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# A quantitative comparison of the diets of sympatric pelagic sharks in gulf and shelf ecosystems off southern Australia

Paul J. Rogers[1,2]*, Charlie Huveneers[1,2], Brad Page[1], Derek J. Hamer[1,3], Simon D. Goldsworthy[1], James G. Mitchell[2], and Laurent Seuront[2,4]

[1]*SARDI Aquatic Sciences, Henley Beach, South Australia, Australia 5022*
[2]*School of Biological Sciences, Flinders University, GPO Box 2100, South Australia, Australia*
[3]*Australian Marine Mammal Centre, Australian Antarctic Division, 203 Channel Highway, Kingston, Tasmania, Australia, 7050*
[4]*Centre National de la Recherche Scientifique, France*

**Corresponding Author: tel: +61 (0)8 8207 5487; fax: +61 (0)8 8207 5406; e-mail: paul.rogers@sa.gov.au*

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Predator–prey dynamics represent an important determinant in the functioning of marine ecosystems. This study provides the first quantitative investigation of the diets of sympatric pelagic shark species in gulf and shelf waters off southern Australia. Stomachs of 417 sharks collected from fishery catches between 2007 and 2011 were examined, including 250 bronze whalers, 52 shortfin makos, 49 dusky sharks, 39 smooth hammerheads, and 27 common threshers. Dusky sharks had the highest dietary diversity of the five species examined. We found overlap in the consumption of cephalopods, small pelagic teleosts, crustaceans, and benthic teleosts in bronze whalers, dusky sharks, and smooth hammerheads, and preliminary evidence of specialization in the highly migratory species, the common thresher and the shortfin mako. Findings were discussed and compared with previous studies in other temperate marine ecosystems. This study will significantly improve the understanding of the ecological roles of these top predators in the gulf and shelf habitats off southern Australia, and enhance the ecosystem models being developed for this unique bioregion.

**Keywords:** Ecosystems, foraging, partitioning, specialization.

## Introduction

High-trophic-level predators play key roles in marine ecosystems (Baum *et al.*, 2003), and removal by fisheries can lead to trophic cascades (Myers *et al.*, 2007). Long-term impacts of removing high-trophic-level predators can be predicted using mass–balance ecosystem models that integrate matrices of dietary, fishery, and distributional information for different trophic levels (Jennings and Kaiser, 1998; Kitchell *et al.*, 2002). Stevens *et al.* (2000) used an ecosystem model to show that removal of sharks can lead to differential responses in biomass of prey or exertion of 'top–down' control over some trophic groups. Predation risk also plays an important role in ecosystem function, as predator avoidance comes with an associated cost in terms of lost foraging time (Ripple and Beschta, 2004; Heithaus *et al.*, 2008).

Recent studies of the diets of sharks in other ecosystems have included (i) morphological analyses of prey items in stomachs (Wood *et al.*, 2009); (ii) estimation of trophic levels using stable isotopes (Domi *et al.*, 2005; MacNeil *et al.*, 2005; Logan and Lutcavage, 2010); (iii) evacuation of the stomachs of live animals (Webber and Cech, 1998); and (iv) DNA analysis of prey remains (Barnett *et al.*, 2010). Each method has proven successful for resolving dietary patterns, and recent studies have applied combinations of these approaches, e.g. Barnett *et al.* (2010). Previous diet studies based on analysis of hard and soft remains have shown that shortfin makos (*Isurus oxyrinchus*) consume teleosts, pelagic cephalopods, other elasmobranchs, and marine mammals (Stevens, 1984; Cliff *et al.*, 1990; MacNeil *et al.*, 2005; Maia *et al.*, 2006; Wood *et al.*, 2009; Preti *et al.*, 2012). The diets of dusky sharks have been studied in several regions, including off south-western Western Australia, and include small pelagic teleosts, cephalopods, and elasmobranchs (Smale, 1991; Gelsleichter *et al.*, 1999; Simpfendorfer *et al.*, 1999). Common thresher sharks (*Alopias vulpinus*) predominantly feed on small pelagic teleosts and cephalopods in the Southern Californian Bight (Preti *et al.*, 2012). The diet of the bronze whaler (*Carcharhinus brachyurus*) has only been described for populations off southern Africa and Argentina, where small pelagic teleosts and cephalopods were important (Smale, 1991; Smale and Cliff, 1998; Lucifora *et al.*, 2009). Similarly, studies of the diet of the smooth hammerhead (*Sphyrna zygaena*) have been limited to a single multi-species study (Smale and Cliff 1998).

One gap in the datasets required to develop ecosystem models for the continental shelf waters and adjacent gulf systems off southern Australia is the paucity of dietary information for pelagic sharks. The pelagic shark assemblage in this region is made up of eight key species: the white shark (*Carcharodon carcharias*), shortfin mako, porbeagle (*Lamna nasus*), blue shark (*Prionace glauca*), bronze whaler, dusky shark, common thresher, and the smooth hammerhead. Spatial distributions of these species range from the gulfs and shelves, e.g. the bronze whaler, dusky shark, and smooth hammerhead, to shelves and oceanic, such as the porbeagle, shortfin mako, and blue shark, and finally gulfs to oceanic, such as the white shark and common thresher (Last and Stevens, 2009; Stevens, 2010).

This study represents the first investigation of the dietary patterns of five species of pelagic sharks in the gulf and adjacent shelf ecosystems off southern Australian waters, including the bronze whaler, dusky shark, smooth hammerhead, shortfin mako, and common thresher. The main aim of this study was to examine, quantify, and compare the diets of these pelagic sharks in shelf waters of the Great Australian Bight (GAB), the adjacent Bonney Upwelling Region (BUR) off Port MacDonnell, and two adjacent gulfs, including Spencer Gulf and Gulf St Vincent (Figure 1). We also aimed to provide the necessary data to enhance the ecosystem models being developed for this region and facilitate comparisons with other boundary current systems, such as those off southern Africa, the Southern Californian Bight, and South America.

## Material and methods

### Study area and sample collection

Stomachs were collected from sharks taken by commercial fishers in shelf waters of the GAB, Spencer Gulf, and Gulf St Vincent (Figure 1), and in shelf waters in the BUR off southeastern South Australia (SE SA) during game fishing competitions between January 2007 and May 2010 (Figure 1). Gear types used in the commercial fisheries sampled included surface and bottom-set longlines, handlines, and large mesh monofilament gillnets (6–6.5 inch mesh).

The Commonwealth-managed Gillnet Hook and Trap (GHAT) Fishery operates along a large part of the southern coastline (although it excludes the two gulfs) and targets gummy shark (*Mustelus antarcticus*) (Figure 1). Gillnets were ~4200 m long with a 3 m drop. The headline consisted of floating rope, and the footline consisted of sinking rope of a smaller diameter than the headline. Longlines consisted of floating rope mainlines (~7 mm diameter) with 1.7 mm stainless steel leaders with up to 400 hooks attached to the mainline at regular intervals by way of a stainless steel clip. Mainlines were up to 14 km long, and terminal ends were anchored and marked with large buoys. Small buoys were used between the hooks to suspend the mainline

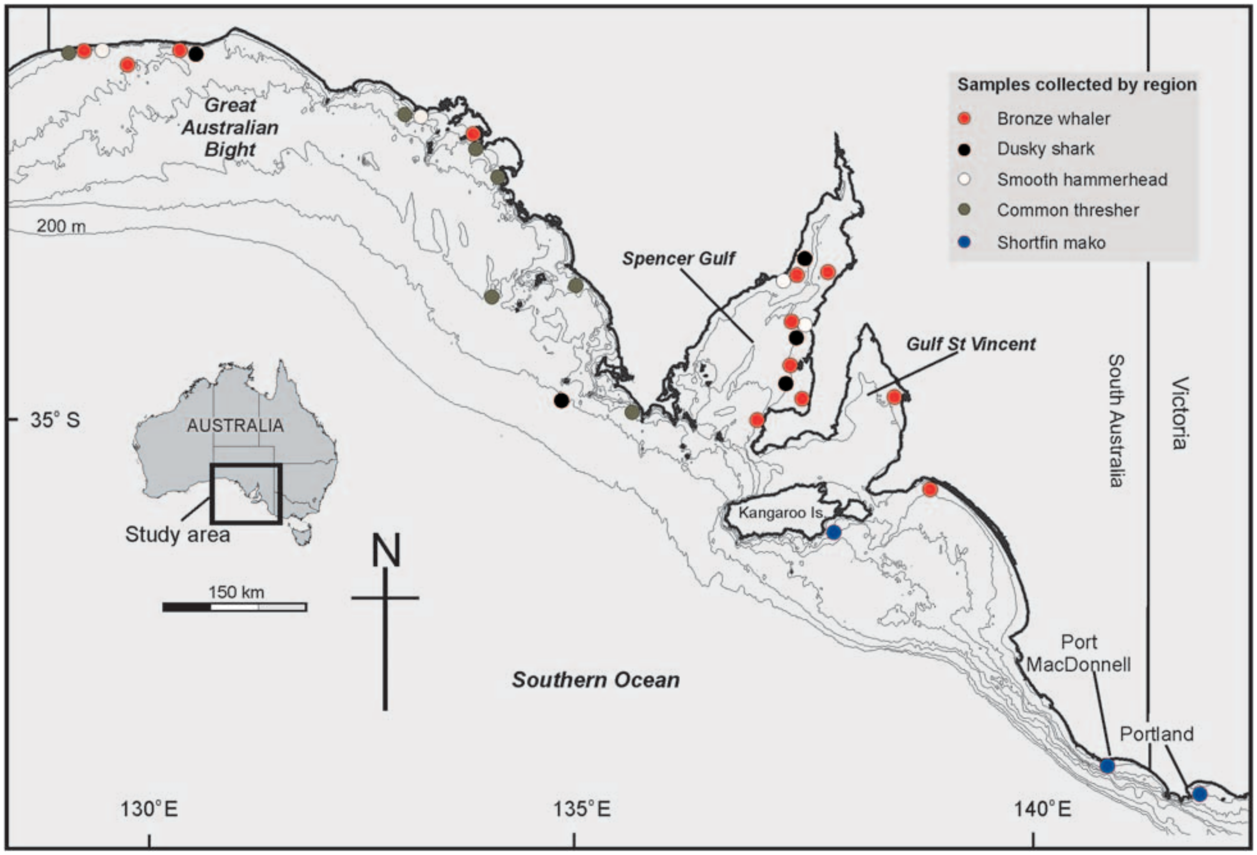

**Figure 1.** Regions where samples were collected in gulf and shelf waters of South Australia and Victoria between 2007 and 2010.

near the surface. Game fishers suspended bait under balloons from boats and metropolitan jetties in Gulf St Vincent, using recreational fishing gear (30–80 lb line) and leaders of 1.5–1.7 mm nylon-coated wire attached to size 12/0–14/0 hooks. The species, sex, and lengths [natural total lengths (TL) in some cases, and fork length (FL) in others; ±1 cm] were recorded (Francis, 2006). Shark foreguts from anterior of the oesophagus to the pyloric sphincter were removed, placed in labelled bags, then frozen or kept on ice for analysis in the laboratory.

