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Abstract
Large predatory fish that alter the behaviour of smaller species may affect visual estimates of abundance by making organisms more or less difficult to observe and quantify. To evaluate the non-consumptive influence of large predators on rocky reef fishes observed with Baited Remote Underwater Video (BRUV), we tested the hypothesis that fish assemblages monitored when large (ca 1.5 m) piscivorous sharks, Mustelus antarcticus, were present differ from those observed when sharks were absent. We did this in two ways using recordings from rocky reefs in Batemans Marine Park, NSW, Australia. First, we examined 6 min of each 30 min tape; 3 min when sharks were present and 3 min when they were absent, in a paired sample design from 17 sites. Second, we compared fish assemblages for complete tapes (30 min) at sites with sharks present compared to sites where they were absent. The diversity and total abundance of fishes was consistently lower in the presence of sharks; we detected significant assemblage-wide change (PERMANOVA, $P < 0.05$). Importantly, the diversity and total abundance of fishes for complete tapes (30 min) decreased in the presence of sharks by 18 % and 36 %, respectively, underscoring the likelihood that sharks influence observed fish assemblages. Individual species responses were variable and while the abundance of many fish species decreased in response to sharks, others increased 6-fold. Overall, these results highlight the need to consider systematic differences in the abundance of large predators to avoid biases when testing hypotheses about fish assemblages using non-destructive visual methodologies.

The influence of gummy sharks, *Mustelus antarcticus*, on observed fish assemblage structure

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Abstract

Large predatory fish that alter the behaviour of smaller species may affect visual estimates of abundance by making organisms more or less difficult to observe and quantify. To evaluate the non-consumptive influence of large predators on rocky reef fishes observed with Baited Remote Underwater Video (BRUV), we tested the hypothesis that fish assemblages monitored when large (ca 1.5 m) piscivorous sharks, *Mustelus antarcticus,* were present differ from those observed when sharks were absent. We did this in two ways using recordings from rocky reefs in Batemans Marine Park, NSW, Australia. First, we examined 6 mins of each 30 min tape; 3 mins when sharks were present and 3 mins when they were absent, in a paired sample design from 17 sites. Second, we compared fish assemblages for complete tapes (30 mins) at sites with sharks present compared to sites where they were absent. The diversity and total abundance of fishes was consistently lower in the presence of sharks; we detected significant assemblage-wide change (PERMANOVA, $P<0.05$). Importantly, the diversity and total abundance of fishes for complete tapes (30 mins) decreased in the presence of sharks by 18% and 36%, respectively, underscoring the likelihood that sharks influence observed fish assemblages. Individual species responses were variable and while the abundance of many fish species decreased in response to sharks, others increased 6-fold. Overall, these results highlight the need to consider systematic differences in the abundance of large predators to avoid biases when testing hypotheses about fish assemblages using non-destructive visual methodologies.

Additional Keywords: Species interactions, elasmobranch, predator avoidance, fish species composition, rocky reef fishes.

Introduction

Large marine predators can alter the behaviour and space-use patterns of smaller species without actually killing them (Grabowski and Kimbro 2005; Wirsing *et al.* 2008). In the presence of a large marine predator (e.g. sharks, seals, dolphins, etc.) smaller fish may employ a range of strategies to minimise predation risk, such as (i) moving to an area with fewer predators or greater protection, (ii) utilising camouflage or defensive adaptations, (iii) reducing conspicuous behaviours or increasing vigilance, (iv) altering the timing of activities or (v) schooling (Lima & Dill 1990; Pitcher 1993; Godin 1997). In general, predator-response behaviours have energetic costs reducing the time available for other essential activities (e.g. foraging, courtship, etc.) leading to risk-based trade offs (Lima and Dill 1990; Lima 1998) with potentially strong ecological consequences (Frid *et al*. 2008). Predator-response behaviours can also influence visual estimates of abundance of marine organisms by making them either more or less difficult to observe and quantify (Wirsing *et al.* 2007; Wirsing *et al.* 2008). In some cases, predator-response behaviours that affect visual quantification may be induced by an actual threat (e.g. sharks, seals, etc.). However, in other cases the threat may simply be perceived by the organism being sampled. For example, it is well known that reef fish respond either positively or negatively to divers undertaking visual surveys influencing their estimates of fish assemblages (Cole 1994; Kulbicki 1998; Willis and Babcock 2000; Watson and Harvey 2007). Such biases need to be carefully considered when hypotheses require comparisons of areas where systematic differences in large predators may exist (e.g. comparisons of areas inside and outside 'no take' marine reserves). Given the increasing importance of quantitative visual assessments in marine conservation and fisheries management, it is necessary to investigate potential biases in these methodologies to ensure management decisions and policies are made using the best available information.

