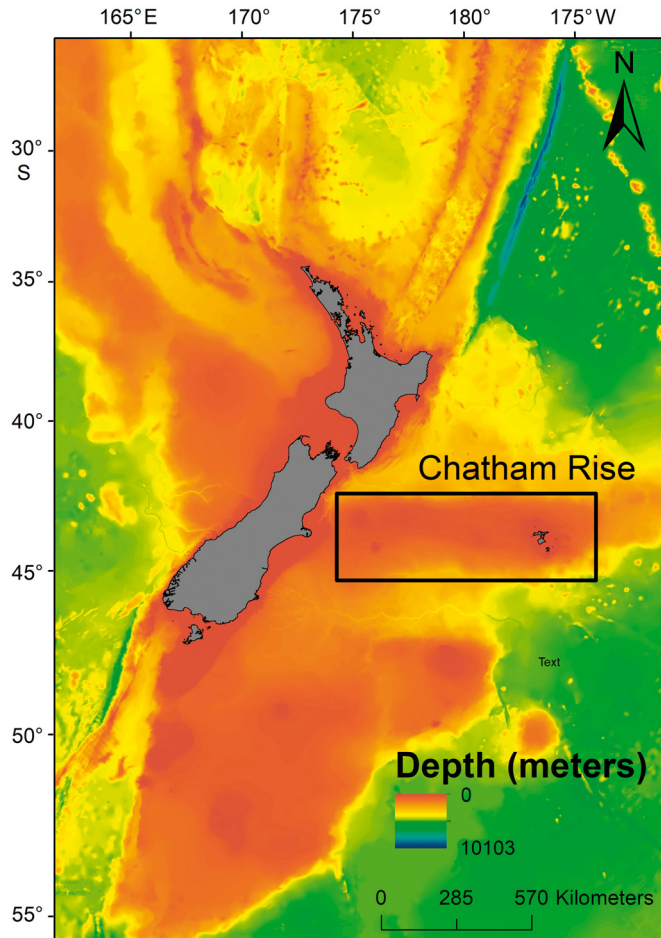
Fig. 1. Bathymetry of the New Zealand region, showing the Chatham Rise. Shallow waters are shown in red and deep waters in blue. The depth range of Chatham Rise is 0–5000 m

Fig. 2. Morphological measurements taken during the survey: (a) gape height (G_H) and gape width (G_W); (b) total length (TL); (c) head width (H_W). The image also showcases the heterogeneity of the community sampled and species body shape

45° S; Fig. 1) at depths of 200–1300 m (O'Driscoll et al. 2011), during January 2018. Samples were collected from bottom trawl catches at 130 spatially stratified locations (O'Driscoll et al. 2011). Each catch was sorted and weighed on board, and up to 200 specimens of each species were sexed and measured for total length (TL; in mm) and mass (M; compensated for boat motion, to 0.1 g), following NIWA protocol (O'Driscoll et al. 2011). Additional measurements of morphology were made for up to 14 specimens of each common species, and all specimens of uncommon species (Table S1 in the Supplement at www.int-res.com/articles/suppl/m637p225_supp.pdf). A photograph of each specimen was taken with a scale (30 cm ruler) in each picture and then 4 measurements were made by hand (Fig. 2). Gape height (G_H) was defined as the maximum linear distance between the upper and lower jaws with the mouth stretched open. Gape width (G_W) was defined as the maximum linear distance between the left and right
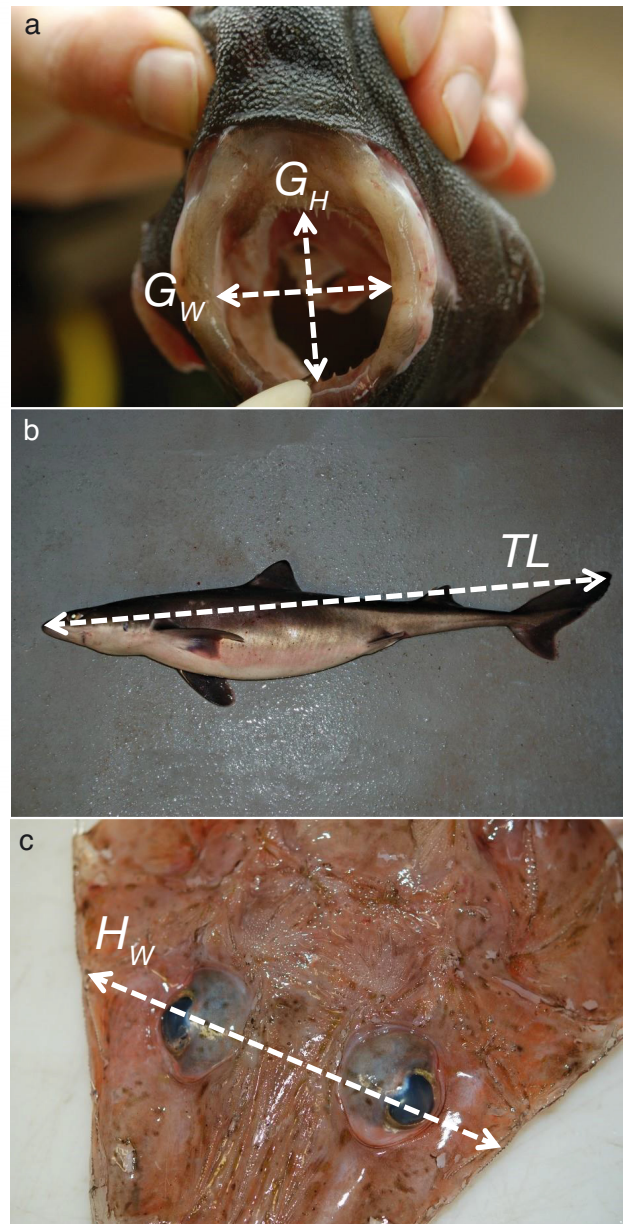
corners of the open mouth. Head width (H_W) was measured as the distance across the head at the midpoint of the eye. A few specimens of rarer species that were measured for gape were not measured for length and weight as part of the routine catch sample. For these samples, total length was estimated from the photograph using ImageJ (Schneider et al. 2012), and mass was estimated from the log(TL) ~ log(M) relationship, estimated from all specimens of

that species from the trip (Stevens et al. 2019). Gape area (G_A) was calculated as per Erzini et al. (1997): $G_A = \pi 0.25(G_H G_W)$. A species-level arithmetic mean was calculated for all continuous traits.

