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Do agonistic behaviours bias baited remote underwater video surveys of fish?

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Abstract

Marine environments require monitoring to determine the effect of climate change, human development, pollution and conservation measures. Marine protected areas are being established globally and require periodic monitoring to determine whether their objectives are being met. Baited underwater video systems are becoming a popular method for monitoring change within protected fish populations, because they are less damaging to habitats than more established methods such as bottom trawling and allow for more statistical powerful relative comparisons and to determine spatial and temporal patterns and trends in the relative abundances, lengths and biomass of demersal and pelagic fishes. However, much remains uncertain about how interactions between the fish and bait and between the fish themselves affect the results obtained. Agonistic behaviours are frequently observed around the bait of the camera and potentially bias fish density estimates by altering the number and size classes seen at cameras. Here we counted the number of agonistic behaviours between pink snappers (*Pagrus auratus*), the size of fish involved and whether the fish left the field of view following such behaviours. The study consisted of 20 baited underwater video deployments inside a New Zealand marine reserve and 20 in adjacent open areas, providing a large range of fish densities. We observed a significant relationship between the peak number of fish observed at the camera and the total number of agonistic behaviours, as well as the number of both aggressor and subordinate fish leaving the camera field of view following interactions. The slope of the latter relationship and thus the absolute numbers of fish leaving were higher for subordinate fish. As subordinates were significantly smaller than aggressors the apparent size frequency distribution is likely skewed away from smaller size classes. The staying time of the fish and thus the maximum number of fish present at the camera will be reduced by agonistic behaviours and the absolute magnitude of this effect appears to be greater at high fish densities. Our results suggest that an overall effect of these phenomena is to underestimate the differences in abundance between MPAs and open areas, but also to overestimate differences in average size.

Introduction

Marine coastal areas are increasingly being subjected to anthropogenic disturbances (Marinesque et al. 2012). To reduce these pressures and slow the resultant loss of marine biodiversity the parties to the Convention on Biological Diversity (CBD) agreed to aim for “at least 10% of each of the world’s marine and coastal ecological regions effectively conserved by 2020” (Fox et al. 2012). One tool to reach these conservation aims is the establishment of marine protected areas (MPAs); defined by Kelleher & Kenchington in 1992 as "an area of intertidal or sub-tidal terrain, together with its overlying water and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environments". In response to the CBD and other agreements MPA networks are being developed globally to help conserve marine ecosystems (O'Leary et al. 2012).

In some MPAs it is hoped that protection from fishing pressures will allow targeted species to recover, increasing in abundance and achieving more natural size frequency distributions (Willis et al. 2003; Jennings 2009). Therefore, it is important that fish populations inside MPAs are monitored to determine whether these management objectives are being met (Watson et al. 2005). In temperate regions the monitoring of fish populations is often conducted via trawl surveys which can provide detailed data on the size, age and abundance of fish assemblages (Cronin et al. 2012). Bottom trawl surveys are considered inappropriate in MPAs due to their destructive nature and are impractical in many nearshore areas owing to shallow depths and obstructions on the sea bed (Fernandes et al. 2003). The development of further non-destructive methods to survey inshore fish populations has been recommended and remotely operated camera systems are a possible solution (Ellis & DeMartini 1995, Cappo et al. 2001, 2003 and 2006).

Baited underwater video (BUV) cameras are now widely used in the assessments of fish biodiversity, relative density (Watson et al. 2005; Heagney et al. 2007; Malcolm et al. 2007) and stock size structure (Harvey et al. 2002; Willis et al. 2003; Willis & Millar 2005). The increased attraction of carnivorous fish to the BUC makes it less likely to produce low or zero abundance estimates allowing for more statistical powerful relative comparisons and to determine spatial and temporal patterns and trends in the relative abundances, lengths and biomass of demersal and pelagic fishes (Willis et al. 2000, Wills and Babcock, 2000, Stoner et al. 2008). BUV have been used to monitor fish populations within several MPAs; and have recorded an increase in coral trout abundance (*Plectropomus leopardus*) in deep reef areas of the Great Barrier Reef (Cappo et al. 2012) and the response of reef fish assemblages to protection in Western Australia (Harvey et al. 2012).

As well as abundance estimates BUV cameras also provide insight into the behaviour of fish and in particularly the behaviours performed during foraging (Jamieson et al. 2006). BUV surveys have allowed both inter and intra-specific agonistic behaviours between fish to be observed (Armstrong et al. 1992; Jones et al. 2003; Cappo et al. 2004, 2007; Farnsworth et al. 2007; Stoner et al. 2008) and some studies have highlighted the possibility that fish may be discouraged from approaching a BUV by the presence of another fish (Jones et al. 2003). These studies have suggested that fish commonly avoid competition (Willis et al. 2003) or predation by larger or more aggressive individuals around the camera (Lampitt et al. 1983; Cappo et al. 2004, 2007; Harvey et al. 2007). It has been speculated that this could result in large size cohorts dominating and becoming overrepresented in BUV data at the expense of non-aggressive species, sizes and trophic groups (Stoner & Ottmar 2003; Harvey et al. 2007; Malcolm et al. 2007; Stoner et al. 2008). In general, the attraction of feeders to a spatial concentration of resources can promote an increase in agonistic behaviours; behavioural adjustments associated with fighting including attack, escape, threat, defence and appeasement (Scott & Fredericson 1951). This has been documented in dominant convict cichlids (Cichlasoma nigrofasciatum) (Grant & Guha 1993) and Harris sparrows (Zonatrichia querula) (Rohwer & Ewald 1981) both defending clumped resources.

