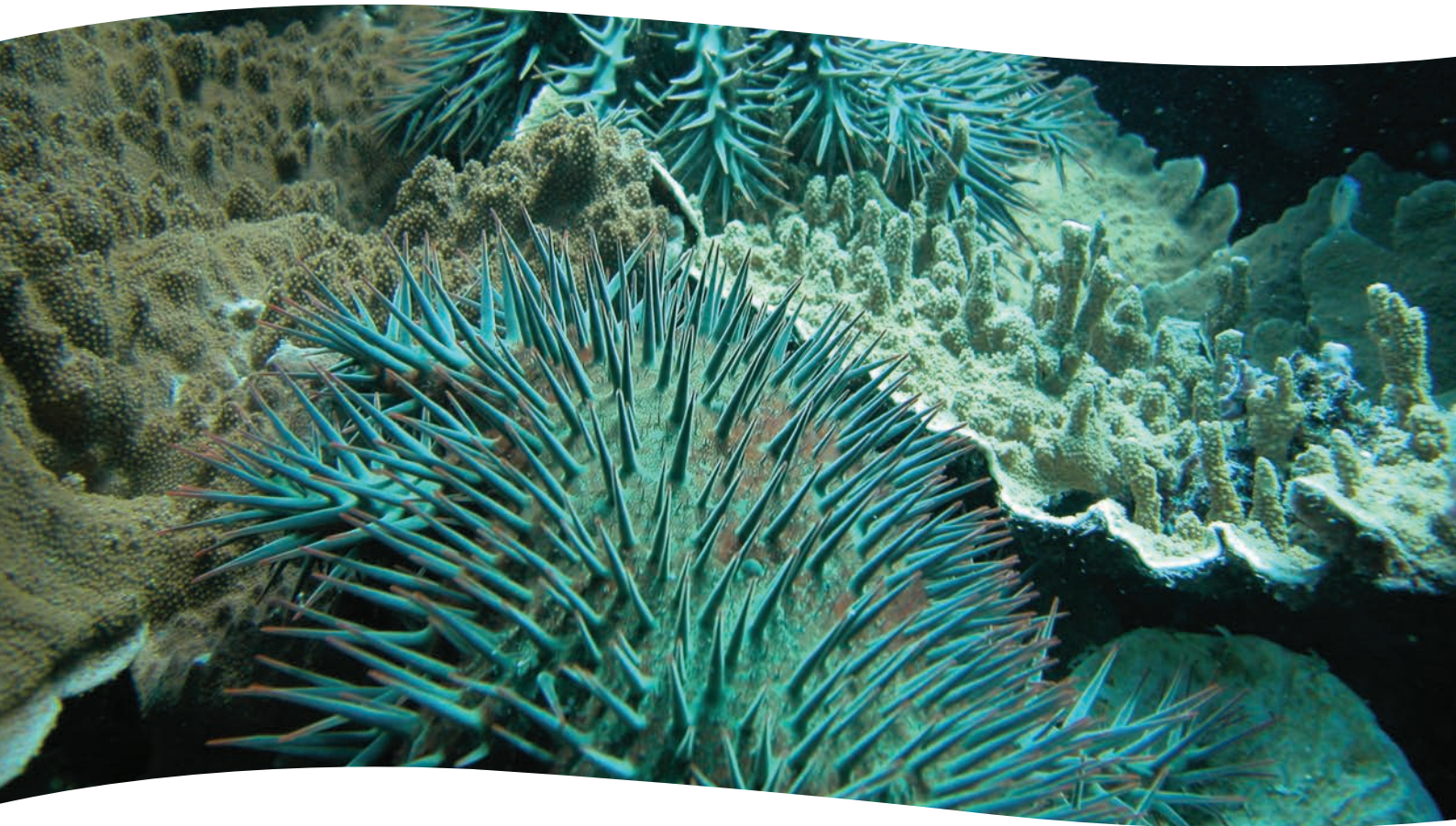


Do no-take zones reduce the likelihood of outbreaks of the Crown-of-thorns starfish?

Hugh Sweatman and Mike Cappel



Australian Government



AUSTRALIAN INSTITUTE
OF MARINE SCIENCE

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Hugh Sweatman¹ and Mike Cappel¹

¹ Australian Institute of Marine Science



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ACRONYMS

ABT	Aggregated Boosted Trees
AIC	Akaike's Information Criterion
AIMS	Australian Institute of Marine Science
COTS	Crown-of-thorns Starfish
CRC	Cooperative Research Centre
GBR	Great Barrier Reef
GBRMP	Great Barrier Reef Marine Park
GBRMPA	Great Barrier Reef Marine Park Authority
LTMP	Long-term Monitoring Program
MPA	Marine Protected Area
NESP	National Environmental Science Program
RIMReP	Reef 2050 Integrated Monitoring and Reporting Program
TWQ	Tropical Water Quality

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EXECUTIVE SUMMARY

Several studies have independently suggested that reduction in fishing activity on reefs is correlated with lower local abundance of *Acanthaster cf. solaris* and hence lower coral mortality, but the episodic and boom-bust nature of the population dynamics of *A. cf. solaris* spp. in large, interconnected reef systems such as the Great Barrier Reef (GBR) complicate analyses. Here we re-examine the evidence that no-take zones reduced the likelihood of outbreaks of *Acanthaster cf. solaris* on the GBR. First we examined the definition of “outbreaks” in terms of densities of starfish that consume coral faster than it recovers. Our results support the suggestion that the current definition is conservative, meaning that lower densities of starfish do result in net loss of coral cover. Secondly, we looked for evidence that no-take status reduces the likelihood of starfish outbreaks at a reef, using data from the wave of outbreaks 1994-2004 and from the current wave, 2011-present. We applied two criteria to identify reefs that were likely to have developed outbreaks and three definitions of outbreak densities, including a new lower value (0.12 starfish per two minute manta tow) suggested by this study. The results were variable: while there tended to be fewer outbreaks on no-take reefs, the differences were generally not significant. Other analyses have also shown inconsistent effects, suggesting that zoning has a weak effect on the occurrence of outbreaks.

1.0 INTRODUCTION

Changes in predation rates were among the first causes that were put forward to explain the sudden occurrence of outbreaks of crown-of-thorns starfish, *Acanthaster* spp., on coral reefs (Endean 1969). From initial focus on predators of adult starfish such as the Triton's trumpet shell (*Charonia tritonis*) and certain large fishes (Endean 1969, Owens 1971, Ormond et al. 1990), interest broadened to predators of all life stages (Keesing & Halford 1992a, 1992b, Cowan et al. 2016, 2017) along with associated population modelling (McCallum 1990, 1992, Morello et al. 2014, Babcock et al. 2016). There has been a parallel interest in the effects of fishing pressure on starfish population dynamics and the potential role of marine protected areas as ways of mitigating outbreaks of *Acanthaster* spp. to protect coral cover on reefs.

On the basis of RNA COI-barcoding Vogler et al. (2008, 2013) distinguished four substantially allopatric clades within the *A. planci* species group, which has since been split into four probable species and some possible sub-species. Most research on population ecology of *Acanthaster* spp. has come from Australia, Japan, Guam and Fiji, all within the geographic range of the clade that has been tentatively re-named *Acanthaster* cf. *solaris* (Haszprunar & Spies, 2014).

The evidence that protection from fishing reduces the incidence of outbreaks is limited. Many individual *A. cf. solaris* show evidence of past predation attempts in the form of missing arms or stubby arms that are regenerating and this is taken to indicate a high frequency of predatory attempts. A short-term study that used densities of human populations on an archipelago in Fiji as a proxy for fishing pressure found that densities of *A. cf. solaris* on reefs was inversely related to the densities of predatory reef fishes and the distance from island population centres (Dulvy et al. 2004). On the Great Barrier Reef (GBR), the occurrence of outbreaks of *A. cf. solaris* over an eleven year period was much lower on reefs that were closed to fishing than on reefs where fishing was permitted (Sweatman 2008). As a result, coral cover was generally higher on no-take reefs in that period (McCook et al. 2010). The broad scale declines in coral cover on the GBR (De'ath et al. 2012), a series of large and destructive cyclones (Cheal et al. 2017) and recurring severe bleaching events (Hughes et al. 2017) have led to renewed and urgent interest in measures to protect coral on GBR reefs wherever possible, and outbreaks of *A. cf. solaris* have been a major cause of coral mortality (De'ath et al. 2012).

In this study we re-examine the evidence for a link between fishing and the frequency of destructive outbreaks of *A. cf. solaris*. First, we re-examine the definition of an outbreak. Outbreaks are frequently identified in terms of the densities of starfish that cannot be sustained by the existing coral cover. We use extensive monitoring data to re-examine the definition of an outbreak in terms of the relationship between starfish densities and damage to coral cover. We then use several definitions of an outbreak to re-examine the evidence for a relationship between closing reefs to fishing (Green zones) and the probability of outbreaks of *A. cf. solaris* in the third wave of outbreaks up until 2004. We then apply the same logic to data from the current, fourth wave of outbreaks on the GBR.

2.0 WHAT CONSTITUTES AN OUTBREAK OF *A. cf. solaris*?

2.1 Introduction

Acanthaster cf. solaris exists in two population states: background population levels and outbreak densities. At background population levels, the starfish occur at very low densities when averaged over an individual platform reef, and they do not generally form aggregations at finer scales within a reef. In contrast, during outbreaks, starfish densities are frequently 2-3 orders of magnitude greater and starfish are often aggregated at a local scale (hundreds of m², e.g. Ormond & Campbell 1974; Pratchett 2005). Two other attributes are frequently considered in definitions of outbreaks: firstly some authors consider that outbreaks arise abruptly, rather than by gradual accumulation of starfish over successive recruitments. Secondly, outbreak densities of starfish consume coral faster than the corals recover and grow, so are too great to be sustained by local coral resources (Lourey et al, 2000). This means that the threshold density of starfish that constitutes an outbreak will be related to coral cover. Adult *A. cf. solaris* are highly mobile and certainly move within areas of continuous reef to find and exploit patches of high coral cover, probably using chemical cues (Beach et al. 1975, Sloan & Campbell 1982). Thus the appropriate scale for assessing starfish density in relation to feeding impact is quite large: an entire platform reef or an area of continuous fringing reef. In practice outbreaks have been defined as populations whose densities exceed some value. A great range of values has been used, reflecting different survey methods and locations (see Moran 1986, Moran & De'ath 1992, Pratchett et al. 2014). Most authors give no justification for their chosen threshold density for outbreaks. However the categorisation is presumably based on the logic that, since background densities are very low and the animals are dispersed, the presence of any substantial number of starfish in an area of reef on a scale that is typically assessed by divers indicates an outbreak. A similar approach was formalised by Vanhatalo et al. (2017) who identified outbreaks if there was a 10-fold increase in starfish density above the modelled long-term mean value for a reef, based on latitude and position on the continental shelf.

Two exceptions are studies by Moran & De'ath (1992) and Keesing and Lucas (1992). Moran and De'ath (1992) took an existing scheme for categorising the outbreak status of GBR reefs. In this scheme, reefs with "Active Outbreaks" were those that had high densities of starfish (generally a total of >40 starfish recorded by manta tow) and obvious areas of dead coral (>30%). Reefs had "No Outbreak" where starfish numbers were low (<10 per reef recorded in manta tow surveys) and there was little evidence (<10%) of recently killed coral. Reefs were "Recovering", where there were few starfish and coral cover was low but increasing (and it was known that *A. cf. solaris* numbers had been high in the past and were the likely cause of past coral loss). Inspecting the range of densities of starfish seen on reefs with and without Active Outbreaks, a value of 1,500 starfish km⁻² was higher than the highest values on No Outbreak reefs but low for a reef with an Active Outbreak. Allowing for the low rate of detection by observers using manta tow (Fernandes et al. 1990), this corresponds to 0.22 starfish per 2-minute manta tow, which was then taken by AIMS and GBRMPA as a threshold density for an Active Outbreak.

Secondly, Keesing and Lucas (1992) looked at feeding rates, feeding preferences, and movement of *A. cf. solaris*. They combined these observations with field estimates of coral

cover to model consumption. For reefs with coral cover in the range commonly recorded on the GBR, models suggested that there would be little decline in coral cover until starfish densities exceeded 1,000 km⁻². This figure was broadly similar to the 1,500 km² of Moran & De'ath (1992).

In the mid-1990s there was a move to increase the threshold density for outbreaks on GBR reefs, based on the assumption that most studies occurred in summer and lower water temperatures in winter would be expected to reduce prey consumption over some of the year. Some areas of the GBR also have higher coral cover than others. Engelhardt et al (1997) suggested an arbitrary threshold of 30 starfish ha⁻¹ (0.75 individuals per 250 m²) which was formalised as 1.0 starfish per 2-minute manta tow by the AIMS survey team. The presence of 0.22 *A. cf. solaris* per tow was reclassified as an "Incipient Outbreak" while 1.0 starfish per tow was named an "Active Outbreak."

The concept of an outbreak being an unsustainable density of starfish was extended by De'ath (2003), who examined the predictive value of information on *A. cf. solaris* numbers, coral cover and the outbreak status of reefs from manta tow surveys and fine-scale surveys by divers. He used regression trees to develop models from time series of coral cover and numbers of *A. cf. solaris* based on manta tow surveys of 447 GBR reefs made between 1984 and 2000. The cover of living coral that was recorded at a reef at one survey was a reasonable predictor of living coral cover at the next survey, but the predicted coral cover was 4-10% lower if either Active Outbreaks or Incipient Outbreaks of *A. cf. solaris* were present on that reef at the time of the initial survey. De'ath (2003) combined Active Outbreak and Incipient Outbreak reefs and considered them as one category, but did state that coral cover declined on reefs where either class of outbreak was present. If the threshold for an outbreak is the highest density of starfish that can be sustained by existing coral cover, De'ath found that a density threshold for Incipient Outbreak of 0.22 starfish per 2-minute manta tow was too high, and lower densities also caused coral cover to decline. He recommended that a new outbreak category "Potential Outbreak" be applied where reef-wide mean density on a platform reef was greater than 0.1 starfish per tow. He also recommended that "Incipient Outbreaks" be renamed "Active Outbreaks" while populations where the density is greater than 1.0 starfish per tow (presently "Active Outbreaks") be renamed "Severe Outbreaks."

