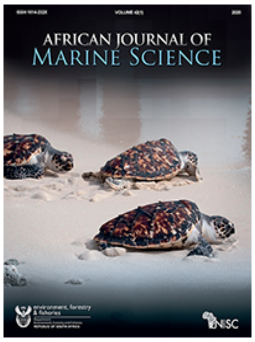


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# Chondrichthyans as an umbrella species-complex for conserving South African biodiversity

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**Conservation surrogates, such as umbrella and flagship species, could help focus South Africa's limited resources for research and management and enhance the conservation gains from marine protected areas (MPAs). Sharks, rays and chimaeras (Chondrichthyes), which are charismatic and ecologically diverse, are potential umbrella candidates, but tests of the ecological suitability of putative marine umbrella species are lacking. Using baited remote underwater video in and around two MPAs in the Western Cape Province, we assessed the potential of chondrichthyans as an umbrella species-complex by quantifying the relationships and co-occurrence patterns between chondrichthyan abundance and diversity and those of other taxa (primarily teleosts and crustaceans). Sites with abundant chondrichthyans, with catsharks or large sharks (>1 m total length), all had significantly greater abundance and diversity of these other taxa, and associations with species of commercial and conservation interest (e.g. roman *Chrysoblephus laticeps*). Endemic scyliorhinids (notably dark catshark *Haploblepharus pictus*) and the broadnose sevengill shark *Notorynchus cepedianus* also had many strong positive co-occurrences (28% and 21% of interactions, respectively). The puffadder catshark *H. edwardsii* had the highest centrality of any species, denoting its high connectedness to other taxa. Overall, chondrichthyans, especially the dark and puffadder catsharks and the broadnose sevengill shark, show strong potential as an umbrella species-complex in South Africa.**

**Keywords:** baited remote underwater video, *Chrysoblephus laticeps*, co-occurrence, *Jasus lalandii*, marine protected areas, *Notorynchus cepedianus*, Scyliorhinidae, Western Cape

**Online supplementary material:** Table S1, available at https://doi.org/10.2989/1814232X.2020.1729859, provides a list of observed species from each taxon (other than Chondrichthyes) and their frequency of occurrence; Table S2 provides the centrality metrics for the top-five most-central species by each measure of centrality.

## Introduction

South Africa's marine ecosystems are biologically diverse and brimming with endemism, but are also heavily impacted by several threats, including exploitation and habitat destruction, particularly on the west coast (Lombard et al. 2004; Griffiths et al. 2010). Fisheries have severely reduced the biomass of many important linefish (hook-and-line) species, including the culturally and commercially important endemic seabream, roman *Chrysoblephus laticeps* (Attwood and Farquhar 1999; Götz et al. 2008). Additionally, west coast rock lobster *Jasus lalandii*, one of South Africa's economically most valuable species, is estimated to have declined to less than 3% of its historical biomass (DAFF 2014). Marine protected areas (MPAs) have shown promise for conserving exploited species in South Africa (Götz et al. 2008; Kerwath et al. 2013; Mann et al. 2016), but currently comprise only 5% of the country's exclusive economic zone (DEA 2018). Additionally, few of South Africa's MPAs have a no-take component, resulting in sub-optimal protection (Currie et al. 2012), and many exclude habitat types that are important for species of conservation concern (Griffiths et al. 2010; Solano-Fernández et al. 2012; Sink 2016). Poaching of culturally and commercially important species like the west coast rock lobster is also widespread due to a poor capacity for enforcement and a failure to address social issues that could improve compliance (Brill and Raemaekers 2013; Sowman and Sunde 2018). South Africa's biodiversity would benefit from an expansion of its MPA network (Solano-Fernández et al. 2012), although improved monitoring and enforcement are required to ensure the effectiveness of MPAs (Marinesque et al. 2012). In a country where responses to MPA declarations can have large social repercussions (Faasen and Watts 2007), there is a need to ensure that these MPAs at least achieve their ecological goals.

When resources are scarce, managers and conservation practitioners may focus efforts on select threatened species, termed surrogates, with the hopes of benefiting other species (Caro and O'Doherty 1999). One example is the 'umbrella species' concept, in which habitat protection focused on one or a few species aims to also conserve a multitude of co-occurring species of conservation concern (Caro and O'Doherty 1999). A 'flagship species' is another form of surrogacy, where species with cultural appeal are used to raise public awareness and funds for

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broader conservation goals (Veríssimo et al. 2014; Jepson and Barua 2015). A species could serve as a combined flagship–umbrella species if it is centred both in existing cultural norms and in networks of ecological interactions (Caro 2010; Jepson and Barua 2015).

The effectiveness of conservation surrogates is, however, equivocal and context-dependent, with recognition of many putative umbrella and flagship species failing to optimally protect diversity at local scales, by focusing resources on too few species or failing to account for the ecological needs of other threatened species (Roberge and Angelstam 2004; Caro 2010, 2015; Joseph et al. 2011). Traditionally, umbrella species have been chosen based on species-specific traits, such as body size, home-range size, or trophic level and diet, without directly verifying ecological suitability or relationships to diversity and abundance of other species, resulting in reduced protection for other areas and species of high conservation priority (Branton and Richardson 2011; Stuber and Fontaine 2018). There have been calls to abandon the umbrella species concept (Roberge and Angelstam 2004), but when niche overlap and habitat associations between umbrella species and other species of conservation concern are explicitly considered, umbrella species can lead to conservation success (Maslo et al. 2016; Fourcade et al. 2017; Stuber and Fontaine 2018), even among unrelated taxa (Bichet et al. 2016). Testing co-occurrence of threatened species is an important first step in evaluating potential umbrella species (Cushman et al. 2010). Also, conservation outcomes could be improved using focal-species complexes, where multiple surrogate species with heterogeneous ecological needs and sensitivities to different potential threats generate wider appeal and a more diverse representation of habitats and landscape elements (Lambeck 1997; Roberge and Angelstam 2004; Veríssimo et al. 2014). The use of a flagship–umbrella species-complex could be a way to increase funding for, and effectiveness of, both current and future conservation measures in South Africa.

Here, we propose the Chondrichthyes (sharks, skates, rays and chimaeras) as a potential flagship–umbrella species-complex for South Africa, because the country is a global hotspot for chondrichthyan diversity (Ebert and van Hees 2015). Many chondrichthyans are charismatic (Albert et al. 2018) and they support a thriving dive tourism industry in South Africa that creates economic opportunities out of conservation (Dicken and Hosking 2009; Gallagher and Hammerschlag 2011; Dicken 2014). The ecological and evolutionary diversity of chondrichthyans also widens their collective niche, making them good candidates for a flagship–umbrella taxon (Cortés 1999; Roff et al. 2016; Stein et al. 2018). Whereas some shark species are large, mobile apex predators, fitting the traditional definition of an umbrella species (Andelman and Fagan 2000; Sergio et al. 2008), chondrichthyans also include many smaller mesopredators, which might better reflect biodiversity at local scales. The Batoidea (skates and rays) exemplify the diversity of form within chondrichthyans, with their unique disc-like body shape, and also are ecologically diverse (Aschliman et al. 2012; Martinez et al. 2016). Many chondrichthyan populations are threatened (Stevens et al. 2000; Dulvy et al. 2014, 2017) and need enhanced protection (Dulvy et al. 2017). Severely threatened species do not always make the best umbrellas, as their rarity limits the extent of niche overlap with other species, but chondrichthyans are diverse in their conservation status (Dulvy et al. 2014; Macdonald et al. 2017). Despite these qualities, no study has rigorously examined the suitability of chondrichthyans as a flagship–umbrella taxon. Such suitability needs explicit testing to ensure that long-term conservation goals can be met in the specific systems for which an umbrella is proposed (Cushman et al. 2010). Only a few studies have tested the umbrella-species concept in marine ecosystems (Zacharias and Roff 2001; Olds et al. 2014; Weng et al. 2015), including just one chondrichthyan, a ray species (Gilby et al. 2017). Unless co-occurrence is demonstrated, charismatic and wide-ranging surrogate species will not be useful in conserving biodiversity (Andelman and Fagan 2000).

