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Trophic Interactions and Distribution of Some Squaliforme Sharks, Including New Diet Descriptions for *Deania calcea* and *Squalus acanthias*

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Abstract

Squaliforme sharks are a common but relatively vulnerable bycatch in many deep water fisheries. Eleven species of squaliforme shark are commonly caught at depths of 200–1200 m on Chatham Rise, New Zealand, and their diversity suggests they might occupy different niches. The diets of 133 *Deania calcea* and 295 *Squalus acanthias* were determined from examination of stomach contents. The diet of *D. calcea* was characterised by mesopelagic fishes, and *S. acanthias* by benthic to pelagic fishes, but was more adaptive and included likely scavenging. Multivariate analyses found the most important predictors of diet variability in *S. acanthias* were year, bottom temperature, longitude, and fish weight. The diet of the nine other commonly caught squaliforme sharks was reviewed, and the spatial and depth distribution of all species on Chatham Rise described from research bottom trawl survey catches. The eleven species had a variety of different diets, and depth and location preferences, consistent with niche separation to reduce interspecific competition. Four trophic groups were identified, characterised by: mesopelagic fishes and invertebrates (*Centroselachus crepidater*, *D. calcea*, and *Etmopterus lucifer*); mesopelagic and benthopelagic fishes and invertebrates (*Centroscymnus owstoni*, *Etmopterus baxteri*); demersal and benthic fishes (*Centrophorus squamosus*, *Dalatias licha*, *Proscymnodon plunketi*); and a generalist diet of fishes and invertebrates (*S. acanthias*). The trophic levels of the species in each of the four groups were estimated as 4.18–4.24, 4.20–4.23, 4.24–4.48, and 3.84 respectively. The diet of *Oxynotus bruniensis* and *Squalus griffini* are unknown. The different niches occupied by different species are likely to influence their vulnerability to bottom trawl fisheries. Some species may benefit from fisheries through an increased availability of scavenged prey.

Introduction

Deep-sea sharks are abundant and widely distributed on Chatham Rise, New Zealand [1], where they are a common bycatch in longline and trawl fisheries [2]. Sharks share a number of biological characteristics that make them susceptible to over-utilisation [3], but the status of populations on Chatham Rise is unknown [2,4]. Of the squaliforme shark species commonly caught by deep water (>400 m) research bottom trawls on Chatham Rise, *Proscymnodon plunketi* and *Dalatias licha* are listed by the IUCN as "near threatened", and *Squalus acanthias* and *Centrophorus squamosus* are listed as "vulnerable"; the other seven commonly caught species, *Centroscymnus owstoni*, *Centroselachus crepidater*, *Deania calcea*, *Etmopterus baxteri*, *Etmopterus lucifer*, *Oxynotus bruniensis* and *Squalus griffini*, are listed as "least concern" or "data deficient". Although there is international concern over the vulnerability of sharks to commercial exploitation [5–8], research bottom trawl surveys on Chatham Rise suggest shark population sizes have not declined substantially over the last 20 years [9].

Squaliforme sharks are expected to be important predators on the continental slope, yet the diet of most species is poorly known. The diversity of sympatric shark species on Chatham Rise suggests they might occupy different niches. Some sharks are known to predate directly upon species targeted by important commercial fisheries on Chatham Rise, for example on hoki *Macruronus novaezelandiae* eggs [10] or juveniles and adults [11], and others compete with commercial finfishes for food resources [11]. Better understanding of the trophic role of sharks can therefore be potentially valuable to fishery managers. For example, assessments of stock status and sustainable yields may be improved by estimating variability in natural mortality rate (*M*), where *M* is estimated from predator (i.e., including sharks) abundance and diet [12,13]. As top predators, sharks demonstrating adaptive foraging may also help to bring stability to ecosystems impacted by fishing [14]. Understanding the trophic role of sharks may also help identify threats to their own species conservation [15].

The shovelnose dogfish, *Deania calcea*, and the spiny dogfish, *Squalus acanthias*, are the most commonly caught shark species during research bottom trawl surveys on Chatham Rise, with maximum catch rates of about 1.5 t km^{-2} and 5.4 t km^{-2} respectively [9]. In New Zealand waters, reported annual commercial catches in recent years have been about 300 t of *D. calcea*, and 3000–7000 t of *S. acanthias* [4], but true catches are likely to be higher as many sharks are discarded and not recorded [2]. Some aspects of the biology of both species are known from international studies, and *S. acanthias* is a relatively well studied, but the diet of neither species on Chatham Rise has been described before.

Chatham Rise is an undersea ridge which runs eastwards for about 1000 km from the east coast of the South Island of New Zealand (Fig. 1). The subtropical front (STF) forms over Chatham Rise, where the mixing of subantarctic and subtropical water masses produces a region of heightened primary productivity [16], supporting abundant mesopelagic biomass [17]. Pronounced ecosystem changes across the STF on Chatham Rise have been correlated with changes in diet for several fish species [18–20], presumably because of variations in environmental conditions and prey availability.

This paper first provides a quantitative description of the diets of *D. calcea* and *S. acanthias* on Chatham Rise. We then review and classify the trophic role of *D. calcea*, *S. acanthias* and nine other squaliforme sharks commonly caught on Chatham Rise, using other New Zealand and international studies. We combine our trophic classification with an analysis of each species' spatial and depth distribution on Chatham Rise, allowing us to evaluate multiple components of potential niche separation for all eleven species. We discuss the veracity of the proposed niche separation, and how this may affect each species' interaction with commercially targeted fish stocks and fisheries.

Materials and Methods

Ethics

This study was exempt from ethical approval by the NIWA Animal Ethics Committee.

Diet descriptions for *Deania calcea* and *Squalus acanthias*

Samples were obtained from stratified-random research bottom trawl surveys on the Chatham Rise during December 2004–January 2005 and December 2005–January 2006 [9]. The sampling strata were defined by location and depth, covering about 146 855 km^2, depths between 200 and 1200 m, and all but the far southeast corner of Chatham Rise. A full–wing bottom trawl was towed by *RV Tangaroa* at each station for c. 3 nautical miles (5.6 km), at a speed of 3.5 knots (6.5 km/h), and at about 100 stations per year.