De'ath's (2003) analysis was based on data collected up to the year 2000. Many more data have been gathered since 2000, and statistical techniques involving regression trees have also evolved in the meantime, so it is appropriate to revisit the definitions of outbreaks.

2.2 Methods

Aggregated boosted regression trees (ABT) are a powerful tool for analysing ecological data (see De'ath 2007 and Elith et al. 2008). ABT is a machine learning technique for regression and classification problems based on "gradient boosting", which produces a prediction model from an ensemble of models in the form of decision trees. Models are built in a step-wise fashion and then generalised by allowing optimization of two differentiable loss functions. The full data set is repeatedly divided at random into "training" and "validation" subsets, and these are used to optimise two loss functions down a gradient. Optimizing training loss (fit to validation datasets) encourages predictive models. A model showing a good fit to training data should be close to the underlying distribution. Optimizing regularization (adjusting model

complexity to give optimal predictions) encourages simple models that have smaller variance in future predictions, making prediction more stable. The approach can be used with a variety of response types that are relevant to marine ecology (e.g. presence/absence, skewed, zero-inflated count data). The models represent the effect of each predictor (e.g. *A. cf. solaris* densities) after accounting for the effects of other predictors (e.g. coral cover). Complex interactions amongst predictors are clearly represented, and models are robust to missing values and outliers.

The methods and models developed here extend those of De'ath (2003), as there have been major advances and improvements in ABT since that study, as well as more than a decade of additional monitoring. We also extended this approach by adding disturbance history as a covariate to *A. cf. solaris* densities.

Data

We used monitoring data from 65 reefs that had been surveyed more than once in the period (1993-2016) using manta tows of the reef perimeters. This gave 747 estimates of mean *A. cf. solaris* density and of mean coral cover derived from these repeated tows. Because 1993 was used as a baseline for changes in coral cover and *A. cf. solaris*, there were 682 rows in the overall dataset. De'ath (2003) used data from more reefs, but our analysis was restricted to reefs with relatively well known disturbance histories.

Manta towing involves towing a snorkeler at slow speed behind a tender. The observer aims to scan a 10 m wide band of reef while being towed for periods of 2 minutes. After each tow, the boat driver idles the engine to allow the observer to record observations of a datasheet attached to the manta board. The procedure is described in Miller et al. (2009). On average each 2-minute tow covers 200 m of reef edge (Figure 1). The variation comes about because of differences in towing speed, and differences in the speed and direction of wind and currents.

Observed densities of *A. cf. solaris* were characterised by a very large proportion of zero values, and few high outliers. The median count per tow was zero, the mean was 0.4555 and the 3rd quartile was only 0.034 starfish per tow. Only 244 of the 682 values (~36%) were greater than zero, and only 25% of the non-zero values were greater than 0.034, yet the maximum mean count was 54.33 starfish per tow. This represents a sparse “parameter space” for model predictions of the effects of varying *A. cf. solaris* densities. The mean *A. cf. solaris* densities (*A. cf. solaris* per tow) were transformed by $\log_{10}(x+1)$ for analysis.

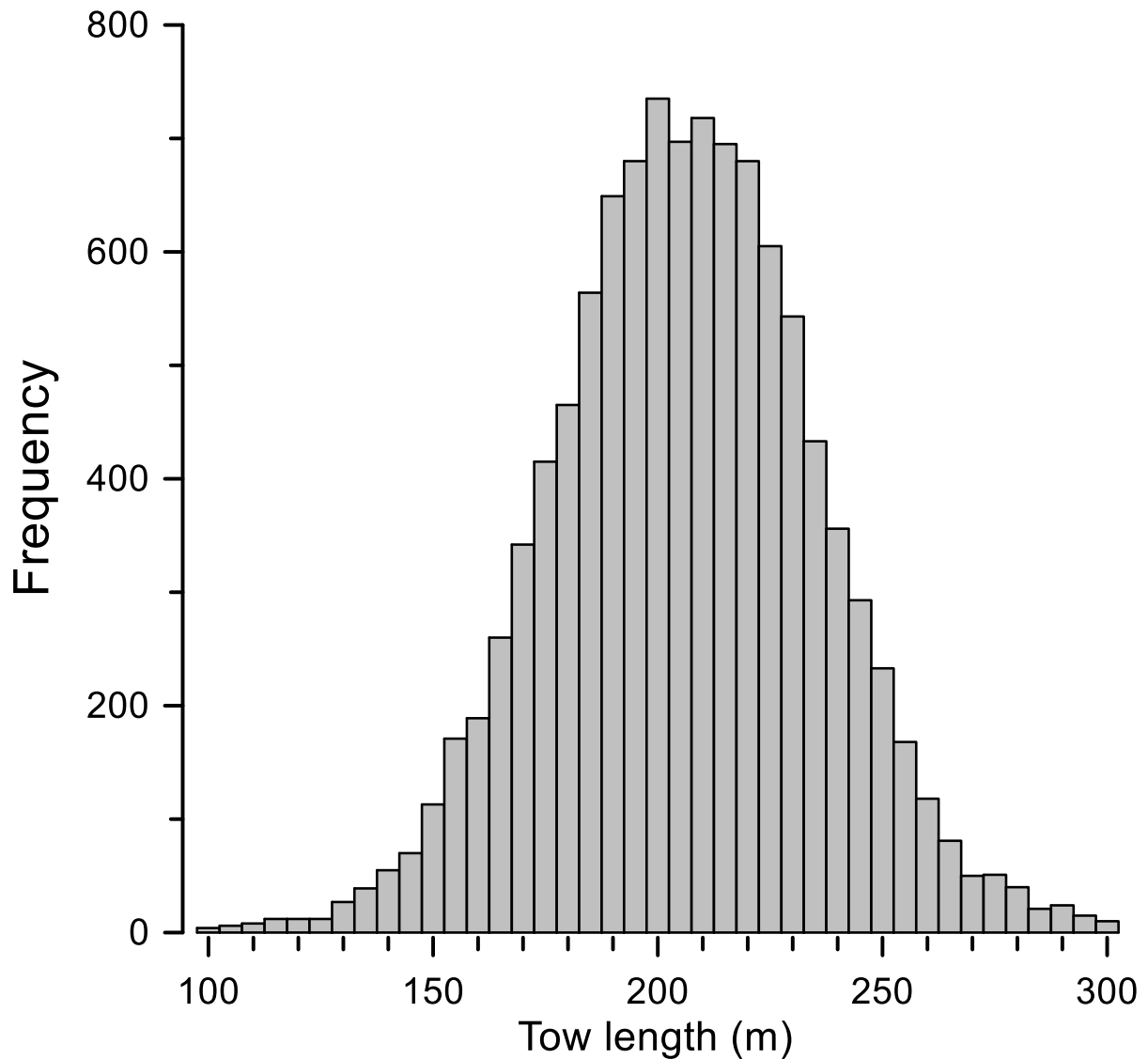


Figure 1: Distribution of distances covered in a 2-minute manta tow, based on GPS tracks from 10,739 tows made between August 2014 and May 2018. Mean tow distance = 204.05 m (95% Confidence Interval: 203.45 - 204.65 m).

Model

Univariate models were constructed using ABT (De'ath 2007, Ridgeway 2006). Coral cover is temporally auto-correlated (as are *A. cf. solaris* densities). Coral cover in a given year depends in part on cover in the previous year, and the magnitude of change is constrained by the spatial limits of the reef habitat. There cannot be major increases in coral cover on a reef where all suitable space is covered by coral, nor can there be further loss of coral cover at a reef with zero coral. Hence we chose to use the annualised rate of change in coral cover (positive growth or negative loss) from the preceding survey to the current survey as the response variable in univariate models. The response was predicted using the following covariates:

- the $\log_{10}(x+1)$ of the mean *A. cf. solaris* per tow in the *previous* survey
- the $\log_{10}(x+1)$ of the mean *A. cf. solaris* per tow in the *current* survey
- the mean % coral cover in the *previous* survey

- the presence (1) or absence (0) of any type of major disturbance between the *previous* and *current* surveys (cyclones, disease, bleaching, other)
- the location of each of the 65 reefs, across the shelf, and along the shelf. “Across” took the value 0 at the Queensland coast, and 1 on the 80 metre isobath. “Along” took the value 0 at the southern-most boundary of the GBR Marine Park (GBRMP) and 1 at the northern-most boundary. These indices of location were developed by Fabricius and De’ath (2000) to account for the vast differences in lagoon width between the northern and southern regions of the GBRMP.

Three separate models were run without interactions (main effects only) and then for 2-way and 3-way interactions, using a Gaussian error distribution. The performance of each of these interaction levels was compared on the basis of their prediction error. Prediction error was measured by 5-fold cross validation. The learning rate (shrinkage) was lowered (from 0.01 to 0.001), and the number of trees was raised (from 1,000 to 10,000) as models became more complex. Prediction errors were plotted at each change to check for stability and convergence. The final model was selected on the basis of an improvement in prediction error of more than 5%. For example, a simple “main effects only” model, with no interactions amongst predictors, would be preferred if its prediction error was within 5% of those of more complex models with 2-way and 3-way interactions.

The ABT analysis gives the relative influence of all covariates in explaining and predicting the response. These are portrayed as partial dependency plots, which show the overall effect of one particular covariate on change in coral cover when the effects of all others held constant (Friedman 2002; Friedman & Meulman 2003). Partial interaction plots showed the influence of current *A. cf. solaris* densities on change in coral cover, given 5 levels of *A. cf. solaris* densities in the survey immediately before (previous). A response of zero change in coral cover indicates no inter-annual change, and positive values represent nett coral growth. Inspection of the partial interaction plots allows critical *A. cf. solaris* densities to be identified above which there is nett loss of coral cover.

All analyses used the library “abt” and function “across-along” (pers comm. G. De’ath) in the open source package “R” (R Core Team, 2016).

2.3 Results

The best model included 2-way interactions and had an r^2 of 35.8%. The level of coral cover in the previous survey (“prev.cover%” in Figure 2) had the highest relative influence in the modelled change in coral cover between surveys (39.5%). The presence or absence of a disturbance in the period between surveys (“disturbnc” in Figure 2) had the next greatest influence (27.0%). The density of *A. cf. solaris* in the previous survey (“Log10.prev.COTs” in Figure 2, 11.5%) and the position of the reef “Along” the GBR (10.3%) had similar levels of influence, followed by the density of *A. cf. solaris* at the current survey (“Log10.current.COTs” in Figure 2, 7.6%) and lastly by cross-shelf position of the survey reefs (“Across”, 4.0%, Figure 2). The importance of the history of disturbances prior to the current survey was a notable feature of the model, showing cumulative effect of losses on coral cover.

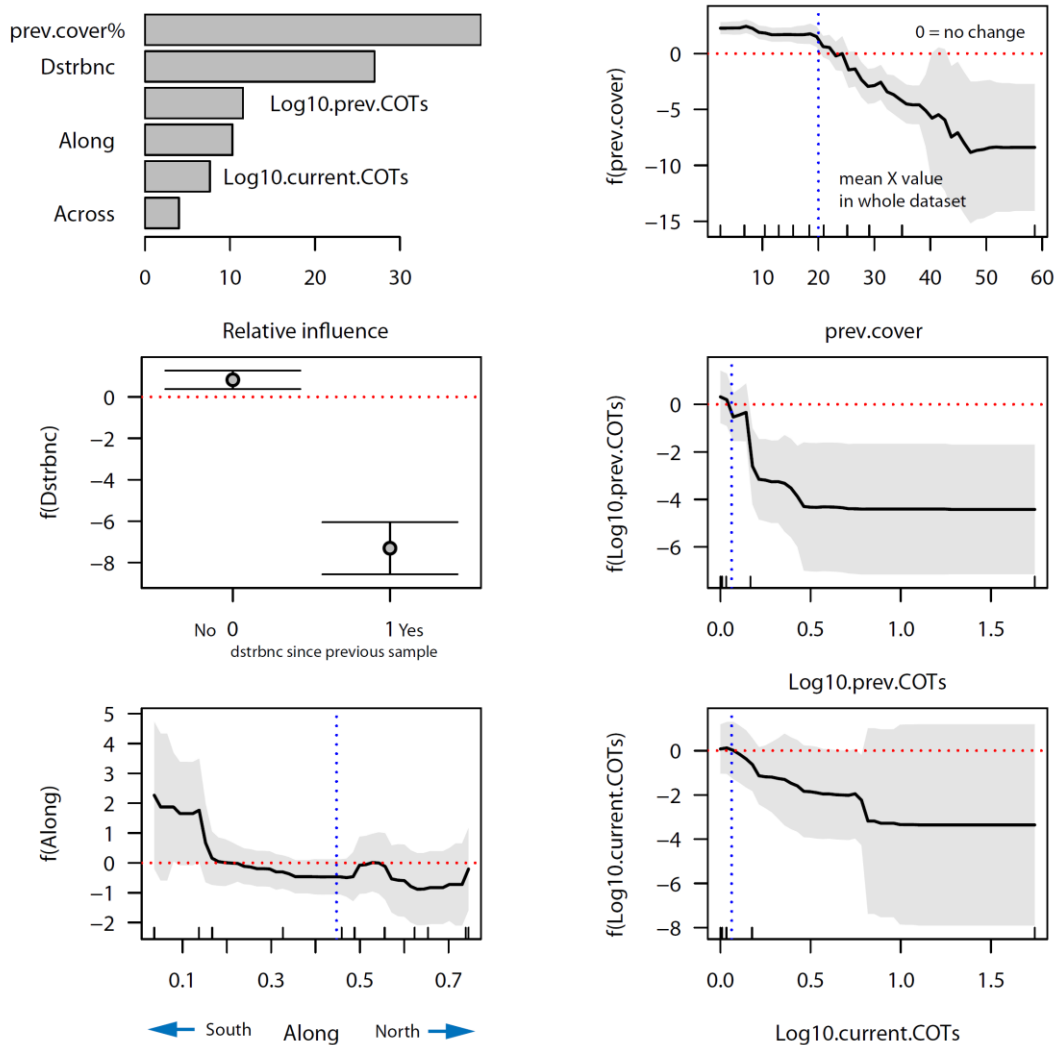


Figure 2: Relative importance histograms, and partial dependency plots for response of change in coral cover over the distribution of observations. Rug plots on the X axes show distribution (in deciles) of samples across values of the explanatory covariates. An equilibrium, zero nett change in change in coral cover is shown by the red horizontal reference lines on the Y axes. Mean values of each of the model predictors are shown by vertical blue lines on the X axes. The transformed density of *A. cf. solaris* (COTS) density in the “current” survey had the highest influence, accounting for ~35% of the deviance explained ($r^2 = 12.5\%$). The response curves show the effect of each individual predictor on change in coral cover, if all other covariates are kept to a constant, or average, value.