We assessed the potential of chondrichthyans to serve as an umbrella species-complex in the Western Cape Province, South Africa, using an extensive dataset from baited remote underwater videos (BRUVs) (Osgood et al. 2019). The Western Cape is an important area for marine conservation in South Africa as it has experienced fisheries collapses (Attwood and Farquhar 1999) and is still impacted by heavy fishing pressure (Moloney et al. 2013; da Silva et al. 2015). There are multiple MPAs in the region, including two in our study area (Figure 1): the 113 km$^2$ Walker Bay Whale Sanctuary and the 20 km$^2$ Betty's Bay MPA. Both prohibit boat-based activity, although only seasonally (July–December) for the Walker Bay Whale Sanctuary, and shore angling occurs in both year-round. First, we related the abundance, diversity and community composition of six other major taxonomic groups (teleosts, crustaceans, cephalopods, Myxinidae, birds and mammals) to the presence of chondrichthyans overall and to specific chondrichthyan groups: catsharks, large sharks (>1 m total length [TL]) and batoids. Second, we compared the co-occurrence patterns among chondrichthyans and these other taxa to assess the strength and centrality of chondrichthyans within the local ecological network. We also estimated the co-occurrence among chondrichthyans and species of conservation concern in the Western Cape, with a focus on two species of economic importance, roman and west coast rock lobster. To supplement our co-occurrence analysis, we calculated centrality measures for all species, which reflect the connectedness of a species with the network of its ecological community (Freeman 1978). Finally, in addition to statistical analyses of the BRUV data, we simulated small marine reserves based on our sampled sites to investigate whether designing marine reserves based upon knowledge of chondrichthyan occurrences would protect a greater abundance of species of conservation concern, as well as more overall community diversity, compared with designs in which sites were either selected at random or by habitat type.

## Materials and methods

### *Study site and BRUV data collection*

At 167 sites along the South African coastline, we conducted a total of 419 BRUV deployments, over multiple time-points, between July 2016 and July 2018 (details

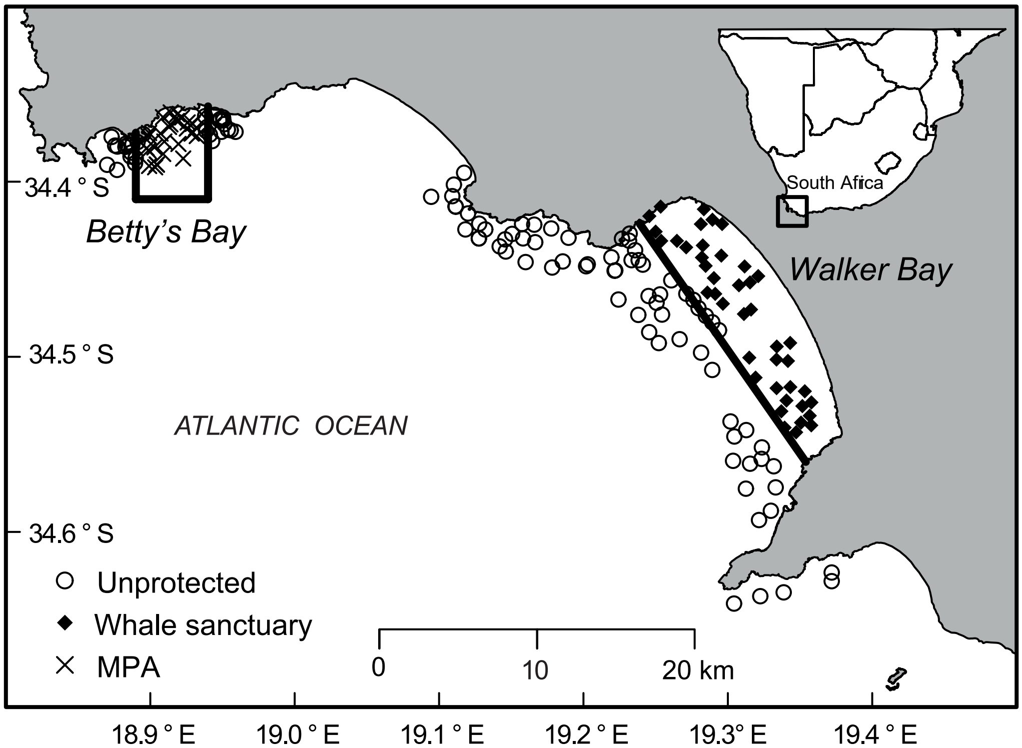


**Figure 1:** Baited remote underwater video (BRUV) sampling sites along the coast of South Africa, categorised by protection status

in Osgood et al. 2019). Sites were randomly placed and stratified across two protected areas: inside (*n* = 40 sites, 109 deployments) and outside (*n* = 69 sites, 131 deployments) the Walker Bay Whale Sanctuary, and inside (*n* = 29 sites, 85 deployments) and outside (*n* = 29 sites, 94 deployments) the Betty's Bay MPA (Figure 1). When possible (i.e. barring weather and equipment constraints), deployments were conducted at each site in each season and each year. On average, a site received 2.5 replicate BRUV deployments over the study period. We selected sites to be 500 m apart from one another, other than within the Betty's Bay MPA where the smaller area dictated a 100–200 m minimum distance between sites; sites closer than 400 m apart were not sampled on the same day, if resources allowed. Sample size per habitat type (rocky reef, kelp forest, and sand) within each of the four sampled areas was dictated by habitat frequency within the area.

Each BRUV system was composed of a mild-steel cross-shaped base with a bait canister and camera set 111 cm apart from one another and raised 20–30 cm off the bottom of the system (details in Osgood et al. 2019). One kilogram of chopped, defrosted sardine *Sardinops sagax* was placed into the bait canister for each deployment. We used GoPro® cameras (Hero 1, Hero 2, Hero 3 Silver Edition, and Hero+) set to 720p to prolong battery life and save memory-card space. We deployed all BRUVs in daylight, between 08:00 and 16:00. Mean deployment time was 62.7 min (SD 10.7, range 20.7–103.2).

For every chondrichthyan, teleost, cephalopod, crustacean, myxinid, bird and mammal recorded during each BRUV deployment, we identified individuals to species level when possible. We then recorded the maximum number of individuals of a species observed at any one time on the entire video recording (MaxN) as a conservative measure of relative abundance (Cappo et al. 2004). We also recorded habitat type (sand, rocky reef, kelp) as well as visibility in broad categories (1 = <1 m; 2 = 1–5 m; 3 = 5–10 m; 4 = >10 m) for each BRUV video, using the distance to the bait canister as a reference. Visibility ranged from 0.5 m to approximately 20 m on the BRUV deployments. We recorded depth using an HDS-8m Gen2 Lowrance chartplotter for deployments in Betty's Bay and using one-meter markings on the BRUV rope in Walker Bay. Site depths ranged between 3 and 55 m (mean 25.3 m [SD 12.2]). For reef and kelp sites, we also estimated the profile of the habitat, ranging between '0' for a flat profile and '4' for the steepest profile. We assigned a profile of '0' to all sand sites.