Baited Remote Underwater Video (BRUV) is a relatively new and cost-effective tool for assessing the diversity and abundance of fishes (Willis and Babcock 2000; Cappo *et al.* 2004).

This technique has been used extensively in marine reserves, where non-destructive sampling of fish populations is desirable, and at depth considered unsafe for SCUBA (e.g. Babcock *et al.* 1999; Malcolm *et al.* 2007; Zintzen *et al.* 2011). The efficacy of BRUV methodology has been assessed by comparisons with other census techniques such as Underwater Visual Census (UVC) (Willis and Babcock 2000; Colton and Swearer 2010; Watson *et al.* 2010); UVC and angling (Willis *et al*. 2000), and trawling (Cappo *et al*. 2004). In general, it has been concluded that BRUV provides robust estimates of fish diversity and abundance, yielding almost the same or significantly higher estimates compared to other methods. Nevertheless, anecdotal evidence suggests that observations of reef fish assemblages made using BRUV may be strongly influenced by the presence of large elasmobranchs and seals (authors' personal observations).

We sought to investigate effects of large predators on BRUV studies by recording the responses of reef fishes to the presence of gummy sharks, *Mustelus antarcticus* (Günther 1870) in southern NSW, Australia. Gummy sharks are abundant off south-eastern Australia (Gomon *et al*. 2008) and are regularly observed in BRUV monitoring. They grow to ca. 1.7m in length and mostly feed on cephalopods and crustaceans, but are also known to take bony fish (Walker 2007; Gomon *et al*. 2008). The presence of gummy sharks has the potential to invoke avoidance behaviour in fishes, which in turn can influence the observed fish diversity and abundance using BRUV because of its limited field of view. To investigate the influence of shark presence on BRUV monitoring, we tested the hypothesis that the observed fish assemblages on videos with sharks present would differ from those observed when sharks were absent.

Materials and methods

Study site and collection methods

Between January and May 2008, 96 sites were sampled with BRUV in the Batemans Marine Park on the south coast of New South Wales, Australia. This 85,000 ha multi-use Park was declared in

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June 2007 and includes NSW State waters (3 nm from the coast) from Bawley Point (35º31.87'S) to Wallaga Lake (36º22.290'S). For each site, a frame containing a video camera (mini DV SONY) and bait bag was deployed on rocky reef for more than 30 minutes duration at depths of 20-40 m. Cameras were housed within high-pressure PVC (polyvinyl chloride) pipe with flat acrylic end-ports yielding a field of view of 110°. The bait bag was at the end of 1.5 m long bait arm held in a horizontal orientation to the substratum (Fig. 1). Prior to each deployment, the bait bag was filled with 400 g of crushed pilchards (*Sardinops sagax*).

Fig. 1 A gummy shark, *Mustelus antarcticus*, approaches as a silver sweep, *Scorpis lineolata*, and a school of mado, *Atypichthys strigatus,* congregate around the BRUV bait bag at a site in Batemans Marine Park, NSW Australia.

Video analysis

In order to test hypotheses, sites (tapes) were used in which gummy sharks were visible for at least 5 mins. For 17 sites that fitted this criterion, we analysed influence of sharks on observed fish assemblages in two ways. First, we quantified fish assemblage data from 3 mins of video in which sharks were present and a further 3 mins of the same video in which sharks were absent, drawn at random from each tape – a paired sample design. In this way we minimised the site-related variation in the data set. We ensured that at least 5 mins separated the two segments we

viewed on each tape. Second, we reviewed diversity and abundance of fish for the entire 30 minutes of tape and contrasted this with tapes from 17 different sites in which sharks did not appear, making 34 sites in total. The sites with sharks absent were randomly selected via random number generation. We note that there is a chance of spatial confounding in these data as there may be differences in fish assemblages at sites independent of the presence of sharks. We are not aware of any reason why this may be the case, but recommend interpreting these data cautiously.