2.2. Trophic level estimates

We primarily used mean trophic level (τ) based on nitrogen isotopic signatures ($\delta^{15}N$) of muscle tissue from the epaxial muscle for many species from Chatham Rise (Pinkerton et al. 2015, 2017). These were calculated as mean τ for each species, collected from adult-sized individuals to encompass only the species' last ontogenetic phase. In those studies, τ was calculated using a trophic fractionation of 3.4‰ after Post (2002) and a $\delta^{15}N$ baseline from the average between surface particulate organic matter and zooplankton signatures (3.3‰) from the study area, or $\tau = \delta^{15}N$ fish/3.4. For species not recorded in the report, τ was first sought from the primary literature from species in the same latitudinal zone. Trophic levels for catsharks *Apristurus* spp. (Koefoed, 1927), *Chimaera lignaria* (Didier 2002), broadnose sevengill shark *Notorynchus cepedianus* (Peron, 1807), plunket shark *Centroscymnus plunketi* (Waite, 1910), ragfish *Icichthys australis* (Haedrich, 1966) and Pacific spookfish *Rhinochimaera pacifica* (Mitsukuri, 1895) came from Pethybridge (2010). Trophic levels for Ray's bream *Brama brama* (Bonnaterre, 1788), hake *Rexea solandri* (Cuvier, 1832) and short-snouted lancetfish *Alepisaurus brevirostris* (Gibbs, 1960) came from Revill et al. (2009). Both studies estimated trophic level in Australia from white muscle tissue, reported $\delta^{15}N$, and the values were divided by the mean trophic fractionation factor of 3.4 (Post 2002) to estimate τ. The τ for 24 other species were sourced from FishBase (Froese & Pauly 2017). The estimate of both $\delta^{15}N$ baseline (calculated from measurements over a wide spatial area) and average trophic enrichment factor (from the literature) were used throughout the whole study.

2.3. Statistical analyses

Exploratory data analysis was conducted on all variables to look for possible relationships and variables that needed transformation, using pairs plots (in the R package 'PerformanceAnalytics'). All continuous variables (G_A, TL, M), except τ, were found to be strongly skewed, and were log transformed. The relationships between G_A and H_W, TL and M were examined using simple linear regression. The best

predictor of G_A was used to create a relative gape area (rG_A) to remove the effect of body size on G_A for comparisons with τ. Some groups of fishes with unusual shapes (highlighted in Section 3) were excluded from the final models. Longnosed spookfish *Harriotta raleighana* (Goode & Bean 1895) were removed from the analysis because measurements of their mouths were inconsistently reported.

A simple linear regression was used to investigate the relationship between τ values found in FishBase and those estimated by isotopes. Linear mixed-effects (LME) models were used to investigate the relationships between τ and G_A, rG_A, TL and M. A random effect of taxonomy (as 'Order') was added to the model, where only orders with 3 or more species represented were included in the model as in Romanuk et al. (2011). A lower taxonomic classification could not be used, as there were too few replications at the family or genus level, and there was only a single τ value for each species. Model selection used Akaike's information criterion corrected for small sample sizes (AICc). The amount of variance explained by the random effect in the LME models was assessed through the difference in the marginal (fixed effect only) and conditional (all model variables) R^2. The assumptions of homoscedasticity, normality, homogeneity and independence were investigated by plotting predicted vs. fitted residuals, QQ-plots, Cleveland dot-plots and ACF plots (Zuur et al. 2009). All analysis was completed in R (version 3.4.2; R Development Core Team 2017).

3. RESULTS

In total, 134 fish species were sampled; of these, 28 were cartilaginous and 106 were bony fishes. The study included fish with large gapes ($G_A = 158.0$ cm^2, hapuku *Polyprion oxygeneios* Schneider and Forster, 1801; Table S1) and small gapes ($G_A = 0.1$ cm^2, crested bellowsfish *Notopogon lilliei* Regen, 1914; Table S1). There was a large range of fish length (max. $TL = 123.0$ cm, school shark *Galeorhinus galeus* Linneus, 1758; min. $TL = 8.1$ cm, fangtooth *Anoplogaster cornuta* Valenciennes, 1833; Table S1) and mass (max. $M = 11\,452.3$ g, smooth skate *Dipturus innominatus* Garrick and Paul, 1974; min. $M = 40.0$ g, blackspot rattail *Lucigadus nigromaculatus* McCulloch, 1907; Table S1).

A simple linear regression revealed that τ values found in FishBase were not related to those estimated by isotopes (Fig. 1); therefore, the relationship between rG_A and τ was first investigated using all data, and then without FishBase estimates. The slopes of the

Table 1. Simple linear regression for the relationship between log(mass, M) (g), log(total length, TL) (cm) and log(head width, H_W) (cm) with log(gape area, G_A). Relationships are shown for all species together, and for bony fishes and sharks separately. AICc: Akaike's information criterion corrected for small sample size

