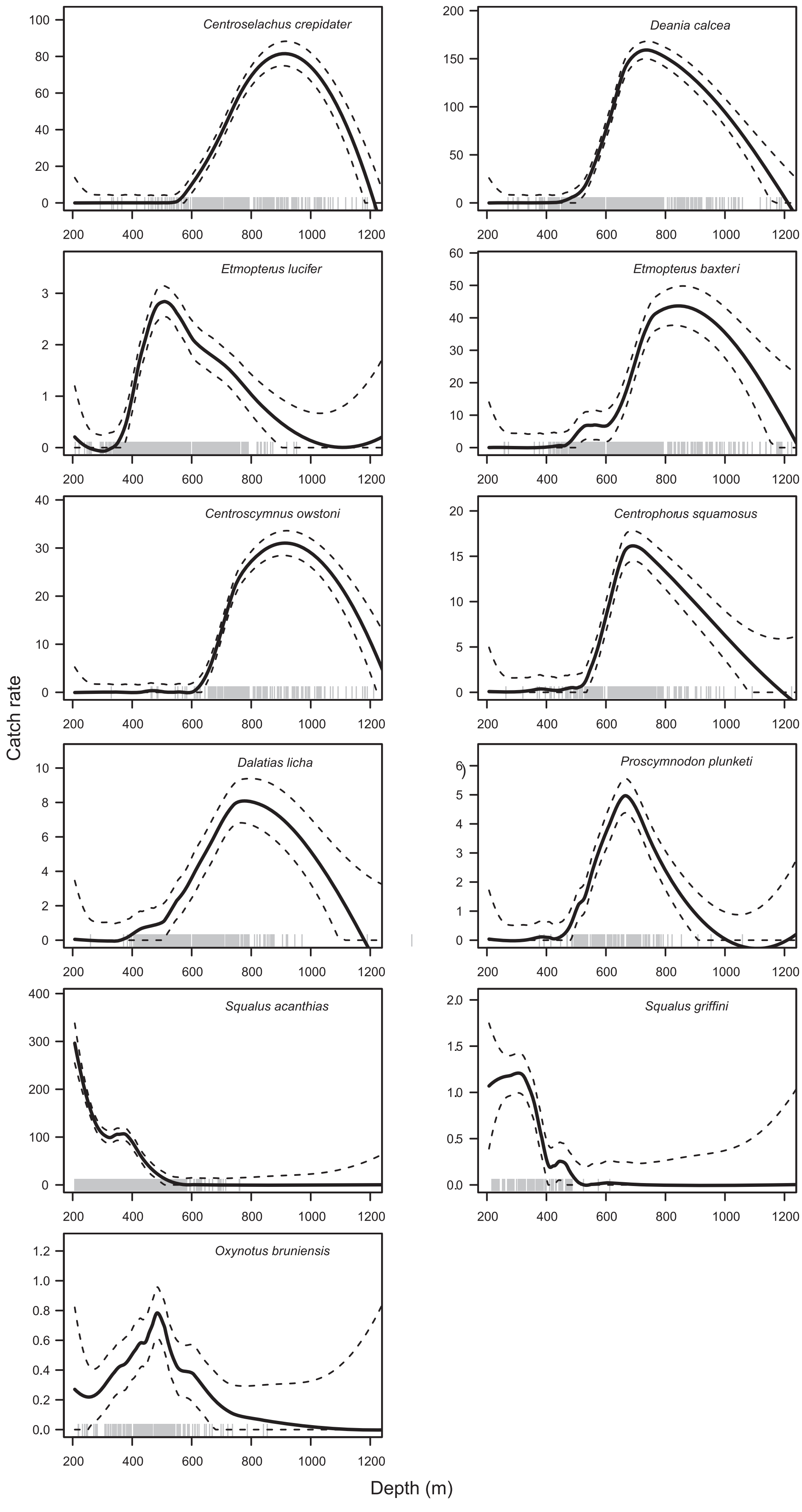
Centroselachus crepidater
Deania calcea
Etmopterus lucifer
Etmopterus baxteri
Centroscymnus owstoni
Centrophorus squamosus
Dalatias licha
Proscymnodon plunketi
Squalus acanthias
Squalus griffini
Oxynotus bruniensis
Catch rate
Depth (m)

Figure 4. Catch rate (kg km^{-2}) of squaliforme sharks on Chatham Rise by species and depth. The solid line shows the LOESS regression fitted to catch rate; broken lines indicate the 95% confidence intervals. The vertical lines above the x-axis indicate the location of catches of that species.
doi:10.1371/journal.pone.0059938.g004

Although we classified the sharks into four diet groups, the prey were not exclusive, and it seems likely that all species show some dietary overlap and adaptive foraging. Fatty acid signatures from myctophid prey have been identified in several sympatric deepwater sharks, including *S. acanthias*, *C. crepidater*, *D. licha*, *P. plunketi*, *C. owstoni*, *D. calcea*, and *E. baxteri* [33]. Scavenging of natural food fall, or of discarded offal from fishing vessels, has also been reported or suspected in a variety of deep-sea sharks [11,32,41], although the difficulty in identifying scavenged prey means it may be more widespread and important than currently thought. This also means that local fishing practices may bias shark diet, and from this the interpretations of foraging behaviour. The conclusions from our study are therefore contingent on our samples, and the degree of dietary and distributional overlap may well vary with time and location, and potentially other biological factors such as ontogeny.