In each 3 minute segment of tape and for the entire tape, we recorded species diversity and total *max* N. The metric, *max* N, is the maximum number of fish observed of any given species in a single frame. Although this provides an independent measure of the abundance of each fish species, it is likely to underestimate total abundance. We used a field of view two metres behind the bait bag, which represents a standardised area of $9.4m^3$ (Malcolm et al. 2007). This distance was estimated from the size of the bait bag (15cm in diameter) and allowed comparison between tapes with variable underwater visibility. Tapes with significant portions of the field of view obscured were rejected. For each tape and segment of the tape, we also determined the *max* N of six common fish species (mado [*Atypichthys strigatus* (Günther 1860)], silver sweep [*Scorpis lineolata* (Kner, 1865)], maori wrasse [*Ophthalmolepis lineolatus* (Valenciennes, 1839)], yellowtail scad [*Trachurus novaezelandiae* (Richardson 1843)], snapper [*Pagrus auratus* (Bloch & Schneider, 1801)] and chinaman leatherjacket [*Nelusetta ayraudi* (Quoy and Gaimard, 1824)]).

Statistical analyses

Multivariate hypotheses about fish assemblages were tested with PERMANOVA (Anderson 2001). In comparing three minute sections of video we analysed two-factors in a repeated measures design; shark presence and absence (fixed with 2 levels) and sites (random with 17 levels), with the interaction term being excluded (Anderson *et al.* 2008). For each analysis, Bray Curtis distances were generated from untransformed data.

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Prior to analysis of univariate variables, a Quantile-Quantile plot was used to test the assumption of normality. For the variables with normal distributions, hypotheses were tested with either a paired sample *t*-test or a standard *t*-test depending on whether fish were being compared within 3 minute segments or among sites with and without sharks, respectively. Where data were not normal, we used a Wilcoxon signed-rank test (Zar 1999).

Results

The first appearance of gummy sharks on a tape was spread across the 30 minute period of recording and ranged from 3 minutes 2 seconds through to near the end of recordings, with a mean (±SE) of 19 minutes 29 seconds (±2 minutes 23 seconds). Sharks maintained a presence on a tape from between 25 to 2160 seconds. On average (±SE) they were present for 471±15 seconds, which equates to almost 8 minutes.

In comparisons of 3 minute segments within a tape, the presence of gummy sharks significantly influenced the structure of the fish assemblages observed with BRUV (PERMANOVA, Pseudo-$F_{1,16}$=2.19, *P*<0.05). Univariate comparisons of 3 minute segments showed reduced relative abundance (total *max* N) and diversity of fish assemblages when gummy sharks were present, although these trends were not statistically significant (t=1.66 df=16 *P*=0.116; t=1.53 df=16 *P*=0.145; Table 1). In addition, four of the six common species (silver sweep, maori wrasse, yellowtail scad and snapper) were significantly less abundant when gummy sharks were present. In contrast, mado and chinaman leatherjacket were significantly more abundant in the presence of gummy sharks. For mado, there was a 15% increase, while chinaman leatherjacket were almost 6-fold more abundant.

Table 1: Summary of diversity and abundance (*max* N) from segments of video tape (3 minutes) in the presence and absence of gummy sharks (*Mustelus antarcticus*) in a paired-sample design (n=17). Univariate response variables are presented, as well as results of SIMPER analyses (untransformed data). Only species contributing >5% to the overall dissimilarity are presented. Average dissimilarity between the two groups = 82.8%. Data for individual

species was not normal and were analysed with a Wilcoxon signed-rank test. We present Median and third Quartiles as well as Mean (± SE).

Variable	Shark present Mean (SE)	Shark absent Mean (SE)	Shark present Median (Q_3)	Shark absent Median (Q_3)	P	SIMPER Contrib %
Diversity	3.9 (0.5)	4.5 (0.5)	-	-	0.145	-
Total *max* N	9.5 (2.5)	12.2 (2.8)	-	-	0.116	-
Mado (*Atypichthys strigatus*)	3.8 (2.0)	3.2 (1.5)	0 (3.5)	0 (3)	<0.001	22.9
Silver sweep (*Scorpis lineolata*)	1.2 (0.5)	1.7 (0.8)	0 (1.5)	0 (3)	<0.001	13.3
Maori wrasse (*Ophthalmolepis lineolatus*)	1.2 (0.3)	1.8 (0.4)	1 (2)	2 (2)	<0.05	11.2
Yellow-tailed scad (*Trachurus novaezelandiae*)	0.3 (0.2)	1.8 (1.5)	0 (0)	0 (0.5)	<0.001	8.2
Snapper (*Pagrus auratus*)	0.5 (0.2)	0.6 (0.3)	0 (1)	0 (1)	<0.001	7.4
Chinaman leatherjacket (*Nelusetta ayraudi*)	0.5 (0.2)	0.1 (0.1)	0 (1)	0 (0)	<0.001	5.9