The potential impact of agonistic behaviours on the number of fish observed by the BUV, however, has not been quantified or examined in detail. Video observations of American lobsters (*Homarus americanus*) within traps found that larger lobsters excluded smaller individuals from entering and that agonistic behaviours between individuals had the greatest impact on the lobsters caught per unit effort. Lobster population estimates from these observations inside lobster traps would falsely conclude that they contained a much higher proportion of large individuals (Jury et al. 2001).

To appreciate the impact of the number of fish at the camera on the number of agonistic behaviours and leaving events a range of population densities with the minimum of differences in habitat, species composition and climate should be studied. Such local variation in fish population density can be found by comparing successful marine reserves to nearby open areas.

New Zealand was one of the first countries to establish a MPA network and now supports some of the world's oldest marine reserves (Denny et al. 2004; Marinesque et al. 2012). Cape Rodney to Okakari Point Marine Reserve (CROP), fully established in 1977, North Eastern Northland (Fig. 1) (Willis & Babcock 2000; Sivagura 2008) is the longest established reserve in New Zealand and has been extremely successful in the recovery of the snapper (*Pagrus auratus*). Snapper population in CROP were the first to be monitored using a novel remote BUV camera system (Willis et al. 2003; Willis & Millar 2005) which has recorded a higher number of individuals above the legal minimal catch limit (fork length > 270 mm) inside the reserve compared to outside (Babcock et al. 1999; Willis & Millar 2005). Surveys in 2003 recorded 27.7 times more snapper inside the reserve which was a significant increase from the previous surveys in 2001 and 2002 which recorded 10.39 and 12.81 more individuals (Taylor et al. 2005; Sivagura 2008). One reason for reserve establishment was to improve the spawning stock biomass of the populations through an increase in larger individuals that represent the reproductive element of the population (Willis et al. 2001).

The characteristics of the CROP provides an opportunity to quantify agonistic behaviours and their possible effects on estimates of snapper relative density between reserve and adjacent non-reserve areas. We quantified the number of agonistic interactions between snapper in BUV deployments inside the reserve and in adjacent non-reserve areas. Interactions could affect relative density estimates if they cause fish to leave the camera field of view therefore we examined how often fish left the camera field of view following an interaction. We predicted that the number of agonistic behaviours would increase with the number of fish as the camera and that the dominance of large aggressors would lead to the non-random departure of smaller subordinate size classes.

Material and Methods

Study Area

CROP (36°16' S, 174°48' E, n = 48), located in the North Western Hauraki Gulf, New Zealand, was fully established in 1977 (Willis et al. 2000). For the purpose of this survey, we broke the study area into 6 reserve and 6 non-reserve areas that represent the habitat variability of the area (Fig. 1). Within each area we randomly selected the deployment locations within the constraints of weather and current conditions and positioned the BUV system on relatively level bottom topography on soft substrate within 50 m of rocky reef habitat (Willis et al. 2003; Taylor et al. 2005).

We made twenty BUV deployments within the reserve and twenty at adjacent non-reserve sites, between May 28 and June 12, 2007, which were also part of the New Zealand Department of Conservation MPA fish monitoring programme. Reserve and non-reserve sites had similar habitats, consisting of both patchy and solid sub-tidal reefs and sand. At all study sites we made deployments at an overall depth range between 3 and 24.5 m.

Each BUV camera unit consisted of a SONY XC-999P high resolution colour video camera mounted on a stainless steel stand 115 cm above a triangular base. We pointed the camera vertically downwards towards a sealed and punctured plastic bait canister in the centre of the camera field of view, containing 4 fresh whole pilchards (*Sardinops neopilchardus*) and an external pilchard tied to the lid (Willis & Babcock 2000). We refreshed bait between deployments. To reduce field time we deployed two camera systems simultaneously. Both systems used a self-contained video camera in an underwater housing marked by a surface buoy to allow retrieval after a 30 minute video sequence had been recorded. The 30 minutes began from when the unit touched the seabed. We used no artificial light. The equipment and deployment methodology are described in further detailed in Willis & Babcock 2000 and Taylor et al. 2005.

Data Collection

We recorded the maximum number of P. auratus present in the BUV field of view at any one time in the entire 30 minute video sequence (Max_{sna}). This measure has been identified as the most suitable to quantify fish numbers in the BUV footage as it prevents the same fish being counted repeatedly (Willis & Babcock 2000; Willis et al. 2000). We developed an ethogram to describe the five agonistic behaviours observed between snapper (Table 1) and also described the scenarios under which the behaviour occurred and the possible responses of the aggressor and subordinate snapper. Studies that have described similar behaviours in other fish species were referenced in the ethogram. We used the ethogram to quantify the number of agonistic behaviours between snapper during each deployment. We documented whether snapper left the camera field of view immediately following an agonistic encounter, either as a subordinate or as an aggressor. Inter-specific agonistic behaviours were observed to occur, but represented only 25.06% of agonistic behaviours and were therefore deemed to have less of an impact on snapper numbers than intra-specific behaviours and were discounted from the study.