The sharks were sampled opportunistically, from most tows where they were caught. Fish were measured (total length (TL) to
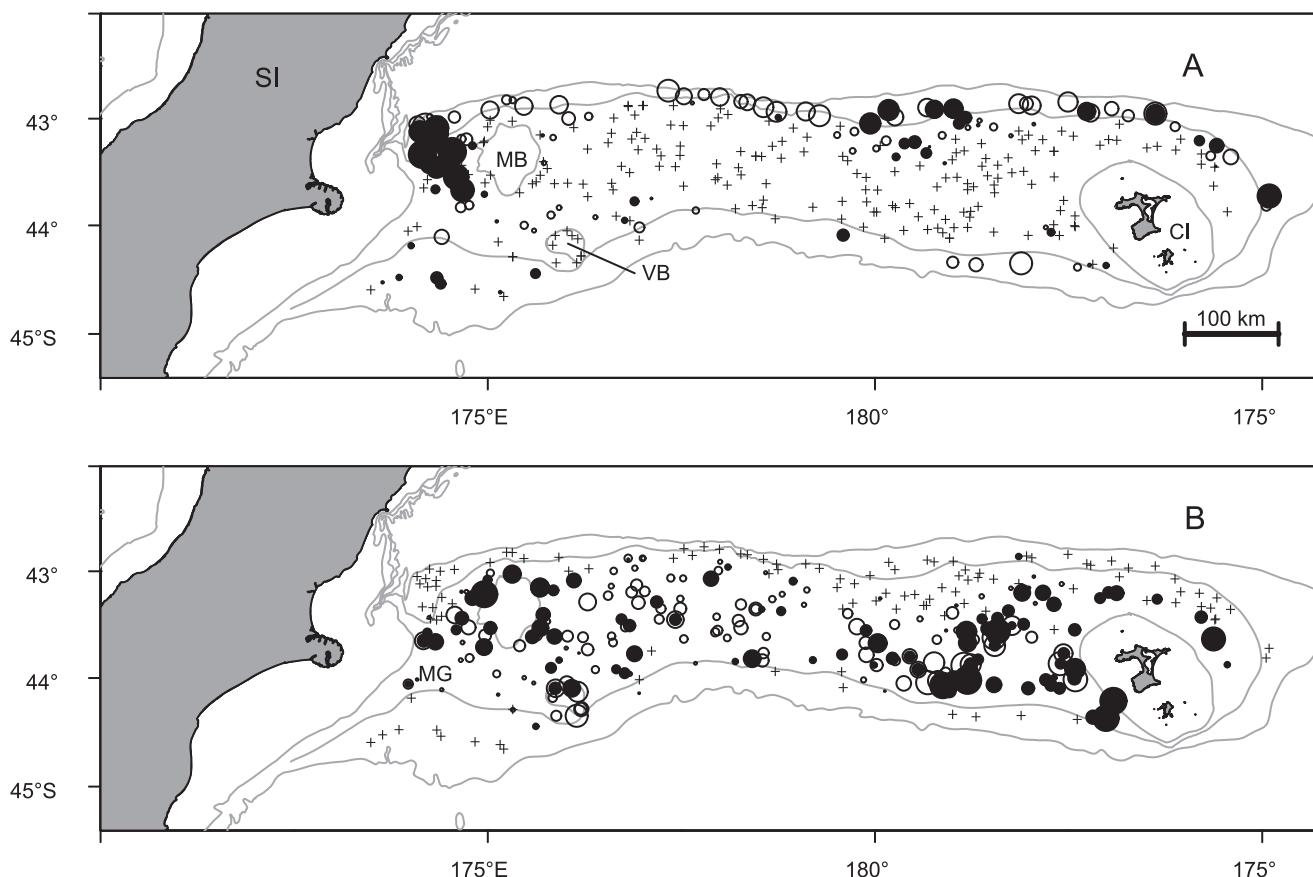
Figure 1. Locations on Chatham Rise of the research trawl tows (crosses), and tows where a) *Deania calcea*, **and b)** *Squalus acanthias* **were caught (open circles) and non-empty stomach samples were obtained (filled circles).** Circle sizes are proportional to catch (max. 189 kg for *D. calcea* and 264 kg for *S. acanthias*) and stomach sample size (max. 51 for *D. calcea* and 49 for *S. acanthias*). Grey lines show the 200 m, 600 m, and 1000 m isobaths; SI, South Island of New Zealand; CI, Chatham Islands; MG, Mernoo Gap; MB, Mernoo Bank; VB, Veryan Bank.
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the nearest mm), weighed (to the nearest 5 g), and sexed. Fish with obviously regurgitated or everted stomachs were not sampled. At sea, stomachs were sealed by fixing a cable-tie around the oesophagus, then the oesophagus was cut in front of the tie, the intestines cut below the pyloric sphincter, and the stomach removed, labelled, frozen at $-20°C$ and returned to the laboratory.

Each stomach was thawed, the wet weight of stomach and contents recorded, the stomach contents removed and rinsed with water, and the wet weight of the empty stomach recorded. Recognisable prey items were then identified. For each prey category, the individual prey items were counted, and the wet–weight recorded after removal of surface water by blotting paper.

The contribution of different prey items to the diet was determined by numerical importance (%N), frequency of occurrence (%F), mass (%W) and percentage index of relative importance (%IRI) [21,22]. Bootstrap methods, consisting of 1000 replicates of random samples, with replacement, of stomachs from the original data set, stratified by tow, were used to estimate 95% confidence intervals around the dietary statistics [23].

To conduct analyses of diet variability the prey items were aggregated into taxonomic categories. The prey categories were chosen to achieve maximum prey resolution, whilst maintaining sample size, and varied with the ability to identify different prey taxa. Invertebrate prey were classified to phylum, class, or order level, except for shrimps and prawns which were classified together as Natantia, and Astacidea, Achelata, Anomura, and Brachyura which were classified together as Reptant Decapoda; vertebrate prey were classified to order or family level, except for discarded fish offal which was classified together as 'discarded fish'. Discarded fish offal was recognisable as cleanly severed fish heads and/or tails, or filleted fish frames. The unidentifiable prey, sand, rocks, shell fragments, nematode and trematode parasites found in the stomachs, and prey classified as well digested, were excluded from detailed analyses. The knowledge of prey ecology was generally poor, and considered insufficient to allow a convincing functional grouping of prey.

To assess the adequacy of the samples, the cumulative diversity (Brillouin index of diversity, H) of categorised stomach contents was plotted against the cumulative number of stomachs containing food [24]. The mean and 95% credible interval were calculated from 1000 curves based upon different random orders of the stomachs. The sample was considered adequate for analyses of diet variability if the mean sample diversity (H) was ≥95% of the asymptotic diversity (H_A), estimated from a fitted curve of the form $H = an/(1+bn)$ [25].