Comparisons of the entire 30 minutes tapes with and without sharks demonstrated that the abundance (total *max* N) of fish was significantly reduced in sites at which gummy sharks were present (t=2.3, df=32, $P < 0.05$, Fig. 2). A similar trend was apparent for the diversity of fishes, but it proved marginally non-significant (t=1.7, df=32, $P = 0.09$). We did not detect impacts in the overall composition of the assemblage however (PERMANOVA, Pseudo-$F_{1,32}$=1.26, P=0.23). In contrast to analyses of 3 minute segments, there were no significant differences in the *max* N of mado (t=1.6, df=32, $P = 0.12$), silver sweep (t=1.49, df=32, $P = 0.15$), maori wrasse (t=0.10, df=32, $P = 0.92$), yellowtail scad (t=0.9, df=32, $P = 0.35$), snapper (t=0.74, df=32, $P = 0.45$) and chinaman leatherjacket (t=0.24, df=32, $P = 0.81$) (Fig. 2) in 30 min comparisons.

Discussion

Impacts of predators on BRUV data

The presence of gummy sharks influenced the structure of fish assemblages we observed using BRUV. Comparison of the 3 minute segments with and without sharks on a single video tape, revealed significant shifts in fish assemblage structure and abundances of common species.

Although the species diversity and abundance (total *max* N) were reduced by 13% and 22% respectively when sharks were present, we failed to detect significant changes. However, if the swamping effects of the common planktivorous mado were removed from comparisons of total *max* N within 3 minute segments, there were significantly fewer fish observed when sharks present than when they are absent ($t=2.1$, df=16, $P < 0.05$). Similar to these 3 minute segments, the abundance (total *max* N) and diversity of fish assemblages over 30 minutes at sites with sharks was 36% and 18% lower than at sites without sharks, respectively. We contend, therefore, that either the perceived or actual threat from large predatory species may bias outcomes when using visual techniques, such as BRUV, to assess fish community structure. Moreover, studies that overlook the non-consumptive effects of predation may underestimate the overall impact predators have on their communities (Wirsing et al. 2008).
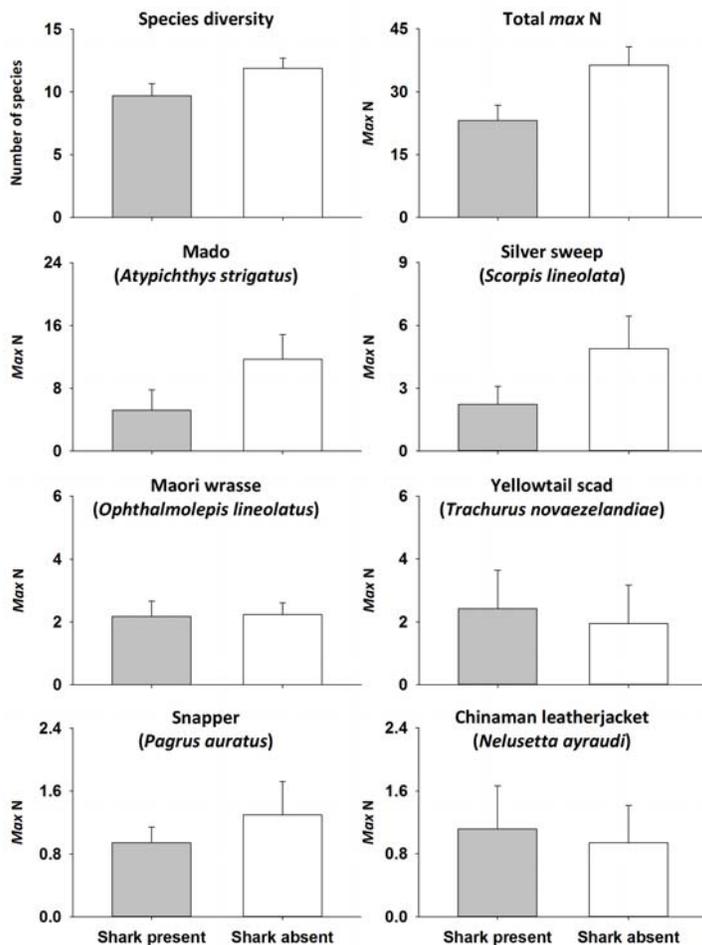