	Intercept	Slope	SE	p	R^2	logLik	AICc
All species							
Log(TL)	−2.018	1.218	0.066	<0.001	0.307	−1046.18	2098.361
Log(M)	−1.184	0.576	0.022	<0.001	0.466	−927.993	1861.985
Log(H_W)	1.044	1.168	0.056	<0.001	0.369	−938.247	1882.494
Bony fishes							
Log(TL)	−2.701	1.425	0.083	<0.001	0.324	−854.39	1714.779
Log(M)	−1.931	0.708	0.026	<0.001	0.545	−726.704	1459.408
Log(H_W)	1.007	1.260	0.067	<0.001	0.372	−786.727	1579.454
Sharks							
Log(TL)	−4.134	1.623	0.15	<0.001	0.425	−151.904	309.808
Log(M)	−0.304	0.407	0.047	<0.001	0.330	−151.363	308.726
Log(H_W)	−0.633	1.885	0.122	<0.001	0.633	−98.246	202.491

relationships between τ and rG_A did not change regardless of whether FishBase estimates were included or not (bony fishes with FishBase: $\tau = -0.012(rG_A) + 1.231$ vs. bony fishes without FishBase: $\tau = -0.015(rG_A) + 1.210$; cartilaginous fishes with FishBase: $\tau = -0.003(rG_A) + 1.352$ vs. cartilaginous fishes without FishBase: $\tau = -0.016(rG_A) + 1.182$).

Log(G_A) was significantly and positively related to log(TL) (cm), log(M) (g) and log(H_W) (Table 1, Fig. 3). *N. lilliei* and banded bellowsfish *Centriscops humerosus* (Richardson, 1846) (Macrorhamphosidae) did not fit these relationships because of their unusual shapes (Figs. 3 & 4). For all species, log(M) was the best predictor of log(G_A) (as judged by the AICc), which was also true for bony fishes when analysed sep-
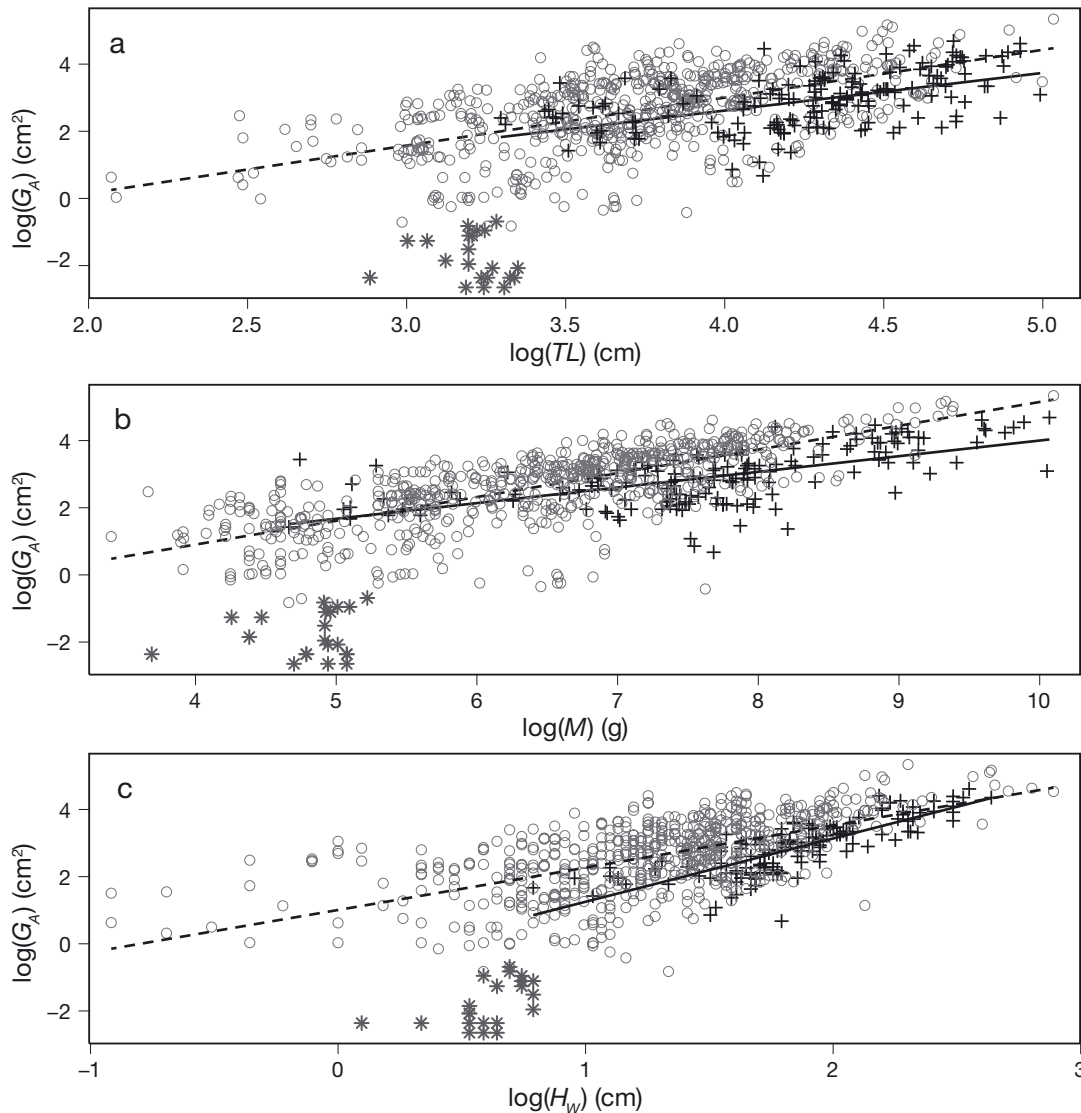

Fig. 3. Relationship between the log(gape area, GA) and (a) log(total length, TL), (b) log(mass, M) and (c) log(head width, HW) for 642 specimens of 106 bony fish species and 166 specimens of 28 shark species from the Chatham Rise. Crosses (+) with solid goodness of fit line represent sharks (chondrichthyans), and open circles (O) with dashed goodness of fit line represent bony fishes (osteichthyans). Asterisks (✳) represent bellowsfishes and are not included in predictions. See Section 3 for the equations and fit statistics

Fig. 4. Banded bellowsfish *Centriscops humerosus* (Richardson, 1846), from the Macrorhamphosidae family, showing its unique body morphology

Fig. 5. Plot of trophic levels collected from FishBase and those estimated using isotopes

arately (Table 2). For cartilaginous fishes, $\log(H_W)$ was a better predictor of $\log(G_A)$ than $\log(M)$ and $\log(TL)$. For comparative purposes, $\log(rG_A)$ was estimated as the ratio of G_A to M^2, as more of the variance was explained than $\log(TL)$ and $\log(H_W)$ for all species.