Distance-based linear model (DistLM) analysis in PRIMER v6 [26] was used to identify which of the potential predictors explained most of the variability in diet. Data were first standardised, then square-root transformed, and a dissimilarity matrix calculated using Bray-Curtis distances. The potential predictors were fish total length, weight, and sex, and the tow year, time of day, depth, latitude and longitude (the latter three all a mean of the start and finish positions), and bottom water temperature. Significant and relevant correlations between predictors are reported in the results. The most significant predictors were selected using the ''best'' selection method, which used both the Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) [27], with the most parsimonious model selected by plotting the top 50 models chosen using each criterion as a scatter plot, and selecting the models which appeared in both criteria and had the lowest combined criterion scores [26]. The results of the DistLM analysis were a marginal test, fitting each predictor individually, and a conditional test, fitting each predictor

conditional on the predictor(s) already in the model. To further investigate the effects of the predictors identified from the DistLM analysis, the continuous predictors were binned, with bin limits chosen so that the number of observations in each bin was approximately equal. The target number of samples in each bin was sufficiently large to describe >95% of the estimated diversity of the overall diet. The binned data were averaged (mean of normalised proportions of prey species), square-root transformed, and then the characteristic prey groups identified with SIMPER (similarity percentages) [28]. The actual mean percentage weight of the prey groups identified by SIMPER was then calculated to show the main differences in diet composition between bins.

Review of squaliforme shark diet

The diet of common squaliforme sharks on Chatham Rise was reviewed from previously published New Zealand and worldwide studies. The species reviewed were *Centroscymnus owstoni*, *Centrophorus squamosus*, *Centroselachus crepidater*, *Dalatias licha*, *Deania calcea*, *Etmopterus baxteri*, *Etmopterus lucifer*, *Oxynotus bruniensis*, *Proscymnodon plunketi*, *Squalus acanthias*, and *Squalus griffini*. There were insufficient data for all of these species on Chatham Rise to complete quantitative diet comparisons. Three species that were rarely encountered were not included in the diet review; *Centroscymnus coelolepis* (2 occurrences in 21 years of Chatham Rise research trawl surveys, [9]), *Etmopterus pusillus* (1 occurrence), and *Etmopterus molleri* (1 occurrence). For each species and study where quantitative diet composition data were provided, the trophic level was estimated following Cortés [22]. Where unidentified or unidentifiable prey were included as part of the diet composition statistics these categories were ignored, and the identified prey re-scaled. Trophic level was not estimated where prey descriptions were incomplete, for example where 'minor' prey were not listed. The trophic level was estimated from prey occurrence descriptions only when this could be interpreted as percentage numerical importance (%N). The overall tropic level for each species was a weighted (by sample size) mean of the individual studies [22]. The review by Cortés [22] was not included in the present review as this would duplicate some data sources.

Distribution analyses

The spatial distribution of the shark species included in the diet review was then evaluated by estimating species abundance by location (latitude, longitude, and depth) on Chatham Rise. Standardised tow-by-tow catch rates (kg km^{-2}) were obtained from 21 annual stratified-random research bottom trawl surveys [9]. For each species, the mean catch rate per $0.3°$ latitude and longitude cell was plotted, as well as the catch rate against depth. Although the average catch rate would better represent by the median than the mean (because catch rates are usually approximately log-normally distributed), the mean was preferred as it ensured cells with a single non-zero catch had an average that was greater than zero. The trend in catch rate at depth was evaluated by fitting LOESS regressions. LOESS smooths the data by fitting a local quadratic regression using weighted least squares, and was implemented using the *loess* function in R (http://www.R-project.org).

Results

Diet of *Deania calcea*

Deania calcea were not caught at the majority of tow locations, and were sampled predominantly from two areas; the western end of Chatham Rise, and on the north Chatham Rise east of 180° longitude (Fig. 1a). Of 314 specimens examined, 100 (32%) had

empty stomachs. The number of prey items per stomach ranged between 1 and 7, with 55% containing only a single prey item. Prey remains were all unidentifiable or well digested in 81 stomachs, leaving 133 for detailed analyses of diet. The 133 specimens were sampled from a median depth of 573 m (range 420–727 m), and had a median length of 81.9 cm TL (range 37.7–109.8 cm TL), and a TL (cm) to weight (g) relationship of $W = 0.00078 \times TL^{3.34}$ ($R^2 = 0.99$; Std. errors 0.00017 and 0.049 respectively) The diversity of prey categories reached 90% of the estimated asymptote after 94 stomachs, but did not reach 95% of the asymptote (Fig. 2a). As a result, although the sample described diet reasonably well, it was not considered large enough for analyses of diet variability.

The diet of *D. calcea* was characterised by teleost fishes, the majority of which could not be identified, and natant decapods (Table S1). Myctophids were the most frequent and numerous of the identifiable fish prey, with at least five species consumed. However in terms of prey weight myctophids were relatively unimportant, because they were relatively small, and other prey categories of larger fish were more important, particularly merlucciids and macrourids, as well as various squids.

Diet of *Squalus acanthias*

Squalus acanthias were caught in most tows within the depth range 200–400 m, and were sampled predominantly from two areas; the western end of Chatham Rise, and to the west of the Chatham Islands (Fig. 1b). Of 550 specimens examined, 63 (11%) had empty stomachs. The number of prey items per stomach ranged between 1 and 252, with 61% containing only a single prey item. Prey remains were all unidentifiable or well digested in 192 stomachs, leaving 295 for detailed analyses of diet. The 295 specimens were sampled from a median depth of 380 m (range 209–761 m), and had a median length of 74.4 cm TL (range 55.2–105.7 cm TL), and a TL (cm) to weight (g) relationship of $W = 0.0032 \times TL^{3.08}$ ($R^2 = 0.98$; Std. errors 0.00049 and 0.035 respectively) The diversity of prey categories reached 95% of the estimated asymptote after 47 stomachs (Fig. 2b), indicating the sample was large enough for analyses of diet variability.

The diet of *S. acanthias* was characterised by teleost fishes, and although the majority of the fish prey could not be identified, at least 24 species were consumed, having habits ranging from benthic to mesopelagic (Table S2). Other important prey were salps, euphausiids, and squids. The most important fish prey category was scavenged jack mackerel (*Trachurus* spp.), followed by Merluccidae (entirely hoki *Macruronus novaezelandiae*) and macro-

urids (at least four species). Salps and euphausiids were the most numerous prey, but squids were most important by prey weight, followed by unidentified fish, scavenged fish, hoki, and octopods. The squid prey were most frequently identified as arrow squid *Nototodarus* spp., and the scavenged fish were heads and/or tails only of jack mackerel *Trachurus* spp. or hoki.

The DistLM analysis indicated significant relationships between diet and several of the predictors (Table 1), with the sequential model having the predictors year, bottom temperature, longitude, and fish weight, together explaining 13.2% of the deviance.

The diet of *S. acanthias* was characterised by salps, copepods, euphausiids and squids in 2005 (Table 2). In 2006 the diet featured more squids and reptant decapods (which were predominantly *Metanephrops challengeri*), and in 2007 the diet featured more discarded fishes and macrourids. There were no strong correlations between year and any other predictor ($r^2 \le 0.23$).