Various thresholds in effects of *A. cf. solaris* can be inferred by examining partial dependency plots, particularly in relation to a zero nett change in coral cover. This represents an equilibrium below which coral cover is declining. The partial dependency of change in coral cover on current and previous *A. cf. solaris* densities from Figure 2 are expanded in Figure 3.

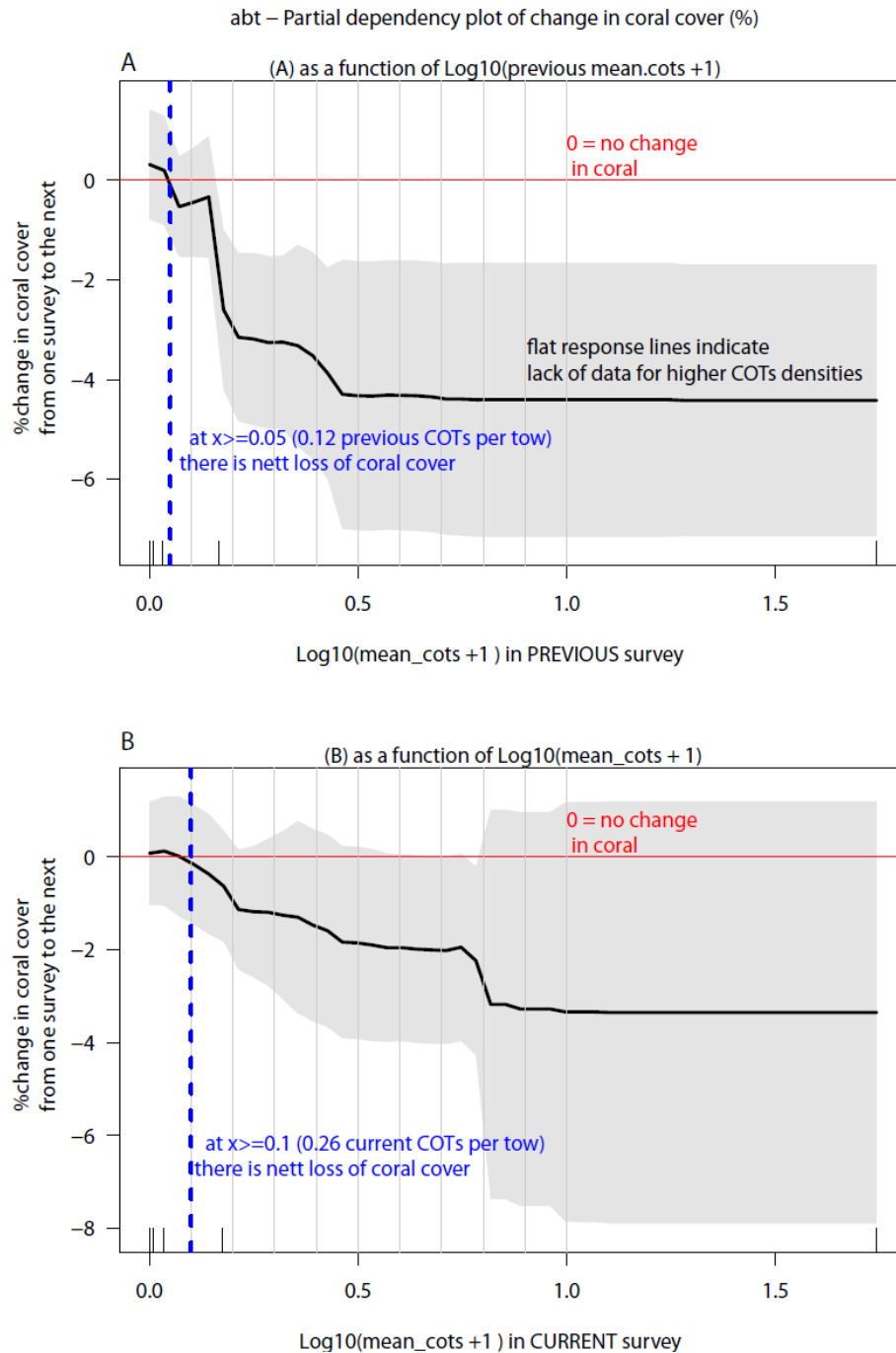


Figure 3: Partial interaction plots of the response of coral cover (change in percent cover per year) as a function of (A) density of *A. cf. solaris* at the preceding survey, and (B) as a function of density of *A. cf. solaris* (COTS) in the current survey. Coral cover recorded at the preceding survey was the best predictor of current coral cover (Figure 2), but depensation below average coral cover was evident for *A. cf. solaris* densities of $> \sim 0.12$ per tow at the preceding survey.

When all the other covariates in the model were accounted for, coral cover declined whenever densities of *A. cf. solaris* were greater than ~ 0.12 starfish per tow at the preceding survey (where the response line crosses the reference line indicating zero change in coral cover between surveys, Figure 3A). The nett loss increased rapidly to -4% per year as the observed densities of *A. cf. solaris* increased, and then flattened due to uncertainty caused by the lack of observations of high *A. cf. solaris* densities in the surveys. The “rugs” on the x-axes show

that only 10% of the observed *A. cf. solaris* densities were greater than ~0.5 starfish per tow. The density of starfish recorded in the current survey had lower influence in the model (Figure 3), but there was a nett loss of coral cover when current starfish densities increased beyond ~0.26 starfish per tow (Figure 3B). The rate of nett loss of coral flattened out at around -3% per year after dropping steeply when current starfish densities reached ~4.6 starfish per tow (0.75 on the log transformed scale, Figure 3B).

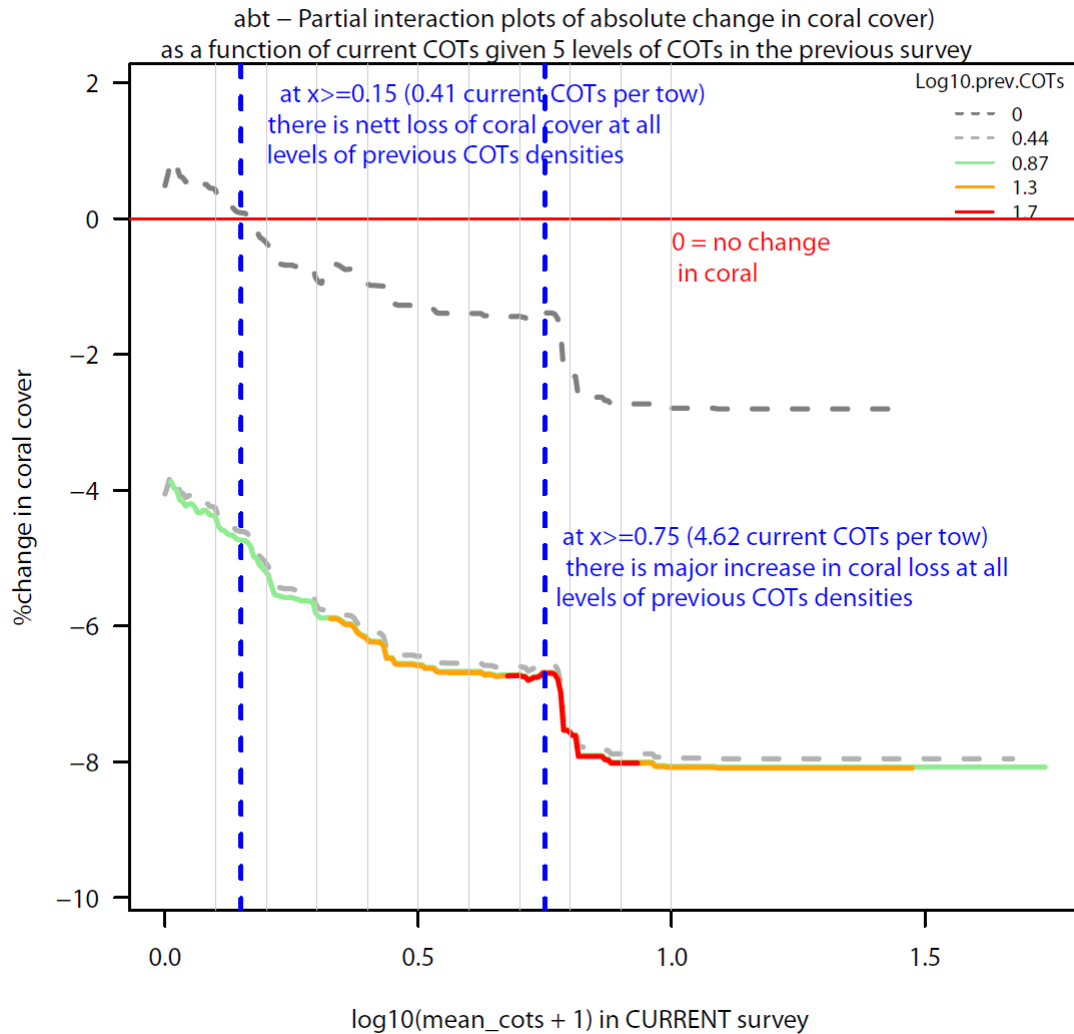


Figure 4: Partial dependency plot of annual change in coral cover as a function of density of *A. cf. solaris* (COTS) in the current survey, given 5 levels of starfish density in the preceding survey. If the density of starfish was >0.41 per tow in the current survey, there was a nett loss of coral cover since the previous survey regardless of the density of starfish recorded at that previous survey (including zero).

Coral cover declined between surveys when densities of *A. cf. solaris* in the current survey were greater than ~0.41 per tow, regardless of the density of starfish at the previous survey (Figure 4). Similarly, there was a steep increase in loss of coral cover when densities of *A. cf. solaris* in the current survey reached ~4.62, regardless of the density of starfish seen in the previous survey (Figure 4). The lines showing the change in coral cover for different densities of starfish in Figure 4 are parallel, indicating a lack of interaction between the main effects in the model. The grouping of response curves for a range of densities of *A. cf. solaris* recorded

in the previous survey may be due to a lack of data for those levels, or a similarity in nett coral loss for a range of higher previous *A. cf. solaris* densities.

There was a nett loss of coral when the average density of *A. cf. solaris* at the previous survey reached 0.41 starfish per tow regardless of the coral cover at the previous survey (Figure 5), though the extent of the change was increased for higher cover values.