Size Categories

We also measured the fork length of each snapper involved in an agonistic interaction using image analysis software SigmaScan Pro and assigned to one of 7 size categories based on fork length (Table 2). Fish in size category 3 or below have a fork length below the recreational catch limit (270 mm) and were considered juveniles.

Data Analysis

Max_{sna}, the number of behaviours and leavings are count data and are over-dispersed, a variance greater than the mean, therefore the effect of reserve was modelling using a Generalized Linear Model (GLM) with a negative binomial distribution. Data sets with more than 50% zeros were modelled using a zero-inflated GLM with a negative binomial distribution in R (v2.15) using the statistical package pscl. GLMs have are particularly useful for modelled count data that has a non-normal distribution (Zeileis et al. 2008).

Size class data was over-dispersed, therefore the mean size class of aggressors and subordinates in non-reserve and reserve deployments was modelled using a zero-inflated or non-zero-inflated GLM with a negative binomial distribution.

The relationship between Max_{sna} and the number of agonistic behaviours and leaving events within reserve and non-reserve deployments was analysed using a zero-inflated or non-zero-inflated GLM with a negative binomial regression and compared to the null model using a likelihood ratio test.

Results

The maximum number of snapper observed in a single image (Max_{sna}) was significantly (z-value = -2.19, $P < 0.029$) higher in reserve (mean 16.5 ± SE 0.40) than in adjacent non- reserve sites (5 ± 0.65). Significantly (z-value = 3.80, P = 0.001) more agonistic behaviours were performed between snapper in the reserve (131.11 behaviours per deployment ± SE 3.84) than in non-reserve deployments (5 ± 0.65). In reserve deployments, significantly (z- value = -3.39, P = 0.001) more aggressors left the field of view following an agonistic behaviour (6.89 leaving events per deployment ± SE 0.29) than in non-reserve sites. Subordinates left the field of view more often than aggressors and the number of agonistic behaviours resulting in a subordinate leaving in the reserve deployments was significantly (z- value = -7.98, $P < 0.001$) higher (37.55 leaving events per deployment ± SE 1.61) than in non-reserve deployments (0.15 ± 0.03) (Fig. 2).

The mean size category of aggressors and subordinates was significantly (z-value = 6.32, $P < 0.001$ and z-value = 5.96, $P < 0.001$) larger inside the reserve (mean 4.89 ± SE 0.03 and 4.26 ± 0.05) than in non-reserve sites (3.14 ± 0.05 and 3.07 ± 0.07). The mean size category of aggressors were larger than the subordinates in reserve sites (z-value = 4.56, $P < 0.05$).

The number of agonistic behaviours increased with Max_{sna} in both reserve and non-reserve deployments (z-value = 8.39, $P < 0.001$)(Fig. 3a). The number of aggressors leaving the field of view after agonistic behaviours also increased significantly with Max_{sna}, but only in reserve deployments resulting in a significant interaction between Max_{sna} and protection status (z-value = 6.34, $P < 0.001$) (Fig. 3b). Subordinates left the field of view more often in deployments with higher recorded Max_{sna} in both reserve and non-reserve areas (z-value = 6.02, $P < 0.001$)(Fig. 3c).

Discussion

This study took advantage of the well established CROP and its dense snapper population to determine whether agonistic interactions are likely to influence the abundance of fish observed via BUV monitoring systems. The number of agonistic behaviours increased with the number of fish present within the BUV field of view as did the number of aggressors and subordinates leaving events following these interactions. The number of agonistic behaviours and leaving events were very low at non-reserve sites due to the low number of fish observed there. In these areas agonistic behaviours will have a limited impact on the Max_{sna} values recorded by the BUV. In addition it is likely that there will be a reduction in the number of subordinate fish (which are on average smaller fish) observed in reserve areas as a result of the greater instance of subordinate leaving events. This effect is likely to bias results towards larger size classes, especially at reserve sites where higher densities occur.

Previous studies have highlighted the possibility that fish may be discouraged from approaching the bait on a BUV by the presence of another aggressive, often larger, fish due an increased chance of competition (Jones et al. 2003; Willis et al. 2003; Cappo et al. 2004) or predation (Lampitt et al. 1983; Harvey et al. 2007). Guarding of the bait with agonistic behaviours by large aggressive individuals was observed particularly in high density reserve deployments. Malcolm et al. 2007 predicted that agonistic interactions may result in aggressive individuals dominating the bait and being overrepresented in BUV studies and Harvey et al. 2007 expressed concern that this may result in a reduction in the number of fish, especially of certain non-aggressive species and trophic groups.

A pattern of gradually increasing density of legal sized snapper has been observed through BUV surveys in the reserve between 1998 and 2002. The same level of population recovery has not been observed for juvenile snapper (Sivagura 2008) and this may be partly because of juveniles being partially excluded from the BUV field of view thus reducing their estimates. The build-up of numbers of fish at the camera (and thus the MAX_{sna} value obtained) is dependent on the abundance of the fish in the surrounding area and their staying time (Bailey & Priede 2002). Agonistic behaviours reduce staying time, especially for smaller fish.