On the western flank of Chatham Rise (173.9–177.4°E), the diet of *S. acanthias* was characterised by euphausiids and squids, and to a lesser extent by salps, macrourids, and reptant decapods (Table 3). Moving eastwards across Chatham Rise, the diet featured more fishes, including merlucciids and macrourids, and then more copepods, salps, and discarded fishes. Squids were least important towards the centre of Chatham Rise (177.8°E – 177.8°W). Longitude was moderately correlated with latitude ($r^2 = 0.39$), which was caused by the absence of samples from the southeast Chatham Rise, but weakly correlated with other predictors ($r^2 \le 0.21$).

The diet of small (≤ 1090 g) *S. acanthias* was characterised by salps, small crustaceans, and myctophids (Table 4). Euphausiids featured in the diet of all sizes of *S. acanthias*. As *S. acanthias* got larger, the diet featured less salps, the crustacean component changed from amphipods and copepods to reptant decapods, the fish component changed from myctophids to macrourids, discarded fishes, and eventually to merlucciids, and the cephalopod component featured squids throughout, but octopods only in larger (≥ 1425 g) *S. acanthias*. Fish weight was moderately correlated with latitude ($r^2 = 0.42$; larger fish on south Chatham

Figure 2. Cumulative diversity of prey categories (solid lines) and 95% credible intervals (broken lines) in the analyses of diet of a) *Deania calcea*, **and b)** *Squalus acanthias*. Dotted lines are the fitted curves from which asymptotic diversities were estimated.
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Table 1. *Squalus acanthias* results of the DistLM analysis marginal and conditional tests, using all stomachs containing prey ($n = 295$).

Variable	d.f.	P	r²
Marginal model			
Length	2	0.001	0.032
Weight	2	0.001	0.036
Sex	2	0.006	0.010
Year	3	0.001	0.057
Time of day	2	0.080	0.006
Depth	2	0.001	0.026
Latitude	2	0.001	0.020
Longitude	2	0.001	0.025
Bottom temperature	2	0.001	0.030
Conditional (sequential) model			
Year	3	0.001	0.057
+ Bottom temperature	5	0.001	0.089
+ Longitude	6	0.001	0.111
+ Weight	7	0.001	0.132

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Table 2. *Squalus acanthias* diet by year.

	2005	2006	2007
n	145	33	117
Salpidae	24.0[c]	3.6	12.1[b]
Copepoda	14.4[b]	1.5	0.0
Euphausiacea	15.5[b]	1.5	10.2[a]
Reptant Decapoda	5.5	17.6[a]	2.6
Macrouridae	3.3	0.1	12.3[b]
Discarded fishes	1.4	9.1	25.8[c]
Teuthoidea	9.9[a]	47.6[c]	10.3[a]

Mean of standardised percent prey weight within each year, for the prey types together contributing at least 90% of the SIMPER within group similarity for one or more groups. SIMPER percentage contribution to within group similarity:
[a]3–10%;
[b]10–30%;
[c]>30%; no superscript, not identified by SIMPER as characteristic for that group; n, sample size.
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Table 4. *Squalus acanthias* diet by fish weight.

	655–1090	1095–1415	1425–2395	2400–3030	3100–5000
n	60	58	58	59	60
Salpidae	31.5[c]	26.9[c]	17.6[c]	5.1	4.2
Amphipoda	6.2	6.8[a]	3.9	2.1	0.5
Copepoda	11.6[a]	15.6[b]	0.6	3.4	5.0
Euphausiacea	19.0[b]	11.3[a]	8.5[a]	11.6[b]	8.6[a]
Reptant Decapoda	3.1	3.9	8.1[a]	5.1[a]	8.2
Merlucciidae	0.0	0.0	4.9	3.4	11.0[a]
Myctophidae	8.3[a]	0.1	4.1	0.0	1.7
Macrouridae	0.5	5.2	8.8[a]	13.5[b]	4.6
Discarded fishes	0.0	8.6	8.6[a]	22.0[c]	20.4[b]
Teuthoidea	6.9	13.8[b]	14.8[b]	8.5[a]	27.2[c]
Octopoda	0.0	0.0	5.7[a]	4.9	3.6

Mean of standardised percent prey weight within each fish weight (g) group, for the prey types together contributing at least 90% of the SIMPER within group similarity for one or more groups. SIMPER percentage contribution to within group similarity:
[a]3–10%;
[b]10–30%;
[c]>30%; no superscript, not identified by SIMPER as characteristic for that group; n, sample size.
doi:10.1371/journal.pone.0059938.t004

Rise) and sex ($r^2 = 0.40$), but weakly correlated with other predictors ($r^2 \leq 0.19$).

In cooler water ($\leq 7.5°C$), the diet was characterised by salps, amphipods, macrourids, and squids (Table 5). The diet then changed with increasing water temperature, and included copepods at $7.6–8.1°C$, at $\geq 8.2°C$ featured more discarded fishes and squids, and at $\geq 10.0°C$ was dominated by euphausiids. Bottom temperature was strongly correlated with depth ($r^2 = 0.85$; cooler in deeper water) and moderately correlated with latitude ($r^2 = 0.50$; cooler to the south), and weakly correlated with other predictors ($r2 \leq 0.20$).

Review of squaliforme shark diet

The sample sizes used to describe diet were generally small ($n < 50$) (Table 6). There was a paucity of diet samples for some species, with a total of <20 samples for *P. plunketi* and *C. owstoni*, and none for *Oxynotus bruniensis* and *Squalus griffini*. Yano & Tanaka [56] examined a large sample of *C. owstoni* ($n = 336$) and reported pelagic and benthopelagic fishes and squids, but their quantitative data were combined with *C. coelolepis* ($n = 64$) for analyses, and therefore their data were excluded from this review. *Squalus acanthias* was well studied, and the review for this species was not exhaustive.

The diets reported for each species were categorised on the basis of their diet, being most often (I) mesopelagic fishes and invertebrates (*C. crepidater*, *D. calcea*, and *E. lucifer*), (II) mesopelagic and benthopelagic fishes and invertebrates (*C. owstoni*, *E. baxteri*), (III) demersal and benthopelagic fishes (*C. squamosus*, *D. licha*, and *P. plunketi*), and (IV) generalist diet of fishes and invertebrates (*S. acanthias*). Invertebrate prey were typically numerically dominated by crustaceans, with cephalopods less frequent and numerous but

Table 3. *Squalus acanthias* diet by longitude.