The University of Victoria Animal Care Committee authorised all observations of live animals (AUP 2016-032[1]). This study was conducted under the authority of a joint research permit issued by the then South African Department of Agriculture, Forestry and Fisheries: Branch Fisheries Management and Department of Environmental Affairs: Branch Oceans and Coasts (RES2017-31 and RES2018-59).

### *Data analysis*

For each BRUV site, we first averaged the MaxN and species richness (total number of species) for all BRUV deployments replicated at the site. Then we assessed the relationship between the relative abundance (mean MaxN) and mean richness of all chondrichthyans to the mean MaxN and Shannon diversity index (calculated from mean MaxN) of species from all the other taxonomic groups pooled using Spearman rank correlations. Next, we assessed the associations between the MaxN of other taxa averaged per site and the presence of three chondrichthyan groups (catsharks, large sharks [>1 m TL], batoids) at a site using generalised linear models (GLMs) with a gamma distribution. We used *t*-tests to examine the relationships between the presence of these chondrichthyan groups and the mean Shannon diversity of the other taxa, because they were normally distributed. We also used a gamma GLM and a *t*-test to assess whether sites with an above-average abundance of chondrichthyans (mean MaxN >3) had a greater total MaxN and Shannon diversity, respectively, of other taxa than sites with fewer chondrichthyans.

Next, we assessed whether the community composition of teleosts, cephalopods, crustaceans, myxinids, birds and mammals differed between sites with and without catsharks, large sharks, batoids, and abundant chondrichthyans, using a PERMANOVA. We determined which species of these other taxa were most responsible for any differences in community composition observed, based on significant Dufrêne–Legendre indicator (DLI) values greater than 0.20 (Gilby et al. 2017).

To assess co-occurrence patterns between chondrichthyans and species from the other taxa, we used the package 'co-occur' in R (Griffith et al. 2016). We qualitatively compared the percent of positive and negative co-occurrences as well as the strength (effect size) of co-occurrences among chondrichthyan species as well as across specific groups: all chondrichthyans, catsharks, large sharks, and batoids. The effect size of a species pair's co-occurrences is calculated as the observed number of co-occurrences minus the number of co-occurrences expected assuming random associations, standardised by number of sites, and ranges from −1 to +1. We also qualitatively compared the mean percent and strength of co-occurrences among chondrichthyans and, respectively, teleosts, cephalopods and crustaceans, the taxa with the most observed species. We then determined which species had centrality within the network of these co-occurrences based on degree, betweenness, local bridging, closeness, and eigenvalue centrality. Centrality measures the importance of a node in a network (Freeman 1978), and in the case of ecological communities reflects the connectedness of a species to others through co-occurrence.

We examined the relationships between chondrichthyans and all species of conservation concern (red-listed by either the IUCN [www.iucn.org] or South African Sustainable Seafood Initiative [wwfsassi.co.za]), and also roman and west coast rock lobster, two species of local economic and conservation importance, based on habitat and co-occurrence. We ran a redundancy analysis (RDA) using habitat type, depth, habitat profile, and area as constraints to assess how the MaxN of chondrichthyans and species of conservation concern correlated based on habitat. We used non-averaged data (i.e. all 419 BRUV videos) owing to small habitat heterogeneity at a site. We determined the strength of positive co-occurrences between chondrichthyans and these species of conservation concern, and we determined specifically which chondrichthyans had strong positive co-occurrences, both inside and outside the protected areas, with roman and west coast rock lobster. We also determined the mean strength of positive and negative co-occurrences between species of conservation concern and all other species to compare the connectivity of these threatened species, and their suitability as umbrella species, with that of chondrichthyans.

Finally, we simulated the creation of a small MPA (i.e. encompassing four sites) by randomly selecting a site of high chondrichthyan abundance and then joining it with its three closest sites. We repeated this procedure basing an MPA instead on sites with low chondrichthyan abundance, both over all habitats and over just reef and kelp habitats, to assess whether reef and kelp sites alone, even without high chondrichthyan abundance, would provide comparable conservation benefits. From this simulation, we calculated the percent increase in the Shannon diversity and species richness of all taxa, defining percent increase as the difference between the value for the MPA simulated based on abundant chondrichthyans and the value for the MPA based on fewer chondrichthyans, divided by the mean value for both MPAs. We also calculated the percent increase for the abundance of species of conservation concern along with the percent increase for both roman and west coast rock lobster abundance, specifically. We repeated the simulation 1 000 times.

## Results

In total, we observed on the BRUVs 18 chondrichthyan species and 52 other species: 39 teleosts, seven crustaceans, two cephalopods, two birds, one myxinid (the sixgill hagfish *Eptatretus hexatrema*) and one mammal (the Cape fur seal *Arctocephalus pusillus*) (Table 1; Supplementary Table S1). Two-thirds of these other species were found only at sites where we also observed chondrichthyans ($n$ = 147 sites), including 29 teleosts, two crustaceans (Cape rock crab *Guinusia chabrus,* sandflat crab *Danielita edwardsii*), one cephalopod (chokka-squid *Loligo reynaudii*), one bird (Cape cormorant *Phalacrocorax capensis*), and the single myxinid species (Supplementary Table S1). At least one chondrichthyan species occurred with every species of teleost, crustacean, and cephalopod at a minimum of one site. Both chondrichthyan total abundance and richness at a site were moderately correlated ($\rho$, range 0.42–0.53) with each of the total abundance and Shannon diversity of the other taxa present, with stronger correlations occurring in the MPAs (Table 2).

There was also a significantly higher abundance of other taxa at sites with catsharks (likelihood ratio test [LRT], $\chi^2$ = 37.84, df = 1, $p$ < 0.001) and large sharks (LRT, $\chi^2$ = 4.82, df = 1, $p$ = 0.00513), but not batoids (LRT, $\chi^2$ = 0.039, df = 1, $p$ = 0.794), compared with sites lacking these species (Figure 2a). Similarly, the Shannon diversity of other taxa was also significantly higher at sites with catsharks (two-sample $t$-test, $t$ = 3.75, df = 165, $p$ < 0.001) and large sharks (two-sample $t$-test, $t$ = 2.13, df = 165, $p$ = 0.0342) but not batoids (two-sample $t$-test, $t$ = 0.31, df = 165, $p$ = 0.754) (Figure 2b). Sites with abundant chondrichthyans had both a significantly higher abundance (LRT, $\chi^2$ = 11.48, df = 1, $p$ < 0.001) (Figure 2a) and higher mean Shannon diversity (two-sample $t$-test, $t$ = 7.94, df = 165, $p$ < 0.001) (Figure 2b) of other taxa, relative to sites with few chondrichthyans.