τ estimated from stable isotopes was unrelated to τ estimates from FishBase: FishBase = 3.25 + 0.18(Isotope) (p = 0.258, R^2 = 0.031; Fig. 5). As a result, relationships between TL (cm), M (g) and rG_A were examined with and without FishBase estimates. τ was unrelated to
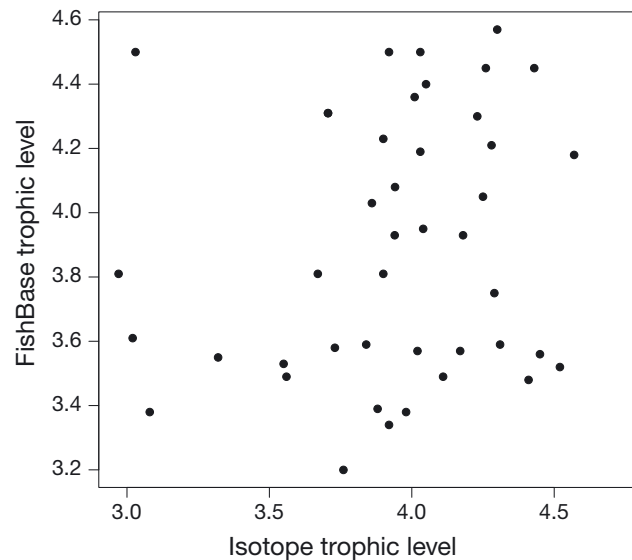
TL (cm) for bony fish: τ = 3.65 + 0.14($\log(TL)$) (p = 0.226, R^2 = 0.021); and sharks: τ = 3.18 + 0.20($\log(TL)$) (p = 0.412, R^2 = 0.036) (Fig. 6a, Table 2). τ was also unrelated to M (g) for bony fish: τ = 3.44 + 0.07($\log(M)$) (p = 0.099, R^2 = 0.040); and sharks: τ = 3.99 + 0.01 ($\log(M)$) (p = 0.902, R^2 = 0.001) (Fig. 6b, Table 2). τ was unrelated to rG_A for bony fish: τ = 3.70 – 0.02($\log(rG_A)$) (p = 0.538, R^2 = 0.006); and sharks: τ = 3.78 – 0.02 ($\log(rG_A)$) (p = 0.581, R^2 = 0.016) (Fig. 6c, Table 2). τ was also unrelated to G_A for bony fish: τ = 3.70 – 0.06($\log(rG_A)$) (p = 0.211, R^2 = 0.011); and sharks: τ = 4.21 – 0.04($\log(rG_A)$) (p = 0.626, R^2 = 0.012) (Table 2). However, when order was included as a random effect, more of the variance in the relationships could be explained. This was because some orders had positive relationships, some negative, and in others, there was no relationship. Completing the analyses separately for bony fishes and cartilaginous fishes improved the variance explained by the models for cartilaginous fishes, but not for bony fishes (Table 2). This was also true when FishBase estimates were removed where the relationship for cartilaginous fishes appears to be moderate

Table 2. Linear mixed-effects models for the relationship between mass (M, g), total length (TL, cm), gape area (G_A) and relative gape area (rG_A) with trophic level (τ), with order as a random effect. Relationships are shown for all species together and for bony fishes and sharks separately. See Section 2.3 for explanation of 'fixed' and 'all' R^2 values