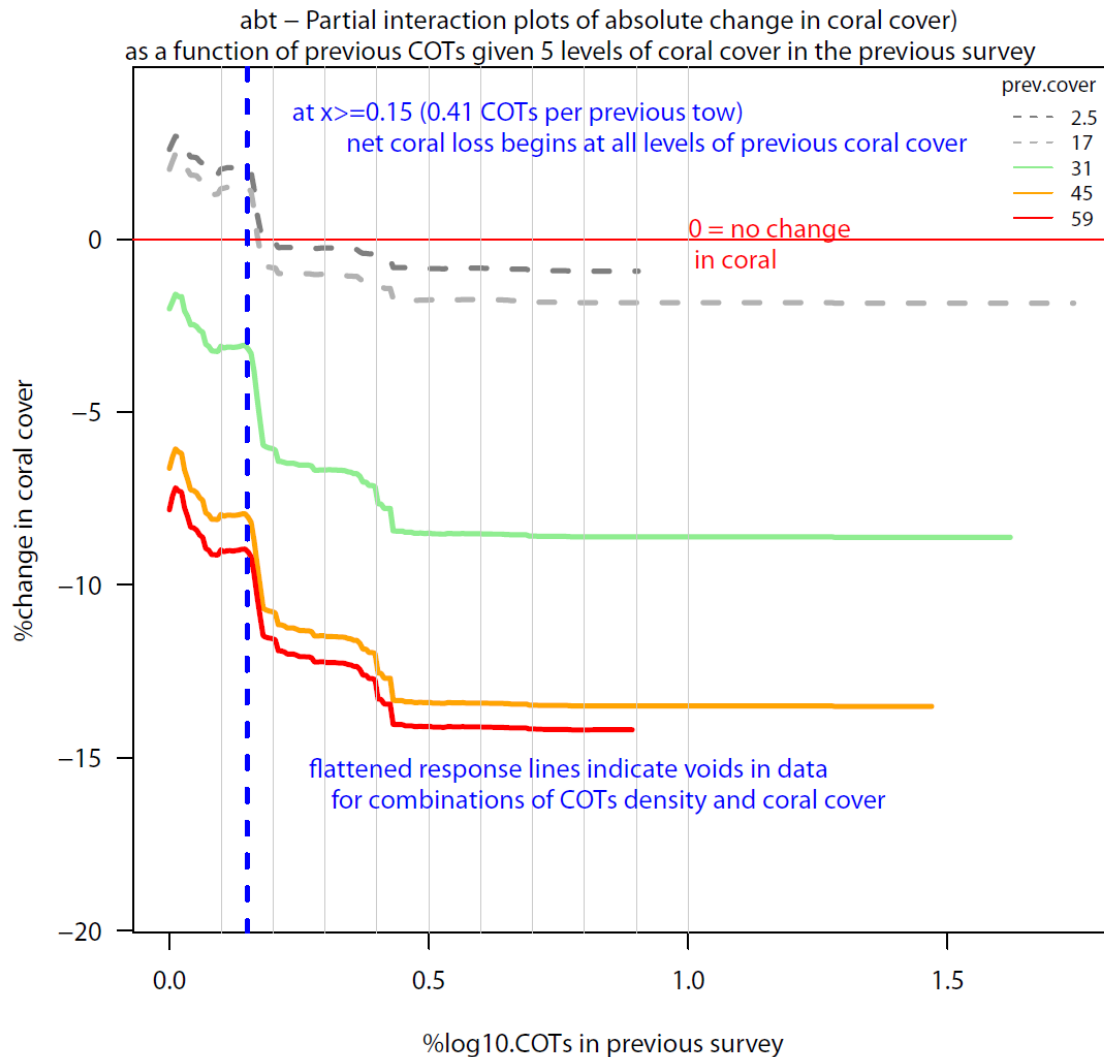


Figure 5: Partial dependency plot of change in coral cover between surveys as a function of the density of *A. cf. solaris* (COTS) at the preceding survey for 5 levels of coral cover recorded at the preceding survey. Coral cover declined steeply between surveys when starfish densities reached ~ 0.41 *A. cf. solaris* per tow, regardless of the level of the coral cover that was present at the preceding survey.

2.4 Discussion

These new analyses support De'ath's (2003) suggestion that, if the definition of an outbreak is to be based on the threshold density of starfish that cannot be sustained by local coral biomass, then the density of 0.22 starfish per tow (equivalent to 1,500 starfish km^{-2}) is too high. Our analyses indicate that coral cover will decline over one or two years (the interval between surveys) if starfish densities reach 0.12 starfish per tow (~ 820 starfish km^{-2}). Our statistical models also included the occurrence of other disturbances that affect coral cover, such as

storms and coral bleaching, and such disturbances had greater relative influence on change in coral cover than the density of starfish at the preceding or at the current survey. It was only possible to include the presence or absence of other disturbances in the model and then only if the disturbance occurred in the interval between the previous survey and the most recent survey. This did not account for differences in the intensity of such disturbances, or for any residual effects of disturbances that occurred in the more distant past, prior to the preceding survey. A quantitative estimate of the effects of disturbances would allow the relationship between starfish densities and decline in coral cover could be estimated with greater precision.

From a reef manager's perspective, there is no benefit to overestimating the densities of *A. cf. solaris* that a reef can sustain, so this lower threshold should be adopted and used in reporting. However, this lower outbreak threshold density raises some practical issues. For all the reefs that have been surveyed on the GBR, the median number of manta tows required to survey the reef perimeter is 42. This outbreak threshold of 0.12 starfish per tow accounts for the low detection rate by manta tow (Fernandes et al. 1990), but it means that the sighting of just 5 starfish in 42 tows would indicate their presence at densities that will cause coral cover to decline on an average reef, and even lower counts of starfish will indicate unsustainable populations on about half the reefs of the GBR. This will affect the reliability of detecting outbreaks.

2.5 Summary

- Change in coral cover between surveys was most strongly related to the coral cover at the preceding survey. Reefs with higher coral cover tended to lose more coral.
- The occurrence of other disturbances besides *A. cf. solaris* outbreaks at a reef has a strong influence on change coral cover, but we used a truncated history (only back to the previous survey) in our analyses
- The effect of *A. cf. solaris* numbers in the *previous* survey outweighs the effect of the *A. cf. solaris* count in the *current* survey. This effect may be as great as a 40% decrease below average coral cover values
- This level of 0.12 *A. cf. solaris* per tow may be a better estimate of the density at which coral cover is no longer sustained, so is an "outbreak" threshold density and should be adopted for reporting.
- There was a proportional, nett loss of coral cover from year to year at current *A. cf. solaris* densities above ~0.41 per tow, regardless of all previous densities of *A. cf. solaris* and all previous levels of coral cover

3.0 DOES PROTECTION FROM FISHING DECREASE THE PROBABILITY OF OUTBREAKS OF CROWN-OF-THORNS STARFISH ON REEFS?

3.1 Introduction

An important feature of the biology *A. cf. solaris* is that outbreaks occur intermittently. Four large-scale outbreak episodes have been recorded on the GBR since 1960. These waves of outbreaks start on reefs to the north of Cairns, though within that region locations from Green Is (17°S) to Lizard Is (14.6°S) have been identified as the starting point (Brodie et al. 2005, Fabricius et al. 2010, Wooldridge and Brodie 2015, Furnas et al. 2013, Vanhatalo et al. 2017). Over succeeding years, starfish then spread to other reefs, presumably as larvae are transported by prevailing currents. It has been suggested that adult starfish may migrate between reefs (Endean 1969) but there are no observations to support this. The southerly progression through the central region of the GBR is well documented (Talbot & Talbot 1971, Miller 2002, Vanhatalo et al. 2017). Reefs in the far northern GBR have been surveyed much less regularly than central and southern reefs, but there is limited evidence that outbreaks progress northwards as well (Moran et al. 1992). This is presumably because larvae are transported by the Hiri Current. Outbreaks have also been recorded on clusters of reefs in the southern Swains region that are not synchronised with the southerly progression through the central GBR and may arise independently (Reichelt et al 1990, Moran et al. 1992).

Starfish numbers on individual reefs may build gradually or rapidly, and then decline after a number of years, probably due to starvation and disease (Pratchett 1999, Pratchett et al. 2014). This temporary and progressive nature of outbreaks means that not all reefs on the GBR are equally likely to have outbreaks at any point in time. In order to test for differences in the likelihood of outbreaks, it is important to distinguish those reefs where larval supply and coral cover would potentially allow outbreaks to develop during the period of interest (e.g. reefs that are “at risk”), from other reefs in regions where outbreaks are unlikely at that time. There are some stable geographic patterns: *A. cf. solaris* are rare on exposed outer reefs compared with midshelf and inshore reefs (James and Scandol 1992). The intermittent occurrence of outbreaks means that timing of surveys is also important, since surveys made well before or well after a wave of outbreaks passes through a particular region are unlikely to find high numbers of starfish.

If reefs where outbreaks are unlikely to occur are included in analyses of outbreak frequencies, any effect of marine park zoning on the probability of outbreaks occurring will be diluted. It is not possible at present to estimate larval supply, so here we explore the effects of different definitions for reefs being at risk. Our approach is based on the simple assumption that reefs that are close to one another share a common hydrodynamic setting and are likely to be exposed to similar currents that transport starfish larvae. Comparing reefs that receive similar numbers of potential recruits, but that are zoned as no-take areas or are open to fishing, may show effects of zoning on the probability of starfish developing to adult size in outbreak numbers.

3.2 Methods

We examined the effect of no-take zoning on the occurrence of outbreaks in two waves of outbreaks: the 3rd recorded wave which began in the early 1990s, and the current (4th) wave which began around 2011.

Identifying reefs that are at risk of developing outbreaks of *Acanthaster*

If reefs have secondary outbreaks of *A. cf. solaris*, they must have received substantial numbers of *A. cf. solaris* larvae. Neighbouring reefs are likely to experience similar hydrodynamic conditions and can be expected to receive similar supplies of larvae. Thus the most obvious category of reefs that could be considered to be at risk of developing outbreaks would be those that are adjacent to reefs where high densities of starfish are recorded. The most extensive record of *A. cf. solaris* populations on GBR reefs is based on manta tow surveys (Miller et al. 2009), so we used these data to identify reefs with outbreaks.

We identified sets of reefs that were likely to have been exposed to significant settlement of *A. cf. solaris* larvae under two different criteria:

1. Firstly we identified the reefs where overall average densities of ≥ 0.22 *A. cf. solaris* per manta tow had been observed. This corresponds to the long-accepted threshold for Incipient Outbreaks based on studies by Moran & De'ath (1992) and Keesing and Lucas (1992).
2. In view of the analysis in the previous section, we also considered reefs where overall average densities of ≥ 0.12 *A. cf. solaris* per manta tow had been observed.

Having identified focal reefs that had received substantial numbers of larvae by these criteria, we assumed that reefs situated within a belt 25 km north or south of these focal reefs experienced similar hydrodynamic conditions, and so were likely to receive similar numbers of *A. cf. solaris* larvae, meaning that outbreaks were equally likely to develop there. For this reason (and subject to other conditions below), we included in the analysis every reef that lay within a 25km belt of latitude to the north or south of a reef that had either (1) average density of *A. cf. solaris* ≥ 0.22 starfish per tow (Incipient Outbreak, Miller et al. 2009), or (2) average density of *A. cf. solaris* ≥ 0.12 starfish per tow (based on the previous section of this report).

In order to focus on reefs where conditions were likely to support outbreaks, we excluded all outer shelf reefs from analyses, as outbreaks rarely occur on these (James and Scandol 1992). Secondly the timing of the study relative to the implementation of zoning measures is important. The GBRMP was initially zoned sequentially by region. The Cairns Section of the GBRMP was zoned early on, and the first zoning plan for that region was proclaimed in 1981. Zoning of the Cairns section was amended in 1989 after other regions had been zoned. The substantially-revised Amalgamated Zoning Plan for the entire GBRMP, which included a much greater proportion of no-take zones, came into force in mid-2004. Since the ecological effects of closure to fishing depend in part on seasonal processes such as recruitment, the effects of Marine Protected Areas (MPAs) develop over a period of years (e.g. Edgar et al. 2014). In the case of the 3rd wave of outbreaks, we allowed the effects of zoning to develop for five years after the implementation of the revised zoning plan for the Cairns Section, and so (following Sweatman 2008) we only considered the pattern of outbreaks recorded after 1994 but before

mid-2004, when the Amalgamated Zoning Plan came into effect. The first outbreaks of the 4th wave were seen in 2011, more than six years after the Amalgamated Zoning Plan came into effect, so we assumed that any effects of zoning on the reef communities were at least partially developed by that time.

The different GBR management zones permit several levels of fishing and the use of different types of gear. Additionally, on some reefs, fishing is permitted in some areas, but not in others. For analysis, if line fishing was allowed on any part of a reef, we considered that reef to be open to fishing. Only reefs where no fishing for benthic species was permitted in any area were classed as no-take. Trolling for pelagic species was the only fishing permitted on some reefs; we judged pelagic fishes to be unlikely predators of *A. cf. solaris* and considered such reefs to be no-take zones.

The probability of detecting outbreaks when they occur will increase with the survey effort at a reef. For this reason we only included reefs that were surveyed a minimum of three times between 1994 and 2004 (3rd Wave) and at least twice between 2011 and 2016 (4th Wave). We also excluded reefs in the far northern GBR (<14°S) because these were surveyed infrequently and irregularly.

Having identified reefs that were arguably both at risk of developing outbreaks and had been sampled adequately by these multiple criteria, we compared the relative occurrence of outbreaks on reefs that were open to fishing and reefs that were no-take zones at the time of each wave of outbreaks. We used three different density thresholds for outbreaks: the existing category “Incipient outbreak” (average for a reef of ≥ 0.22 starfish per 2 minute tow), the existing category “Active outbreak” (average for a reef of ≥ 1.0 starfish per 2 minute tow), and following Section 2, the new lower criterion of ≥ 0.12 starfish per 2-minute tow. The relationship between occurrence of outbreaks (by the three definitions) and Marine Park zoning status was modelled for each wave. Log-linear models included terms for the two waves of outbreaks (Wave 3 (1994-2004) and Wave 4 (2011 to 2017)), for whether a reef was a no-take zone or not, and for whether an outbreak was recorded at that reef in that period. Separate analyses considered inshore plus midshelf reefs, or only midshelf reefs. Models were selected using analysis of deviance and Akaike’s Information Criterion (AIC). Effect sizes were estimated using odds ratios.