## Laboratory analyses

Stomachs were thawed and the contents were removed, washed with water using 1 mm and 0.5 mm sieves, and weighed. Identification of prey items was based on intact and remaining hard items including cephalopod beaks, sagittal otoliths, and exoskeletal remains. Recognizable prey items were identified to the lowest possible taxonomic level.

Cephalopod beaks were identified using a reference collection, images of beaks of known identification, and a published guide (Lu and Ickeringill, 2003). Stomach contents identified as fishing bait after communication with the fishers were excluded from the analyses. The number of empty stomachs together with those containing only bait were recorded and expressed as a percentage of the total number examined, and discarded. The wet mass of each item was weighed to ±0.01 g.

Prey found in stomachs were: (i) identified to the lowest taxonomic level; and (ii) separated into taxonomic categories that we refer to as trophic groups (Goldsworthy *et al.*, 2011). These included Chordata (Ascidians), Asteroidea (sea stars), crustaceans (crabs and prawns), small pelagic teleosts, benthic cephalopods (squid, cuttlefish, and octopus spp.), pelagic cephalopods (Ommastrephidae), unidentified cephalopods, unidentified teleosts, benthic teleosts, large pelagic teleosts, elasmobranchs (small demersal sharks, skates, and rays), Aves (birds), and marine mammals (cetaceans and pinnipeds).

## Quantitative assessment of adequacy of sample sizes

Cumulative prey curves were fitted to the number of stomachs sampled and the number of prey taxa and trophic groups identified to assess if the numbers of samples analysed for each shark species were statistically adequate to describe the diet and to include in intraspecies multivariate comparisons. To eliminate potential biases, the number of new prey items in each stomach was determined after the order of the stomachs had been randomized ten times (Ferry and Cailliet, 1996; Bizzarro *et al.*, 2007). The mean number of prey species (lowest taxon) or trophic group in each stomach was plotted against the number of stomachs analysed. The incidence of an asymptotic relationship between (i) the mean number of prey taxa identified (to the lowest possible taxon) and (ii) the broader trophic group level (as used in Ecopath), and the number of stomachs analysed signifies that sufficient samples had been collected and analysed. The premise is that collection of additional samples would not provide any further benefit in terms of describing the diet of each shark species (Preti *et al.*, 2001). Asymptotes of cumulative prey curves were estimated by fitting the general Gompertz model to describe the relationship between the number of prey taxa identified and the number of stomach samples collected. This model is represented by the equation:

$$N_t = ae^{-\varepsilon b^{-cx}}$$

where $N_s$ represents the number of taxa analysed at sample size, $s$, $a$ is the asymptote of the model fit (theoretical number of samples required), $b$ and $c$ are constants, and $x$ represents the number of samples analysed. The model was solved for $x$ to estimate the number of samples required to reach the asymptotic number ($Na$) of: (i) prey taxa and (ii) prey trophic groups. Fitting of the curves was achieved using the Levenberg–Marquardt non-linear curve-fitting routine in Curve Expert Professional (Ver. 1.2.3, Microsoft).

Data describing the diets of each shark species were pooled across years and regions to calculate the standard relative metrics of prey quantity and importance including:

(i) percentage numerical importance (%$N$) = number of one prey divided by the total number of all prey × 100;

(ii) percentage frequency of occurrence (%$F$) = number of stomachs containing prey of one taxon/total number of stomachs that contained prey × 100;

(iii) percentage by weight (%$W$) = weight of one prey/total weight of all prey × 100 (Preti *et al.*, 2001).

Percentage numerical importance provides insights about feeding behaviour and preference of prey, percentage frequency of occurrence shows how consistently the predatory species selects a given prey species, and percentage by weight may reflect the relative metabolic value of a prey type (Tirasin and Jørgensen, 1999). To allow intraspecific comparisons, and to compare the findings with previous studies, two dietary indices were calculated, the index of relative importance (IRI) (Cortés, 1997) and the geometric index of importance (GII) (Assis, 1996). These are expressed as:

$$\begin{aligned} \mathrm{IRI} &= (\%N + \%W) \times \%F \\ \mathrm{GII} &= (\%N + \%W + \%F)/\sqrt{3} \end{aligned}$$

IRI values were subsequently converted to percentages to allow comparisons with previously published studies (Cortés, 1997; Preti *et al.*, 2012).

## Comparison of diets between shark species

To quantify and compare prey consumption among the four shark species highlighted as having adequate sample sizes at the trophic group level, and to test for evidence of assemblage structure, we used analysis of similarities (ANOSIM), and similarity percentages (SIMPER) in PRIMER (Ver. 6, PRIMER-E Ltd., Plymouth, UK). We generated a Euclidean distance-based resemblance matrix using fourth-root-transformed prey abundance data. Each prey group represented the variables and each shark specimen represented a single sample. The factor 'shark species' was included in the analysis. Other factors, such as size, sex, season, and region, were not investigated due to inadequate sample sizes, and/or sampling coverage (e.g. by region/season).

Statistical differences in the prey consumed by each shark species were assessed using ANOSIM, which is analogous to the niche overlap index developed by Schoener (1968). Pairwise $R$-values were used to describe the extent of similarities (Hyndes *et al.*, 1997), where values near 1 indicated separation in dietary niches, while values closer to 0 indicated similarity. Dietary overlap between shark species was calculated using Horn's (1966) index ($R_0$). Values of 0–0.29, 0.3–0.59, or >0.6 indicated low, medium, or high overlap, respectively (Langton, 1982). Diet diversity or breadth was calculated using the combined index

(CI) (Cortés *et al.*, 1996), calculated by taking the average of the Levin's index (B) and the Shannon–Weiner index ($H_0$) standardized to a scale of 0–1 (Krebs, 1999).

SIMPER was used to assess the relative contributions of the prey trophic groups to the overall differences in consumption by portion of the assemblage represented by the four shark species examined. Indicator species analysis (ISA) (Dufrêne and Legendre, 1997) in PC ORD (Ver. 5) was used to determine the prey trophic groups that best characterized the observed differences in diets of the five shark species. Monte Carlo tests were used with 4999 permutations of observed maximum indicator values (IVs) for each prey group. The IVs ranged from 0, where in the case of this study it provided no indication of the level of representation of a particular prey species to a particular predatory group, to 100, where it indicated perfect indication of representation of a prey species to a particular group (McCune and Mefford, 1999).

## Results

In total, 417 stomachs were collected from dead sharks of five species captured by commercial and game fisheries in the GAB, Spencer Gulf, Gulf St Vincent, and the BUR in the SE SA between 2007 and 2010 (Figure 1). The sharks comprised 250 bronze whalers (71–305 cm, TL), 52 shortfin makos (94–267 cm, TL), 49 dusky sharks (96–256 cm, TL), 39 smooth hammerheads (98–174 cm, TL), and 27 common threshers (145–296 cm, TL). Shortfin makos were caught on rod and reel during game fishing competitions, and common threshers were sampled from commercial demersal gillnets. Totals of 82 and 18% of dusky sharks, 86 and 14% of bronze whalers, and 51 and 49% of smooth hammerheads were taken on longlines and demersal gillnets, respectively.

Of the 417 stomachs examined, 318 (76%) contained prey that could be identified and classified into one of 13 broad trophic groups. Stomachs of shortfin mako were collected from specimens weighed in during game fishing competitions at Port MacDonnell, South Australia and Portland, Victoria (BUR; Figure 1) between 2008 and 2010. Those from common threshers were collected during commercial gillnetting sets in the eastern and central GAB in 2007 and 2009 (Figure 1), and stomachs from bronze whalers, dusky sharks, and smooth hammerheads were collected during commercial gillnet sets in the GAB during 2007, and from longline sets in Spencer Gulf and Gulf St Vincent between 2008 and 2010. The majority of sharks sampled were juveniles or subadults, with the exception of two pregnant bronze whalers, and three male shortfin makos. Loose otoliths found in stomachs ($n = 23$, all shark species) were highly eroded and most were difficult to identify when not associated with other recognizable hard parts (e.g. teleost jaw bones and spines).

### Cumulative prey curves: sample size by shark species

Cumulative prey curves did not reach asymptotes for any of the five species when prey were examined at the lowest taxonomic level (Figure 2). Gompertz model fits to the number of stomachs collected with prey, the number of prey taxa, and trophic groups represented showed that asymptotes were reached for bronze whalers and shortfin makos when prey taxa were combined and examined at the trophic group level (Table 1). We considered that the data were: (i) adequate to investigate and qualitatively compare the diets of the five species; (ii) sufficient to provide a preliminary quantitative comparison of the diets of bronze whalers, dusky sharks, smooth hammerheads, and shortfin makos; (iii) not adequate for describing rarer prey, those for which consumption may be seasonally and or spatially separated, those restricted to life history stages not sampled (i.e. neonates and adult sharks), or otherwise limited in availability; and (iv) not adequate to draw conclusions about common threshers ($n < 20$) from multivariate analyses.