From our examination of the agonistic behaviours occurring around the BUV it is plausible that more frequent agonistic behaviours exclude or remove fish from the field of view and as a result BUV studies may underestimate the difference in fish abundance between high and low density areas. The density of juvenile snapper in particular could be underestimated within the CROP reserve, making it difficult to determine the success of the CROP reserve on this age class, or to track the growth of cohorts. It is important to note, however, that agonistic interactions are not the only factor that may influence abundance estimates derived using BUV methodology. For example, the approachability of snapper to divers varies throughout the CROP reserve (Cole 1994). “Bolder” fish that allow divers to approach more closely are more common in the CROP reserve than in adjacent non-reserve areas (Cole 1994) and presumably may also be more likely to swim under a potentially threatening object such as a large camera stand. Such a situation could potentially lead BUV systems overestimating the difference in fish abundance between reserve and non-reserve areas (the opposite of the effect described here).

This study illustrates that the impact of agonistic behaviours and resultant leaving events on BUV density estimates will vary with fish population density and warrants further study to ensure that the method is generating accurate results of MPA success. Modelling approaches were developed in the deep sea to generate density estimates from BUV footage (Farnsworth et al. 2007) and this approach is beginning to be expanded into shallow water studies. Most modelling approaches used to date assume independent movement and behaviour by the animals involved. Other studies have presented evidence that this might not be the case (Armstrong et al. 1992; Jones et al. 2003; Cappo et al. 2007; Stoner et al. 2008) and the effect is quantified here. Improved modelling approaches will provide the opportunity to estimate absolute fish population densities but studies such as this are essential to provide underlying behavioural information. Agonistic behaviours also potentially prevent fish from entering the camera field of view at all and the current study would not be able to assess this affect. An additional camera viewing the BUV and the area outside the field of view would enable information to be gathered on the component of the fish population potentially excluded from the survey.

Baited underwater video systems with a horizontal view are now the most commonly used worldwide (Cappo et al. 2006; Harvey et al. 2012) and the vertical view system described in this study is generally only employed in the New Zealand Department of Conservation MPA fish monitoring programme. Horizontal BUV systems provide a larger field of view (Watson et al. 2005) than the vertical BUV, allowing those fish that are chased directly away from the bait to remain in the field of view. However, individuals chased to the right, left or towards the camera will leave the field of view. This study highlights that horizontal BUV systems have an advantage in reducing the number of individuals leaving the camera field of view following agonistic behaviours. However, individuals that do move further from the bait and the camera due to agonistic behaviours will be more difficult to identify and measure. This study illustrates that the impact of agonistic behaviours and resultant leaving events on BUV density estimates will vary with fish population density and warrants further study to ensure that the method is generating accurate results that properly assess the effects of MPA implementation.

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Conclusions

Snapper agonistic interactions have a greater potential to affect BUV density estimates in reserve sites due to an increase in the numbers of subordinate and aggressor fish leaving the field of view at higher population densities. As smaller individuals are more likely to be the subject of aggressive interactions than larger fish, it is likely that the observed size frequency is skewed upwards as a result. Agonistic behaviours in P. auratus cause fish to leave the camera field of view and this effect increases as more fish compete for the bait. This effect probably reduces the apparent difference in population density between the CROP reserve and adjacent open areas.

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References

Adams C.E., Huntingford F.A., Krpal J., Jobling M., Burnett S.J. (1995) Exercise, agonistic behaviour and food acquisition in Arctic charr, Salvelinus alpinus. Environmental Biology of Fishes, 43, 213–218.

Armstrong J.D., Bagley P.M., Priede I.G. (1992) Photographic and acoustic tracking observations of the behaviours of the grenadier Coryphaenoides (Nematoburus) armatus, the eel Synaphobranchus bathybius, and other abyssal demersal fish in the North Atlantic Ocean. Marine Biology, 112, 535–544.

Babcock R.C., Kelly S., Shears N.T., Walker J.W., Willis T.J. (1999) Changes in community structure in temperate marine reserves. Marine Ecology Progress Series, 189, 125–134.

Bailey D.M., Priede I.M. (2002) Predicting fish behaviour in response to abyssal food falls. Marine Biology, 141, 831–840.

Caballero C., Castro J.J. (1999) Effect of residence and size asymmetries upon the agonistic interactions between juvenile white-seabream (Diplodus sargus cadenati de la Paz, Bauchot and Daget, 1974). Aggressive Behavior, 25, 297–303.

Caballero C., Castro J.J. (2003) Effect of competitor density on the aggressiveness of juvenile white seabream (Diplodus sargus cadenati de la Paz, Bauchot and Daget, 1974).

Aggressive Behavior, 29, 279–284. Cappo M., Speare P., Wassenberg T.J., Harvey E., Rees M.,

Heyward A., Pitcher R. (2001) Use of Baited Remote Underwater Video Stations (BRUVS) to survey demersal fish – how deep and meaningful? In: Harvey E.S., Cappo M. (Eds). Direct Sensing of the Size Frequency and Abundance of Target and Non-target Fauna in Australian Fisheries. Fisheries Research and Development Corporation, Rottnest Island, Western Australia, 4–7 September 2000: 63–71.