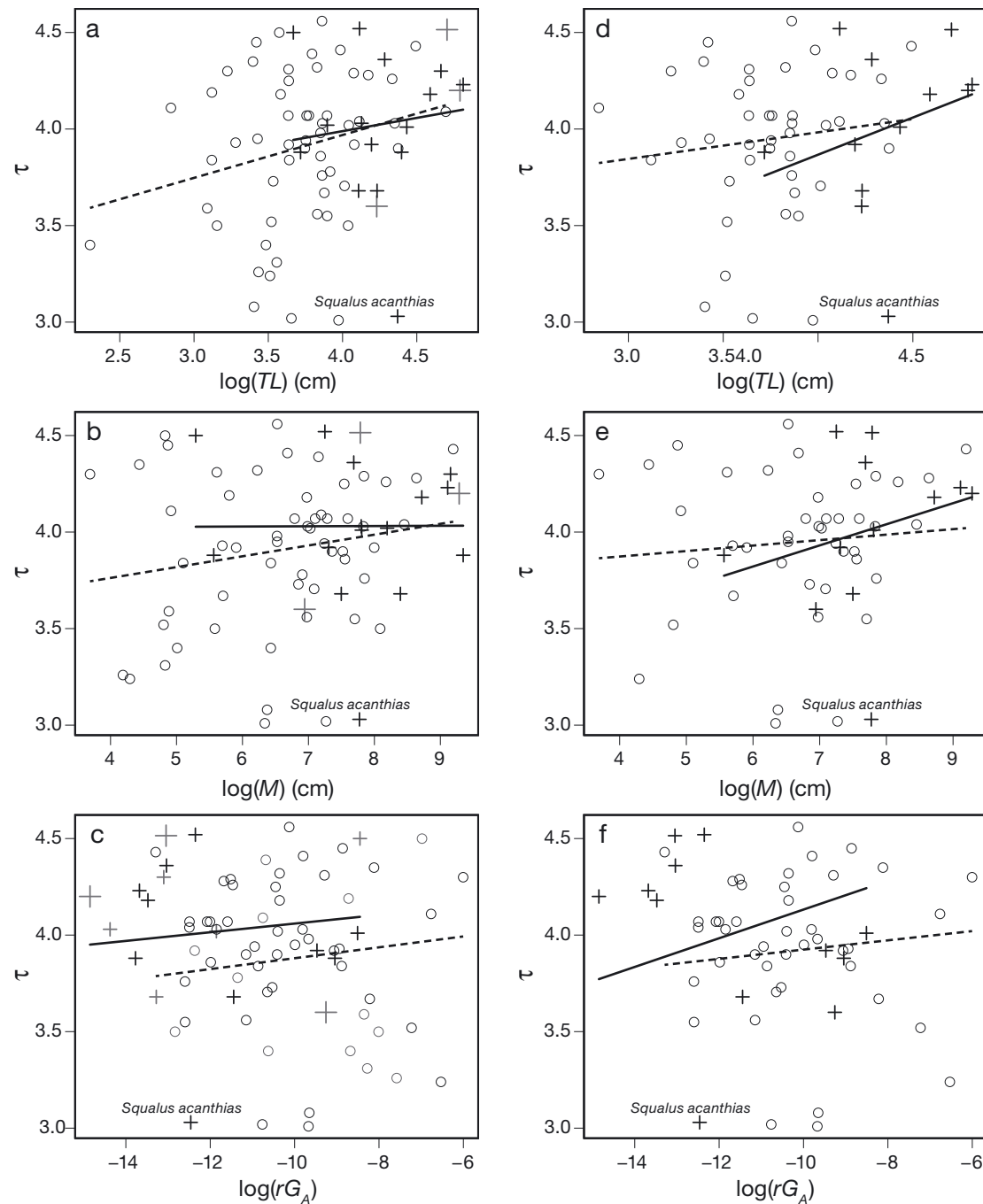|	All trophic level values				Without FishBase trophic level values			
	AICc	LogLik	R^2 (fixed)	R^2 (all)	AICc	LogLik	R^2 (fixed)	R^2 (all)
All species (n = 74)					**(n = 55)**			
Log(TL)	80.299	−36.15	0.063	0.063	62.159	−27.079	0.029	0.166
Log(M)	84.478	−38.239	0.043	0.067	63.565	−27.783	0.043	0.236
Log(G_A)	85.658	−38.829	0.011	0.011	65.410	−28.710	0.001	0.154
Log(rG_A)	85.787	−38.893	0.032	0.045	63.637	−27.818	0.072	0.263
Bony fishes (n = 56)					**(n = 44)**			
Log(TL)	64.407	−28.203	0.054	0.054	49.742	−20.871	0.009	0.087
Log(M)	67.553	−29.777	0.050	0.089	51.714	−21.857	0.021	0.171
Log(G_A)	67.635	−29.818	0.028	0.028	52.563	−22.282	<0.001	0.073
Log(rG_A)	69.442	−30.721	0.020	0.039	52.270	−22.135	0.043	0.195
Sharks (n = 17)					**(n = 11)**			
Log(TL)	15.878	−3.939	0.011	0.454	20.42	−6.21	0.084	0.463
Log(M)	18.495	−5.247	0.002	0.486	22.304	−7.152	0.104	0.533
Log(G_A)	17.617	−4.809	0.012	0.411	14.100	−3.050	0.045	0.759
Log(rG_A)	21.072	−6.536	0.030	0.219	13.331	−2.666	0.236	0.771

Fig. 6. Relationship between trophic level (τ) and the mean of log(total length, TL), log(mass, M) and log(relative gape area, rG_A) for 132 species from the Chatham Rise, (a–c) show the fit for all (τ) estimates. (d–f) show the fits without FishBase estimates of (τ) Crosses (+) with solid goodness of fit line represent sharks (chondrichthyans) and open circles (O) with dashed goodness of fit line represent bony fishes (osteichthyans). Spiny dogfish *Squalus acanthias* were removed from the analysis of sharks, as the assumption of normality was violated. See Section 3 for the equations and fit statistics

(Table 2, Fig. 6d,e). However, the sample size (n = 11) is too small to make any definite conclusions (Table 2, Fig. 6e). Spiny dogfish *Squalus acanthias* (Linneus, 1758) were removed from the analysis of artilaginous fishes, as the assumption of normality was violated

(based on inspecting the residual plots), because of the relatively low trophic level of this species. The diet of spiny dogfish around New Zealand is highly variable, and the potential for a biased τ estimate is therefore relatively high (Dunn et al. 2013).

4. DISCUSSION

We found a strong positive relationship between gape size and body size for deep-sea fishes: in general, bigger fishes had bigger size-corrected gapes. These relationships can help inform deep-sea food web studies and ecosystem models with gape-limitation assumptions, as we have a better understanding of the likely range of possible gape sizes of different species, and also how their characteristics may have evolved and become adaptive (Jennings et al. 2001, Fulton et al. 2004a, Blanchard et al. 2009, Smith et al. 2015). Here, total length, mass and head width were all positively related to gape area for both cartilaginous fishes and bony fishes, but the strength of the relationships changed across the groups. Cartilaginous fishes with larger-than-average mouths (relative to body size) had larger heads than bony fishes. This could be because some cartilaginous fishes will take chunks of larger prey, rather than capturing and swallowing their prey whole; specimens of *Hoplostethus atlanticus* and smooth oreo *Pseudocyttus maculatus* (Gilchrist 1906) have been observed with shark-sized bites taken from their dorsal-posterior region that has subsequently healed (M. R. Dunn pers. obs.). Taking chunks of prey has 2 consequences. First, morphometrically, biting prey likely requires more bite force than is necessary for fishes that swallow their prey whole. As bite force increases with increasing head size (Huber et al. 2005, 2006), cartilaginous fishes with larger heads may be more capable of feeding this way. Second, biting prey into smaller pieces means that cartilaginous fishes can consume prey, including scavenged prey, much larger than their gape size. For cartilaginous fishes, we may then expect gape to be less related to the size of prey than for other predators.