Fig. 2 Mean (±1 SE) diversity, Total *max* N as well as *max* N for common fish species from 30 minute comparisons (n=17). Sharks present and absent are indicated by grey and white bars, respectively. * *P*<0.05.

Individual fish species responded differently to the presence of sharks. Most species moved away from the bait when gummy sharks were present and this was particularly noticeable for yellowtail scad with relative abundance (*max* N) declining 6-fold; an observation consistent with predator avoidance behaviour. In contrast to fish species that moved away from the bait in the presence of sharks, the relative abundance of mado and chinaman leather jacket increased when sharks were present. These species are generally attracted to disturbances, making the commotion associated with the presence of relatively large sharks a potential attractant. Alternatively, the presence of large sharks attacking the bait bag may enhance the dispersion of the bait plume and associated particles, producing tradeoffs in their use of space by potential prey. Consequently, species may use energetically profitable locations despite the risks (Lima 1998). An additional explanation may be the existence of complex species interactions which cascade through the assemblage when sharks are present; so their presence displaces one species which allows another to increase in number. Other workers have observed complex territorial intra and inter-specific interactions among fishes around BRUVs (Willis et al. 2003; Fetterplace 2011; anon. reviewer, pers. comm.).

Similar to these 3 minute segments, the abundance (total *max* N) and diversity of fish assemblages over 30 minutes at sites with sharks were depressed by 36% and 18% respectively. However, these similarities were not reflected in comparisons of the abundances of common species. There may be several explanations for these results. First, fish can respond quickly to the presence of a predation threat, but may return to a bait shortly after a large predator moves away. As the amount of time gummy sharks were observed varied substantially over the 30 min tapes (ca. 8 minutes on average), the differences in *max* N among sites with and without sharks should thus be less pronounced than the paired-comparisons of 3 minutes segments within sites. Second, inter-site differences (e.g. structural complexity, hydrodynamics, food availability or reproductive potential, etc.) also influence fish assemblage structure (Kingsford and Battershill

1998) increasing variation in the structure of fish assemblages and decreasing effect sizes associated with predator-response behaviours. Third, sharks may have been near the bait and influencing fish assemblages, but remained out of the field of view as has been shown for scavengers (Collins *et al*. 1999). This is unlikely to have occurred regularly, however, because sharks tend to circle an area before approaching a bait making it likely that they will appear in the field of view at some stage.

Implications for BRUV sampling

Comparing results from 3 vs. 30 min comparisons made in this study allows some consideration of how predator-response effects on BRUV data may vary in response to different BRUV deployment times. We note that increased deployment times did not diminish the impact of predator-response behaviours on *max* N or diversity. If fish behaviours change rapidly in the presence of a large predator, increasing the drop (soak) time of each BRUV relative to the average time sharks are observed around the bait bag (perhaps calculated via a pilot study) will reduce biases associated with predator-responses when estimating abundance via *max* N. This is because *max* N is an instantaneous measure of fish abundance that can occur at any time during an individual BRUV drop (i.e. either when sharks are present or absent). We also note that even at the longer deployment time of 30 min, predator-response behaviour means that less common and rare species are likely to be under-estimated in the presence of sharks, given that common species abundances were the same but total *max* N and diversity were significantly lower. However, the results also show that under-estimation of individual species abundances are likely to be less pronounced than additive community response variable such as total *max* N. Importantly, given sufficient quantitative information, it may also be possible to statistically correct for the effects of large predators on observed fish assemblages using BRUV (e.g. Anderson *et al*. 2005). Farnsworth and co-workers (2007) have made advances in quantitative

modeling in this regard; however, these techniques require accurate information about shark abundances.