Cappo M., Harvey E.S., Malcolm H., Speare P. (2003) Advantages and applications of novel 'video-fishing' techniques to design and monitor Marine Protected Areas. In: Beumer J.P., Grant A., Smith D.C. (Eds), Aquatic Protected Areas – What Works Best and How Do We Know? Proceedings of the World Congress on Aquatic Protected Areas. Australian Society of Fish Biology, Cairns, August 2002: 455–464.

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. Journal of Experimental Marine Biology and Ecology, 302, 123–152.

Cappo M., Harvey E.S., Shortis M. (2006) Counting and measuring fish with baited video techniques – an overview. In: Lyle J.M., Furlani D.M., Buxton C.D. (Eds), Cutting-edge Technologies in Fish and Fisheries Science. Australian Society for Fish Biology Workshop Proceedings, Hobart: 101–114.

Cappo M., De'ath G., Speare P. (2007) Inter-reef vertebrate communities of the Great Barrier Reef Marine Park determined by baited remote underwater video stations. Marine Ecology Progress Series, 350, 209–221.

Cappo M., Stowar M., Stieglitz T., Lawrey E., Johansson C., Macneil A. (2012) Measuring and communicating effects of MPAs on deep 'shoal' fisheries. Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia, 9–13 July 2012: 1–5.

Castro J.J., Caballero C. (1998) Dominance structure in small groups of juvenile white-seabream (Diplodus sargus cadenati de la paz, Bauchot and Daget 1974). Aggressive Behavior, 24, 197–204.

Castro J.J., Caballero C. (2004) Effect of the light intensity upon the agonistic behaviour of juvenile of white-seabream (Diplodus sargus cadenati de la paz, Bauchot and Daget, 1974). Aggressive Behavior, 30, 313–318.

Castro J.J., Santiago J.A. (1998) The influence of food distribution on the aggressive behaviour of juvenile white-seabream (Diplodus sargus cadenati de la paz, Bauchot and Daget, 1974). Aggressive Behavior, 24, 379–384.

Cole R.G. (1994) Abundance, size structure, and diver-oriented behaviour of three large benthic carnivorous fishes in a marine reserve in northeastern New Zealand. Biological Conservation, 70, 93–99.

Cronin M.A., Gerritsen H.D., Reid D.G. (2012) Evidence of low spatial overlap between grey seals and a specific whitefish fishery off the west coast of Ireland. Biological Conservation, 150, 136–142.

Denny C.M., Willis T.J., Babcock R.C. (2004) Rapid recolonisation of snapper Pagrus auratus: Sparidae within an offshore island marine reserve after implementation of no-take status. Marine Ecology Progress Series, 272, 183–190.

Ellis D.M., DeMartini E.E. (1995) Evaluation of a video camera technique for indexing the abundances of juvenile pink snapper, Pristipomoides filamentosus, and other Hawaiian insular shelf fishes. Fishery Bulletin, 93, 67–77.

Farnsworth K.D., Thygesen U.H., Ditlevsen S., King N.J. (2007) How to estimate scavenger fish abundance using baited camera data. Marine Ecology Progress Series, 350, 223–234.

Fernandes P.G., Stevenson P., Brierley A.S., Armstrong F., Simmonds E.J. (2003) Autonomous underwater vehicles: future platforms for fisheries acoustics. ICES Journal of Marine Science, 60, 684–691.

Fox H.E., Soltanoff C.S., Mascia M.B., Haisfield K.M., Lombana A.V., Pyke C.R., Wood L. (2012) Explaining global patterns and trends in marine protected area (MPA) development. Marine Policy, 36, 1131–1138.

Grant J.W.A., Guha R.T. (1993) Spatial clumping of food increases its monopolization and defense by convict cichlids, Cichlasoma nigrofasciatum. Behavioral Ecology, 4, 293–296.

Harvey E., Fletcher D., Shortis M. (2002) Estimation of reef fish length by divers and by stereo-video – A first comparison of the accuracy and precision in the field on living fish under operational conditions. Fisheries Research, 57, 255–265.

Harvey E., Cappo M., Butler J.J., Hall N., Kendrick G.A. (2007) Bait attraction affects the performance of remote underwater video stations in assessment of demersal fish community structure. Marine Ecology Progress Series, 350, 245–254.

Harvey E.S., Newman S., McLean D.L., Cappo M., Meeuwige J.J., Skepperb C.L. (2012) Comparison of the relative efficiencies of stereo-BRUVs and traps for sampling tropical continental shelf demersal fishes. Fisheries Research, 125, 108–120.

Heagney E.C., Lynch T.P., Babcock R.C., Suthers I.M. (2007) Pelagic fish assemblages assessed using mid-water baited video: standardising fish counts using bait plume size. Marine Ecology Progress Series, 350, 255–266.

Jamieson A.J., Bailey D.M., Wagner H.J., Bagley P.M., Priede I.G. (2006) Behavioural responses to structures on the seafloor by the deep-sea fish Coryphaenoides armatus: implications for the use of baited landers. Deep-Sea Research Part I: Oceanographic Research Papers, 53, 1157–1166.

Jennings S. (2009) The role of marine protected areas in environmental management. ICES Journal of Marine Science, 66, 16–21.

Jones E.G., Tselepides A., Bagley P.M., Collins M.A., Priede I.G. (2003) Bathymetric distribution of some benthic and benthopelagic species attracted to baited cameras and traps in the deep eastern Mediterranean. Marine Ecology Progress Series, 251, 75–86.