We found 2 main outliers in our analysis, the bellowsfishes *Centriscops humerosus* and *Notopogon lilliei* and spiny dogfish *Squalus acanthias*. Bellowsfishes have an unusual shape, with a very small mouth on the end of an extended snout (Fig. 4), and they appear to feed on plankton and microbenthos (Graham 1939). For spiny dogfish, the lack of relationship between trophic level and morphology can be attributed to its ecology. *S. acanthias* is known to be an especially adaptive forager, with high diet variability (Dunn et al. 2013).

Romanuk et al. (2011) hypothesized that there would be a positive correlation between body size (total length or mass) and relative gape area with trophic level of fishes in a given ecosystem. In an environment where generalists predominate, and

scavenging is common, it seems unlikely that this hypothesis would be supported. In bathypelagic environments '… it is an advantage to be able to take the largest possible meal that comes along, and at the same time, not to turn aside from a copepod' (Marshall 1960, p. 108). Our analysis of 106 species of teleost fishes and 28 species of cartilaginous fishes from the deep sea (89 of which are generalists; Table S1) revealed no relationship between body size (total length or mass) or gape size (relative gape area), and trophic level, regardless of whether estimates of trophic level from FishBase were included or not (Table 2). This result contrasts with prior research showing a relationship between trophic level and fish size (total length, mass or gape; Cortés 1999, Karpouzi & Stergiou 2003, Ebert & Bizzarro 2007, Karachle & Stergiou 2011, Romanuk et al. 2011, Hayden et al. 2019). The likely difference in the results stem from the source of the trophic level estimate. Previous research has relied on estimates from diet (Cortés 1999, Karpouzi & Stergiou 2003, Ebert & Bizzarro 2007, Karachle & Stergiou 2011) or FishBase (Romanuk et al. 2011, Hayden et al. 2019), whereas we used estimates predominantly from stable isotopes. Trophic level estimates from stomach samples rely on knowing the trophic level of all items found in the stomach, which is difficult for understudied deep-sea systems. FishBase and diet studies rely on estimates of prey found in the stomach which give an indication of recent diet, whereas stable isotopes give an indication of diet over a longer period, depending on which tissues were sampled.

Estimates from stable isotopes and FishBase for deep-sea fishes are unrelated (Fig. 1) in contrast to studies of lagoon fish (Mancinelli et al. 2013) and 3 estuarine systems and 5 pelagic systems (Carscallen et al. 2012), where strong relationships between FishBase and stable isotope estimates were found. Our data do, however, reflect results found by Cresson et al. (2014), in a bay environment, and Chassot et al. (2008), in open pelagic waters, demonstrating differences in trophic level estimated from diet and from isotopes. Results vary depending on the time of year and the location where fish are sampled (Chassot et al. 2008, Cresson et al. 2014). They are also heavily influenced by the fishes' diet (Chassot et al. 2008, Cresson et al. 2014) and their taxonomy (Table 2). The fishes in this study were predominantly generalists (Table S1) which was assumed to influence the overall lack of very high or very low trophic levels. The effect of order was demonstrated to be far more influential in predicting trophic level of deep-sea fishes than size, emphasising this important factor in fish diet.

Our results suggest that the deep sea functions differently to shallow water or pelagic environments (Karpouzi & Stergiou 2003, Carscallen et al. 2012, Hayden et al. 2019), which may be explained by the low-productivity environment the fishes occupy. A diet study with deep-sea species from New Zealand showed that, although 63% of the species displayed diet overlap of at least 40%, food items usually comprised a large range of trophic level species, from small invertebrates to fish (Jones 2012). Opportunistic foraging would likely include scavenging of dead items (in natural systems), or consumption of behaviourally compromised or dead items escaping from nets or discarded by fishing vessels (in exploited systems). It can be difficult, or impossible, to determine whether a prey item was ingested live, or scavenged, but some prey of a few deep-sea fishes have been confidently identified as scavenged, for example where prey are just fish heads and/or tails discarded by fishing vessels (e.g. Dunn et al. 2010, Forman & Dunn 2012), or human waste from vessels (e.g. a pork chop, Dunn et al. 2010). Deep-sea fish diets may be linked to habitat use and ontogenetic stage, which usually do not overlap (Drazen & Sutton 2017), suggesting that resource use is linked to niche guilds and life stage, and therefore, size. Although this is not in line with what was shown by our models, where we focussed on bottom-associated species of adult size, our results corroborate with diet analysis that shows the broad range of food items ingested by all species (Jones 2012). It is also possible that spatially and temporally separate sampling of different predator species might attribute prey differences to the predator, where the true difference was different prey availability to generalist predators. This problem may be pronounced in deep-sea studies where sampling is relatively difficult and expensive, and samples are consequently small and/or spatially and temporally distinct.

Theoretical studies predict that, as species become larger, they should eat larger prey to maximise net energy return (Werner & Gilliam 1984). If this is replicated across all organisms in an ecosystem, there should be a general increase in trophic level with individual size. Although some empirical studies have found a positive relationship between body size (total length or mass) and trophic level across different species of fish (Cortés 1999, Karpouzi & Stergiou 2003, Ebert & Bizzarro 2007, Karachle & Stergiou 2011, Romanuk et al. 2011), this has not always been detected (Jennings et al. 2001, Dalponti et al. 2018). For the deep sea, ecological theory predicts that fishes should have evolved to consume any item of food encoun-

tered, resulting in more generalists occupying this habitat (Ebeling & Cailliet 1974). In species that are discriminate feeders, there may be some aspects of their morphology or physiology (or likely a combination of the two, i.e. banded bellowsfish) that can predict what types of prey they consume (Eggers 1977).