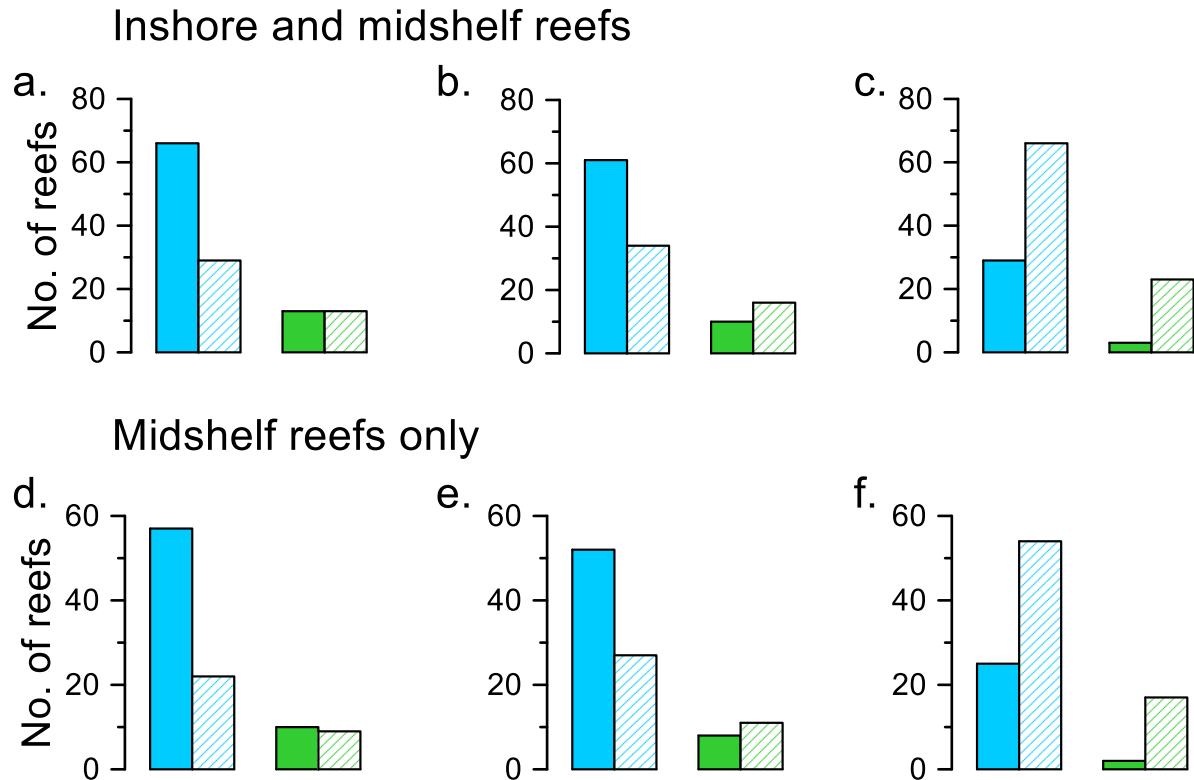


Figure 6: Numbers of reefs that were open to fishing (blue) or no-take areas (green) where outbreaks were recorded (solid fill) or no outbreaks were recorded (hatched) based on summed data from the two waves of outbreaks. Reefs were considered at risk of developing outbreaks and included in these analyses if they lay near a reef where densities of ≥ 0.22 *A. cf. solaris* per tow were observed in the study period. The upper panels include both midshelf and inshore reefs; lower panels only include midshelf reefs. Panels (a) and (d) give the numbers using outbreak threshold density of 0.12 starfish per tow (see previous Section); panels (b) and (e) use an outbreak threshold of 0.22 starfish per tow; panels (c) and (f) use an outbreak threshold of 1.0 starfish per tow.

3.3 Results

In no case was there evidence that the effect of marine park zoning of a reef on probability of recording an outbreak differed between the two waves of outbreaks (no significant 3-way interactions, Appendix 1). When either criterion was used to identify reefs where outbreaks could be expected, the models could be reduced to Zone x Outbreak (the term of interest) plus a simple effect of Wave (Appendix 1). We therefore combined the observations from Waves 3 and 4 for analysis. The raw numbers for each wave are shown in Appendix 1.

Reefs designated “at risk” of developing outbreaks if near reefs with 0.22 starfish per tow

Taking outbreak density to be ≥ 0.12 starfish per tow and considering only midshelf reefs, there was no evidence that no-take reefs were consistently less likely to have outbreaks of *A. cf. solaris* (Figure 6d, Figure 7a). This was also true if both inshore and midshelf reefs were included in the analysis (Figure 5a, Figure 6a).

Taking outbreak density to be ≥ 0.22 starfish per tow and including only midshelf reefs, there was no evidence that no-take reefs were consistently less likely to have outbreaks of *A. cf.*

solaris (Figure 6e, Figure 7b). If both inshore and midshelf reefs were included in the analysis then reefs that were open to fishing were nearly three times more likely to develop outbreaks of *A. cf. solaris* than on no-take reefs (Figure 6b, lower 95% confidence limit = 1.17, Figure 7b).

Taking outbreak density to be ≥ 1.0 starfish per tow and including only midshelf reefs, there was no evidence that no-take reefs were consistently less likely to have outbreaks of *A. cf. solaris* (Figure 6f, Figure 7c). This was also true if both inshore and midshelf reefs were included in the analysis (Figure 6c, Figure 7c).

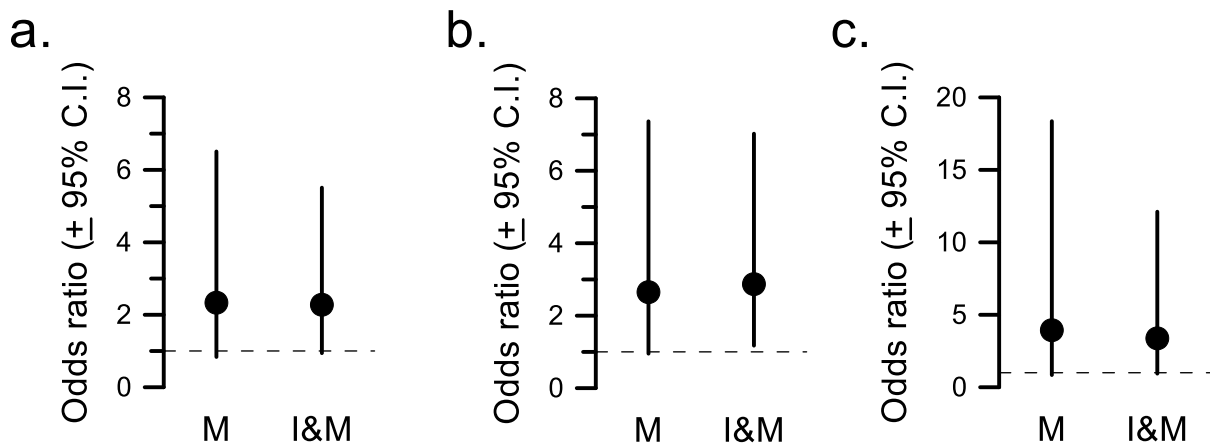


Figure 7: The effect of marine park zone on the likelihood of finding outbreak densities of *A. cf. solaris*, based on three definitions of outbreak: (a) an average density of 0.12 starfish per manta tow, (b) 0.22 starfish per manta tow (Incipient Outbreak), and (c) 1.0 starfish per manta tow (Active Outbreak). Reefs were considered at risk of developing outbreaks and were included in these analyses if they were near a reef where densities of ≥ 0.22 *A. cf. solaris* per tow were observed in the study period. Odds ratios ($\pm$ 95% confidence intervals) are a measure of effect size. The point indicates the estimated odds ratio, error bars are 95% confidence intervals. The expected value of the ratio in the absence of an effect is 1.0, indicated by the dashed horizontal reference line. A ratio >1.0 indicates that outbreaks are more likely on reefs that are open to fishing. Inference is based on whether the confidence intervals include 1.0. M denotes the ratio based on midshelf reefs only, I&M denotes the ratio for inshore and midshelf reefs combined. Note the different scales on the Y-axes.

Reefs designated “at risk” of developing outbreaks if near reefs with 0.12 starfish per tow

If the outbreak threshold density was ≥ 0.12 starfish per tow and only midshelf reefs were considered, then reefs that were open to fishing were nearly three times more likely to develop outbreaks of *A. cf. solaris* than reefs where fishing was prohibited (Lower confidence limit = 1.03, Figure 8d, Figure 9a). However this was not true if both inshore and midshelf reefs were included in the analysis (Figure 8a, Figure 9a).

Taking outbreak density to be ≥ 0.22 starfish per tow and including only midshelf reefs, then reefs that were open to fishing were nearly three times more likely to develop outbreaks of *A. cf. solaris* than were no-take reefs (Lower confidence limit = 1.07, Figure 8e, Figure 9b). This was also true if both inshore and midshelf reefs were included in the analysis (Lower confidence limit = 1.11, Figure 8b, Figure 9b).

Taking outbreak density to be ≥ 1.0 starfish per tow and including only midshelf reefs, there was no evidence that no-take reefs were consistently less likely to have outbreaks of *A. cf.*

solaris (Figure 8c, Figure 9c). If both inshore and midshelf reefs were included in the analysis, then reefs that were open to fishing were 3.6 times more likely to develop outbreaks of *A. cf. solaris* than on no-take reefs (Figure 8c, lower confidence limit = 1.01, Figure 9c).

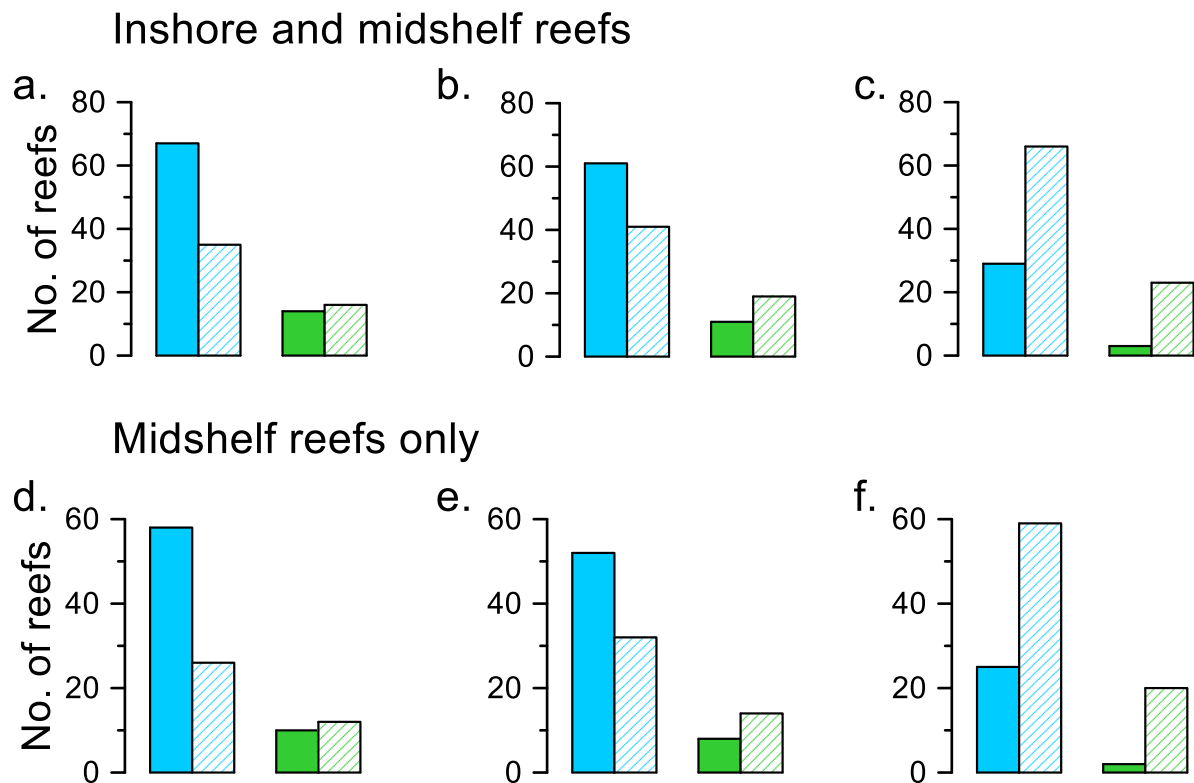


Figure 8: Numbers of reefs that were open to fishing (blue) or no-take areas (green) where outbreaks were recorded (solid fill) or no outbreaks were recorded (hatched) based on summed data from the two waves of outbreaks. Reefs were considered at risk of developing outbreaks and included in these analyses if they lay near a reef where densities of ≥ 0.12 *A. cf. solaris* per tow were observed in the study period. The upper panels include both midshelf and inshore reefs; lower panels only include midshelf reefs. Panels (a) and (d) give the numbers using outbreak threshold density of 0.12 starfish per tow (see previous Section); panels (b) and (e) use an outbreak threshold of 0.22 starfish per tow; panels (c) and (f) use an outbreak threshold of 1.0 starfish per tow.

3.4 Discussion

We have presented 12 different analyses of the relationship between the prohibition of fishing at reefs and the likelihood of outbreaks of *A. cf. solaris*. It is important to note that these are not independent results, but 12 different ways of looking at the same data. The approaches differ in the criteria used to identify reefs that were at risk of outbreaks in the study period, in the threshold density for outbreak status, and whether inshore reefs are included in analyses. All the analyses estimated the likelihood of outbreaks to be lower on no-take reefs. However in many cases, the possibility that the true difference was zero could not be discounted. On present knowledge, it is hard to say if any of the approaches is better than the others. If reefs neighbouring those reefs that had the lower density of 0.12 starfish per tow were considered likely to develop outbreaks, more cases were included in the analyses (106 vs 98 midshelf reefs only; 132 vs 121 inshore & midshelf reefs) which should give marginally greater statistical power. However, using 0.12 starfish per tow as the threshold density for outbreaks only showed a significant effect of zoning when just the midshelf reefs were included, but not when

inshore reefs were considered as well (Figure 9a). The effect of zoning was significant for both sets of reefs if 0.22 starfish per tow was used as the outbreak density threshold (Figure 9b).