### Prey consumption by shark species

#### *Bronze whaler*

Of the 250 stomachs of bronze whalers examined, 162 (65%) contained prey made up of 39 taxonomic groups and nine trophic groups (not including the unidentified categories). Table 2 shows the prey compositions and dietary indices for bronze whaler in the GAB, and the two adjacent gulf systems between 2007 and 2010. The small pelagic teleost, benthic teleost, and benthic cephalopod trophic groups were the most important, respectively (Table 2). Sardine *Sardinops sagax* and southern calamary *Sepioteuthis australis* were the dominant prey in terms of IRI and GII. Many of the teleosts could not be identified. Consumption of four Platycephalidae (*Leviprora* sp. and *Platycephalus* spp.) that inhabit shallow seagrass and sand habitats in gulf waters represented a notable dietary difference of the bronze whaler, when compared with dusky shark and smooth hammerhead.

Notably, the two large (3 m TL) pregnant specimens contained remains of other elasmobranchs, suggesting that a prey shift may occur in larger individuals and/or during gestation. Prey that were not necessarily abundant in the diet, but are characteristic of inshore soft sediment, seagrass, and reef habitats, included the western king prawn *Melicertus latisulcatus*, red swimmer crab *Nectocarcinus integrifrons*, western striped trumpeter *Pelates octolineatus*, and rock ling *Genypterus tigerinus*.

#### *Dusky shark*

Of the 49 stomachs of dusky sharks examined, 32 (65%) contained prey made up of 22 taxonomic groups and ten trophic levels (not the unidentified categories). This included the broadest range of prey of the five shark species ranging from Ascidians to marine mammals. Table 3 shows the prey compositions and dietary indices in the GAB and the two adjacent gulf systems between 2007 and 2010. Unidentified teleosts and unidentified cephalopods were prominent in the stomachs of dusky sharks. Benthic cephalopods, unidentified cephalopods, unidentified teleosts, large pelagic teleosts, and elasmobranchs were the most important trophic groups (prey) in terms of the prey indices, IRI and GII. At the species level, the barracouta *Thyrsites atun*, snapper *Chrysophrys auratus*, and southern calamary were prominent. Notably the juveniles sampled also showed evidence of consuming other elamobranchs, a bird, and a marine mammal.

#### *Shortfin mako*

Of the 52 stomachs examined, 45 (87%) contained prey made up of seven taxa (not including the unidentified categories) and six trophic groups. Table 4 shows the prey compositions and dietary indices of predominantly juvenile and subadult sharks sampled at game fishing competitions at Port MacDonnell, in the SA SE (BUR), and at Portland, Victoria, between 2008 and 2010. The large pelagic teleost and pelagic cephalopod trophic groups were dominant in stomachs in terms of IRI and GII. Scombrids, *T. atun*, and a male short-beaked common dolphin *Delphinus delphis* all showed evidence of removal of the caudal fin at the

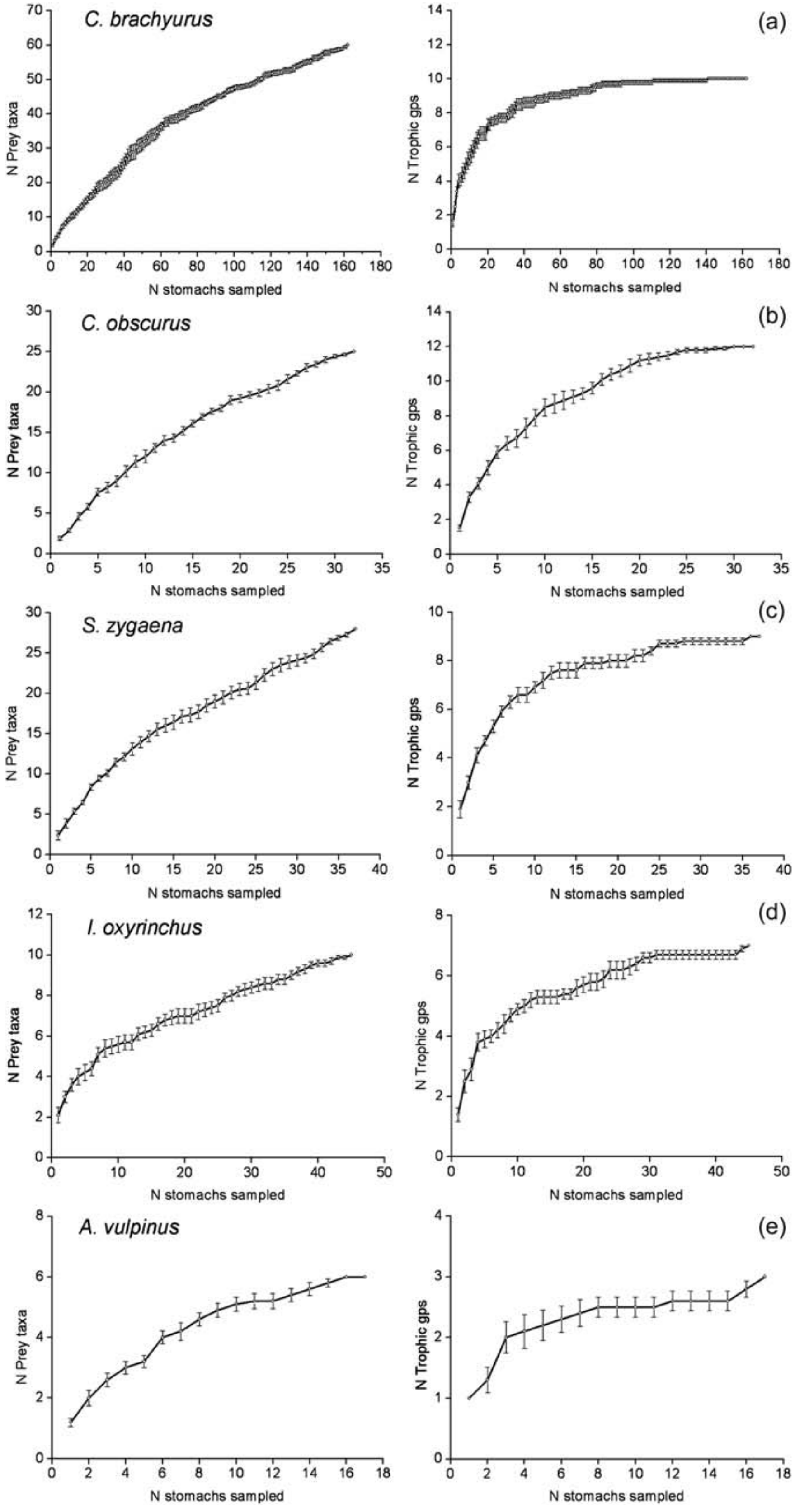

**Figure 2.** Randomized cumulative prey curves showing the relationship between the number of stomachs with prey examined and the number of prey taxa identified to the lowest possible level (left) and by trophic groups (right). (a) Bronze whaler, (b) dusky shark, (c) smooth hammerhead, (d) shortfin mako, and (e) common thresher. Error bars represent standard error of the means.

**Table 1.** Summary of results of Gompertz model fits to numbers of stomachs collected with prey, the number of prey taxa identified, and trophic groups represented in diets of five species of pelagic sharks in southern Australian gulf and shelf waters.

| Shark species | Prey identification level | *a* | *b* | *c* | s.e. | *s* | *Na* | *r* |
|---|---|---|---|---|---|---|---|---|
| Bronze whaler | Lowest taxonomic | 59.86 | 0.80 | 0.02 | 1.32 | 162 | 330 | 0.99 |
| | Trophic group | 9.81 | 0.09 | 0.05 | 0.28 | | 138 | 0.99 |
| Dusky shark | Lowest taxonomic | 26.57 | 0.81 | 0.10 | 0.63 | 32 | 119 | 0.99 |
| | Trophic group | 12.13 | 0.55 | 0.15 | 0.33 | | 43 | 0.94 |
| Smooth hammmerhead | Lowest taxonomic | 29.8 | 0.67 | 0.08 | 0.92 | 37 | 127 | 0.99 |
| | Trophic group | 8.66 | 0.35 | 0.19 | 0.29 | | 50 | 0.99 |
| Shortfin mako | Lowest taxonomic | 10.85 | 0.23 | 0.05 | 0.30 | 45 | 185 | 0.99 |
| | Trophic group | 6.80 | 0.12 | 0.11 | 0.27 | | 43 | 0.98 |
| Common thresher | Lowest taxonomic | 6.12 | 1.08 | 0.14 | 0.15 | 17 | 33 | 0.97 |
| | Trophic group | 2.66 | 0.34 | 0.41 | 0.14 | | 17 | 0.99 |

Parameters of the Gompertz model: *a*, asymptote of model fit; *b* and *c*, constants; *s*, number of stomachs analysed with prey; *Na*, number of stomach samples with prey required to reach the asymptote; s.e. standard error of model fit; *r*, correlation coefficient for each fit.