**Table 1:** Chondrichthyan species observed using baited remote underwater video (BRUV) in the Western Cape Province, South Africa, and categorised by the major groupings used in the analysis of presence and co-occurrence

| Family | Species | Common name |
|---|---|---|
| | *Catsharks* | |
| Scyliorhinidae | *Haploblepharus pictus** | Dark catshark |
| Scyliorhinidae | *Haploblepharus edwardsii** | Puffadder catshark |
| Scyliorhinidae | *Poroderma africanum** | Pyjama catshark |
| Scyliorhinidae | *Poroderma pantherinum** | Leopard catshark |
| Scyliorhinidae | *Halaelurus natalensis** | Tiger catshark |
| | *Large sharks (>1 m total length)* | |
| Triakidae | *Mustelus mustelus* | Common smooth-hound shark |
| Hexanchidae | *Notorynchus cepedianus* | Broadnose sevengill shark |
| Triakidae | *Galeorhinus galeus* | Soupfin shark |
| Triakidae | *Triakis megalopterus** | Spotted gully shark |
| Carcharhinidae | *Carcharhinus brachyurus*† | Bronze whaler |
| Sphyrnidae | *Sphyrna zygaena*† | Smooth hammerhead shark |
| | *Batoids* | |
| Rajidae | *Raja straeleni** | Biscuit skate |
| Rajidae | *Rostroraja alba* | Spearnose skate |
| Dasyatidae | *Bathytoshia brevicaudata* | Short-tail stingray |
| Rhinobatidae | *Acroteriobatos annulatus** | Lesser guitarfish |
| Myliobatidae | *Myliobatis aquila* | Eagleray |
| | *Other chondrichthyans* | |
| Squalidae | *Squalus acutipinnis*† | Bluntnose spiny dogfish |
| Callorhinchidae | *Callorhinchus capensis** | St Joseph |

†Species with only one occurrence in the BRUV

*Species endemic to southern Africa

**Table 2:** The Spearman correlation coefficients between total relative abundance (MaxN) and species richness of chondrichthyans at a site, and the relative abundance and Shannon diversity indices of other taxa, in both protected and unprotected areas, observed using baited remote underwater video in the Western Cape Province, South Africa

| Chondrichthyes | Other taxa | |
|---|---|---|
| | Relative abundance | Shannon diversity |
| Relative abundance | | |
| Overall | 0.47 | 0.53 |
| Protected | 0.69 | 0.62 |
| Unprotected | 0.33 | 0.44 |
| Richness | | |
| Overall | 0.42 | 0.48 |
| Protected | 0.62 | 0.61 |
| Unprotected | 0.33 | 0.46 |

Community composition differed significantly in the presence of catsharks (PERMANOVA, df = 1, 165, Pseudo-$F$ = 31.75, $p$ = 0.001), large sharks (PERMANOVA, df = 1, 165, Pseudo-$F$ = 5.32, $p$ = 0.002), batoids (PERMANOVA, df = 1, 165, Pseudo-$F$ = 3.59, $p$ = 0.007), and abundant chondrichthyans (PERMANOVA, df = 1, 165, Pseudo-$F$ = 13.07, $p$ = 0.001). Sixteen species were significantly more likely to occur at sites with catsharks or with abundant chondrichthyans, while 19 species were more likely to occur with large sharks. These both included three species of conservation interest: roman, red stumpnose *Chrysoblephus gibbiceps*, and west coast rock lobster. Only six species were more likely at sites with batoids, including bluefin gurnard *Chelidonichthys kumu* and the three-spotted swimming crab *Portunus sanguinolentus*, which were more likely to occur when catsharks and large sharks were absent.

Across all taxa, the number of positive and negative co-occurrences varied considerably by species (Figure 3). For chondrichthyans, the percentage of co-occurrences that were significantly positive, excluding species observed only once, ranged from 1.45% (with a mean strength of 0.0060) for lesser guitarfish *Acroteriobatus annulatus* to 36.23% (with a mean strength of 0.074) for the dark catshark *Haploblepharus pictus* (Figures 4a, 5a). Overall, 13.2% of chondrichthyan associations were significantly positive (Figure 4), with a mean strength of 0.048 (SD 0.037, range 0.006–0.17) per positive co-occurrence (Figure 5b). In contrast, only 4.8% of chondrichthyan associations were negative (Figures 3, 4); these had a mean strength of −0.041 (SD 0.031, range −0.015 to −0.16) per negative co-occurrence (Figure 5b). Chondrichthyan negative co-occurrences ranged from 0.0% of associations for each of lesser guitarfish, short-tail stingray *Bathytoshia brevicaudata*, soupfin shark *Galeorhinus galeus*, and common eagleray *Myliobatis aquila*, and up to 20.3% for biscuit skate *Raja straeleni*. The common smooth-hound shark *Mustelus mustelus*, tiger catshark *Halaelurus natalensis*, and dark catshark also had a high percentage of negative co-occurrences (11.6%) (Figure 4a). The biscuit skate also had moderately strong mean positive and negative co-occurrences, at 0.035 and −0.033, respectively (Figure 5a). The catsharks had the highest percentage

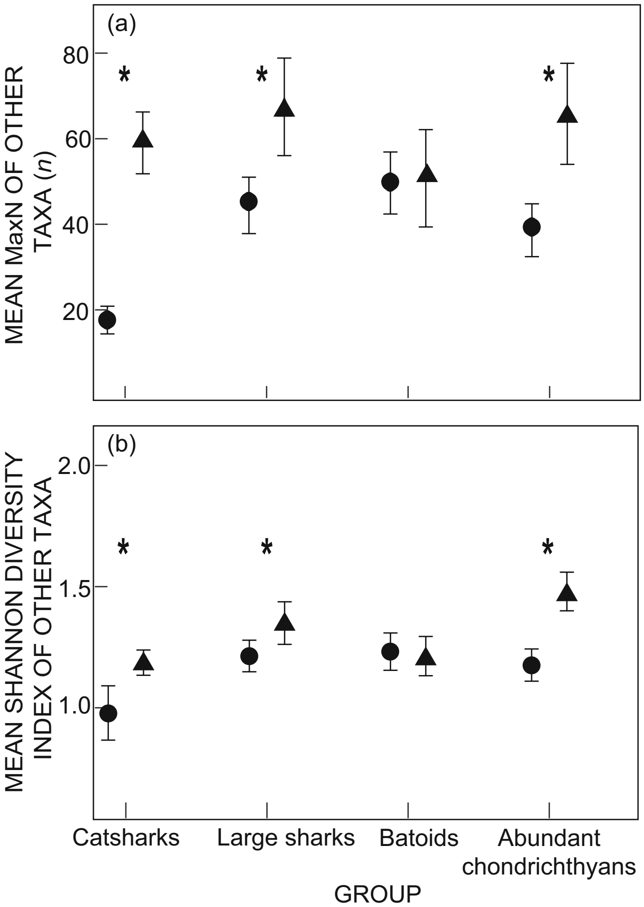


**Figure 2:** (a) Mean relative abundance (MaxN, with 95% confidence interval based on the Gamma distribution) for the overall marine community (i.e. teleosts, cephalopods, crustaceans, birds, mammals and Myxinidae), and (b) mean Shannon diversity index (with 95% confidence interval based on the normal distribution) of the overall marine community at sites without (circles) and with (triangles) the given groups. *Significant differences ($p < 0.05$)

(overall 27.8%) and strength of both positive and negative co-occurrences on average among chondrichthyans, due largely to the many strong positive and negative co-occurrences of the dark catshark, pyjama catshark *Poroderma africanum*, and leopard catshark *P. pantherinum* (Figures 4, 5a, b). In fact, 13 of the 20 strongest interactions across the whole community involved one of these species. The dark catshark was one of the top-three most-strongly co-occurring species for 15 species, followed by the pyjama catshark and the roman, with each being one of the top-three co-occurring species for 12 other species. Large sharks and batoids co-occurred about half as strongly as the catsharks, almost tying for the smallest mean percentage of positive co-occurrences across all groups (Figure 5b). The broadnose sevengill shark (mean strength of 0.039) had the strongest positive co-occurrences among these species, with positive co-occurrences making up 20.9% of its associations (Figures 4a, 5a). These included an effect size of 0.053 with west coast rock lobster and 0.037 with roman.