The diets we estimated for *D. calcea* and *S. acanthias* on Chatham Rise were similar to that reported elsewhere, with *D. calcea* primarily a mesopelagic piscivore, and *S. acanthias* primarily an adaptive piscivore. All reports of *D. calcea* off New Zealand, Australia, and southern Africa indicated a diet dominated by pelagic fishes such as myctophids and mackerels (Carangidae) with relatively low prey diversity [29,32,33,37]. In the North Atlantic, mesopelagic prey did feature, but there were higher proportions of demersal fishes in the diet [30,38]. Although sample sizes were relatively small and discrete, there appear to be no obvious differences in reported sample characteristics (e.g., season, depth, fish size) that might explain the difference in diet, so it could well be related to location and local prey availability. Therefore, although *D. calcea* may specialise on mesopelagic prey, it apparently retains some ability to forage adaptively.

The diet of *S. acanthias* on Chatham Rise was characterised by fishes, although the commonest fish prey were suspected to be scavenged offal from fishing vessels. Compared to other sharks, *S. acanthias* reportedly has an exceptionally adaptive or ‘‘opportunistic’’ foraging behaviour, a conclusion supported by substantial spatial and temporal variations in diet [24,46,53,54]. Whilst adaptive foraging could potentially mask diet changes with ontogeny, we found smaller sharks eating notably more small crustaceans and salps, and larger sharks more large and scavenged fishes. Whilst most other studies [24,47,49,54], but not all [45,53], have reported similar ontogentic shifts in diet, some form of diet change with size is expected [63]. The study of *S. acanthias* off the east coast of the South Island of New Zealand appears to have reported an exceptional diet, being dominated by crustaceans instead of fishes, and including cannabilism [44]. The relative availability of different potential prey for *S. acanthias* on Chatham Rise (this study) and the east coast South Island [44] is unknown. Whilst differences in diet could well reflect real persistent regional differences, such differences could easily be confused by variable prey availability and restricted sampling if combined with pronounced adaptive foraging. Pronounced adaptive foraging may make a species relatively resilient to fisheries-induced ecosystem change, and accordingly *S. acanthias* was the only squaliforme shark to increase in abundance during research trawl surveys between 1992 and 2010 [9].

Fisheries may affect deep-sea shark populations in two main ways. First, capture in nets causes fishing mortality, and escape from nets may result in behavioural impairment and subsequent natural mortality [64]. Second, fishing may influence population productivity, or natural mortality, through the modification of habitats and resources. The sharks foraging on mesopelagic and benthopelagic fishes are directly competing for food resources with hoki, the most abundant species in bottom trawl surveys [9], and the most important commercial fish stock on Chatham Rise [4]. Although the hoki stock has been depleted by fishing to about 50% of its original size [4], the resulting reduction in competition has apparently not resulted in a net benefit to sharks foraging on mesopelagic and benthopelagic resources; the research survey biomass trends for *C. crepidater*, *D. calcea*, and *E. lucifer* have all shown no trend in population size between 1992 and 2010 [9]. It may be that increased mortality from fishing compensates for any decrease in competition. On the east coast of the North Island of New Zealand, research trawl surveys over 600–1500 m and between 1992–94 and 2010 showed a significant increase in biomass of *E. lucifer*, no change in *D. calcea*, and a significant decrease in *C. crepidater* [65]. *Etmopterus lucifer* may be the species most likely to benefit from reduced competition with hoki, because its small size means it could most readily escape trawl nets, and so suffer relatively low fishing mortality.

In principle, the greater the association a shark has with the sea bed the more vulnerable it may be to bottom trawling. The species foraging primarily on mesopelagic prey must spend part of their time in mid-water, where they are not vulnerable to bottom trawls. Demersal foraging shark species in greatest abundance on the west and northwest Chatham Rise, where bottom trawl effort is focused [66], may therefore be at greatest risk from fishing mortality. Assuming that there is not movement of sharks outside of Chatham Rise, the shark most at risk would probably be *P. plunketi*, followed by *O. bruniensis*, *D. licha*, and then to a lesser extent *E. baxteri*, *C. owstoni*, and *S. acanthias*. Although predominantly a demersal species, the north-eastern distribution of *C. squamosus* would make it lower risk. However, none of these species have shown a strong biomass trend in research trawl surveys between 1992 and 2010 [9]. *Proscymnodon plunketi* biomass apparently declined on the northeast Chatham Rise between 1984 and 1994 [57], and in the same surveys, *E. baxteri* biomass also decreased (to 26% in 1994), but *C. owstoni*, *C. crepidater*, and *D. calcea* biomass increased.

Demersal foraging sharks would probably have greatest competition for resources with large and relatively abundant piscivorous bony fishes such as hake *Merluccius australis* and ling *Genypterus blacodes* [67]. Both hake and ling are targeted by commercial fisheries on Chatham Rise [4]. The ling has been found to consume substantial amounts of scavenged offal, most likely discards from fishing vessels [67], and it seems likely that benthic skates [60] and demersal sharks do the same [11]. The increase in the availability of scavenged prey may provide a positive feedback to shark productivity, which may compensate, to some extent, for the increase in fishing mortality. Sharks may also benefit from predating behaviourally impaired fish, of many species, that have escaped trawl nets [64]. Changes to fishing regulations and fishing practices, in order to reduce by-catch and discards, could therefore have a negative effect on the food supply, and therefore productivity, of demersal foraging sharks.

Supporting Information

Table S1 Stomach contents composition for *Deania calcea* from the Chatham Rise 2005, 2006 and 2007 combined.
(DOCX)

Table S2 Stomach contents composition for *Squalus acanthias* from the Chatham Rise 2005, 2006 and 2007 combined.
(DOCX)

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Author Contributions

Conceived and designed the experiments: MD. Performed the experiments: JF DS AC. Analyzed the data: MD. Contributed reagents/materials/analysis tools: MD DS JF AC. Wrote the paper: MD DS.

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