**Table 2.** Prey compositions and dietary indices for bronze whalers ($n = 250$) in the Southern Ocean and two adjacent gulf systems

| Trophic group | Trophic group no. | Prey taxa | *F* | *N* | %*N* | *W* | %*W* | %*F* | IRI | %IRI | GII |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Crustacean | 3 | Brachyura | 1 | 1 | 0.20 | 3 | 0.02 | 0.62 | 0.14 | 0.004 | 0.58 |
| Crustacean | 3 | Decapoda | 1 | 1 | 0.20 | 3 | 0.02 | 0.62 | 0.13 | 0.004 | 0.57 |
| Crustacean | 3 | *Nectocarcinus integrifrons* | 2 | 2 | 0.40 | 22 | 0.15 | 1.23 | 0.67 | 0.021 | 1.26 |
| Crustacean | 3 | *Melicertus latisulcatus* | 2 | 2 | 0.40 | 2 | 0.01 | 1.23 | 0.51 | 0.016 | 1.12 |
| Crustacean | 3 | Isopoda | 2 | 11 | 2.19 | | 0.00 | 1.23 | 2.70 | 0.084 | 2.90 |
| **Small pelagic teleost** | **4** | ***Sardinops sagax*** | **26** | **242** | **48.11** | **3048** | **20.57** | **16.05** | **1102.30** | **34.138** | **77.95** |
| Unid. small pelagic teleost | 4 | Unidentified | 1 | 1 | 0.20 | | 0.00 | 0.62 | 0.12 | 0.004 | 0.56 |
| Small pelagic teleost | 4 | *Engraulis australis* | 1 | 2 | 0.40 | 25 | 0.17 | 0.62 | 0.35 | 0.011 | 0.92 |
| Small pelagic teleost | 4 | *Scomber australasicus* | 3 | 3 | 0.60 | 53 | 0.36 | 1.85 | 1.77 | 0.055 | 2.02 |
| Small pelagic teleost | 4 | *Trachurus* spp. | 5 | 5 | 0.99 | 462 | 3.12 | 3.09 | 12.68 | 0.393 | 5.89 |
| Small pelagic teleost | 4 | *Arripis georgianus* | 2 | 2 | 0.40 | 204 | 1.38 | 1.23 | 2.19 | 0.068 | 2.49 |
| Small pelagic teleost | 4 | *Hyporhamphus menanochir* | 3 | 3 | 0.60 | 107 | 0.72 | 1.85 | 2.44 | 0.076 | 2.39 |
| Small pelagic teleost | 4 | *Hyperlophus vittatus* | 2 | 2 | 0.40 | 15 | 0.10 | 1.23 | 0.61 | 0.019 | 1.21 |
| Benthic cephalopod | 5 | Octopoda | 9 | 9 | 1.79 | 605 | 4.08 | 5.56 | 32.63 | 1.011 | 9.08 |
| **Benthic cephalopod** | **5** | ***Sepia* sp.** | **24** | **30** | **5.96** | **1092** | **7.37** | **14.81** | **197.57** | **6.119** | **21.89** |
| **Benthic cephalopod** | **5** | ***Sepioteuthis australis*** | **25** | **39** | **7.75** | **1430** | **9.65** | **15.43** | **268.56** | **8.317** | **26.31** |
| Pelagic cephalopod | 6 | Ommastrephid spp. | 7 | 8 | 1.59 | 52 | 0.35 | 4.32 | 8.39 | 0.260 | 4.44 |
| Unid. cephalopod | 7 | Unidentified | 7 | 8 | 1.59 | 597 | 4.03 | 4.32 | 24.29 | 0.752 | 8.12 |
| **Unid. teleost** | **8** | Unidentified | **76** | **78** | **15.51** | **2270** | **15.32** | **46.91** | **1446.22** | **44.789** | **57.91** |
| Benthic teleost | 9 | Monocanthidae | 3 | 3 | 0.60 | 185 | 1.25 | 1.85 | 3.42 | 0.106 | 2.91 |
| Benthic teleost | 9 | *Thamnoconus degeni* | 1 | 1 | 0.20 | 4 | 0.03 | 0.62 | 0.14 | 0.004 | 0.58 |
| Benthic teleost | 9 | *Pelates octolineatus* | 2 | 2 | 0.40 | 35 | 0.23 | 1.23 | 0.78 | 0.024 | 1.34 |
| Benthic teleost | 9 | *Notolabrus* spp. | 1 | 1 | 0.20 | 105 | 0.71 | 0.62 | 0.56 | 0.017 | 1.26 |
| Benthic teleost | 9 | *Merlangius* sp. | 1 | 1 | 0.20 | 3 | 0.02 | 0.62 | 0.14 | 0.004 | 0.58 |
| Benthic teleost | 9 | Labridae | 1 | 1 | 0.20 | 25 | 0.17 | 0.62 | 0.23 | 0.007 | 0.72 |
| Benthic teleost | 9 | *Chrysophrys auratus* | 2 | 2 | 0.40 | 326 | 2.20 | 1.23 | 3.21 | 0.099 | 3.31 |
| Benthic teleost | 9 | *Platycephalus* spp. | 12 | 12 | 2.39 | 1188 | 8.02 | 7.41 | 77.07 | 2.387 | 14.68 |
| Benthic teleost | 9 | *Platycephalus longispinus* | 1 | 1 | 0.20 | 75 | 0.51 | 0.62 | 0.44 | 0.014 | 1.06 |
| Benthic teleost | 9 | *Leviprora inops* | 2 | 2 | 0.40 | 629 | 4.24 | 1.23 | 5.73 | 0.177 | 5.35 |
| Benthic teleost | 9 | *Platycephalus bassensis* | 1 | 1 | 0.20 | 263 | 1.78 | 0.62 | 1.22 | 0.038 | 2.33 |
| Benthic teleost | 9 | *Scorpaenidae* | 4 | 6 | 1.19 | 139 | 0.94 | 2.47 | 5.27 | 0.163 | 3.56 |
| Benthic teleost | 9 | *Argyrosomus japonicus* | 1 | 1 | 0.20 | 80 | 0.54 | 0.62 | 0.46 | 0.014 | 1.10 |
| Benthic teleost | 9 | *Cnidoglanis macrocephalus* | 2 | 2 | 0.40 | 157 | 1.06 | 1.23 | 1.80 | 0.056 | 2.17 |
| Benthic teleost | 9 | *Sphyraena novaehollandiae* | 1 | 1 | 0.20 | 70 | 0.47 | 0.62 | 0.41 | 0.013 | 1.03 |
| Benthic teleost | 9 | *Sillago* sp. | 1 | 1 | 0.20 | 10 | 0.07 | 0.62 | 0.16 | 0.005 | 0.62 |
| Benthic teleost | 9 | *Aldrichetta forsteri* | 2 | 2 | 0.40 | 83 | 0.56 | 1.23 | 1.18 | 0.037 | 1.67 |
| Benthic teleost | 9 | *Haletta semifaciata* | 1 | 1 | 0.20 | 64 | 0.43 | 0.62 | 0.39 | 0.012 | 0.99 |
| Benthic teleost | 9 | *Genypterus tigerinus* | 3 | 3 | 0.60 | 441 | 2.98 | 1.85 | 6.62 | 0.205 | 4.64 |
| Large pelagic teleost | 10 | *Thyrsites atun* | 2 | 2 | 0.40 | 110 | 0.74 | 1.23 | 1.41 | 0.044 | 1.85 |
| Elasmobranch | 11 | Rajidae | 1 | 1 | 0.20 | 76 | 0.51 | 0.62 | 0.44 | 0.014 | 1.07 |
| Elasmobranch | 11 | Unidentified | 3 | 3 | 0.60 | 507 | 3.42 | 1.85 | 7.44 | 0.230 | 5.09 |
| Elasmobranch | 11 | Urophidae | 4 | 4 | 0.80 | 252 | 1.70 | 2.47 | 6.16 | 0.191 | 3.92 |

Prey taxa with $>5\%$ IRI are in bold.

**Table 3.** Prey compositions and dietary indices for dusky sharks ($n = 49$) in the Great Australian Bight.

| Trophic group | Trophic group no. | Prey taxa | *F* | *N* | %*N* | *W* | %*W* | %*F* | IRI | %IRI | GII |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Chordata | 1 | Ascidian | 1 | 1 | 1.54 | 90 | 1.08 | 3.13 | 8.19 | 0.385 | 4.42 |
| Crustacean | 3 | *Nectocarcinus integrifrons* | 1 | 1 | 1.54 | 11 | 0.13 | 3.13 | 5.22 | 0.245 | 3.47 |
| Crustacean | 3 | *Melicertus latisulcatus* | 1 | 1 | 1.54 | 21.47 | 0.26 | 3.13 | 5.61 | 0.264 | 3.60 |
| Crustacean | 3 | Isopoda | 1 | 4 | 6.15 | 2 | 0.02 | 3.13 | 19.31 | 0.907 | 7.98 |
| Small pelagic teleost | 4 | *Sardinops sagax* | 1 | 3 | 4.62 | 83 | 1.00 | 3.13 | 17.54 | 0.824 | 7.42 |
| Small pelagic teleost | 4 | Scombridae | 1 | 2 | 3.08 | 682 | 8.19 | 3.13 | 35.21 | 1.654 | 13.07 |
| Small pelagic teleost | 4 | *Trachurus* spp. | 1 | 2 | 3.08 | 973 | 11.69 | 3.13 | 46.14 | 2.168 | 16.57 |
| Benthic cephalopod | 5 | *Octopus* sp. | 1 | 1 | 1.54 | 830 | 9.97 | 3.13 | 35.96 | 1.689 | 13.31 |
| **Benthic cephalopod** | **5** | ***Sepia* sp.** | **6** | **8** | **12.31** | **462.7** | **5.56** | **18.75** | **334.97** | **15.736** | **28.69** |
| Benthic cephalopod | 5 | *S. australis* | 3 | 3 | 4.62 | 533.18 | 6.40 | 9.38 | 103.31 | 4.853 | 16.43 |
| Pelagic cephalopod | 6 | Ommastrephidae | 3 | 3 | 4.62 | 551.7 | 6.63 | 9.38 | 105.43 | 4.953 | 16.66 |
| **Unid. cephalopod** | **7** | Unidentified | **7** | **9** | **13.85** | **63.88** | **0.77** | **21.88** | **319.67** | **15.018** | **27.24** |
| **Unid. teleost** | **8** | Unidentified | **11** | **12** | **18.46** | **62.2** | **0.75** | **34.38** | **660.30** | **31.020** | **39.06** |
| **Benthic teleost** | **9** | ***Chrysophrys auratus*** | **2** | **2** | **3.08** | **1180** | **14.17** | **6.25** | **107.81** | **5.065** | **20.86** |
| Benthic teleost | 9 | *Sphyraena novaehollandiae* | 1 | 1 | 1.54 | 50 | 0.60 | 3.13 | 6.68 | 0.314 | 3.94 |
| Benthic teleost | 9 | *Silligonodes* spp. | 1 | 1 | 1.54 | 17 | 0.20 | 3.13 | 5.45 | 0.256 | 3.55 |
| Benthic teleost | 9 | *Haletta semifaciata* | 1 | 1 | 1.54 | 5.4 | 0.06 | 3.13 | 5.01 | 0.235 | 3.41 |
| Benthic teleost | 9 | *Kathetostoma* sp. | 1 | 1 | 1.54 | 88.45 | 1.06 | 3.13 | 8.13 | 0.382 | 4.41 |
| Benthic teleost | 9 | *Genypterus tigerinus* | 1 | 1 | 1.54 | 10 | 0.12 | 3.13 | 5.18 | 0.243 | 3.46 |
| **Large pelagic teleost** | **10** | ***Thyrsites atun*** | **2** | **2** | **3.08** | **1572** | **18.88** | **6.25** | **137.24** | **6.447** | **25.57** |
| **Elasmobranch** | **11** | Unidentified | **3** | **3** | **4.62** | **794.75** | **9.55** | **9.38** | **132.76** | **6.237** | **19.57** |
| Elasmobranch | 11 | *Heterodontus portusjacksoni* | 1 | 1 | 1.54 | 87 | 1.04 | 3.13 | 8.07 | 0.379 | 4.39 |
| Bird | 12 | Aves | 1 | 1 | 1.54 | 149 | 1.79 | 3.13 | 10.40 | 0.489 | 5.13 |
| Marine mammal | 13 | Cetacea | 1 | 1 | 1.54 | 6 | 0.07 | 3.13 | 5.03 | 0.236 | 3.41 |