Both teleosts and cephalopods had a similar percentage of positive and negative co-occurrences to chondrichthyans on average, although catsharks still had the highest mean percentage of positive co-occurrences across all groups examined (Figures 3, 4). However, two teleosts, roman and hottentot seabream *Pachymetopon blochii*, had the highest percentage of positive interactions across all taxa (Figure 3). Hottentot also had the strongest positive co-occurrences among all species (mean co-occurrence strength = 0.075), but the dark, pyjama, and leopard catshark species had interaction strengths nearly as strong (0.070–0.074). Despite having a lower mean percentage of positive co-occurrences to teleosts, cephalopods and chondrichthyans (Figure 4b), crustaceans had strong positive co-occurrences on average, largely due to the west coast rock lobster (Figure 3). The strongest positive co-occurrences involving any species occurred between the dark catshark and each of the west coast rock lobster (0.17) and hottentot seabream (0.16).

The puffadder catshark had the highest centrality of any species of any taxonomic group based on every measure except eigenvalue centrality, for which the teleost hottentot seabream was highest (Supplementary Table S2). However, the pyjama catshark and puffadder catshark had the second and fourth highest values of eigenvalue centrality, respectively. The pyjama catshark and hottentot seabream also tied with the puffadder catshark for the highest values for degree and closeness centrality.

Chondrichthyans had similar scores on the RDA to species of conservation concern, suggesting occurrences in similar habitats generally. The pyjama, leopard, and puffadder catsharks had similar scores on both axes of the RDA to roman, as well as red steenbras *Petrus rupestris*, with large scores on the first axis and negative scores on the second axis indicating a shared preference for deeper reef sites (Figure 6). The dark catshark had similar scores on both axes to the west coast rock lobster, because of similar abundance on shallow kelp sites in the Betty's Bay MPA (Figure 6).

Chondrichthyans co-occurred positively and significantly with seven species of conservation interest (Table 3). The strength of positive co-occurrences of chondrichthyans with species of conservation interest was mildly greater than the mean strength of their co-occurrences with other taxa in general (Figure 5b). The pyjama catshark (mean co-occurrence strength = 0.13) and dark catshark (0.11) were the second- and third-strongest species of any taxa co-occurring positively with roman, behind hottentot seabream (0.14). The pyjama catshark and dark catshark co-occurred more strongly with roman within protected areas (0.18 and 0.13, respectively) than outside them (0.091 and 0.099). The dark catshark co-occurred most strongly (0.17) and the pyjama catshark third strongest (0.14) with the west coast rock lobster. These two catsharks also co-occurred more strongly with west coast rock lobster in protected areas (0.20 and 0.17, respectively) than outside them (0.15 and 0.12, respectively). Only the west coast rock lobster and roman had co-occurrences stronger than chondrichthyans on average; most species of conservation concern did not have strong co-occurrences with other species (Figure 5c).

Compared with selecting a random site of low chondrichthyan abundance, the mean Shannon diversity

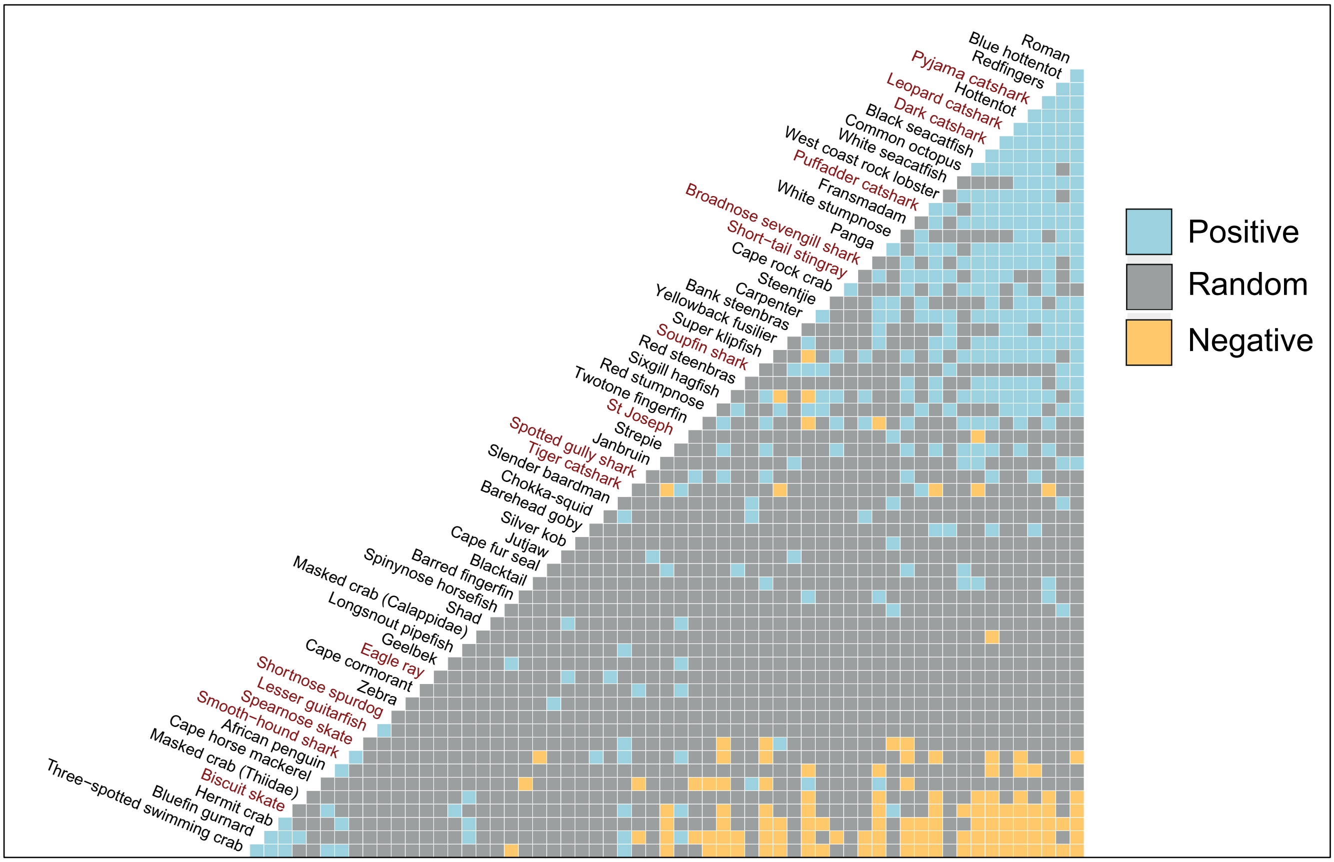


**Figure 3:** Species co-occurrences in the BRUV data, categorised as positive, negative or random. Species are ordered from most-positive occurrences to most-negative occurrences. Red font indicates chondrichthyan species

was 12.2% (95% CI 1.4) higher, species richness was 22.8% (2.3) higher, abundance of species of conservation concern was 33.5% (1.2) higher, and roman abundance was 97.6% (6.5) higher in simulations of MPAs based on sites of high chondrichthyan relative abundance. When compared with selecting a reef or kelp site of low chondrichthyan abundance, Shannon diversity was still 5.3% (1.1) higher, species richness 4.1% (1.5) higher, abundance of species of conservation concern 5.0% (3.1) higher, and roman abundance 20.2% (5.7) higher in simulations of MPAs based on sites of high chondrichthyan relative abundance. However, the abundance of west coast rock lobster was 17.0% (8.6) lower in the MPAs simulated based on high chondrichthyan abundance compared with those based on reef and kelp sites with few chondrichthyans. This species' abundance was, however, 58.8% (9.4) higher in the former simulated MPAs when compared with sites of low chondrichthyan abundance over all habitats.