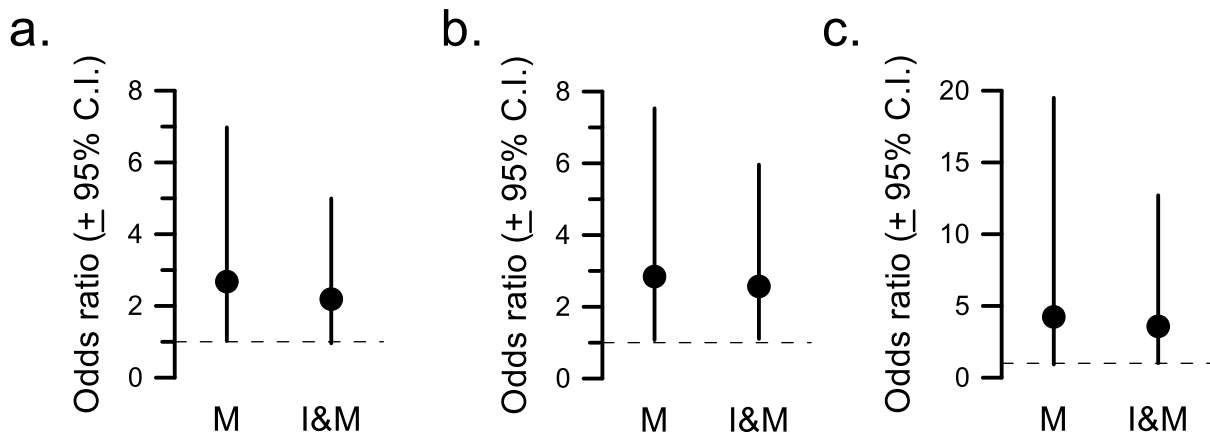


Figure 9: The effect of marine park zone on the likelihood of finding outbreak densities of *A. cf. solaris*, based on three definitions of outbreak: (a) an average density of 0.12 starfish per manta tow, (b) 0.22 starfish per manta tow (Incipient Outbreak), and (c) 1.0 starfish per manta tow (Active Outbreak). Reefs were considered at risk of developing outbreaks and were included in these analyses if they were near a reef where densities of ≥ 0.12 *A. cf. solaris* per tow were observed in the study period. Odds ratios ($\pm$ 95% confidence intervals) are a measure of effect size. The point indicates the estimated odds ratio, error bars are 95% confidence intervals. The expected value of the ratio in the absence of an effect is 1.0, indicated by the dashed horizontal reference line. A ratio >1.0 indicates that outbreaks are more likely on reefs that are open to fishing. Inference is based on whether the confidence intervals include 1.0. M denotes the ratio based on midshelf reefs only, I&M denotes the ratio for inshore and midshelf reefs combined. Note the different scales on the Y-axes.

The episodic nature of *A. cf. solaris* outbreaks, in combination with the reasonable assumption that outbreaks are mainly propagated by larval dispersal between reefs, means that not all reefs are equally likely to have outbreaks at any time. For this reason, a simple overall analysis of the occurrence of outbreaks by zone on all reefs across all years will give an unsatisfactory estimate of the relative likelihood of outbreaks on reefs in each marine park zone, because the inclusion of reefs where outbreaks are unlikely in all treatment groups will tend to dilute any evidence of differences. To circumvent this, we have tried to focus on reefs that were at risk of outbreaks. The criteria that we used to identify reefs where outbreaks could be expected are overly simple and somewhat arbitrary. The use of a band of latitude is obviously a crude representation of proximity of reefs and the setting of the width of the band at 25 km was arbitrary. The selection of a minimum number of surveys during each wave before a reef was included in analyses was also arbitrary. The criteria for identifying reefs that are at risk of developing outbreaks could in principle be refined using the advanced hydrodynamic models of the GBR that are becoming available through the eReefs project (Chen et al. 2011). A body of modelling around possible transmission pathways for *A. cf. solaris* outbreaks on the GBR has been developed, combining network theory and advanced hydrodynamic modelling (Hock et al. 2014, 2016). However, we still lack precise knowledge of spawning dates and locations. This is important since currents in the GBR lagoon vary greatly in speed and direction, particularly in summer when the starfish spawn. This means that dispersal trajectories from the same site may differ considerably from week to week (C Ewels, pers comm). At present there is also little information on most aspects of the larval life of *A. cf. solaris* in the wild. This includes the behaviour and location of larvae in the water column, anything about interactions with competitors, or estimates of larval survival under field conditions. Without such

information, hydrodynamic models cannot at present give reliable predictions of larval supply to a reef that could be used to identify those reefs where outbreaks might be expected to develop.

The criteria we used to identify reefs that were at risk of outbreaks differed from those used by Sweatman (2008). In the earlier study, the full geographic spread of reefs (either reefs in all positions on the shelf or just midshelf reefs) between 25km north of the most northerly outbreak and the 25 km south of the most southerly outbreak were all considered to have been at risk. In this study, only reefs within the 25km band of a reef where either a starfish density of 0.12 or 0.22 per tow were seen were included in the analyses. With the new criteria, and with the additional data from the fourth wave of outbreaks since 2011, there are still proportionally more outbreaks on midshelf reefs that are open to fishing than on no-take reefs, but the difference is not statistically significant using a 5% error rate (Figure 6d, Figure 7b), though the effect of zoning was significant when both inshore and midshelf reefs were considered (Figure 6a, Figure 7b).

Vanhatalo et al. (2017) used a statistical model to investigate the effects of zoning on the occurrence of high starfish densities using the same data. Their model estimated “intensity” to capture the variation in relative numbers of starfish geographically and over time. Intensity can be thought of as the expected (average) count of *A. cf. solaris* per manta tow on a reef at a particular location (in terms of latitude and position on the continental shelf) and point in time. Their model included terms for spatial patterns (such as the low occurrence of on outer shelf reefs) and a spatio-temporal term to address the episodic nature of starfish populations. The authors divided the dataset into the periods before and after the implementation of the amalgamated zoning plan for the GBRMP in 2004. They found that intensity did not change substantially with time since a reef was closed to fishing in the period up to 2004, but intensity on reefs that were closed to fishing under the new zoning plan in 2004 declined by half in the following 10 years, when compared with reefs where fishing was permitted.

No-take reefs are expected to differ from reefs that are open to fishing in terms of fishing pressure. This can have direct effects on the abundances of target species and indirect effects on reef communities through trophic cascades. A recent review (Cowan et al. 2017) identified 80 coral reef species that have been recorded eating one or more life stages of *A. cf. solaris* in the field or in laboratory studies. The majority (55) were fishes. Twenty-one species were planktivorous damselfishes that took eggs or larvae, the many of the other fishes were larger species had been observed feeding on moribund or dead starfish. Nine of the 55 species of fishes had been recorded attacking healthy juvenile or adult *A. cf. solaris*. How might these species be affected if their home reef was zoned as a no-take area? The effect of zoning on reef fish communities in a standard habitat has been studied on GBR reefs. Emslie et al. (2015) compared the communities that live on the semi-exposed reef slopes on reefs across the GBR. The abundance of benthic foragers that might prey on juvenile starfish (including wrasses and some butterfly fishes) was greater on no-take reefs offshore, while inshore the reverse was true. The abundance of planktivores (primarily damselfishes) which are potential predators of eggs and larvae did not differ with zoning. Of the larger fishes that attacked healthy juvenile and adult *A. cf. solaris*: the pufferfishes, triggerfishes, and emperors, only the emperors (Lethrinidae) are taken by fishers on the GBR and so might respond directly to zoning. However lethrinids occur in low numbers (at least in the reef slope sites that have been studied) and there is no evidence of an effect of zoning on their abundance on offshore

reefs of the GBR (Figure 10). The other known predators of *A. cf. solaris* are invertebrates. This includes the best-known predator of the crown-of-thorns starfish, the Triton's Trumpet snail (*Charonia tritonis*). There are no *a priori* reasons to think that the abundance these invertebrate species will be affected by fishing pressure and marine park zoning.

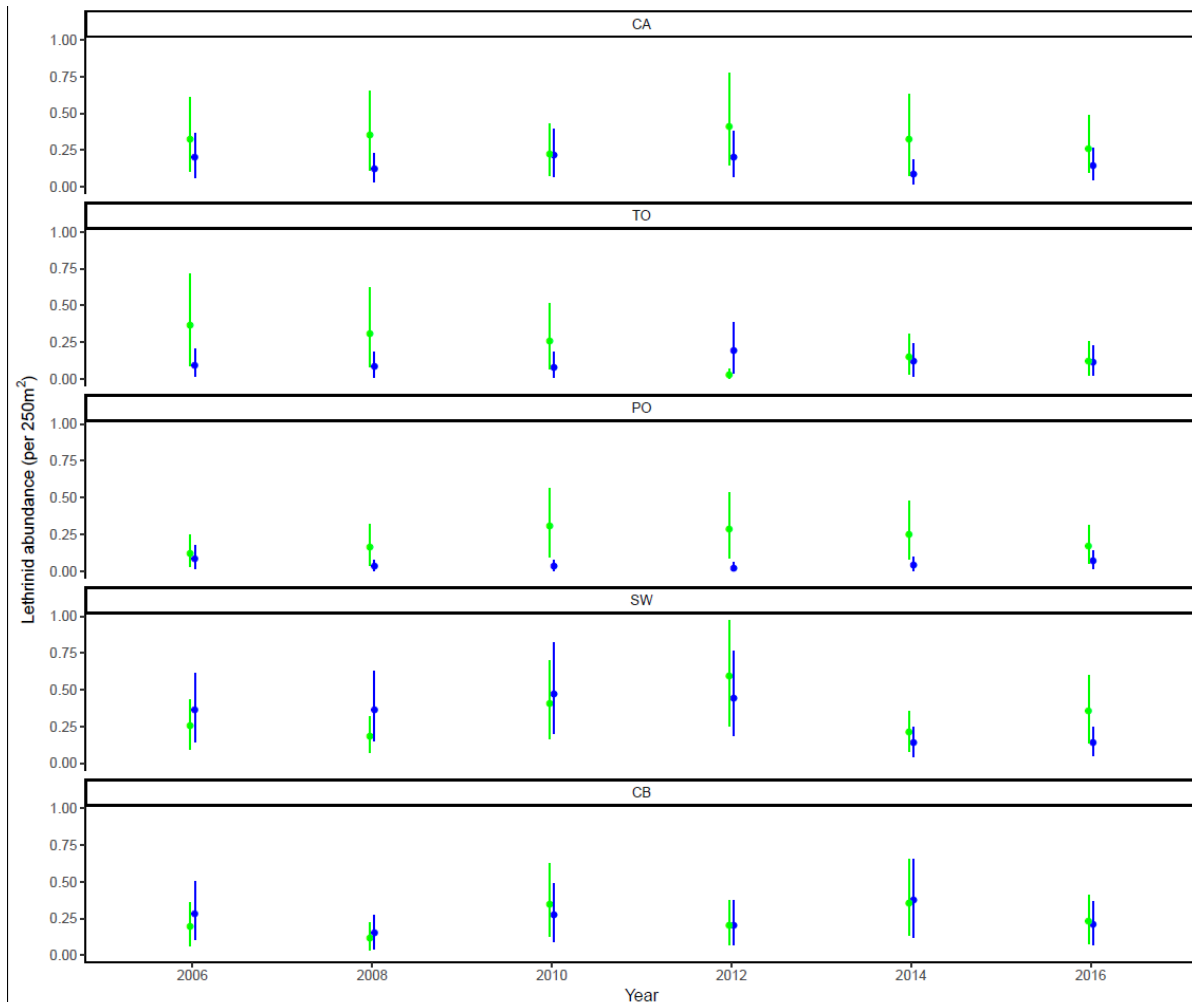


Figure 10: Mean abundance of emperors (Lethrinidae) on no-take reefs (green symbols) and reefs that are open to fishing (blue symbols) in five regions of the Great Barrier Reef from 2006 to 2016. Error bars are 95% uncertainty intervals. Data from AIMS Long-term Monitoring Program. The estimated overall effect size across all regions was that Lethrinids were 12.4% more abundant in no-take zones but the 95% uncertainty interval (-15% to +50%) spans zero.

The primary target species of the reef line fishery on the GBR are piscivores in the genus *Plectropomus*. Coral trout are more numerous and individuals are larger in no-take zones on the GBR (Emslie et al. 2015). However coral trout are most unlikely to prey on adult or juvenile *A. cf. solaris* of any age. Sweatman (2008) suggested that a four-level trophic cascade would be required to link any increase in abundance of large piscivores, such as coral trout, in no-take areas to reductions in abundance of *A. cf. solaris*. An increase in large predatory species could reduce the abundance of species of benthic-feeding carnivorous fishes (such as wrasses) and allow an increase in abundance of small invertebrates such as crabs and polychaete worms that are known prey on small juvenile *A. cf. solaris*. It is also possible that benthic-feeding carnivorous fishes (such as wrasses) prey on smaller juvenile starfish. In this case, reducing the abundance of benthic carnivores would release the starfish from predation

and make outbreaks more likely in no-take zones. At present this is all pure conjecture. Evidence for trophic cascades on coral reefs in general, and on the GBR in particular, is sparse (e.g. Emslie et al. 2015; Rizzari et al. 2015; Casey et al. 2016). This could be because the high diversity of species in many groups on coral reefs could lead to greater functional redundancy than in some other systems, so the ecological functions of species that become less abundant, for instance due to fishing, can be assumed by other species.

In a study of a related topic based on different monitoring data from the GBR, Mellin et al. (2016) found that *A. cf. solaris* outbreaks caused less change in coral community composition on no-take reefs compared with reefs that were open to fishing. Further, the coral communities on no-take reefs returned to their former state more rapidly. Presumably less change in community structure is the result of less intense predation by *A. cf. solaris*, meaning smaller outbreak populations on no-take reefs. The authors mention that a lack of fishing mortality of carnivorous fish in no-take zones could cause trophic cascades that result in more predators of juvenile *A. cf. solaris*, but also comment on the equivocal evidence for trophic cascades on coral reefs.