Prey taxa with >5% IRI are in bold.

**Table 4.** Prey compositions and dietary indices for shortfin mako ($n = 52$) in South-eastern South Australia.

| Trophic group | Trophic group no. | Prey taxa | *F* | *N* | *W* | %*N* | %*W* | %*F* | IRI | %IRI | GII |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Unid. small pelagic teleost | 4 | Unidentified | 1 | 19 |  | 9.55 | 0.00 | 2.22 | 21.22 | 0.266 | 10.83 |
| Small pelagic teleost | 4 | Trachurus spp. | 1 | 1 | 463.27 | 0.50 | 2.53 | 2.22 | 6.73 | 0.084 | 4.31 |
| **Pelagic cephalopod** | **6** | **Ommastrephidae** | **24** | **73** | **1202.79** | **36.68** | **6.56** | **53.33** | **2306.36** | **28.948** | **74.04** |
| Unid. cephalopod | 7 | Unidentified | 6 | 13 | 461.07 | 6.53 | 2.52 | 13.33 | 120.64 | 1.514 | 16.75 |
| **Unid. teleost** | **8** | Unidentified | **26** | **65** | **453.80** | **32.66** | **2.48** | **57.78** | **2030.23** | **25.482** | **68.50** |
| Benthic teleost | 9 | *Nelusetta ayraud* | 2 | 2 | 18.00 | 1.01 | 0.10 | 4.44 | 4.90 | 0.062 | 3.67 |
| Benthic teleost | 9 | Monocanthidae | 1 | 1 | 88.42 | 0.50 | 0.48 | 2.22 | 2.19 | 0.027 | 2.27 |
| **Large pelagic teleost** | **10** | ***Thyrsites atun*** | **20** | **22** | **12102.74** | **11.06** | **66.02** | **44.44** | **3425.44** | **42.994** | **102.73** |
| Large pelagic teleost | 10 | *Scombridae* | 2 | 2 | 90.57 | 1.01 | 0.49 | 4.44 | 6.66 | 0.084 | 4.07 |
| Mammal | 13 | *Delphinus delphis* | 1 | 1 | 3452.06 | 0.50 | 18.83 | 2.22 | 42.96 | 0.539 | 20.62 |

Prey taxa with >5% IRI are in bold.

peduncle. Unidentified teleosts comprised 33% by %*N*. At the species level, arrow squid *Nototodarus gouldi*, and barracouta were dominant. Consumption of Ommastrephids was often only indicated by the presence of their beaks in stomachs. Pre-dorsal squid sucker scarring on the dermal surfaces around the gill slits and mouth was commonly observed on shortfin makos, supporting the dietary composition data indicating the importance of cephalopods. The locations of the sucker scars suggest that the cephalopods attempt to escape during consumption.

### Smooth hammerhead

A total of 39 stomachs were examined from samples collected from commercial catches in the GAB and Spencer Gulf between 2007 and 2010. In total, 37 (95%) stomachs contained prey items, including 22 taxonomic groups (not including the unidentified categories), and nine trophic groups (not including the unidentified categories) (Table 5). This species preyed on a broad variety of benthic cephalopods. This group was dominant in terms of IRI and GII, the most common being southern calamary. Other important prey included benthic teleosts and crustaceans. Ommastrephid squids and cuttlefish species were important prey. The unidentified teleosts, Australian anchovy *Engraulis australis*, and Monocanthids were also important prey items. Prey that were not necessarily abundant, but are characteristic of the patchy seagrass and reef habitats frequented by this species, included the western king prawn and red swimmer crab, Australian anchovy, and southern sea garfish *Hyporhamphus melanochir*.

### Common thresher (A. vulpinus)

Of 27 stomachs examined, 17 (63%) contained prey from five taxonomic groups (not including unidentified categories) and

**Table 5.** Prey compositions and dietary indices for smooth hammerhead ($n = 39$) in the Great Australian Bight and two adjacent gulf systems.

| Trophic group | Trophic group no. | Prey taxa | *F* | *N* | %*N* | *W* | %*W* | %*F* | IRI | %IRI | GII |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Asteroidea | 2 | Asteroidea | 1 | 1 | 0.68 | 0.20 | 0.00 | 2.70 | 1.84 | 0.03 | 2.24 |
| Crustacean | 3 | Decapoda | 1 | 1 | 0.68 | 64.60 | 1.14 | 2.70 | 4.91 | 0.08 | 3.38 |
| Crustacean | 3 | *Nectocarcinus integrifrons* | 1 | 1 | 0.68 | 5.00 | 0.09 | 2.70 | 2.06 | 0.03 | 2.32 |
| Crustacean | 3 | *Melicertus latisulcatus* | 2 | 2 | 1.35 | 100.15 | 1.77 | 5.41 | 16.86 | 0.27 | 6.24 |
| Crustacean | 3 | Isopoda | 1 | 1 | 0.68 | 70.00 | 1.24 | 2.70 | 5.16 | 0.08 | 3.47 |
| Unid. small pelagic teleost | 4 | Unidentified | 2 | 6 | 4.05 |  | 0.00 | 5.41 | 21.91 | 0.36 | 7.17 |
| Small pelagic teleost | 4 | *E. australis* | 5 | 7 | 4.73 | 27.91 | 0.49 | 13.51 | 70.57 | 1.15 | 13.02 |
| Small pelagic teleost | 4 | *Hyporhamphus menanochir* | 1 | 1 | 0.68 | 18.60 | 0.33 | 2.70 | 2.71 | 0.04 | 2.56 |
| **Benthic cephalopod** | **5** | ***Sepia* spp.** | **10** | **12** | **8.11** | **662.00** | **11.68** | **27.03** | **534.89** | **8.72** | **35.39** |
| Benthic cephalopod | 5 | *Sepia apama* | 2 | 3 | 2.03 |  | 0.00 | 5.41 | 10.96 | 0.18 | 5.15 |
| **Benthic cephalopod** | **5** | ***Sepioteuthis australis*** | **13** | **33** | **22.30** | **1554.58** | **27.43** | **35.14** | **1747.34** | **28.48** | **70.02** |
| **Pelagic cephalopod** | **6** | **Ommastrephidae** | **11** | **25** | **16.89** | **807.34** | **14.25** | **29.73** | **925.77** | **15.09** | **48.30** |
| Unid. cephalopod | 7 | Unidentified | 1 | 1 | 0.68 | 315.96 | 5.58 | 2.70 | 16.90 | 0.28 | 7.81 |
| **Unid. teleost** | **8** | Unidentified | **25** | **37** | **25.00** | **657.53** | **11.60** | **67.57** | **2473.23** | **40.31** | **75.61** |
| Benthic teleost | 9 | *Pemphris multiradiata* | 1 | 1 | 0.68 | 3.30 | 0.06 | 2.70 | 1.98 | 0.03 | 2.29 |
| Benthic teleost | 9 | *Belone* sp. | 1 | 1 | 0.68 | 0.90 | 0.02 | 2.70 | 1.87 | 0.03 | 2.25 |
| Benthic teleost | 9 | *Nelusetta ayraud* | 1 | 1 | 0.68 | 5.00 | 0.09 | 2.70 | 2.06 | 0.03 | 2.32 |
| Benthic teleost | 9 | *Monocanthidae* | 4 | 4 | 2.70 | 58.30 | 1.03 | 10.81 | 40.34 | 0.66 | 9.97 |
| Benthic teleost | 9 | *Pelates octolineatus* | 1 | 1 | 0.68 | 50.00 | 0.88 | 2.70 | 4.21 | 0.07 | 3.12 |
| Benthic teleost | 9 | *Sygnathidae* | 1 | 1 | 0.68 | 7.66 | 0.14 | 2.70 | 2.19 | 0.04 | 2.37 |
| Benthic teleost | 9 | *Chrysophrys auratus* | 1 | 1 | 0.68 | 63.00 | 1.11 | 2.70 | 4.83 | 0.08 | 3.35 |
| Benthic teleost | 9 | *Centroberyx australis* | 1 | 1 | 0.68 | 12.80 | 0.23 | 2.70 | 2.44 | 0.04 | 2.46 |
| Benthic teleost | 9 | *Rexea solandri* | 1 | 1 | 0.68 | 1.20 | 0.02 | 2.70 | 1.88 | 0.03 | 2.26 |
| Benthic teleost | 9 | *Arripis georgianus* | 1 | 1 | 0.68 | 120.00 | 2.12 | 2.70 | 7.55 | 0.12 | 4.35 |
| Large pelagic teleost | 10 | *Thyrsites atun* | 4 | 4 | 2.70 | 1060.44 | 18.71 | 10.81 | 231.54 | 3.77 | 27.66 |

Prey taxa with >5% IRI are in bold.

two trophic groups. Table 6 shows the prey compositions and dietary indices for common threshers sampled in the GAB between 2007 and 2009. Our data provide preliminary evidence of specialization on Australian anchovy and sardine, which represented the dominant prey in terms of IRI and GII. Prey diversity was low in the common thresher compared with the other four pelagic shark species, with prey only representing five taxonomic groups. This low diversity of prey occurred despite the common threshers being collected over an extensive spatial range that included inshore waters of the eastern, central, and western GAB (Figure 1).