## Discussion

Our analyses suggest that chondrichthyans could serve as an effective umbrella species-complex for marine conservation in South Africa. We found concordance in the abundance and species richness of this assemblage with that of other marine taxa, and they share habitat with many species of conservation concern in the Western Cape. Among chondrichthyans, the endemic catsharks showed the strongest umbrella-species characteristics, and co-occurred with many species, including a strong association with reef species (roman, west coast rock lobster, and red stumpnose) that are of economic and conservation importance. The umbrella potential of larger shark species was more equivocal owing to their low abundance, but the more common broadnose sevengill shark had strong co-occurrence patterns with a range of taxa. This species has increased its habitat range as a result of the declining presence of the white shark *Carcharodon carcharias* (Hammerschlag et al. 2019), an important predator and competitor, suggesting the broadnose sevengill shark has the wide range and high trophic level of a traditionally defined umbrella species coupled with demonstrated overlap in habitat with other species. A chondrichthyan umbrella species-complex including both catsharks and the broadnose sevengill shark would cover biodiversity over multiple scales, optimising their role as surrogate species (Stuber and Fontaine 2018). Some species (biscuit skate, common smooth-hound shark, and tiger catshark) did have high negative co-occurrences, likely reflecting their relative abundance on the sand habitat for which other species did not have the same affinity.

Catsharks found in the Western Cape region of South Africa are small-bodied, locally resident and abundant (Osgood et al. 2019), all qualities not traditionally associated with umbrella species (Roberge and Angelstam

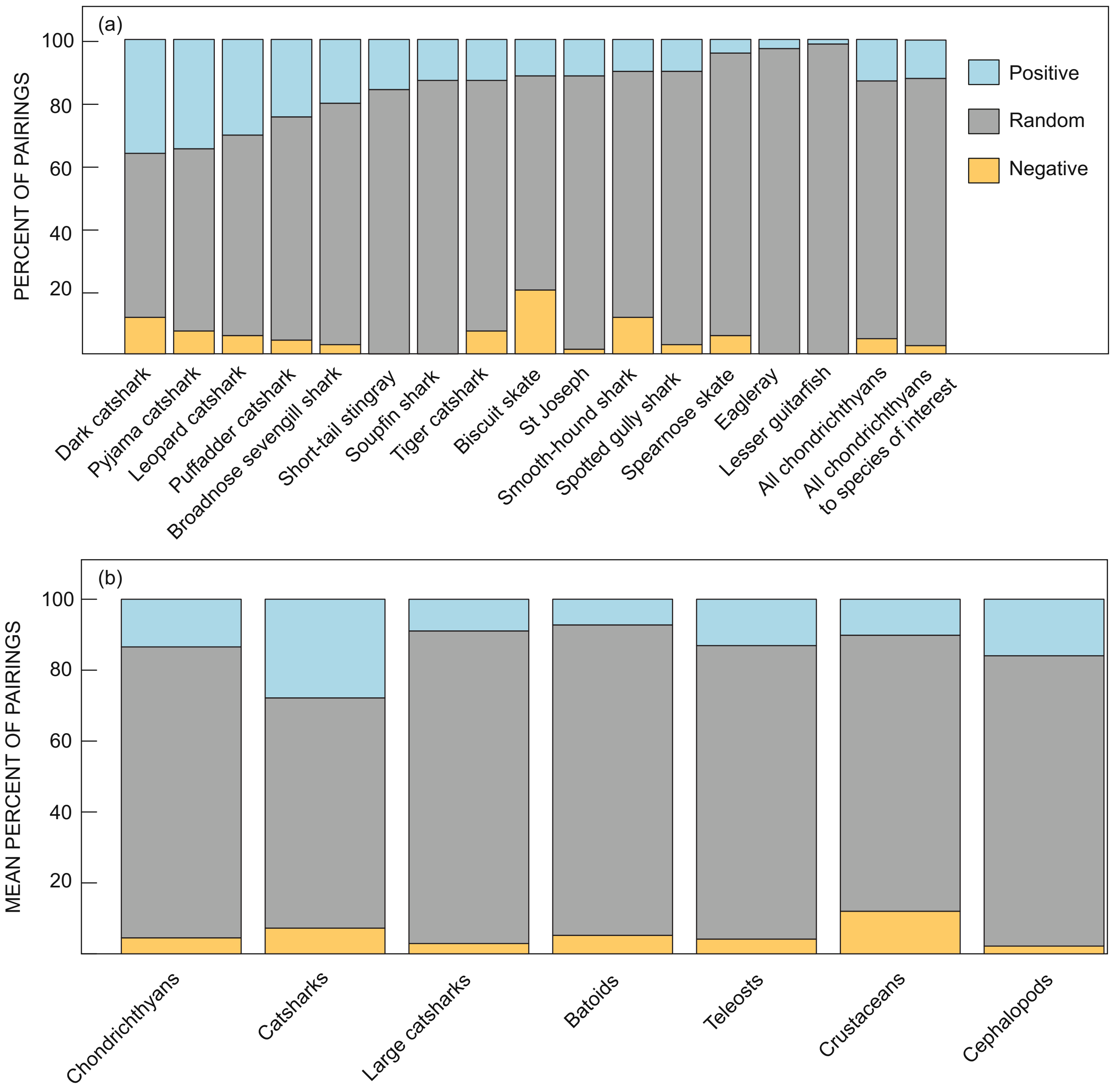


**Figure 4:** (a) The percentage of positive, random, and negative co-occurrences between each chondrichthyan species and all other species, the total for all chondrichthyans, and the total for all chondrichthyans relative only to species of conservation concern. (b) The mean percentage of positive, random, and negative co-occurrences for different groups of chondrichthyans, and for crustaceans and cephalopods

2004; Caro 2010). However, tests of umbrella species that were selected based on large body size, large home range, a generalist diet, and high trophic level have shown that such qualities do not guarantee the protection of high abundance or species richness, even compared with a random selection of species (Andelman and Fagan 2000; Branton and Richardson 2011; Stuber and Fontaine 2018). In fact, in terrestrial systems, small avian species have stronger ecological associations with species richness and greater potential as umbrella species than large mammals (Branton and Richardson 2011). Smaller surrogates with strong associations to local biodiversity can be more useful than umbrella species with large home ranges, as hotspots of biodiversity on these larger scales have already been identified in many regions (Caro 2015). The abundance of catsharks and their ease of capture in the Western Cape aids their use for more precisely identifying local sites of high diversity, and their lower mobility ensures close associations to habitats and local populations of interest. Rarer species are harder to record and study, limiting their use as a practical surrogate for selecting precise locations of conservation need (Fleishman et al. 2000). The use of smaller, localised and endemic umbrella species also supports goals to protect traditionally overlooked biodiversity (Kalinkat et al. 2017).