Wainwright & Richard (1995) found that there was no better predictor of prey choice than body size, because as body size increases so do other morphological features. This has been supported with empirical evidence showing that body size is a more important predictor of diet than taxonomy (Jennings et al. 2001). Contrary to this, our results suggest that taxonomy can explain much more of the variability in trophic level than morphology (total length, mass or relative gape area; Table 2). However, the increased variation in the model arose because there was a unique relationship between trophic level, body size or relative gape area for each species, that varied in direction (positive, negative or none). A similar result was found by Dalponti et al. (2018) where some species had positive relationships between trophic level and body size, some were negative, and no relationship was found for others. This may be because gape size cannot predict the average size predators consume if they eat the widest range of prey sizes (Scharf et al. 2000). Indeed, the maximum trophic level within a population can be predicted by mean body size, but not minimum trophic level (Dalponti et al. 2018). As trophic level measured with isotopes provides an average over time, large fish are likely eating other large fish in the deep, but they are supplementing this diet with other food sources, including smaller prey, and likely scavenged prey.

LITERATURE CITED

Audzijonyte A, Gorton R, Kaplan I, van Putten I, Richards S, Fulton EA (2017) Atlantis user guide. Part I. Physics & ecology. CSIRO, Hobart. https://research.csiro.au/atlantis/?ddownload=111

Blanchard JL, Jennings S, Law R, Castle MD, McCloghrie P, Rochet MJ, Benoît E (2009) How does abundance scale with body size in coupled size-structured food webs? J Anim Ecol 78:270–280

Carscallen WMA, Vandenberg K, Lawson JM, Martinez ND, Romanuk TN (2012) Estimating trophic position in marine and estuarine food webs. Ecosphere 3:1–20

Chassot E, Rouyer T, Trenkel VM, Gascuel D (2008) Investigating trophic level variability in Celtic Sea fish predators. J Fish Biol 73:763–781

Cohen JE, Jonsson T, Carpenter SR (2003) Ecological community description using the food web species abundance and body size. Proc Natl Acad Sci USA 100:1781–1786

Collett R (1889) Diagnoses de poissons nouveaux provenant des campagnes de 'L'Hirondelle.' III.—Description d'une espèce nouvelle du genre *Hoplostethus*. Bull Soc Zool Fr 14:306

Cortés E (1999) Standardized diet compositions and trophic levels of sharks. ICES J Mar Sci 56:707–717

Cresson P, Ruitton S, Ourgaud M, Harmelin-Vivien M (2014) Contrasting perception of fish trophic level from stomach content and stable isotope analyses: a Mediterranean artificial reef experience. J Exp Mar Biol Ecol 452:54–62

Dalponti G, Guariento RD, Caliman A (2018) Hunting high or low: Body size drives trophic position among and within marine predators. Mar Ecol Prog Ser 597:39–46

De Leo FC, Smith CR, Rowden AA, Bowden DA, Clark MR (2010) Submarine canyons: hotspots of benthic biomass and productivity in the deep sea. Proc R Soc B 277: 2783–2792

Didier DA (2002) Two new species of chimaeroid fishes from the southwestern Pacific Ocean (Holocephali, Chimaeridae). Ichthyol Res 49:299–306

Drazen JC, Sutton TT (2017) Dining in the deep: the feeding ecology of deep-sea fishes. Annu Rev Mar Sci 9:337–366

Dunn MR, Griggs L, Forman J, Horn P (2010) Feeding habits and niche separation among the deep-sea chimaeroid fishes *Harriotta raleighana*, *Hydrolagus bemisi* and *Hydrolagus novaezealandiae.* Mar Ecol Prog Ser 407: 209–225

Dunn MR, Stevens DW, Forman JS, Connell A (2013) Trophic interactions and distribution of some squaliforme sharks including new diet descriptions for *Deania calcea* and *Squalus acanthias.* PLOS ONE 8:e59938

Ebeling AW, Cailliet GM (1974) Mouth size and predator strategy of midwater fishes. Deep Sea Res I 21:959–968

Ebert DA, Bizzarro JJ (2007) Standardized diet compositions and trophic levels of skates (Chondrichthyes: Rajiformes: Rajoidei). Environ Biol Fishes 80:221–237

Eggers DM (1977) The nature of prey selection by planktivorous fish. Ecology 58:46–59

Erzini K, Gonçalves JMS, Bentes L, Lino PG (1997) Fish mouth dimensions and size selectivity in a Portuguese longline fishery. J Appl Ichthyol 13:41–44

Forman JS, Dunn MR (2012) Diet and scavenging habits of the smooth skate *Dipturus innominatus.* J Fish Biol 80: 1546–1562

Froese R, Pauly D (2017) FishBase. www.fishbase.org

Fry B (2006) Stable isotope ecology. Springer Science & Business Media, New York, NY

Fulton EA, Smith ADM, Johnson CR (2004a) Biogeochemical marine ecosystem models I: IGBEM—a model of marine bay ecosystems. Ecol Model 174:267–307

Fulton EA, Smith ADM, Johnson CR (2004b) Effects of spatial resolution on the performance and interpretation of marine ecosystem models. Ecol Model 176:27–35

Gardiner JM, Motta PJ (2012) Largemouth bass (*Micropterus salmoides*) switch feeding modalities in response to sensory deprivation. Zoology (Jena) 115:78–83

Goode GB, Bean TH (1895) Scientific results of explorations by the US Fish Commission steamer *Albatross*. No. XXX– On *Harriotta*, a new type of chimaeroid fish from the deeper waters of the northwestern Atlantic. Proc US Natl Mus 17:471–478

Graham DH (1939) Food of the fishes of Otago Harbour and adjacent sea. Trans R Soc NZ 68:421–436

Hayden B, Palomares MLD, Smith BE, Poelen JH (2019) Biological and environmental drivers of trophic ecology in marine fishes — a global perspective. Sci Rep 9:11415

Heupel MR, Knip DM, Simpfendorfer CA, Dulvy NK (2014) Sizing up the ecological role of sharks as predators. Mar Ecol Prog Ser 495:291–298