Jury S.H., Howell H., O’Grady D.F., Watson W.H. (2001) Lobster trap video: in situ video surveillance of the behaviour of Homarus americanus in and around traps. Marine and Freshwater Research, 52, 1125–1132.

Kelleher G., Kenchington R.A. (1992) Guidelines for Establishing Marine Protected Areas. A Marine Conservation and Development Report. International Union for Conservation of Nature and Natural Resources (IUCN), Gland, Switzerland.

Kudoh T., Yamaoka K. (2004) Territorial behavior in juvenile red sea bream Pagrus major and crimson sea bream Evynnis japonica. Fisheries Science, 70, 241–246.

Lampitt R.S., Merrett N.R., Thurston M.H. (1983) Inter-relations of necrophagous amphipods, a fish predator, and tidal currents in the deep sea. Marine Biology, 74, 73–78.

Malcolm H.A., Gladstone W., Lindfield S., Wraith J., Lynch T.P. (2007) Spatial and temporal variation in reef fish assemblages of marine parks in New South Wales, Australia – baited video observations. Marine Ecology Progress Series, 350, 277–290.

Marinesque S., Kaplan D.M., Rodwell L.D. (2012) Global implementation of marine protected areas: is the developing world being left behind? Marine Policy, 36, 727–737.

O’Leary B.C., Brown R.L., Johnson D.E., von Nordheim H., Ardron J., Packeiser T., Roberts C.M. (2012) The first network of marine protected areas (MPAs) in the high seas: the process, the challenges and where next. Marine Policy, 36, 598–605.

Rohwer S., Ewald P.W. (1981) The cost of dominance and advantage of subordination in a badge signaling system. Evolution, 35, 441–454.

Scott J.P., Fredericson E. (1951) The causes of fighting in mice and rats. Physiological Zoology, 24, 273–309.

Sivagura K. (2008) Cape Rodney to Okakari Point Marine Reserve and Tawharanui Marine Park Fish (Baited Under Water Video System) Monitoring Report 2007. Department of Conservation, Auckland, New Zealand: 28.

Stoner A.W., Ottmar M.L. (2003) Relationships between size-specific sediment preferences and burial capabilities in juveniles of two Alaska flatfishes. Journal of Experimental Marine Biology and Ecology, 282, 85–101.

Stoner A.W., Ryer C.H., Parker S.J., Auster P.J., Wakefield W.W. (2008) Evaluating the role of fish behavior in surveys conducted with underwater vehicles. Canadian Journal of Fisheries and Aquatic Sciences, 65, 1230–1243.

Taylor R.B., Anderson M.J., Egli D.P., Usmar N., Willis T.J. (2005) Cape Rodney to Okakari Point Marine Reserve Fish Monitoring 2005: Final Report. Report to the Department of Conservation, Auckland Conservancy, Department of Conservation, Auckland UniService, Auckland: 38.

Watson D.L., Harvey E.S., Anderson M.J., Kendrick G.A. (2005) A comparison of temperate reef fish assemblages recorded by three underwater stereo-video techniques. Marine Biology, 148, 415–425.

Willis T.J., Babcock R.C. (2000) A baited underwater video system for the determination of relative density of carnivorous reef fish. Marine and Freshwater Research, 51, 755–763.

Willis T.J., Millar R.B. (2005) Using marine reserves to estimate fishing mortality. Ecology Letters, 8, 47–52.

Willis T.J., Parsons D.M., Babcock R.C. (2001) Evidence for long-term site fidelity of snapper (Pagrus auratus) within a marine reserve. New Zealand Journal of Marine and Freshwater Research, 35, 581–590.

Willis T.J., Millar R.B., Babcock R.C. (2003) Protection of exploited fish in temperate regions: high density and biomass of snapper Pagrus auratus (Sparidae) in northern New Zealand marine reserves. Journal of Applied Ecology, 40, 214–227.

Zeileis A., Kleiber C., Jackman S. (2008) Regression models for count data in R. Journal of Statistical Software, 27, 1–25.