Given that sharks can influence the observed structure of fish assemblages measured using BRUV, our results raise concerns over BRUV monitoring programs, particularly in situations where sharks are likely to systematically vary among treatments. For example, the effect sizes associated with observed differences between fish assemblages inside and outside 'no-take' marine reserves measured using BRUV may be biased by the occurrence of large predatory fishes. This is because large predators are more abundant in marine protected areas (see Lester *et al.* 2010) and as such their non-consumptive effects on smaller species will be greater inside that outside marine reserves. This problem would be further exacerbated in long-term monitoring programs or Before-After-Control-Impact experiments for newly established marine reserves where the abundance of sharks and other large predators continue to increase inside reserves compared to outside reserves through time (Roberts and Hawkins 2000). It should, however, be noted that this bias is likely to under-estimate overall fish abundance in areas with the larger abundances of sharks. Therefore, previous studies that have used BRUV to compare areas inside and outside no-take marine reserves have, if anything, underestimated effect sizes for most prey species (e.g. Babcock *et al.* 1999; Chapman *et al.* 2006; Watson *et al.* 2007).

Conclusions

Overall, we demonstrate that the structure of fish assemblages quantified using BRUV may be influenced by presence of sharks. This bias has potential to make comparisons of the total abundance of fish in areas with different predator abundances problematic because some of the variation will be attributable to small-scale behavioral responses to predators rather than genuine differences in fish population structures. Variation caused by behavioral responses to predators should, therefore, be carefully considered in long-term or large scale monitoring programs using

BRUV.

Large predators are clearly an integral part of the overall fish assemblage, nevertheless where their presence has the potential to introduce bias, researchers should consider increasing soak times, particularly if predators are present for relatively short periods. The use of longer soak times must be balanced against the dissolution of the bait plume however. We anticipate that long term BRUV monitoring programs in which numbers of large predators fluctuate markedly over time run the greatest risk of introducing bias to the overall dataset. Under these circumstances, we recommend that predator abundance be treated as a covariate in an attempt to minimize effects. Researchers and managers alike need to be aware of the potential for (i) long-term ecological consequences of changes in predator abundance (Lima 1998) and (ii) the introduction of bias in data sets generated by BRUV.

References

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26: 32-46. doi: 10.1111/j.1442-9993.2001.01070.pp.x

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software

and statistical methods. PRIMER-E, Plymouth

Anderson MJ, Millar RB, Blom WM, Diebel CE (2005) Nonlinear multivariate models of successional change in community structure using the von Bertalanffy curve. Oecologia 146:279–286. doi: 10.1007/s00442-005-0195-0

Babcock RC, Kelly S, Shears NT, Walker JW, Willis TJ (1999) Changes in community structure in temperate marine reserves. Mar Ecol Prog Ser 189:125–134. doi: 10.3354/meps189125

Brown JS, Kotler BP (2004) Hazardous duty pay and the foraging cost of predation. Ecol Lett 7:999–1014. doi: 10.1111/j.1461-0248.2004.00661.x

Cappo M, Speare P, De'ath G (2004) Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. J Exp Mar Biol Ecol 302:123–152. doi: 10.1016/j.jembe.2003.10.006

Chapman DDF, Pikitch EK, Babcock EA (2006) Marine parks need sharks? Science 312:526–527. doi: 10.1126/science.312.5773.526d

Cole RG (1994) Abundance, size-structure, and diver-oriented behaviour of three large benthic carnivorous fishes in a marine reserve in northeastern New Zealand. Biol Conserv 70: 93-99. doi: 10.1016/0006-3207(94)90276-3

Collins M, Yau C, Nolan C, Bagley P, Priede I (1999) Behavioural observations on the scavenging fauna of the Patagonian slope. J Mar Biol Ass of the UK 79:963–970. doi: 10.1017/S0025315499001198

Farnsworth KD, Thygesen UH, Ditlevsen S, King NJ (2007) How to estimate scavenger fish abundance using baited camera data. Mar Ecol Prog Ser 350:223–234. doi: 10.3354/meps07190

Fetterplace L (2011) Sand barrens or thriving oasis: sanctuary zone effects on soft sediment fish assemblages. Unpublished B. Mar. Sci. (Hons) thesis, University of Wollongong Pp.107

Frid A, Baker GG, Dill LM (2008) Do shark declines create fear-released systems? Oikos