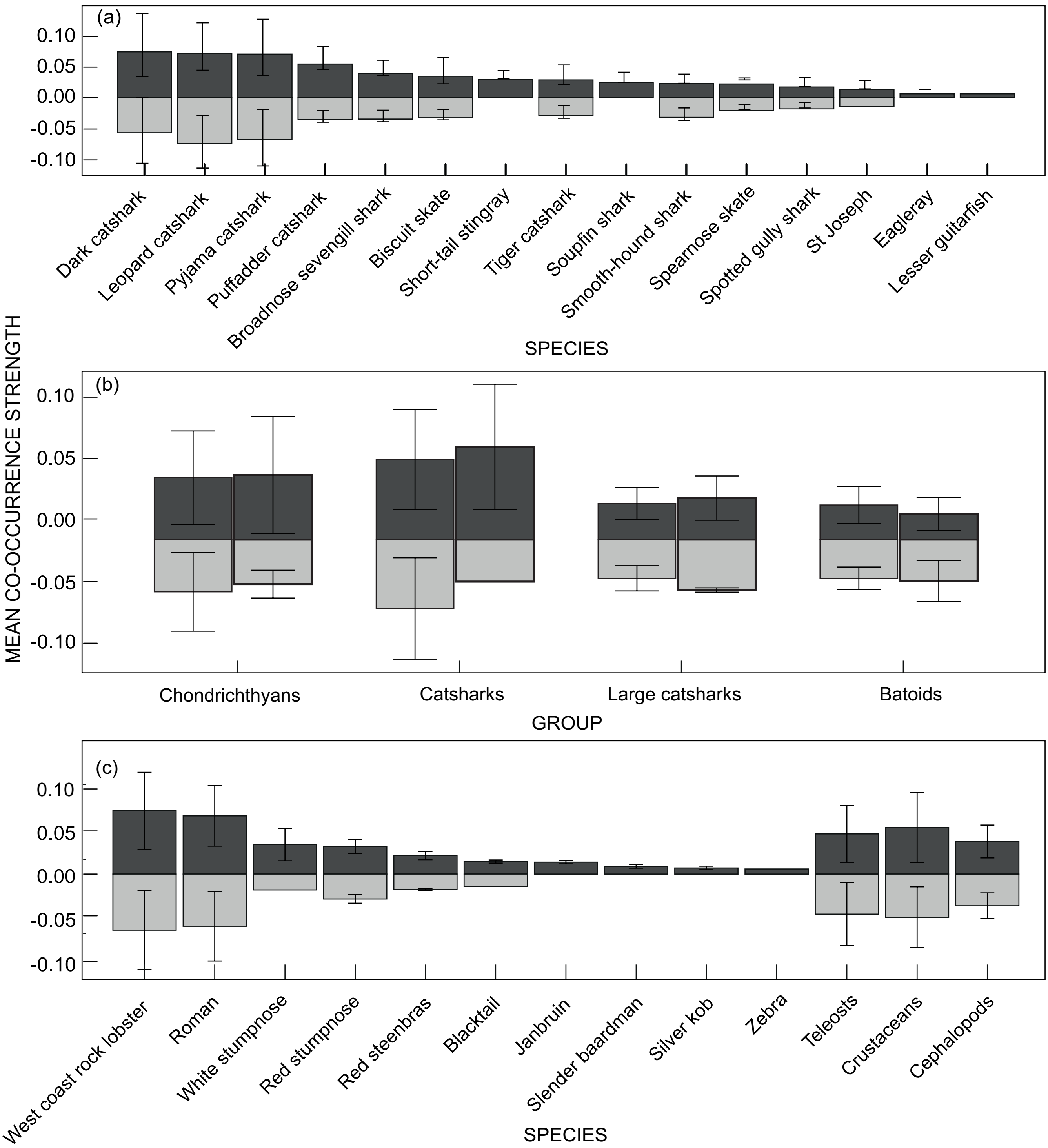


**Figure 5:** The mean strength of positive and negative co-occurrences with all other species, for (a) each chondrichthyan species (see Table 1 for scientific names), (b) each chondrichthyan group (solid box relative only to species of conservation concern), and (c) each species of conservation concern (see Supplementary Table S1 for scientific names) and the groups teleosts, crustaceans and cephalopods. Error bars represent ±SD

Catsharks have other qualities besides habitat associations with species of conservation interest, including high centrality within the ecological community and complementarity in habitat use, that also imply they might serve as effective umbrella species (Lambeck 1997; Andelman and Fagan 2000). Most of the catshark species demonstrated centrality, and therefore high connectedness in the community. The puffadder catshark had high centrality on every metric, suggesting it is closely connected to many other species that do not necessarily co-occur with each

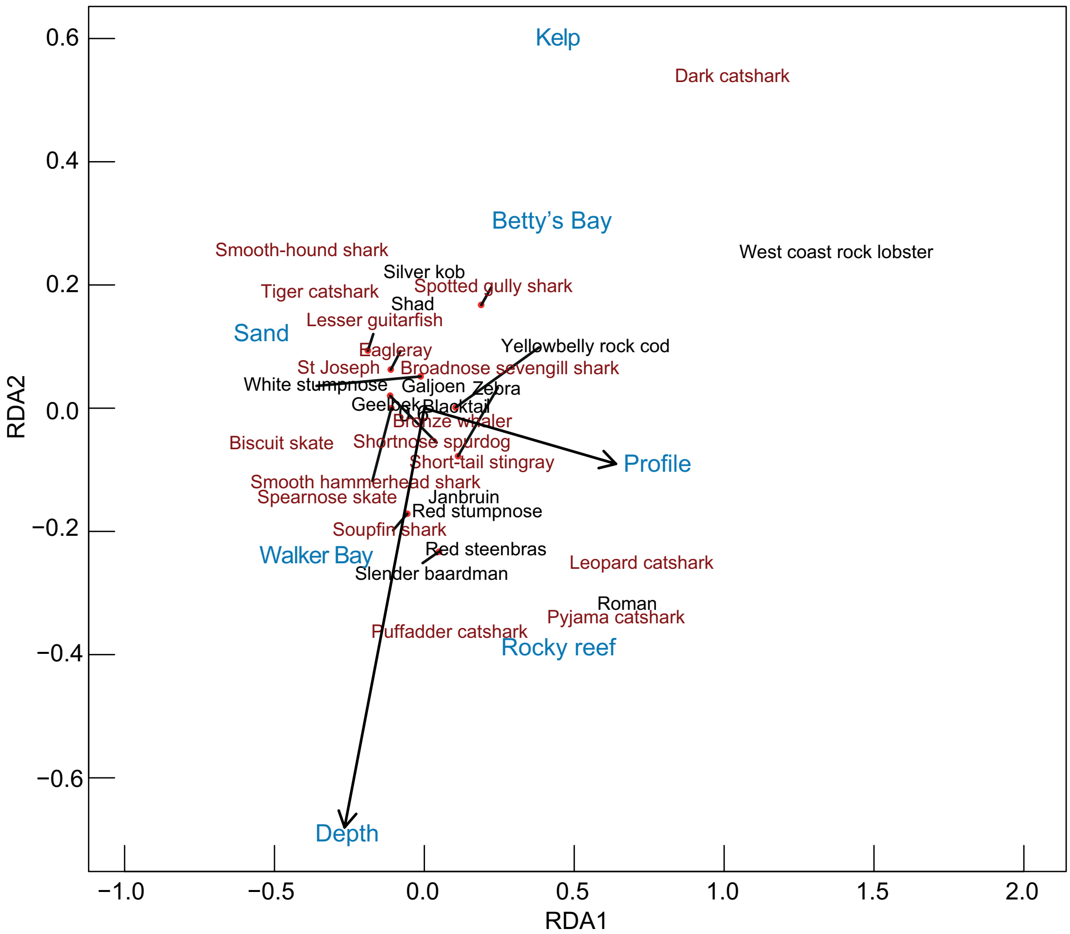


**Figure 6:** The scores of each chondrichthyan species (red font) and each species of conservation concern (black font) on the first two axes of a redundancy analysis (RDA) relative to habitat variables (overall type, profile, depth and area) that were used as constraints (blue font)