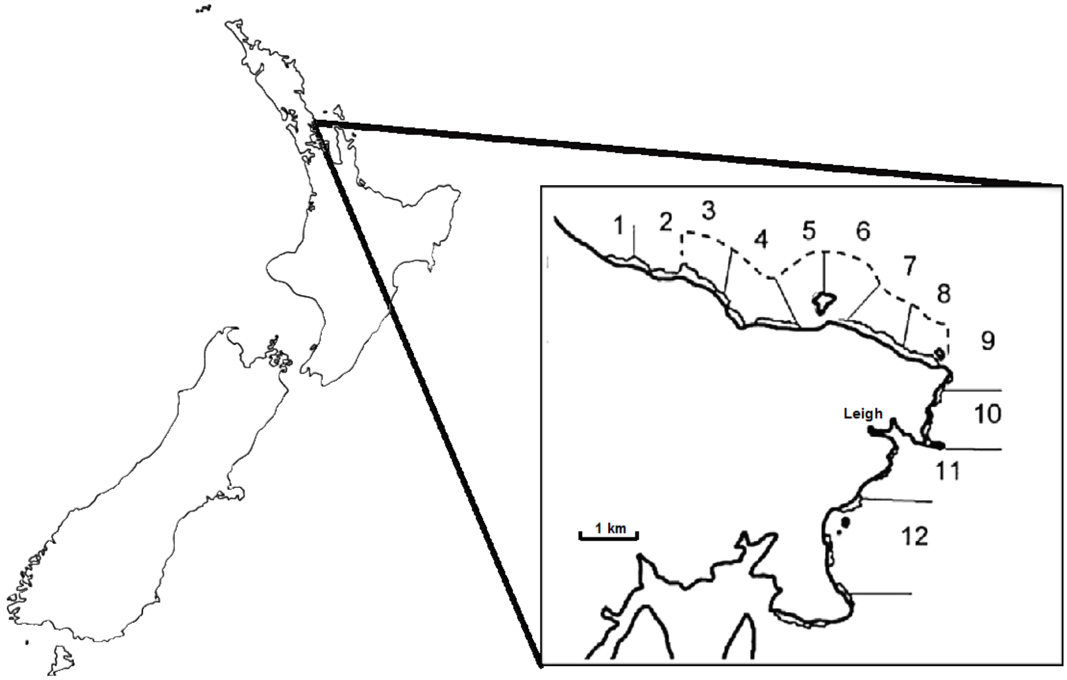


Figure 1. Map of the Cape Rodney to Okakari Point Marine Reserve (areas 3 to 8) and adjacent non-reserve areas (1 to 2 and 9 to 12).

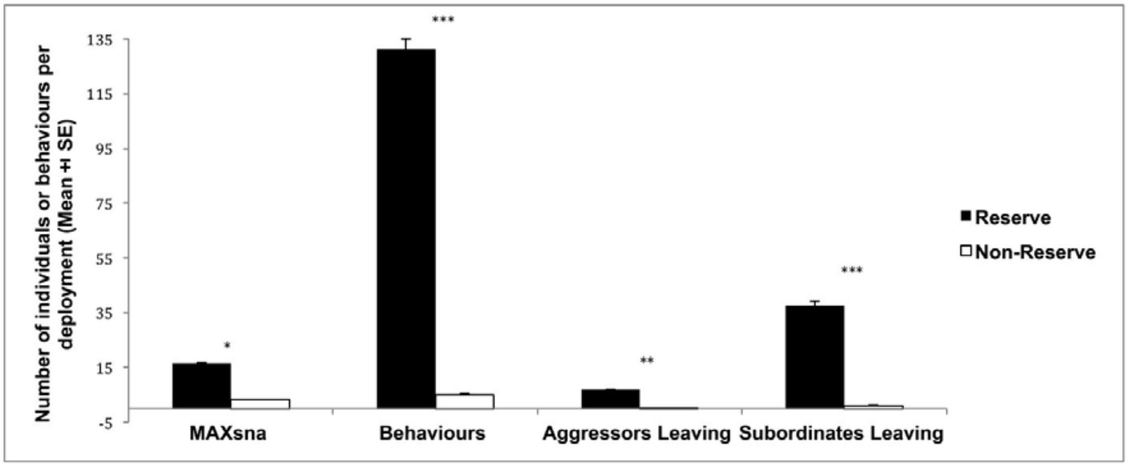
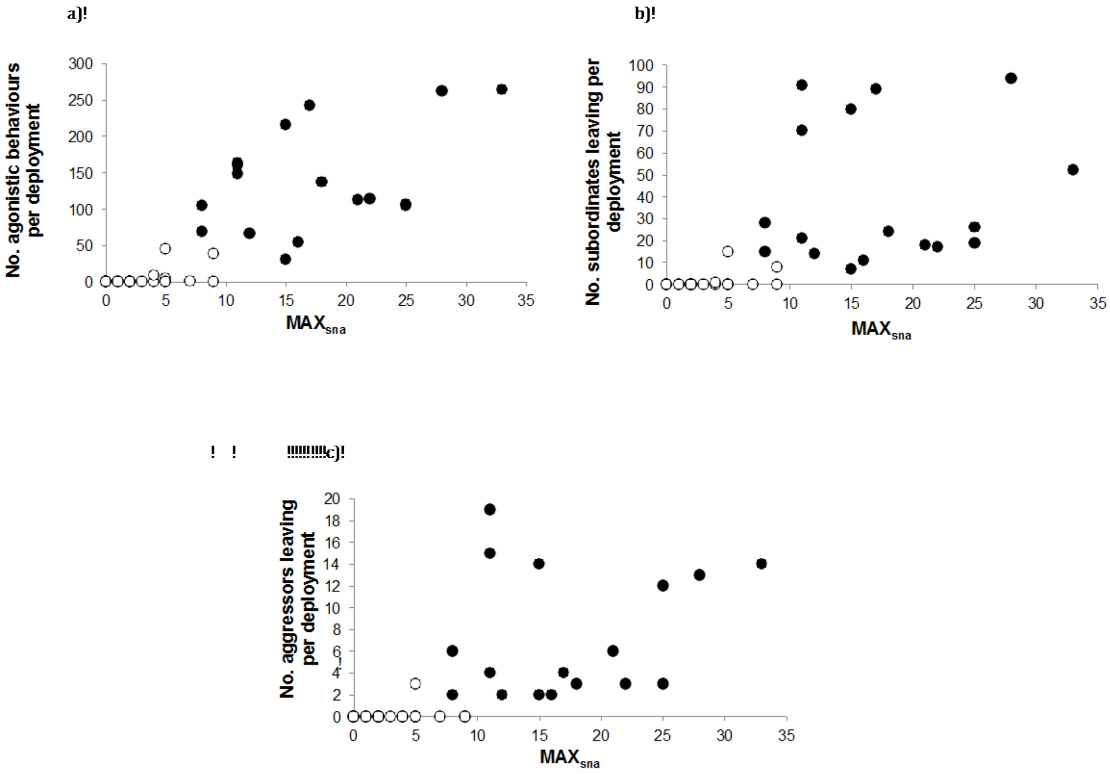