117:191–201. doi: 10.3354/meps07190

Godin JJ (1997) Behavioural Ecology of Teleost Fishes. Oxford University Press, Oxford

Gomon M, Bray D, Kuiter R (2008) Fishes of Australia's Southern Coast. Reed New Holland, Sydney

Grabowski JH, Kimbro DL (2005) Predator-avoidance behavior extends trophic cascades to refuge habitats. Ecology 86:1312–1319. doi: 10.1890/04-1216

Kingsford MJ (1998) Reef fishes. In: Kingsford MJ, Battershill, C (eds) Studying temperate marine environments. pp 132–165

Kulbicki M (1998) How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. J Exp Mar Biol Ecol 222: 11-30. doi: 10.1016/S0022-0981(97)00133-0

Lester S, Halpern BS, Grorud-Colvert K, Lubchenco J, Ruttenberg BI, Gaines SD, Airamé S, Warner RR (2009) Biological effects within no-take marine reserves: a global synthesis. Mar Ecol Prog Ser 384:33–46. doi: 10.3354/meps08029

Lima SL, Dill LM (1990) Behavioural decisions made under the risk of predation: a review and prospectus. Can J Zoolog 69:619–640. doi: 10.1139/z90-092

Lima SL (1998) Nonlethal effects in the ecology of predator-prey interactions: what are the ecological effects of anti-predator decision-making? Bioscience 48:25–34. doi: 10.2307/1313225

Malcolm HA, Gladstone W, Lindfield S, Wraith J., Lynch TP (2007) Spatial and temporal variation in reef fish assemblages of marine parks in New South Wales, Australia—baited video observations. Mar Ecol Prog Ser 350:277–290. doi: 10.3354/meps07195

Pitcher TJ (1993) Behaviour of Teleost Fishes, 2nd edition. Chapman and Hall, London

Roberts CM, Hawkins JP (2000) Fully-protected marine reserves: a guide. WWF Endangered Seas Campaign, Washington DC

Walker TI (2007) Spatial and temporal variation in the reproductive biology of gummy shark

Mustelus antarcticus (Chondrichthyes: Triakidae) harvested off southern Australia. Mar Freshwater Res 58:67–97. doi: 10.1071/MF06074

Watson DL, Harvey ES (2007) Behaviour of temperate and sub-tropical reef fishes towards a stationary SCUBA diver. Mar Freshw Behav Phy 40:85–103. doi: 10.1080/10236240701393263

Watson DL, Harvey ES, Fitzpatrick BM, Langlois TJ, Shedrawi G (2010) Assessing reef fish assemblage structure: how do different stereo-video techniques compare? Mar Biol 157:1237–1250. doi: 10.1007/s00227-010-1404-x

Watson DL, Harvey ES, Kendrick GA, Nardi K, Anderson MJ (2007) Protection from fishing alters the species composition of fish assemblages in a temperate-tropical transition zone. Mar Biol 152:1197–1206. doi: 10.1007/s00227-007-0767-0

Willis TJ, Babcock RC (2000) A baited underwater video system for the determination of relative density of carnivorous reef fish. Mar Freshwater Res 51:755–763. doi: 10.1071/MF00010

Willis TJ, Millar RB, Babcock RC (2000) Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. Mar Ecol Prog Ser 198:249–260. doi: 10.3354/meps198249

Willis TJ, Millar RB, Babcock RC (2003) Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. J Appl Ecol 40: 214-227. doi: 10.1046/j.1365-2664.2003.00775.x

Wirsing AJ, Heithaus MR, Dill LM (2007) Fear factor: do dugongs (*Dugong dugon*) trade food for safety from tiger sharks (*Galeocerdo cuvier*)? Oecologia 153:1031–1040. doi: 10.1007/s00442-007-0802-3

Wirsing AJ, Frid A, Dill LM (2008) Seascapes of fear: evaluating sublethal predator effects experienced and generated by marine mammals. Mar Mammal Sci 24:1–15. doi: 10.1111/j.1748-7692.2007.00167.x

Zar JH (1999). Biostatistical Analysis 4th Edn. Prentice-Hall, New Jersey

Zintzen V, Roberts D, Anderson MJ, Stewart AL, Struthers CD, Harvey ES (2011). Hagfish predatory behaviour and slime defence mechanism. Sci Reports 1:131, 1–6. doi: 10.1038/srep00131