Considering the evidence of predation on the starfish themselves, many *A. cf. solaris* have physical damage in the form of one or more missing or regenerating arms (e.g. Rivera-Posada et al. 2014). This is assumed to be the result of unsuccessful predatory attacks. It is not clear whether the incidence of sub-lethal predation attempts will be positively or negatively related to the rate of lethal predation (McCallum et al. 1989; Birkeland & Lucas 1990; Kettle 1990; Cowan et al. 2017). The incidence of starfish with damaged arms will depend on both the rate of sub-lethal predator attacks and on the rate of healing and tissue regeneration, and the latter varies substantially with the nutritional state of the starfish. Starfish populations in the late stages of an outbreak, when coral food is less available, had a higher incidence of injury (27% to >90% in two years at Helix Reef in the 1980s, Kettle [1990]). Two recent studies have compared the incidence of starfish with damaged arms in no-take areas and on reefs that were open to fishing: The incidence of starfish with damaged arms was marginally lower at two sites that were open to fishing compared with a no-take zone in the Philippines (62% and 53% vs 67%, Rivera-Posada et al. 2014). A much larger sample of 3,846 *A. cf. solaris* from 19 reefs on the GBR found the opposite pattern: the incidence of injury was lowest on no-take reefs ($46.05\% \pm 7.1\% \text{ SE}$) compared with reefs that were open to fishing ($50.15\% \pm 5.92\% \text{ SE}$) and with reefs with restrictions on fishing gear ($53.78\% \pm 12.66\% \text{ SE}$) (Messmer et al., 2017). The authors noted that the differences between overall mean values for reefs in different zones were small compared with the variation among the means for individual reefs within zones. The extent of damage was also similar across zones, with damaged animals in each zone having usually lost a single arm. In summary no clear pattern in likelihood of sub-lethal predatory attacks is evident among zones, though Kettle's work implies that the interpretation of injury rates is not necessarily straight forward.

Overall the evidence for a negative relationship between likelihood of outbreaks and protection from fishing remains weak. Our analyses of manta tow surveys in the GBR Marine Park consistently show that there are relatively fewer outbreaks on no-take reefs, but any effect appears to be small. An alternative approach using a statistical model also found inconsistency in the size of the effect at different times. There is little evidence that abundance of most functional groups of fishes on GBR reefs is affected by marine park zoning. Nor are there differences in cover of hard and soft corals and algae between zones (Emslie et al. 2015).

Evidence of sub-lethal predation also shows contrasting patterns in different studies. The development of more sophisticated models of connectivity in combination with increased knowledge of the basic life history of *A. cf. solaris* may allow more robust tests of the hypothesis, but this is some way in the future.

3.4 Summary

- Different approaches to the analysis of the occurrence of outbreaks in two waves of outbreaks that have affected the GBR found that outbreaks were less likely to occur on no-take reefs, but in many cases the possibility that the difference is zero could not be excluded.
- Other related studies of effects of zoning on starfish numbers which gave inconsistent results at different times. The relationship between protection from fishing and the frequency of starfish that were missing arms was also inconsistent.
- Many species have been observed to prey on different life stages of *A. cf. solaris* in laboratory experiments or in the field, but mechanisms that link abundance of the majority of these predators to marine park zoning are unclear.
- The episodic nature of *A. cf. solaris* outbreaks, the lack of information on much basic biology of the starfish and the relative sparseness of manta tow surveys mean that a definitive test for a relationship between protection from fishing and likelihood of outbreaks remains elusive.
- There is very little information about predation on *A. cf. solaris* of any age-class under natural conditions, but this is particularly so for larvae and small juveniles.

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APPENDIX 1: THE FREQUENCY OF OUTBREAKS OF *A. CF. SOLARIS* IN THE THIRD AND FOURTH WAVES OF OUTBREAKS

Reefs designated “at risk” of developing outbreaks from being near reefs with 0.22 starfish per tow

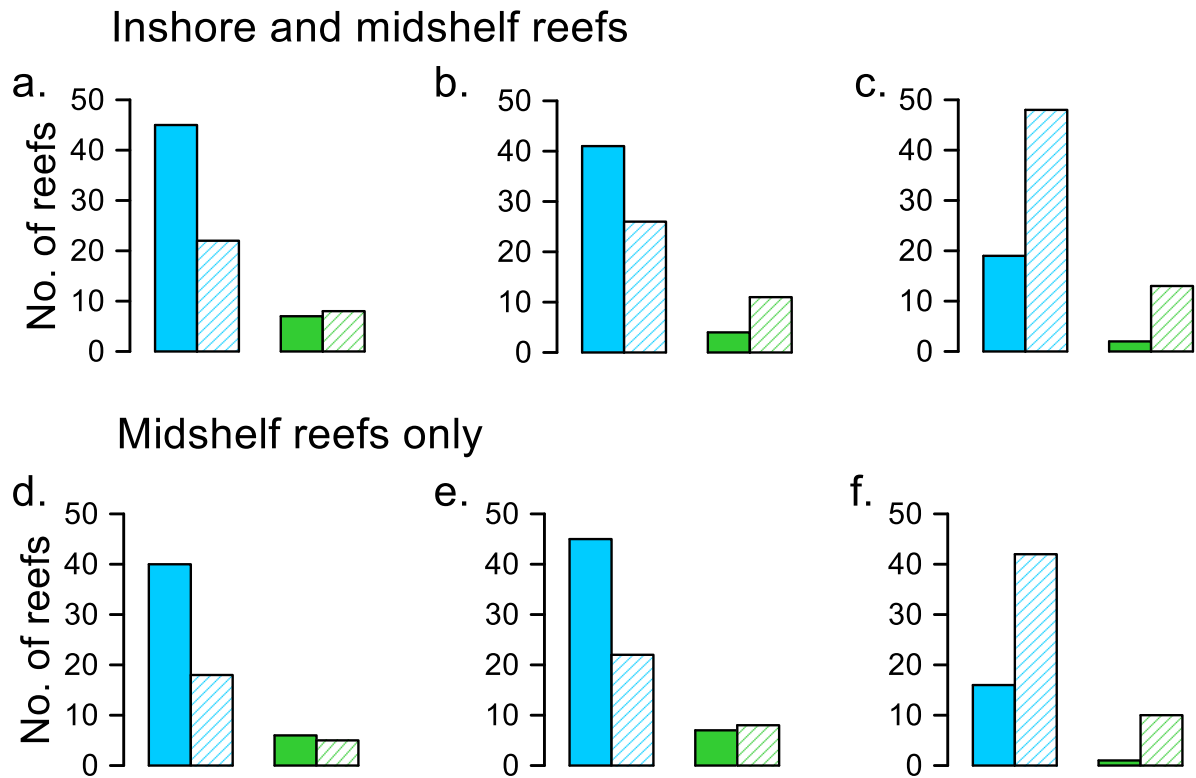


Figure 11: Numbers of reefs that were open to fishing (blue) or no-take areas (green) where outbreaks were recorded (solid fill) or no outbreaks were recorded (hatched) during the third recorded wave of outbreaks on the GBR, 1994-2004. Reefs were considered at risk of developing outbreaks and included in these analyses if they lay near a reef where densities of ≥ 0.22 *A. cf. solaris* per tow were observed in the study period. The upper panels include both midshelf and offshore reefs; lower panels only include midshelf reefs. Panels (a) and (d) are based on an outbreak threshold density of 0.12 starfish per tow (see previous Section); panels (b) and (e) are based on an outbreak threshold density of 0.22 starfish per tow; panels (c) and (f) are based on an outbreak threshold density of 1.0 starfish per tow.

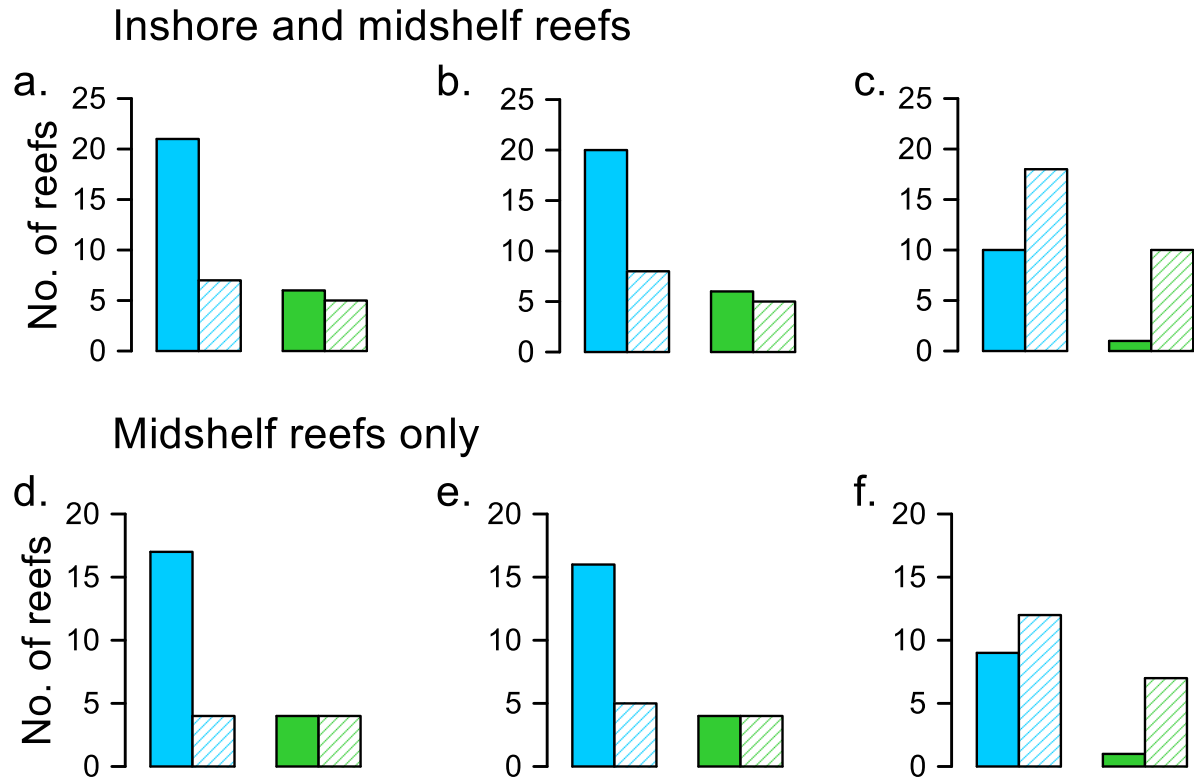


Figure 12: Numbers of reefs that were open to fishing (blue) or no-take areas (green) where outbreaks were recorded (solid fill) or no outbreaks were recorded (hatched) during the fourth recorded (current) wave of outbreaks on the GBR, 2011 to present. Reefs were considered at risk of developing outbreaks and included in these analyses if they lay near a reef where densities of ≥ 0.22 *A. cf. solaris* per tow were observed in the study period. The upper panels include both midshelf and offshore reefs; lower panels only include midshelf reefs. Panels (a) and (d) are based on an outbreak threshold density of 0.12 starfish per tow (see previous Section); panels (b) and (e) are based on an outbreak threshold density of 0.22 starfish per tow; panels (c) and (f) are based on an outbreak threshold density of 1.0 starfish per tow.

Reefs designated “at risk” of developing outbreaks from being near reefs with 0.12 starfish per tow

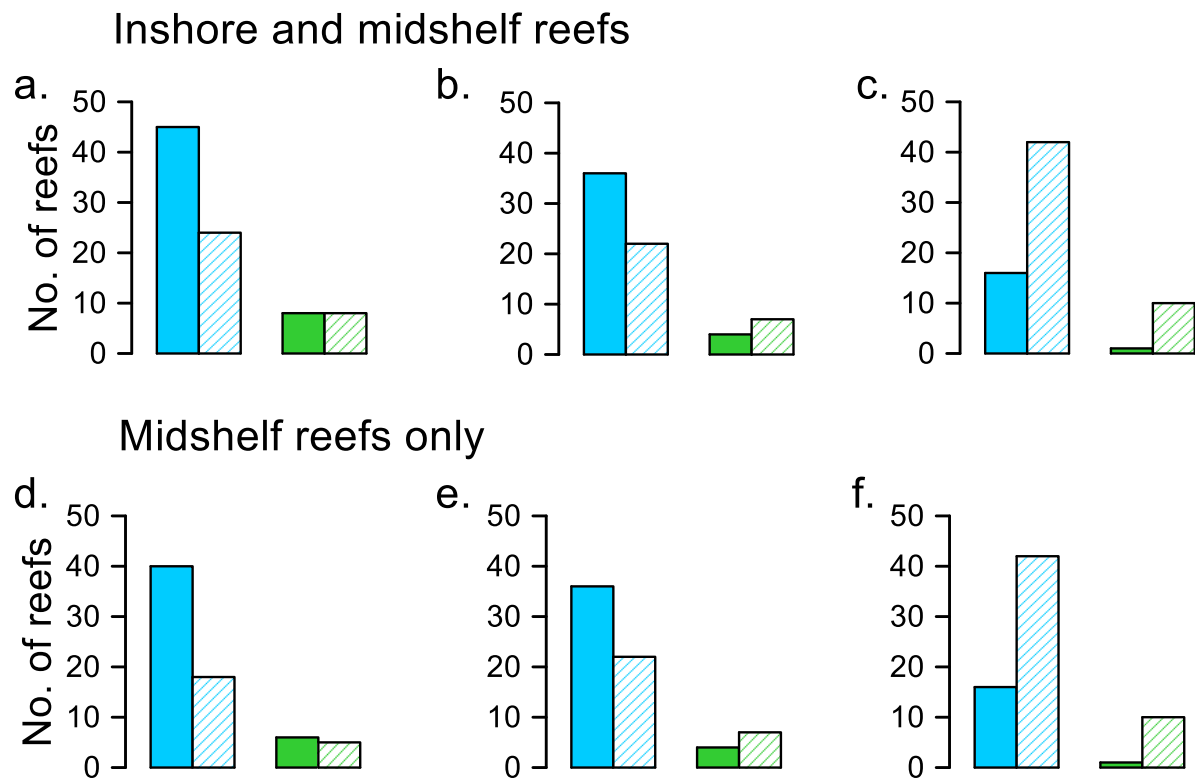


Figure 13: Numbers of reefs that were open to fishing (blue) or no-take areas (green) where outbreaks were recorded (solid fill) or no outbreaks were recorded (hatched) during the third recorded wave of outbreaks on the GBR, 1994-2004. Reefs were considered at risk of developing outbreaks and included in these analyses if they lay near a reef where densities of ≥ 0.12 *A. cf. solaris* per tow were observed in the study period. The upper panels include both midshelf and offshore reefs; lower panels only include midshelf reefs. Panels (a) and (d) are based on an outbreak threshold density of 0.12 starfish per tow (see previous Section); panels (b) and (e) are based on an outbreak threshold density of 0.22 starfish per tow; panels (c) and (f) are based on an outbreak threshold density of 1.0 starfish per tow.