## Interspecies comparisons of prey consumption

There was considerable overlap in the diets of bronze whalers, dusky sharks, and smooth hammerheads, yet ANOSIM (sample statistic, Global $R = 0.204$, $p = 0.0001$) showed that there were statistical differences between each of the pairwise comparisons of the shark species, ranging from $p = 0.001$ for the comparison between bronze whalers and dusky sharks to $p = 0.003$ for the comparison of diets of bronze whalers and shortfin makos (Table 7). The Simplified Morisita Index showed that dietary overlap was highest between dusky sharks and the smooth hammerheads ($C_H = 0.87$), and lowest between bronze whalers and shortfin makos ($C_H = 0.21$) (Table 7). Diets of bronze whalers and dusky sharks also exhibited a high degree of overlap.

Indicator species analyses confirmed that demersal (observed IV value = 28.4) and pelagic cephalopods (Ommastephidae) (observed IV value = 27.2) best explained the statistical differences in the foraging ecologies of the shark species compared in our study. In comparison, demersal and small pelagic teleosts had observed IV values of 20.6 and 8.7, respectively. This aligned with results of the SIMPER analysis (Table 8), which showed that the pelagic cephalopod group explained differences in the diets of three shark species pairs: bronze whaler and shortfin mako, dusky shark and shortfin mako, and smooth hammerhead and shortfin mako. Benthic cephalopods were the prey group that explained the similarities observed in the diets of the bronze whaler, dusky shark, and smooth hammerhead.

Estimates of dietary niche breadth (CI 0.04–0.45) showed that dusky sharks had the most diverse diets (CI = 0.45), followed by bronze whalers (CI = 0.40), shortfin makos (CI = 0.37), and smooth hammerheads (CI = 0.32), which were all similar in terms of the diversity of prey consumed. The common thresher had the lowest prey diversity (CI = 0.03).

## Discussion

This study represents the first investigation of the foraging ecology of five pelagic shark species that inhabit the gulfs and shelves off southern Australia. It provides the first insights into the ecological roles of these species, and the interplays between these predators in this unique marine bioregion. There were significant differences between the dietary niches of the highly migratory, and the gulf- and shelf-associated species. Diets of the gulf- and shelf-associated species were characterized by a suite of teleost and cephalopod prey that aggregate over benthic habitats between spring and summer, and these species exhibited a high degree of dietary overlap. These habitats include combinations of seagrass, macroalgae, low-relief rocky reefs, and sandbanks. In contrast, the diets of the two highly migratory species were characterized by a narrower suite of prey and evidence of foraging specialization. Common

**Table 6.** Prey compositions and dietary indices for common thresher ($n = 27$) in the Great Australian Bight.

| Trophic group | Trophic group no | Prey taxa | *F* | *N* | %*N* | *W* | %*W* | %*F* | IRI | %IRI | GII |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Small pelagic teleost** | **4** | ***Sardinops sagax*** | **4** | **37** | **15.95** | **144.18** | **16.30** | **23.53** | **758.69** | **8.50** | **45.83** |
| **Small pelagic teleost** | **4** | ***Engraulis australis*** | **9** | **179** | **77.16** | **636.70** | **71.96** | **52.94** | **7894.49** | **88.45** | **179.68** |
| Small pelagic teleost | 4 | *Trachurus* spp. | 1 | 1 | 0.43 | 1.00 | 0.11 | 5.88 | 3.20 | 0.04 | 3.94 |
| Small pelagic teleost | 4 | *Arripis georgianus* | 1 | 2 | 0.86 | 60.60 | 6.85 | 5.88 | 45.36 | 0.51 | 11.11 |
| Unid. teleost | 8 | Unidentified | 5 | 5 | 2.16 | 42.20 | 4.77 | 29.41 | 203.67 | 2.28 | 23.91 |
| Benthic teleost | 9 | *Centroberyx australis* | 1 | 8 | 3.45 | 0.08 | 0.01 | 5.88 | 20.34 | 0.23 | 6.85 |

**Table 7.** ANOSIM-based comparison of the fourth-root-transformed prey item abundance data for four pelagic shark species.

| Pairwise tests | *p*-value | $C_H$ |
|---|---|---|
| Bronze whaler, dusky shark | 0.001 | 0.77 |
| Bronze whaler, shortfin mako | 0.003 | 0.21 |
| Bronze whaler, smooth hammerhead | 0.001 | 0.65 |
| Dusky shark, shortfin mako | 0.002 | 0.26 |
| Dusky shark, smooth hammerhead | 0.001 | 0.87 |
| Shortfin mako, smooth hammerhead | 0.003 | 0.30 |

The degrees of dietary overlap between the six pairwise comparisons is shown using values of the Simplified Morisita Index ($C_H$).

threshers had narrow niche breadths and focused on small pelagic teleosts, whereas shortfin makos predominantly targeted large pelagic teleosts and cephalopods, but also consumed a conspecific and a short-beaked common dolphin.

Previous dietary studies based on analysis of stomach contents of Carcharhinids have found that a significant proportion of stomachs were empty; 63% (Cliff and Dudley, 1992) and 51% for bronze whalers (copper shark) (Lucifora *et al.*, 2009), and 53% of sandbar shark *C. plumbeus* (McElroy *et al.*, 2006), whereas studies of the diet of shortfin makos showed that fewer were empty; 12% (Maia *et al.*, 2006), 28% (Preti *et al.*, 2012), and 35% (Young *et al.*, 2010). Similarly, this was not a significant issue during our study as between 63% and 95% of the stomachs from the species we examined contained prey. Previous research has shown that capture durations vary considerably when using game fishing tackle to take pelagic sharks (Heberer *et al.*, 2010), and some species, including shortfin mako (Brunnschweiler *et al.*, 2011), blue sharks (Stevens, 1984), bronze whalers (PJR, unpublished data), and Caribbean reef sharks *C. perezi* (Brunnschweiler *et al.*, 2005) regurgitate their stomachs during capture in what is assumed to be an attempt to rid themselves of the hook(s). This identifies a potential bias in diet studies based on line-caught sharks due to the fact that some structurally complex items, including teleost, ray barbs, and cephalopod beaks, may be retained for longer periods than softer, easy-to-digest prey. Therefore, although samples were obtained from catches using three gear types, and regurgitated stomachs were omitted from the analysis, diet data from hook-based captures need to be viewed in the light of this information, especially in terms of the relative weights of prey ingested.

Our cumulative prey curves did not reach asymptotes when prey were examined at the lowest possible taxonomic level identified, but did reach asymptotes for two shark species when prey were combined at the trophic group level. Fitting of the Gompertz model to the number of samples examined and the number of prey taxa/groups identified showed that asymptotes were obtained at the trophic group level for bronze whalers and shortfin makos, and curves were close to reaching an asymptote for dusky sharks and smooth hammerhead. We consider that fitting these models is a suitable alternative method to that of Bizzarro *et al.* (2007), which relies on fitting regression lines to the last four or five points and comparing slopes. While our fits suggest our sample sizes may not have adequately characterized the rarer prey for all five shark species, they were sufficient to compare the consumption of prey at the broader trophic group levels. Despite this, further data are required in the future to improve the spatial resolution of our dietary analysis. Previous diet studies have also shown that asymptotes in cumulative prey curves have not been reached at the lowest possible taxonomic levels (Simpfendorfer, 1999; McElroy *et al.*, 2006; Papastamatiou *et al.*, 2006; Preti *et al.*, 2008). In the cases of studies of highly mobile pelagic teleosts and elasmobranchs that are logistically difficult to study, it is rarely achievable to collect adequate samples to resolve the diet across all space and time-scales. Despite these limitations, the samples we collected were adequate to show the general differences and similarities between the taxa for the most common ontogenetic stages (juveniles) that inhabit this region.

We found some evidence of differences in niche breadths between the pelagic shark species. The gulf- and shelf-associated species, including the dusky shark and the bronze whalers, had broader niche breadths than the highly migratory shortfin mako, which had a lower niche breadth in the BUR, and targeted large prey, including barracouta and arrow squid. Interestingly, we found evidence of large quantities of Australian anchovy in stomachs of some barracouta that were consumed by shortfin makos, which suggests that this endothermic lamnid may be gaining additional energetic benefits from consuming these large piscivorous teleosts. This shelf upwelling system and the associated thermal frontal zones are the location of spatially concentrated pelagic production during late summer and autumn, which attracts a range of residential and migratory marine predators. Despite the availability of a broad spectrum of alternative benthic, epipelagic, and pelagic prey in the BUR, the same narrow range of prey was consistently found in stomachs of shortfin makos over three seasons, suggesting that this species targets particular prey. This finding was consistent with a study of shortfin makos in the eastern North Atlantic Ocean that showed that diets comprised a low diversity of teleost and cephalopod species (Maia *et al.*, 2006). Similarly, shortfin makos were found to exhibit foraging specialization in the Northwest Atlantic Ocean where a large predatory teleost, the bluefish (*Pomatomus saltatrix*) dominated their diets (Wood *et al.*, 2009).

This study represents the first dietary information for the common thresher in Australian waters. Despite concerted efforts to collect samples at game fishing events and on commercial fishing vessels, stomachs were only collected from 27 specimens.