	173.9–175.0°E	175.3–177.4°E	177.8°E–178.8°W	178.9–177.8°W	177.9–175.6°W
n	54	57	62	63	59
Salpidae	9.6[a]	3.8	26.9[c]	19.3[b]	23.8[c]
Copepoda	0.0	0.0	12.4[b]	21.5[c]	0.2
Euphausiacea	24.6[c]	24.3[c]	2.8	3.4	6.4
Reptant Decapoda	11.3[a]	4.3	4.5	3.2	5.8
Merlucciidae	4.0	7.0[a]	3.6	4.8	0.0
Macrouridae	8.1[a]	13.0[b]	8.1[a]	1.6	2.4
Discarded fishes	3.7	8.7[a]	6.8[a]	23.8[c]	15.3[b]
Teuthoidea	18.7[b]	14.0[b]	9.3[a]	7.9	22.4[c]

Mean of standardised percent prey weight within each longitude group, for the prey types together contributing at least 90% of the SIMPER within group similarity for one or more groups. SIMPER percentage contribution to within group similarity:
[a]3–10%;
[b]10–30%;
[c]>30%; no superscript, not identified by SIMPER as characteristic for that group; n, sample size.
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Table 5. *Squalus acanthias* diet by bottom temperature.

	6.3–7.5	7.6–8.1	8.2–9.1	9.2–9.9	10.0–11.3
n	58	66	58	65	48
Salpidae	30.1[c]	23.5[c]	13.1[b]	10.7[a]	5.5
Amphipoda	11.0[a]	4.7	0.3	0.1	3.7
Copepoda	2.9	27.3[c]	2.6	0.0	0.2
Euphausiacea	3.7	4.3	15.3[b]	1.6	41.7[c]
Macrouridae	12.8[b]	1.9	5.2	6.6[a]	6.5
Discarded fishes	6.9	10.6[a]	14.2[b]	21.5[c]	4.1
Teuthoidea	11.5[a]	5.4	20.9[c]	23.3[c]	9.6[a]

Mean of standardised percent prey weight within each bottom temperature (°C) group, for the prey types together contributing at least 90% of the SIMPER within group similarity for one or more groups. SIMPER percentage contribution to within group similarity:
[a] 3–10%;
[b] 10–30%;
[c] >30%; no superscript, not identified by SIMPER as characteristic for that group;
n, sample size.
doi:10.1371/journal.pone.0059938.t005

relatively important by weight. Within (III), *D. licha* and *P. plunketi* was noted for consuming chunks of flesh. The lowest weighted mean trophic level was estimated for *S. acanthias* (3.84), followed by *E. lucifer* (4.18), *E. baxteri* (4.20), *D. calcea* (4.22), *C. owstoni* (4.23), *C. crepidater* (4.24), *C. squamosus* (4.24), *P. plunketi* (4.32) and *D. licha* (4.48) (Table 6).

Distribution analyses

Amongst the sharks in diet group (I), *E. lucifer* (number of catches, n = 1422) was relatively ubiquitous but most abundant on the south Chatham Rise, particularly west of 180° (Fig. 3), and had a peak catch rate at about 500 m depth (Fig. 4). *Deania calcea* (n = 892) was most abundant along the north Chatham Rise and in particular to the north and east of the Chatham Islands, with a peak catch rate in deeper water, at 750 m. *Centroselachus crepidater* (n = 321) was also most abundant along the north Chatham Rise, and in particular to the east of the Chatham Islands, and the deepest peak catch rate, at about 900 m.

In diet group (II), *C. owstoni* (n = 177) and *E. baxteri* (n = 485) had similar depth distributions, with peak catch rates at about 900–1000 m, but *E. baxteri* was most abundant on the south Chatham Rise, and especially to the south and west of the Mernoo Gap, and *C. owstoni* was abundant only on the north Chatham Rise.

In diet group (III), all three species had an overlapping depth ranges with peaks in catch rate at 700–800 m, but *D. licha* (n = 643) had a relatively ubiquitous distribution but with persistently higher catch rates northeast of the Chatham Islands, *P. plunketi* (n = 186) had a patchier distribution, but was persistently more abundant on the south west and central northern Chatham Rise, and *C. squamosus* (n = 273) was abundant only to the north and east of the Chatham Islands. *Proscymnodon plunketi* had the narrowest depth range, with most catches made between 500–800 m, compared to 400–900 m in *D. licha*, and 400–1000 m in *C. squamosus*.

In diet group (IV), *S. acanthias* (n = 1520) catch rates were greatest at the shallow boundary of the survey (200 m), and then declined with depth, being rare below 500 m. *Squalus acanthias* were relatively ubiquitous, but large catch rates were taken in several years to the west of the Chatham Islands. *Squalus acanthias* had the highest catch rates in this study. *Squalus griffini* (n = 106) had a depth distribution broadly similar to *S. acanthias*, except that the catch rate did not increase at depths <300 m, and it was

caught almost entirely around the Chatham Islands. *Oxynotus bruniensis* (n = 222) was relatively ubiquitous across Chatham Rise, with a peak in catch rate at about 500 m.

Discussion

The eleven squaliforme shark species studied on Chatham Rise showed a variety of different diets, and depth and location preferences, consistent with niche separation to reduce interspecific competition. We described four trophic groups, and within these groups there was some spatial and depth separation of species. Some studies have already suggested that deep-sea sharks may reduce interspecific competition by having different prey preferences (often used to infer foraging depth), and/or different bottom depth preferences [10,29,30,33,38,42,57]. The only previous study of the distribution of deep water sharks on Chatham Rise [1] used catch data from bottom trawl surveys at 700–1500 m depth, and concluded there were no interspecific differences in depth distribution; all sharks were rare below 1200 m, and all extended shallower than 700 m. The depth range we studied, 200–1200 m, was more appropriate for studying shark distribution, but still did not include the shallow depth limits for *S. acanthias*, *S. griffini*, and possibly *O. bruniensis*. The data set we analysed was also more spatially extensive than Wetherbee's [1], and allowed us to identify more detailed spatial differences in distribution. In some cases the spatial separation we found was pronounced. For example, there was relatively little spatial overlap between the mesopelagic and benthopelagic predators *C. owstoni* and *E. baxteri*. Wetherbee [1] also noted *E. baxteri* was more abundant on the south Chatham Rise, and *C. owstoni* more abundant on the north.