**Table 3:** Species of conservation concern that were observed at least twice in the baited remote underwater videos (BRUV) in the Western Cape Province, South Africa, ordered by taxon and the mean strength (effect size) of their positive co-occurrences with chondrichthyans. An asterisk (*) denotes mean effect sizes derived from only significant positive co-occurrences. IUCN = International Union for the Conservation of Nature; SASSI = South African Sustainable Seafood Initiative. IUCN status (version 2019-2): NE = Not Evaluated; LC = Least Concern; NT = Near Threatened; VU = Vulnerable; EN = Endangered

| Species | Common name | IUCN status | SASSI listing | Co-occurrence strength |
|---|---|---|---|---|
| Crustacea | | | | |
| *Jasus lalandii* | West coast rock lobster | LC | Red | 0.09* |
| Teleostei | | | | |
| *Chrysoblephus laticeps* | Roman | NT | Orange | 0.07* |
| *Chrysoblephus gibbiceps* | Red stumpnose | EN | Red | 0.04* |
| *Rhabdosargus globiceps* | White stumpnose | VU | Red | 0.03* |
| *Petrus rupestris* | Red steenbras | EN | Red | 0.02* |
| *Diplodus capensis* | Blacktail | LC | Red | 0.007 |
| *Pomatomus saltatrix*† | Shad | VU | Red | 0.006* |
| *Atractoscion aequidens*† | Geelbek | VU | Red | 0.006* |
| *Umbrina robinsoni* | Slender baardman | NE | Red | 0.006 |
| *Diplodus hottentotus* | Zebra | LC | Red | 0.004 |
| *Gymnocrotaphus curvidens* | Janbruin | LC | Red | 0.004 |
| *Argyrosomus inodorus* | Silver kob | NE | Red | 0.004 |
| *Dichistius capensis*† | Galjoen | NE | Red | 0.004 |
| *Epinephelus marginatus*† | Yellowbelly rock cod | VU | Orange | 0.003 |

†Species with only one occurrence in the BRUV

other, and is therefore an ideal candidate to indicate site-level diversity (Pérez-García et al. 2016). The taxonomic and morphological similarity between the puffadder and dark catsharks encumbers conservation measures based on the former species alone, but both co-occurrence and centrality metrics indicate the dark catshark also had some of the strongest links in the community. The 'friendship paradox' borrowed from social-network theory, which postulates that species (the 'friends') linked to a species chosen at random are more central in the network than the originally chosen species, also provides evidence of the centrality of the dark catshark (Christakis and Fowler 2010; Pires et al. 2017). The co-occurrence patterns of the dark catshark, suggests it is the 'friend' of many species and thus central to the community. It was one of the strongest co-occurring species for each of 15 other species (i.e. it was one of the 'best friends' for these species). The species also associates with the habitat of the commercially important west coast rock lobster. Thus, together the puffadder catshark and dark catshark could form the basis of an umbrella species-complex, motivated further by the Near-Threatened status of the puffadder catshark. In addition to being highly central, the puffadder, pyjama, and leopard catsharks share habitat associations with species of conservation concern, including roman and red steenbras, species that are popular with anglers. The catsharks have some complementarity in habitat preference; although many are abundant on reefs and in kelp (Osgood et al. 2019), the tiger catshark associates strongly with sand, so that as part of an umbrella complex, inclusion of the species could protect diversity over a range of habitats.

Beyond chondrichthyans, our study also identified habitats and a few teleost species that could be used to select sites of conservation potential. Basing selection on habitat was almost as effective at forming speciose and abundant MPAs in our simulations as selecting sites based on chondrichthyan abundance, given that the quality of chondrichthyans as umbrella species comes from their association with productive reef and kelp habitats (Osgood et al. 2019). However, the small benefits observed from the MPAs that were simulated based on chondrichthyan abundance suggests chondrichthyan abundance yields slightly more-precise information on local diversity and abundance useful to MPA placement, other than MPAs that could benefit the west coast rock lobster, possibly due to their greater ubiquity in kelp habitats. Additionally, habitat quality is not well mapped along the Western Cape coastline, limiting its utility for targeting MPA placement. In contrast, the distribution of chondrichthyans, particularly catsharks, is accessible from substantial recreational and commercial fishing effort, and fishery independent surveys. Two teleost species, roman and hottentot seabream, are also potentially effective umbrella candidates since both co-occur with many species in the community. Roman was rarer on our BRUVs than chondrichthyans and not as prevalent across habitats: catsharks had higher co-occurrence and centrality. However, roman is charismatic in South Africa because of its popularity in recreational fisheries and as a food source, so the species could be used in tandem with a chondrichthyan umbrella species-complex in local marketing and research campaigns. Ultimately, the close association of roman with chondrichthyans should help motivate the latter as an umbrella species-complex. Comparatively, hottentot seabream, found predominantly on reefs, does not associate with the same breadth of habitat as do chondrichthyans, and the species is not as charismatic, limiting its potential as either an umbrella or flagship species (Roberge and Angelstam 2004; Roberson et al. 2015).

We propose that chondrichthyans, especially a subset including catsharks and at least the broadnose sevengill shark, should be used as an umbrella species-complex in the Western Cape Province. Additional research on the relationship of these species to different habitats and seascape elements is required to assess their appropriateness for different conservation goals and target species, as co-occurrence can change with time and context (Cushman et al. 2010; Tulloch et al. 2016; Stuber and Fontaine 2018). More-detailed knowledge of multiscale habitat associations that could be used in species-distribution modelling would solidify the ecological suitability of chondrichthyans as umbrella species (MacPherson et al. 2018). Additionally, more data will be needed on the relationship of chondrichthyans to the less-frequently observed species. The bird, mammal and squid species, as well as a few teleost species (e.g. pipefish *Syngnathus temminckii*, silver kob *Argyrosomus inodorus*, and zebra *Diplodus hottentotus*), were observed only opportunistically on the BRUVs, likely because of a combination of rarity and BRUV selectivity. The results were not greatly affected by these sightings, and so more BRUV work, including sampling in the evening and at night, combined with other methods of sampling besides BRUVs, could be done in the future to test chondrichthyan associations with these species.

Chondrichthyans could also serve as a flagship–umbrella species-complex, as they have a cultural presence both internationally and locally in South Africa, and, given the high charisma of sharks in general, attitudes could be shifted for the less-charismatic species with targeted marketing and educational programmes (Albert et al. 2018; Curtin and Papworth 2018). Because of their endemism, catsharks are ideal for raising awareness of South Africa's unique, evolutionarily distinct chondrichthyan biota (Ebert and van Hees 2015). Marketing could also raise the potential of chondrichthyans for the conservation of species like roman. Conservation initiatives are already starting to turn to smaller species when large charismatic species are absent (Kalinkat et al. 2017), and this might be an effective approach in the highly impacted coastal ocean of the Western Cape. However, the spread of the broadnose sevengill shark into former white shark hotspots foreshadows a future for this larger, charismatic species as a flagship in the lucrative shark-related tourism industry of the country (Gallagher and Hammerschlag 2011; Hammerschlag et al. 2019). Chondrichthyans are charismatic, highly connected, and abundant in South Africa, creating promise for them as a flagship–umbrella species-complex. Since successful flagship species on the international stage do not always translate to charisma at the local level, the cultural suitability for different marine species to serve as flagships in South Africa needs to be investigated (Caro 2015; Jepson and Barua 2015). If research into how communities engage with chondrichthyans, both in South Africa and abroad, is incorporated into effective conservation marketing, the taxon could attract conservation attention and funds on both the local and international level (Jepson and Barua 2015; Macdonald et al. 2017). When resources are scarce and diversity is threatened, chondrichthyans can serve as an ecologically, as well as culturally, suitable set of surrogate species to optimise conservation in South Africa.

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