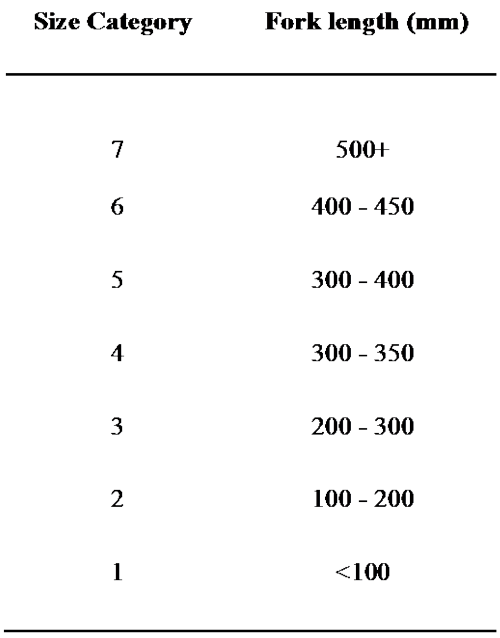
Figure 2. Histogram of the maximum number of snapper observed at once (Max$_{sna}$); number of agonistic behaviours between snapper; and the number of aggressor and subordinate snapper leaving following an agonistic behaviour. All values are means ± SE for both reserve and adjacent non-reserve sites. (*** indicates a P < 0.0001, ** P < 0.001 and * P < 0.01).



Figures 3a - c. Relationship between the maximum number of snappers observed at once (Max$_{sna}$) and (a) agonistic behaviours between snapper (b) aggressor leaving events following an agonistic behaviour and (c) subordinate leaving events following an agonistic behaviour within reserve and adjacent non-reserve sites.

Behaviour	Description	Scenario	Response of Aggressor	Response of Subordinate	References
Short pursuit	Aggressor moved rapidly towards the subordinate, often beginning with a sharp turn. Mouth openings during pursuits were common and increased with intensity. Single or multiple bites, generally towards the competitors' tail or flank, occurred at the highest intensity.	Observed when the subordinate approaches the bait while the aggressor is guarding or feeding.	Left the bait and camera field of view during the pursuit but generally returned to the bait afterwards.	Left bait and sometimes the camera field of view during the pursuit. Some evidence of returning to the bait.	(Castro and Caballero 1998, Castro and Santiago 1998, Caballero and Castro 1999, Caballero and Castro-Hdez 2003, Castro and Caballero 2004) (*Diplodus sargus cadenati*).
Lateral threat display	Aggressor bends body into a curved shape towards the subordinate, often combined with a forward movement. Highest intensity behaviours subordinates forced towards the ground.	Subordinate approached the bait while the aggressor was guarding or feeding.	Moved away from bait vicinity but not field of view. Replaced subordinate at bait or returned to feeding.	Moved away from bait vicinity but not field of view.	(Castro and Caballero 1998, Castro and Santiago 1998, Caballero and Castro 1999, Caballero and Castro-Hdez 2003, Castro and Caballero 2004) (*Diplodus sargus cadenati*).
Frontal threat display	Aggressor took a stationary stance facing the subordinate with their head brought close and slightly lowered. Commonly combined with a slight forward movement, which increased with intensity. Nipping in the highest intensity behaviors.	Subordinate approached the bait while the aggressor was guarding or feeding.	Moved away from bait vicinity or out of field of view. Replaced subordinate at bait or return to feeding.	Moved away from bait vicinity or out of field of view.	(Kudoh and Yamaoka 2004) (*Pagrus major* and *Evynnis japonica*)
Pushing	Aggressor made a rapid movement towards the subordinate with or followed by physical contact.	Aggressor disturbed during feeding in close proximity to the bait.	Moved away from bait vicinity or out of field of view.	Moved away from bait vicinity or out of field of view.	(Adams et al. 1995)(*Salvelinus alpines*)
Biting	Aggressor advanced and made physical contact with the subordinate using its mouth, followed by a biting motion.	Subordinate approached the bait while the aggressor was guarding or feeding.	Moved away from the bait vicinity and often returned to feeding	Moved away from the bait vicinity but not the field of view.	

Table 1. Ethogram of agonistic behaviours between snapper (*Pagarus auratus*) around a baited underwater video system in a New Zealand marine reserve and adjacent non-reserve sites.



Size Category	Fork length (mm)
7	500+
6	400 - 450
5	300 - 400
4	300 - 350
3	200 - 300
2	100 - 200
1	<100

Table 2. Fork length of size categories of the snapper (*Pagarus auratus*) observed in the baited underwater video camera deployments.