**Table 8.** Results of multivariate similarity percentages analysis of the prey group abundance matrix for bronze whalers, dusky sharks, smooth hammerheads, and shortfin makos.

| Prey group | Bronze whaler–dusky shark | Bronze whaler–shortfin mako | Dusky shark–shortfin mako | Bronze whaler–smooth hammerhead | Dusky shark–smooth hammerhead | Shortfin mako–smooth hammerhead |
|---|---|---|---|---|---|---|
| Demersal cephalopods | 17.87 | 11.4 | 10.34 | 22.66 | 19.64 | 17.92 |
| Demersal teleosts | 14.49 | 10.71 | 9.78 | 15.7 | 13.22 | 10.5 |
| Pelagic cephalopods | 5.99 | 21.79 | 20.85 | 6.66 | 7.7 | 20.48 |
| Small pelagic teleosts | 12.74 | 10.68 | 0 | 16.35 | 10.22 | 9.01 |
| Unidentified cephalopod | 11.46 | 0 | 11.59 | 0 | 9.96 | 0 |
| Unidentified teleosts | 20.51 | 18.95 | 19 | 22.19 | 20.49 | 16.55 |
| Elasmobranch | 7.37 | 0 | 5 | 0 | 0 | 0 |
| Large pelagic teleost | 0 | 16.58 | 16.45 | 5.13 | 7.31 | 16.02 |
| Crustaceans | 0 | 0 | 0 | 6.26 | 6.17 | 0 |

Pairwise comparisons indicate the extent to which each prey group explains the similarities between each shark species pair.

A previous diet study of the big eye thresher (*Alopias superciliosus*) was based on a comparable sample size ($n = 26$) in the Northeast Pacific Ocean (Preti *et al.*, 2008). During our study, common threshers consumed the narrowest range of prey of the five shark taxa we examined, with the Australian anchovy, a species with a small body size (14 cm, TL), representing the most important prey species. A previous study that analysed stomachs of common threshers ($n = 107$) in the Northeast Pacific Ocean found that Northern anchovy (*Engraulis mordax*) sardine and Pacific mackerel (*Scomber japonicus*) were the most important prey, respectively (Preti *et al.*, 2001). A subsequent study with a larger sample size ($n = 225$) also found that Northern anchovy and sardine were the dominant prey (Preti *et al.* 2012). Preti *et al.* (2004) suggested that oceanographic patterns driving cool water regimes off California and Oregon in the Northeast Pacific Ocean led to narrow prey preferences in the common thresher, with *E. mordax* and the market squid (*Loligo opalescens*) being important prey. Morphological and co-evolutionary factors may also be important determinants in prey selection. For example, Aalbers *et al.* (2010) found that the caudal fin of the common thresher was used to strike small pelagic teleosts, representing a specialization on small schooling prey (e.g. Northern anchovy) that may be more difficult to feed on consistently using other predation tactics in all environmental conditions (e.g. moon phases and high turbidities), especially given the small mouth gape and the small teeth of this species. In contrast, large pelagic teleosts and large pelagic cephalopods were dominant in the diets of the shortfin mako, reflecting their high swimming performance, dentition, and ability to immobilize and kill prey with large body sizes. The mode by which Scombrids, barracouta, and a short-beaked common dolphin were incised and consumed suggested that these large, highly mobile prey may be immobilized prior to ingestion by removal of the caudal fin at the peduncle. This unique feeding tactic may facilitate foraging overlaps with other similar sized pelagic sharks without exerting competitive impacts in low productivity oceanic ecosystems, e.g. with blue sharks that feed on a range of teleosts and cephalopods (Stevens *et al.*, 1984; McCord and Campana, 2003), and common threshers that have adaptations and behavioural tactics to feed on small prey (Aalbers *et al.*, 2010).

Shortfin makos often had pre-dorsal squid sucker scarring on their lateral surfaces and around the gill slits, which supported the findings of our dietary analyses of stomach contents, and reflected the ecological importance of pelagic cephalopods in shelf waters. This was consistent with findings in the Southern Californian Bight, where shortfin makos feed on jumbo squid (*Dosidicus gigas*) (Vetter *et al.*, 2008), and where market squid (*Loligo opalescens*) also form an important inshore prey species for a range of predators (Zeidberg *et al.*, 2006). The BUR off SE SA where shortfin mako stomach samples were collected also supports the Southern Squid Fishery that targets arrow squid *N. gouldi* (Arnould *et al.*. 2003). The importance of these squid in the diets of shortfin makos suggests that there may be operational and trophic interactions between this fishery and pelagic sharks in this region.

Smooth hammerheads and shortfin makos were similar in that they both consumed pelagic cephalopods and barracouta; however, the broad range of prey consumed by smooth hammerheads suggested that his species has a benthic foraging strategy suited to gulf and inshore shelf bentho-pelagic habitats. ANOSIM and the Morisita Index values suggested that these species had low levels of dietary overlap, which was partly explained by the diverse bentho-pelagic diet of the smooth hammerhead. Interestingly, benthic crustaceans that burrow and shelter in soft sediment, including the red swimmer crab and western king prawn, featured in the diet of smooth hammerheads, suggesting that this species may search for these prey by swimming close to the benthos. They may also utilize their unique flattened morphology to uncover and consume these cryptic burrowing prey. Unidentified teleosts also dominated the diet composition of smooth hammerheads, so unfortunately some of the dietary composition could not be resolved. Future diet studies could benefit from the incorporation of DNA-based analyses of prey items (Barnett *et al.*, 2010) to gain improved resolution of these unidentified components.

Sardine, southern calamary, and cuttlefish were important prey of the bronze whaler and the dusky shark. However, the main distinction between these sympatric species was that juvenile dusky sharks may occupy a higher trophic niche in shelf and gulf waters, and/or be active scavengers, evidenced by their consumption of elasmobranchs, a bird, and marine mammal tissue. These findings were consistent with patterns observed for dusky shark off southern Africa where they occupy a high trophic level evidenced by their consumption of other elasmobranchs (Smale, 1991; Smale and Cliff, 1998; Dudley *et al.*, 2005). ANOSIM and the Morisita Index values suggested there was a high degree of niche overlap between the two sympatric carcharhinids and the smooth hammerhead, yet less overlap between these predominantly coastal species and the shortfin mako. Niche overlap highlighted by the ANOSIM, the indicator species analyses (based on the identifiable prey), and the Morisita Index was largely explained by sharing of cephalopods, which may reflect the importance of this prey group to ecosystem functioning off southern Australia.

The spatial separation of the sampling should also be considered when comparing the diets of the shortfin mako and the coastal pelagic sharks as there is likely to be considerable variations in the prey fields across regions, seasons, and environments that were not resolved due to the patchy nature and availability of samples. The majority of the sharks examined during this study were immature, which reflected the relative rarity of adult sharks in fishery catches, the small sample sizes of the less common species (e.g. the common thresher and the shortfin mako), and the difficulties involved in investigating the larger, less abundant, and highly cryptic adult life history stages. In future, further sampling will be required to resolve ontogenetic variation in diet, and to account for variability in prey availability over broader space- and time-scales. Spatial segregation of sexes and sizes has been described for shorfin makos (Mucientes *et al.*, 2009), and size-based differences in diets may be important in terms of the roles of these predators in marine ecosystems.

The trophic data collected during this study will be included in ecosystem models for the gulfs and shelves off southern Australia, and outputs will be used to inform management processes in Australian State- and Commonwealth-managed waters. Given the ecological roles of pelagic sharks and the current imperative to understand the impacts of climatic variability on the patterns of distribution, abundance, and habitat use of their prey, the assessment of the foraging dynamics of these top predators should continue to represent a research priority in this unique marine bioregion.

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## References

Aalbers, S. A., Bernal, D., and Sepulveda, C. A. 2010. The functional role of the caudal fin in the feeding ecology of the common thresher shark *Alopias vulpinus*. Journal of Fish Biology, 76: 1863–1868.

Arnould, J. P. Y., Trinder, D. M., and McKinley, C. P. 2003. Interactions between fur seals and a squid jig fishery in southern Australia. Marine and Freshwater Research, 54: 979–984.

Assis, C. A. 1996. A generalized index for stomach analysis of fish. Scientia Marina, 60: 385–389.

Barnett, A., Redd, K. S., Frusher, S. D., Stevens, J. D., and Semmens, J. M. 2010. Non-lethal method to obtain stomach samples from a large marine predator and the use of DNA analysis to improve dietary information. Journal of Experimental Marine Biology and Ecology, 393: 188–192.

Baum, J. K., Myers, R. A., Kehler, D. G., Worm, B., Harley, S. J., and Doherty, P. A. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. Science, 299: 389–392.

Bizzarro, J. J., Robinson, H. J., Rinewalt, C. S., and Ebert, D. A. 2007. Comparative feeding ecology of four sympatric skate species off central California, USA. Environmental Biology of Fishes, 80: 197–220.

Brunnschweiler, J. M., Andrews, P. L. R., Southall, E. J., Pickering, M., and Sims, D. W. 2005. Rapid voluntary stomach eversion in a free-living shark. Journal of the Marine Biological Association of the United Kingdom, 85: 1141–1144.

Brunnschweiler, J. M., Nielsen, F., and Motta, P. 2011. *In situ* observation of stomach eversion in a line-caught shortfin mako (*Isurus oxyrinchus*). Fisheries Research, 109: 212–216.

Cliff, G., and Dudley, S. F. J. 1992. Sharks caught in the protective gill-nets off Natal, South Africa. 6. The copper shark *Carcharhinus brachyurus* (Gunther). South African Journal of Marine Science, 12: 663–674.

Cliff, G., Dudley, S. F. J., and Davis, B. 1990. Sharks caught in the protective nets off Natal, South Africa. 3. The shortfin mako shark *Isurus oxyrinchus* Rafinesque. South African Journal of Marine Science, 9: 115–126.

Cortés, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Canadian Journal of Fisheries and Aquatic Sciences, 54: 726–738.

Cortés, E., Manire, A., and Hueter, R. E. 1996. Diet, feeding habits and diel feeding chronology of the bonnethead shark, Sphyrna tiburo, in Southwest Florida. Bulletin of Marine Science, 58: 353–367.