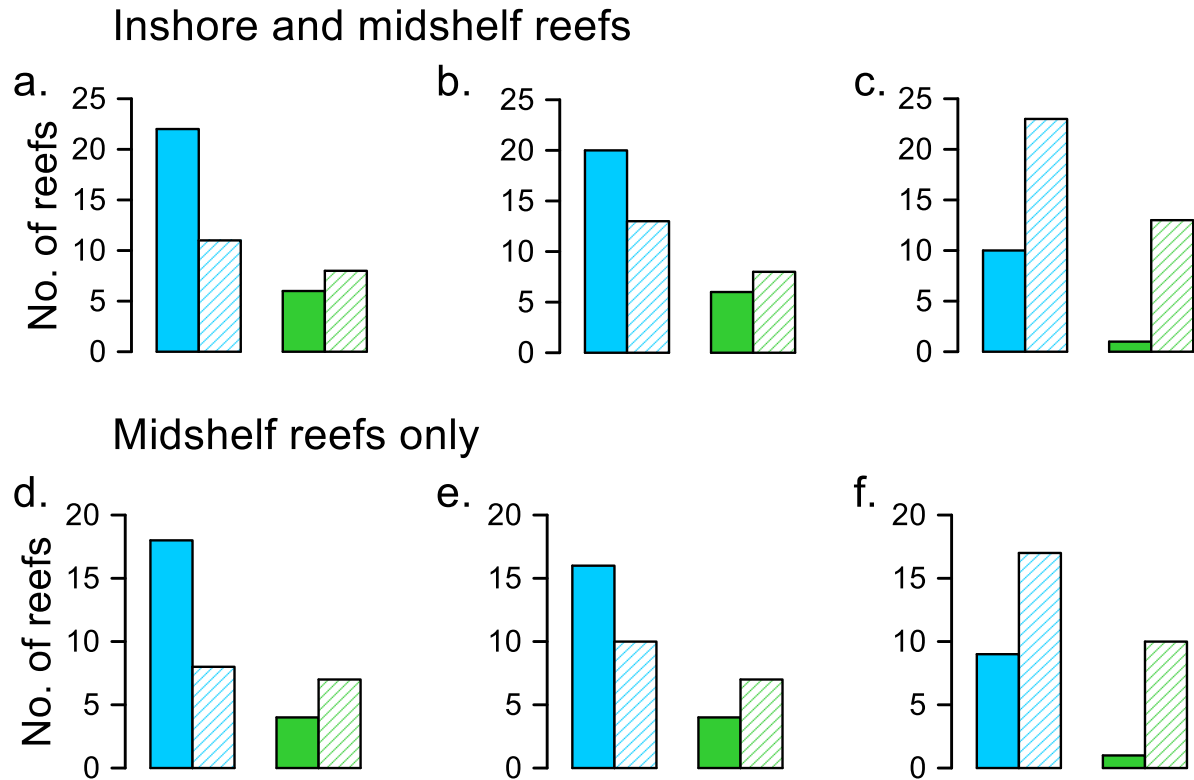


Figure 14: Numbers of reefs that were open to fishing (blue) or no-take areas (green) where outbreaks were recorded (solid fill) or no outbreaks were recorded (hatched) during the fourth recorded (current) wave of outbreaks on the GBR, 2011 to present. Reefs were considered at risk of developing outbreaks and included in these analyses if they lay near a reef where densities of ≥ 0.12 *A. cf. solaris* per tow were observed in the study period. The upper panels include both midshelf and offshore reefs; lower panels only include midshelf reefs. Panels (a) and (d) are based on an outbreak threshold density of 0.12 starfish per tow (see previous Section); panels (b) and (e) are based on an outbreak threshold density of 0.22 starfish per tow; panels (c) and (f) are based on an outbreak threshold density of 1.0 starfish per tow.

APPENDIX 2: MODEL SELECTION

The full model including terms for all factors and interaction was:

*Counts ~ Zone*Outbreak*Wave + Zone*Outbreak + Zone*Wave + Outbreak*Wave + Wave + Zone + Outbreak*

We identified the best model by omitting terms and examining the resulting increase in deviance, a measure of the amount of variation in the data that each model explained. Only terms whose omission resulted in a significant increase in deviance were retained. In each case the best model included the Zone x Outbreak interaction (indicating that the number of starfish outbreaks was different in different marine park zones). The lack of significant change in deviance when the 3-way interaction was omitted in each case indicated that the effect of zoning on the likelihood of outbreaks was similar in the two waves. This allowed the data from the two waves to be combined.

Table 1: The sequence of sub-models used in model selection. W = Wave, Z = Zone, O = Outbreak

Model No.	Model	Notes
1	$W*Z*O + W*Z + W*O + Z*O + W + Z + O$	Full model
2	$W*Z + W*O + Z*O + W + Z + O$	Full model less 3-way interaction
3	$W*Z + W*O + W + Z + O$	Model 2 less $Z*O$
4	$W*Z + Z*O + W + Z + O$	Model 2 less $W*O$
5	$W*O + Z*O + W + Z + O$	Model 2 less $W*Z$
6	$W*Z + W + Z + O$	Main effects + $W*Z$
7	$W*O + W + Z + O$	Main effects + $W*O$
8	$Z*O + W + Z + O$	Main effects + $Z*O$
9	$W + Z + O$	Only main effects

Reefs designated “at risk” of developing outbreaks from being near reefs with 0.22 starfish per tow

Table 2: Model selection sequence for likelihood of outbreaks using threshold density of 0.12 starfish per 2-minute manta tow. Inshore and midshelf reefs were included in the analysis. Numbers in “Model comparison” column refer to models in Table 1.

Model Comparison	Test for	Deviance	P
1 vs 2	$W*Z*O$	0.0050495	0.943
2 vs 3	$Z*O$	3.6406	0.056
2 vs 4	$W*O$	0.73764	0.390
2 vs 5	$W*Z$	1.8303	0.176
6 vs 9	$W*Z$	1.4914	0.222
7 vs 9	$W*O$	0.39868	0.528
8 vs 9	$Z*O$	3.3016	0.069

Table 3: Model selection sequence for likelihood of outbreaks using threshold density of 0.22 starfish per 2-minute manta tow. Inshore and midshelf reefs were included in the analysis. Numbers in “Model comparison” column refer to models in Table 1.

Model Comparison	Test for	Deviance	P
1 vs 2	W*Z*O	0.57527	0.448
2 vs 3	Z*O	6.4136	0.011 *
2 vs 4	W*O	2.435	0.119
2 vs 5	W*Z	2.3905	0.122
6 vs 9	W*Z	1.4914	0.222
7 vs 9	W*O	1.536	0.215
8 vs 9	Z*O	5.5145	0.019 *

Table 4: Model selection sequence for likelihood of outbreaks using threshold density of 1.0 starfish per 2-minute manta tow. Inshore and midshelf reefs were included in the analysis. Numbers in “Model comparison” column refer to models in Table 1.

Model Comparison	Test for	Deviance	P
1 vs 2	W*Z*O	0.32386	0.569
2 vs 3	Z*O	4.4968	0.034 *
2 vs 4	W*O	0.28635	0.593
2 vs 5	W*Z	1.6868	0.194
6 vs 9	W*Z	1.4914	0.222
7 vs 9	W*O	0.090878	0.763
8 vs 9	Z*O	4.3013	0.038 *

Table 5: Model selection sequence for likelihood of outbreaks using threshold density of 0.12 starfish per 2-minute manta tow. Only midshelf reefs were included in the analysis. Numbers in “Model comparison” column refer to models in Table 1.

Model Comparison	Test for	Deviance	P
1 vs 2	W*Z*O	0.55427	0.4566
2 vs 3	Z*O	2.9003	0.08856
2 vs 4	W*O	0.64517	0.4218
2 vs 5	W*Z	2.0171	0.1555
6 vs 9	W*Z	1.6884	0.1938
7 vs 9	W*O	0.3165	0.5737
8 vs 9	Z*O	2.5716	0.1088

Table 6: Model selection sequence for likelihood of outbreaks using threshold density of 0.22 starfish per 2-minute manta tow. Only midshelf reefs were included in the analysis. Numbers in "Model comparison" column refer to models in Table 1.

Model Comparison	Test for	Deviance	P
1 vs 2	W*Z*O	0.010037	0.9202
2 vs 3	Z*O	4.2511	0.03922 *
2 vs 4	W*O	1.7663	0.1838
2 vs 5	W*Z	2.396	0.1216
6 vs 9	W*Z	1.6884	0.1938
7 vs 9	W*O	1.0587	0.303
8 vs 9	Z*O	3.5436	0.0598

Table 7: Model selection sequence for likelihood of outbreaks using threshold density of 1.0 starfish per 2-minute manta tow. Only midshelf reefs were included in the analysis. Numbers in "Model comparison" column refer to models in Table 1.

Model Comparison	Test for	Deviance	P
1 vs 2	W*Z*O	0.040665	0.8402
2 vs 3	Z*O	4.6334	0.03135 *
2 vs 4	W*O	1.6281	0.202
2 vs 5	W*Z	2.3495	0.1253
6 vs 9	W*Z	1.6884	0.1938
7 vs 9	W*O	0.96702	0.3254
8 vs 9	Z*O	3.9724	0.04625 *

Reefs designated "at risk" of developing outbreaks from being near reefs with 0.12 starfish per tow

Table 8: Model selection sequence for likelihood of outbreaks using threshold density of 0.12 starfish per 2-minute manta tow. Inshore and midshelf reefs were included in the analysis. Numbers in "Model comparison" column refer to models in Table 1.

Comparison of models	Tests for:	Deviance	P
1 vs 2	W*Z*O	0.1677	0.682
2 vs 3	Z*O	3.3741	0.066
2 vs 4	W*O	0.0064	0.936
2 vs 5	W*Z	1.9295	0.164
6 vs 9	W*Z	2.0215	0.155
7 vs 9	W*O	0.0983	0.753
8 vs 9	Z*O	3.4661	0.062

Table 9: Model selection sequence for likelihood of outbreaks using threshold density of 0.22 starfish per 2-minute manta tow. Inshore and midshelf reefs were included in the analysis. Numbers in “Model comparison” column refer to models in Table 1.

Model Comparison	Test for	Deviance	P
1 vs 2	W*Z*O	0.26554	0.606
2 vs 3	Z*O	5.1772	0.023 *
2 vs 4	W*O	0.1808	0.671
2 vs 5	W*Z	2.1846	0.139
6 vs 9	W*Z	2.0215	0.155
7 vs 9	W*O	2.1846	0.139
8 vs 9	Z*O	5.014	0.025 *

Table 10: Model selection sequence for likelihood of outbreaks using threshold density of 1.0 starfish per 2-minute manta tow. Inshore and midshelf reefs were included in the analysis. Numbers in “Model comparison” column refer to models in Table 1.

Model Comparison	Test for	Deviance	P
1 vs 2	W*Z*O	0.31778	0.573
2 vs 3	Z*O	4.9104	0.0277 *
2 vs 4	W*O	0.0090673	0.924
2 vs 5	W*Z	2.0025	0.157
6 vs 9	W*Z	2.0215	0.155
7 vs 9	W*O	0.028021	0.867
8 vs 9	Z*O	4.9294	0.026 *

Table 11: Model selection sequence for likelihood of outbreaks using threshold density of 0.12 starfish per 2-minute manta tow. Only midshelf reefs were included in the analysis. Numbers in “Model comparison” column refer to models in Table 1.

Model Comparison	Test for	Deviance	P
1 vs 2	W*Z*O	0.56482	0.452
2 vs 3	Z*O	3.7117	0.054
2 vs 4	W*O	0.17338	0.677
2 vs 5	W*Z	2.3246	0.127
6 vs 9	W*Z	2.6912	0.101
7 vs 9	W*O	0.53999	0.462
8 vs 9	Z*O	4.0783	0.043 *

Table 12: Model selection sequence for likelihood of outbreaks using threshold density of 0.22 starfish per 2-minute manta tow. Only midshelf reefs were included in the analysis. Numbers in “Model comparison” column refer to models in Table 1.

Model Comparison	Test for	Deviance	P
1 vs 2	W*Z*O	0.0005	0.982
2 vs 3	Z*O	4.4622	0.035 *
2 vs 4	W*O	0.0016466	0.968
2 vs 5	W*Z	2.5427	0.111
6 vs 9	W*Z	2.6912	0.101
7 vs 9	W*O	0.15017	0.698
8 vs 9	Z*O	4.6108	0.032 *

Table 13: Model selection sequence for likelihood of outbreaks using threshold density of 1.0 starfish per 2-minute manta tow. Only midshelf reefs were included in the analysis. Numbers in "Model comparison" column refer to models in Table 1.

Model Comparison	Test for	Deviance	P
1 vs 2	W*Z*O	0.043981	0.834
2 vs 3	Z*O	4.9151	0.027 *
2 vs 4	W*O	0.37401	0.541
2 vs 5	W*Z	2.9932	0.084
6 vs 9	W*Z	2.6912	0.101
7 vs 9	W*O	0.072006	0.788
8 vs 9	Z*O	4.6131	0.032 *