Bulman et al. [32] listed *C. owstoni* and *E. baxteri* together with *C. crepidater* and *D. calcea* as "pelagic and benthopelagic piscivores". We agree with the grouping of *C. owstoni* and *E. baxteri*, but suggest these two species are usually more benthopelagic, and *C. crepidater* and *D. calcea* are usually more mesopelagic. Amongst the predators of mesopelagic fishes and invertebrates, the small (for a shark) *E. lucifer* was shallower and more southern in distribution than both *C. crepidater* and *D. calcea*, but the spatial overlap between the latter two species was relatively high, with both species especially abundant to the east of the Chatham Islands. Whilst *C. crepidater* did tend to occur a little deeper than *D. calcea*, there could be separation between *C. crepidater* and *D. calcea* to reduce competition that was not apparent from depth and location, for example the two species might forage at different depths in the mesopelagic layers, or at different times of day. Competition between all three predators of mesopelagic fishes and invertebrates might also be reduced by the relatively high abundance of mesopelagic prey on Chatham Rise [17,37]. Off southern Africa, Macpherson & Roel [31] similarly classified *E. lucifer*, *C. crepidater* and *D. calcea* together as foraging on "myctophids and pelagic cephalopods", but also included *C. squamosus* in this group. The former three species, although variable in size and in different genera, all have relatively slender bodies and flattened heads and snouts (they have a "shovelnose" dogfish appearance). *Centrophorus squamosus* has a stockier body and more rounded snout, and on the basis of diet we classified *C. squamosus* with the similarly large, relatively stocky, and blunt snouted *D. licha*, and *P. plunketi*.

Centrophorus squamosus had a relatively distinct distribution on Chatham Rise, but there was more general overlap between the distributions of *D. licha*, and *P. plunketi*, although the high density areas for each species tended not to overlap. However, both *D. licha*, and *P. plunketi* had relatively low average catch rates given their relatively large size, indicating a relatively low abundance,

Table 6. Summary of Squaliforme shark diet studies for species commonly caught during Chatham Rise bottom trawl surveys.

Species	Length (cm)	Region	n	Diet	Reference	Statistic	Trophic level
Centrophorus squamosus	160	New Zealand	26	Benthic, demersal, and benthopelagic fishes, including scavenging.	[11]	%W	4.27
		North Atlantic	21	Demersal fishes, some cephalopods.	[30]	Occurrence	–
		Southern Africa	18	Mainly cephalopods, teleosts, and some crustaceans.	[29]	%W	4.22
		Southern Africa	Not specified	Mesopelagic fishes and pelagic cephalopods	[31]	Qualitative	–
Centroscymnus owstoni	120	New Zealand	19	Mesopelagic and benthopelagic teleosts, with some cephalopods, crustaceans, and salps.	[11]	%W	4.24
		Australia	2	Benthopelagic teleosts, with some salps.	[32]	%W	4.19
		Australia	Not specified	Fish and cephalopods	[8]	Qualitative	–
Centroselachus crepidater	105	New Zealand	19	Mesopelagic teleosts, some cephalopods and crustaceans	[11]	%W	4.24
		Australia	43	Bathypelagic and mesopelagic teleosts, some cephalopods.	[32]	%W	4.24
		Australia	31	Mainly mesopelagic and bathypelagic teleosts, cephalopods, some crustaceans, and mammals.	[33]	%W	4.23
		Australia	Not specified	Fish and cephalopods	[8]	Qualitative	–
		North Atlantic	97	Cephalopods and mesopelagic teleosts, some crustaceans	[30]	%O	–
		Southern Africa	4	Mesopelagic teleosts.	[29]	%N	4.24
		Southern Africa	Not specified	Myctophids and pelagic cephalopods.	[31]	Qualitative	–
Dalatias licha	160	New Zealand	19	Predominantly benthopelagic fishes, including chunks of flesh.	[11]	%W	4.52
		Aegean Sea	2	Almost entirely cephalopods, traces of fishes and crustaceans.	[34]	%W	4.20
		Australia	5	Predominantly bathypelagic teleosts, some cephalopods, crustaceans, and mammals.	[33]	%N	4.44
		Australia	Not specified	Mainly teleosts, also elasmobranchs, cephalopods and crustaceans. Often chunks of flesh.	[8]	Qualitative	–
		Mediterranean Sea	31 (total)	Fishes, with some cephalopods and natant decapods	[35]	Semi-quantitative	–
		Not specified	Not specified	Primarily mesopelagic and bathypelagic teleosts, but also elasmobranchs, cephalopods, various invertebrates, likely scavenging, and including chunks of flesh.	[36]	Qualitative	–
Deania calcea	120	New Zealand	133	Predominantly mesopelagic and benthopelagic fishes, some cephalopods and natant decapods	This study	%W	4.23
		Australia	10	Almost entirely mesopelagic teleosts, some cephalopods.	[32]	%W	4.24
		Australia	18	Mainly mesopelagic teleosts, bathypelagic cephalopods, some natant decapods.	[33]	%N	4.11
		Australia	27	Almost entirely mesopelagic and pelagic teleosts.	[37]	%O	–
		Australia	Not specified	Fish (mainly myctophids), cephalopods and crustaceans	[8]	Qualitative	–

Table 6. Cont.

Species	Length (cm)	Region	n	Diet	Reference	Statistic	Trophic level
		North Atlantic	66	Mainly mesopelagic teleosts, some demersal teleosts, cephalopods, and natant decapods.	[30]	%N	4.23
		North Atlantic	29	Almost entirely mesopelagic and pelagic teleosts and cephalopods.	[38]	%V	4.23
		Southern Africa	62	Mainly mesopelagic teleosts, some cephalopods and crustaceans.	[29]	%W	4.23
		Southern Africa	Not specified	Myctophids and pelagic cephalopods	[31]	Qualitative	–
		Not specified	Not specified	Mesopelagic fish and natant decapods.	[36]	Qualitative	–
Etmopterus baxteri	85	New Zealand	117	Principally fish, some cephalopods.	[39]	Semi-quantitative	–
		New Zealand	25	Largely teleosts and cephalopods, some mysids and decapod crustaceans.	[40]	%W	4.21
		Australia	27	Largely benthopelagic teleosts, some cephalopods and crustaceans.	[32]	%W	4.27
		Australia	31	Bathypelagic and mesopelagic fishes, cephalopods, and some curstaceans.	[33]	%N	4.15
		Australia	113	Benthopelagic teleosts, with cephalopods, some crustaceans, and other invertebrates.	[41]	%W	4.19
Etmopterus lucifer	45	Australia	Not specified	Squid, teleosts (mainly myctophids) and crustaceans.	[8]	Qualitative	–
		Japan	611 (total)	Mostly mesopelagic squids, with some myctophids and euphausiids.	[42]	%N	4.18
		Southern Africa	Not specified	Myctophids and pelagic cephalopods	[31]	Qualitative	–
Oxynotus bruniensis	70	None	–	–	–	–	–
Proscymnodon plunketi	170	New Zealand	12	Demersal fishes, likely scavenging; no crustaceans	[11]	%W	4.30
		New Zealand	6	Teleosts and cephalopods.	[43]	Qualitative	–
		Australia	5	Fishes, cephalopods, and mammal flesh.	[33]	%N	4.34
		Australia	Not specified	Fish and cephalopods	[8]	Qualitative	–
		Not specified	Not specified	Cephalopods and teleosts.	[36]	Qualitative	–
Squalus acanthias	110	New Zealand	295	Mainly teleosts (benthic to pelagic), scavenging, some salps, crustaceans, cephalopods, and elasmobranchs.	This study	%W	4.20
		New Zealand	5149	Predominantly pelagic crustaceans, some fishes, salps, and cephalopods.	[44]	%N	3.55
		Australia	21	Mainly benthopelagic and pelagic teleosts, with cephalopods and crustaceans.	[33]	%N	4.12
		Black Sea	328	Mainly demersal and pelagic teleosts, some crustaceans, nematodes, and actinarians.	[45]	%O	–
		Black Sea	112	Almost entirely pelagic teleosts, some demersal fishes, crustaceans, cephalopods, and mammal flesh.	[46]	%W	4.22
		Irish Sea	435	Mainly pelagic, demersal, and benthic teleosts, with crustaceans, ctenophores, and cephalopods.	[47]	%V	4.12
		Japan	26	Almost entirely pelagic teleosts, some cephalopods and invertebrates.	[48]	%W	4.23
		Northeast Pacific	3126	Incomplete diet description. Mainly pelagic teleosts and euphausiids.	[49]	–	–