Domi, N., Bouquegneau, J. M., and Das, K. 2005. Feeding ecology of five commercial shark species of the Celtic Sea through stable isotope and trace metal analysis. Marine Environmental Research, 60: 551–569.

Dudley, S. F. J., Cliff, G., Zungu, M. P., and Smale, M. J. 2005. Sharks caught in the protective gill nets of KwaZulu-Natal, South Africa. 10. The dusky shark *Carcharhinus obscurus* (Lesueur 1818). South African Journal of Marine Sciences, 27: 107–127.

Dufrêne, M., and Legendre, P.. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs, 67: 345–366.

Ferry, L. A., and Cailliet, G. M. 1996. Sample size and data analysis: are we characterizing and comparing diet properly? In Feeding Ecology and Nutrition in Fish. Proceedings of the Symposium on the Feeding Ecology and Nutrition in Fish, International Congress on the Biology of Fishes. American Fisheries Society, San Francisco, pp. 71–80. Ed. by D. MacKinlay, and K. Shearer.

Francis, M. 2006. Morphometric minefields—towards a measurement standard for chondrichthyan fishes. Environmental Biology of Fishes, 77: 407–421.

Gelsleichter, J., Musick, J. A., and Nichols, S. 1999. Food habits of the smooth dogfish, *Mustelus canis*, dusky shark, *Carcharhinus obscurus*, Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, and the sand tiger, *Carcharias taurus*, from the northwest Atlantic Ocean. Environmental Biology of Fishes, 54: 205–217.

Goldsworthy, S. D., Page, P., Rogers, P. J., and Ward, T. M. 2011. Establishing Ecosystem-based management for the South Australian Sardine Fishery: Developing Ecological Performance

Indicators and Reference Points to Assess the Need for Ecological Allocations. Final Report to the Fisheries Research and Development Corporation. SARDI Publication No. F2010/000863-1. 173 pp.

Heberer, C., Aalbers, S. A., Bernalc, D., Kohin, S., DiFioree, B., and Sepulveda, C. A. 2010. Insights into catch-and-release survivorship and stress-induced blood biochemistry of common thresher sharks (*Alopias vulpinus*) captured in the southern California recreational fishery. Fisheries Research, 106: 495–500.

Heithaus, M. R., Frid, A., Wirsing, A. J., and Worm, B. 2008. Predicting ecological consequences of marine top predator declines. Trends in Ecology and Evolution, 23: 202–210.

Horn, H. S. 1966. Measurement of 'overlap' in comparative ecological studies. American Naturalist, 100: 419–424.

Hyndes, G. A., Platell, M. E., and Potter, I. C. 1997. Relationships between diet and body size, mouth morphology, habitat and movements of six sillaginid species in coastal waters: implications for resource partitioning. Marine Biology, 128: 585–598.

Jennings, S., and Kaiser, M. J. 1998. The effects of fishing on marine ecosystems. Advances in Marine Biology, 34: 204–314.

Kitchell, J. F., Essington, T. E., Boggs, C. H., Schindler, D. E., and Walters, C. J.. 2002. The role of sharks and longline fisheries in a pelagic ecosystem of the central Pacific. Ecosystems, 5: 202–216.

Krebs, C. J. 1999. Ecological Methodology. Addison-Welsey Educational Publishers, Menlo Park, CA. 620 pp.

Langton, R. J. 1982. Diet overlap between Atlantic cod, *Gadus morhua*, silver hake, *Merluccius bilinearis* and fifteen other Northwest Atlantic finfish. Fishery Bulletin US, 80: 745–759.

Last, P. R., and Stevens, J. D. 2009. Sharks and Rays of Australia, 2nd edn. CSIRO Publishing, Collingwood, Victoria. 644 pp.

Logan, J. M., and Lutcavage, M. E. 2010. Stable isotope dynamics in elasmobranch fishes. Hydrobiologia, 644: 231–244.

Lu, C. C., and Ickeringill, R. 2003. Cephalopod beak identification and biomass estimation techniques: tools for dietary studies of southern Australian finfishes. Museum Victoria Sciences Reports, 6: 1–65.

Lucifora, L. O., Garcia, V. B., Menni, R. C., Escalante, A H., and Hozbor, N. M. 2009. Effects of body size, age and maturity stage on diet in a large shark: ecological and applied implications. Ecological Research, 24: 109–118.

MacNeil, M. A., Skomal, G. B., and Fisk, A. T. 2005. Stable isotopes from multiple tissues reveal diet switching in sharks. Marine Ecology Progress Series, 302: 199–206.

Maia, A., Queiroz, N., Correia, J. P., and Cabral, H. 2006. Food habits of the shortfin mako, *Isurus oxyrinchus*, off the southwest coast of Portugal. Environmental Biology of Fishes, 77: 157–167.

McCord, M. E., and Campana, S. E. 2003. A quantitative assessment of the diet of the blue shark (*Prionace glauca*) off Nova Scotia. Journal of Northwest Atlantic Fisheries Science, 32: 57–63.

McCune, B, and Mefford, M. J. 1999. PC-ORD. Multivariate Analysis of Ecological Data, Version 4. MjM Software Design, Gleneden Beach, OR.

McElroy, W. D., Wetherbee, B. M., Mostello, C. S., Lowe, C. G., Crow, G. L., and Wass, R. C. 2006. Food habits and ontogenetic changes in the diet of the sandbar shark, *Carcharhinus plumbeus*, in Hawaii. Environmental Biology of Fishes, 76: 81–92.

Muceintes, G. R., Queiroz, N., Sousa, L. L., Tarroso, P., and Sims, D. W. 2009. Sexual segregation of pelagic sharks and the potential threat from fisheries. Biology Letters, 5: 156–159.

Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P., and Peterson, C. H. 2007. Cascading effects of the loss of predatory sharks from a coastal ocean. Science, 315: 1846–1850.

Papastamatiou, Y. P., Wetherbee, B. M., Lowe, C. G., and Crow, G. L. 2006. Distribution and diet of four species of carcharhinid shark in the Hawaiian Islands: evidence for resource partitioning and competitive exclusion. Marine Ecology Progress Series, 320: 239–251.

Preti, A., Kohin, S., Dewar, H., and Ramone, D. A. 2008. Feeding habitats of the big-eye thresher shark (*Alopias superciliosis*) sampled from the California-based drift gillnet fishery. California Cooperative Oceanic Fisheries Investigations. Report No. 49, 202–211.

Preti, A., Smith, S. E., and Ramone, D. A. 2001. Feeding habits of the common thresher shark (*Alopias vulpinus*) sampled from the California-based drift gill-net fishery, 1998–1999. California Cooperative Oceanic Fisheries Investigations. Report No. 42, 145–152.

Preti, A., Smith, S. E., and Ramone, D. A. 2004. Diet difference in the thresher shark (*Alopias vulpinus*) during transition from a warm water regime to a cool water regime off California–Oregon, 1998–2000. California Cooperative Oceanic Fisheries Investigations. Report No. 45, 118–125.

Preti, A., Soykan, C. U., Dewar, H., Wells, R. J. D., Spear, N., and Kohin, S. 2012. Comparative feeding ecology of shortfin mako, blue and thresher sharks in the California Current. Environmental Biology of Fishes, in press.

Ripple, W. J., and Beschta, R. L. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems. BioScience, 54: 755–766.

Schoener, T. 1968. The Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology, 65: 1820–1827.

Simpfendorfer, C. A., Goodreid, A., and McAuley, R. B. 1999. Diet of three commercially important shark species from Western Australian waters. Marine and Freshwater Research, 52: 975–985.

Smale, M. J. 1991. Occurrence and feeding of three shark species, *Charcharhinus brachyurus*, *C. obscurus* and *Sphyrna zygaena*, on the Eastern Cape Coast of South Africa. South African Journal of Marine Science, 11: 31–42.

Smale, M. J., and Cliff, G. 1998. Cephalopods in the diets of four shark species (*Galeocerdo cuvier*, *Sphyrna lewini*, *S. zygaena*, and *S. mokarran*) from KwaZulu Natal, South Africa. South African Journal of Marine Science, 20: 241–253.

Stevens, J. D. 1984. Biological observations on sharks caught by sport fishermen off New South Wales. Australian Journal of Marine and Freshwater Research, 35: 573–590.

Stevens, J. D., Bonfil, R., Dulvy, N. K., and Walker, P. A. 2000. The effects of fishing on sharks, rays, and chimeras (chondrichthyans), and the implications for marine ecosystems. ICES Journal of Marine Science, 57: 476–494.

Tirasin, E.M., and Jørgensen, T. 1999. An evaluation of the precision of diet description. Marine Ecology Progress Series, 182: 243–252.

Vetter, R., Kohin, S., Preti, A., McClatchie, S., and Dewar, H. 2008. Predatory interactions and niche overlap between mako shark, *Isurus oxyrinchus*, and jumbo squid, *Dosidicus gigas*, in the California Current. CalCOFI Report, 49: 142–156.

Webber, J. D., and Cech, J. J., Jr. 1998. Nondestructive diet analysis of the leopard shark from two sites in Tomales Bay, California. California Fish and Game, 84: 18–24.

Wood, A. D., Wetherbee, B. M., Juanes, F., Kohler, N. E., and Wilga, C. 2009. Recalculated diet and daily ration of the shortfin mako (*Isurus oxyrinchus*), with a focus on quantifying predation on bluefish (*Pomatomus saltatrix*) in the northwest Atlantic Ocean. Fishery Bulletin, 107: 76–88.

Young, J. W., Lansdell, M. J., Campbell, R. A., Cooper, S. P., Juanes, F., and Guest, M. A. 2010. Feeding ecology and niches segregation in oceanic top predators. Marine Biology, 157: 2347–2368.

Zeidberg, L. D., Hamner, W. M., Nezlin, N. P., and Henry, A. 2006. The fishery for California market squid (*Loligo opalescens*) (Cephalopoda: Myopsida) from 1981 through 2003. Fishery Bulletin, 104: 46–59.

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