Huber DR, Eason TG, Hueter RE, Motta PJ (2005) Analysis of the bite force and mechanical design of the feeding mechanism of the durophagous horn shark *Heterodontus francisci.* J Exp Biol 208:3553–3571

Huber DR, Weggelaar CL, Motta PJ (2006) Scaling of bite force in the blacktip shark *Carcharhinus limbatus.* Zoology (Jena) 109:109–119

Jack L, Wing SR (2011) Individual variability in trophic position and diet of a marine omnivore is linked to kelp bed habitat. Mar Ecol Prog Ser 443:129–139

Jennings S, Pinnegar JK, Polunin NVC, Boon TW (2001) Weak cross species relationships between body size and trophic level belie powerful size based trophic structuring in fish communities. J Anim Ecol 70:934–944

Jones MRL (2012) Diets and feeding relationships of deepsea fish from central and southern New Zealand. PhD dissertation, Auckland University of Technology

Karachle PK, Stergiou KI (2011) Mouth allometry and feeding habits of some Mediterranean fishes. Acta Ichthyol Piscat 41:265–275

Karpouzi VS, Stergiou KI (2003) The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. J Fish Biol 62:1353–1365

King NJ, Bailey DM, Priede IG (2007) Role of scavengers in marine ecosystems: Introduction. Mar Ecol Prog Ser 350: 175–178

Koslow JA, Bell J, Virtue P, Smith DC (1995) Fecundity and its variability in orange roughy: effects of population density condition egg size and senescence. J Fish Biol 47: 1063–1080

MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. Am Nat 100:603–609

Mancinelli G, Vizzini S, Mazzola A, Maci S, Basset A (2013) Cross-validation of δ^{15}N and FishBase estimates of fish trophic position in a Mediterranean lagoon: the importance of the isotopic baseline. Estuar Coast Shelf Sci 135: 77–85

Marshall NB (1960) Swim bladder structure of deep-sea fishes in relation to their systematics and biology. Discov Rep 31. Cambridge University Press, Cambridge

Moss SA (1977) Feeding mechanisms in sharks. Am Zool 17: 355–364

Motta PJ, Wilga CD (2001) Advances in the study of feeding behaviors, mechanisms, and mechanics of sharks. Environ Biol Fishes 60:131–156

O'Driscoll RL, MacGibbon D, Fu D, Lyon W, Stevens DW (2011) A review of hoki and middle-depth trawl surveys of the Chatham Rise January 1992–2010. New Zealand Fisheries Assessment Report 2011/47. National Institute of Water Atmospheric Research, Wellington. http://docs. niwa.co.nz/library/public/FAR2011-47.pdf

Pearcy WG, Ambler JW (1974) Food habits of deep-sea macrourid fishes off the Oregon coast. Deep Sea Res I 21: 745–759

Pethybridge H (2010) Ecology and physiology of deep-water chondrichthyans off southeast Australia: mercury stable isotope and lipid analysis. PhD dissertation, University of Tasmania, Hobart

Pinkerton M, Anderson OF, Bury S, Brown J, Nodder S, Forman J (2015) Marine Trophic Index based on research trawl surveys of the Chatham Rise 1992−2014. National Institute of Water Atmospheric Research and Ministry for the Environment, Wellington

Pinkerton M, Anderson O, Dunn M, Edwards C, Roux MJ (2017) Ocean ecosystem indicators for New Zealand: review of the Marine Trophic Index. National Institute of Water and Atmospheric Research, Wellington

Post DM (2002) Using stable isotopes to estimate trophic position: models methods and assumptions. Ecology 83: 703–718

Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Ramos R, González-Solís J (2012) Trace me if you can: the use of intrinsic biogeochemical markers in marine top predators. Front Ecol Environ 10:258–266

Revill AT, Young JW, Lansdell M (2009) Stable isotopic evidence for trophic groupings and bio-regionalization of predators and their prey in oceanic waters off eastern Australia. Mar Biol 156:1241–1253

Rex MA, Etter RJ, Morris JS, Crouse J and others (2006) Global bathymetric patterns of standing stock and body size in the deep-sea benthos. Mar Ecol Prog Ser 317:1–8

Romanuk TN, Hayward A, Hutchings JA (2011) Trophic level scales positively with body size in fishes. Glob Ecol Biogeogr 20:231–240

Scharf FS, Juanes F, Rountree RA (2000) Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Mar Ecol Prog Ser 208:229–248

Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. Nat Methods 9:671–675

Slaughter JE, Jacobson B (2008) Gape:body size relationship of flathead catfish. N Am J Fish Manag 28:198–202

Smith MD, Fulton A, Day RW, Shannon LJ, Shin YJ (2015) Ecosystem modelling in the southern Benguela: comparisons of Atlantis Ecopath with Ecosim and OSMOSE under fishing scenarios. Afr J Mar Sci 37:65–78

Stevens DW, O'Driscoll RL, Ballara SL, Schimel ACG (2019) Trawl survey of hoki and middle-depth species on the Chatham Rise, January 2018 (TAN1801). New Zealand Fisheries Assessment Report FAR 2018/41. National Institute of Water Atmospheric Research, Wellington. https://fs.fish.govt.nz/Page.aspx?pk=113&dk=24639

Vander Zanden MJ, Rasmussen JB (2001) Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: implications for aquatic food web studies. Limnol Oceanogr 46:2061–2066

Villéger S, Brosse S, Mouchet M, Mouillot D, Vanni MJ (2017) Functional ecology of fish: current approaches and future challenges. Aquat Sci 79:783–801

Wainwright PC, Richard BA (1995) Predicting patterns of prey use from morphology of fishes. Environ Biol Fishes 44:97–113

Ware DM (1978) Bioenergetics of pelagic fish: theoretical change in swimming speed and ration with body size. J Fish Res Board Can 35:220–228

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Annu Rev Ecol Syst 15:393–425

Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer Science & Business Media