Table 6. Cont.

Species	Length (cm)	Region	n	Diet	Reference	Statistic	Trophic level
		Northwest Atlantic	1390	Mainly teleosts, and then cephalopods, bivalves and crustaceans.	[50]	%W	4.08[1]
		Northwest Atlantic	3795	Predominantly demersal and pelagic teleosts, Ctenophores, but spatially and temporally variable.	[51]	Semi-quantitative	–
		Northwest Atlantic	Not specified (n>20)	Sharks <61 cm: primarily cephalopods and fishes, with ctenophores; >60 cm: fishes and some cephalopods.	[52]	Semi-quantitative	–
		Southern Africa	121	Mainly mesopelagic and bathypelagic fishes, some cephalopods, and a few invertebrates.	[29]	%W	4.25
		Southwest Atlantic	2214	1980s: mainly fishes, then cephalopods and invertebrates. 1990s: teleosts and cephalopods, then crustaceans and medusae, salps and ctenophores. 2000s: mainly cephalopods, then teleosts, and crustaceans.	[53]	%W	[2]4.20, 4.13, 4.19
		Southwest Atlantic	223	Teleosts, then ctenophores, cephalopods, scavenging.	[54]	%N	3.95[3]
		Southwest Atlantic	120	Mainly cephalopods, demersal and pelagic teleosts, and some ctenophores and other invertebrates.	[24]	%W	4.20
Squalus griffini	110	None	–	–	–	–	–

Unless specified otherwise, n is the number of stomachs that contained prey and so yielded diet information. Length is the approximate maximum total length, from McMillan et al. [55]. The term *fish* means both teleosts and elasmobranchs. The statistics are %N, percentage number; %W, percentage mass; %N, percentage number;%V, percentage volume; %O, percentage occurrence; Occurrence, presence absence and could not estimate %O; semi-quantitative, quantitative diet description but data not presented in detail (only in figures).
[1], numerous estimates were possible by area and year, but the estimated trophic level did not vary much from the estimated reported here because the diet variation was largely in the proportions of cephalopods and fish, which have similar trophic levels.
[2], estimates for 1980s, 1990s, and 2000s.
[3], estimates were possible for two size classes, but only one trophic level is reported as there was only 0.01 difference between the two.
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which may reduce competition. It is unclear whether the relatively low abundance of *D. licha* and *P. plunketi* on Chatham Rise is natural or a consequence of overfishing. *Proscymnodon plunketi* biomass apparently declined in bottom trawl surveys of the orange roughy spawning grounds (depths of about 800–1200 m) on the northeast Chatham Rise, with biomass in 1994 just 6% of that in 1984 [58]. Subsequent, more extensive trawl surveys, although relatively poor in quality for *P. plunketi* (relatively high coefficients of variation), indicate abundance did not change substantially between 1992 and 2010 [9]. Although the two trawl survey series are not strictly comparable, the biomass trend they could indicate is a large decline in *P. plunketi* during the 1980s and early 1990s, followed by a low but stable biomass level since then. In which case, fishing may have modified the degree of resource competition, and possibly diet and distribution, of *P. plunketi* and *D. licha*.

Squalus acanthias and *S. griffini* do not have the dark colouration typical of many deepsea sharks, and morphologically they are very alike. *Squalus acanthias* has been studied worldwide, with the diet often described as "opportunistic" although usually dominated by pelagic fishes. Although there are no diet data for *S. griffini*, it seems likely that the two species have similar habits, with *S. griffini* being the subtropical congener of the temperate *S. acanthias*.

Very little is known about *Oxynotus bruniensis*, but its relatively small ventral mouth would suggest it eats small benthic prey. The diet of *Oxynotus centrina* in the north Atlantic was found to consist of predominantly benthic worms (Polychaeta and Sipunculidae), with some crustaceans, teleosts, and echinoderms [59]. The diet of *Oxynotus bruniensis* could therefore have greater similarity to chimaeras and the smaller skates and rays [20,60].

The trophic levels estimated for the sharks in diet groups I (*C. crepidater*, *D. calcea*, and *E. lucifer*) and II (*C. owstoni*, *E. baxteri*) were similar, reflecting a broadly similar diet of predominantly teleosts and cephalopods. The trophic levels of the relatively large *D. licha* and *P. plunketi* were slightly higher, primarily because they predated other elasmobranchs, and also chunks of mammal flesh. The latter may indicate these species feed like cookie cutter sharks (*Isistius* spp.) [9]. In the similarly large *C. squamosus*, elasmobranchs were less frequent in the diet, and mammal flesh absent, and the trophic level was accordingly lower (4.24). The trophic level of *S. acanthias* was the lowest, although strongly influenced by the crustacean-focused diet reported in a large sample by Hanchet [44]. If Hanchet's [44] study was removed, the mean weighted trophic level for *S. acanthias* was higher (4.13), although still the lowest of the species studied here.

The trophic levels estimated here were the same as estimated by Cortés [22] for *C. crepidater*, *C. squamosus*, *D. calcea*, and *E. baxteri* (4.2). Cortés [22] estimated the trophic level of *E. lucifer* to be a little lower (4.1) than the present study (4.18). *Squalus acanthias* had the lowest trophic level, with Cortés [22] estimating 3.9 and the present study 3.84. Whilst we estimated a relatively high trophic
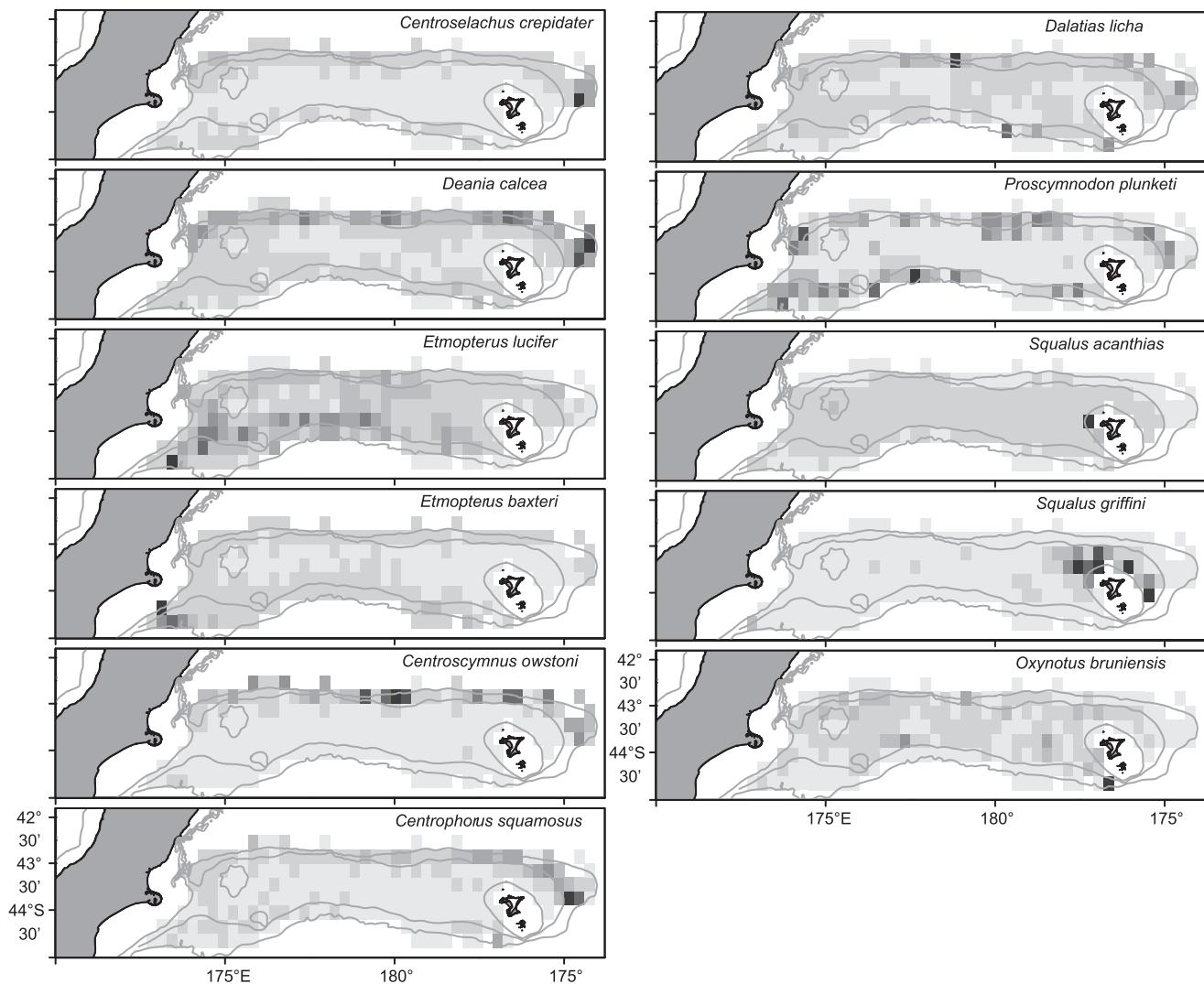
Figure 3. Catch rate (median kg km^{-2}) of squaliforme sharks on Chatham Rise in 0.3° latitude and longitude cells. Cells shaded in the lightest grey were sampled but no catches of that species were made; cells shaded in successively darker grey had higher mean catch rates. Maximum mean catch rates: *Centroselachus crepidater* 686 kg km^{-2}; *Deania calcea* 473 kg km^{-2}; *Etmopterus lucifer* 12 kg km^{-2}; *Etmopterus baxteri* 560 kg km^{-2}; *Centroscymnus owstoni* 98 kg km^{-2}; *Centrophorus squamosus* 100 kg km^{-2}; *Dalatias licha* 52 kg km^{-2}; *Proscymnodon plunketi* 13 kg km^{-2}; *Squalus acanthias* 4630 kg km^{-2}; *Squalus griffini* 10 kg km^{-2}; *Oxynotus bruniensis* 9 kg km^{-2}. Grey lines show the 200 m, 600 m, and 1000 m isobaths.
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level for *D. licha* (4.48), Cortés [22] estimated a relatively low trophic level (4.1) from a reported diet of teleosts, crustaceans, elasmobranchs, cephalopods, and other invertebrates. The relatively large size of *D. licha*, and frequent reports of other elasmobranchs in the diet, suggest this species should have a relatively high trophic level (at least as an adult). Cortés [22] did not report trophic level estimates for *C. owstoni, P. plunketi, S. griffini* or *O. bruniensis*.

Our conclusions about diet and resource partitioning of squaliforme sharks could easily be biased by small sample sizes ($n<50$), which are typical for diet studies of deep sea sharks (see Table 6). Our samples of *S. acanthias* demonstrated the potential for bias: whilst we concluded that the diet of *S. acanthias* on Chatham Rise was varied but predominantly fishes, had we sampled only in 2006 we would have concluded that the diet was predominantly cephalopods. The research trawl survey biomass estimates for *Nototodarus sloanii*, the commonest squid caught during the survey

on Chatham Rise, suggested that in 2006 *N. sloanii* were at least five times more abundant than in 2005 or 2007 [9]. This correlation between *S. acanthias* diet and the relative high abundance of trawl caught squid in 2006 suggests *S. acanthias* has adaptive foraging. It may be that the diets of many deep water sharks are more diverse than existing samples suggest. For example, the apparent absence of crustacean prey in the diet of *C. squamosus* and *P. plunketi* on Chatham Rise could easily be a bias caused by small sample sizes. Although stomach contents analyses do have several potential biases, they are a widely-used and accepted method that can provide information on a species role in food webs [61], and are complementary with other methods [62]. In this study, despite the potential for bias caused by small sample sizes, and by spatially and temporally diverse sampling locations, the diets reported for most deep water sharks were reasonably consistent worldwide.