UNIVERSITY
OF WOLLONGONG
AUSTRALIA

University of Wollongong Research Online

Faculty of Science, Medicine and Health - Papers:
Part B

Faculty of Science, Medicine and Health

2018

Accounting for habitat structural complexity improves the assessment of performance in no-take marine reserves

Matthew Rees

University of Wollongong, mjr849@uowmail.edu.au

Nathan A. Knott

New South Wales Department Of Primary Industries, nknott@uow.edu.au

Joseph M. Neilson

New South Wales Department of Primary Industries

Michelle Linklater

University of Wollongong, ml970@uowmail.edu.au

Ian Osterloh

New South Wales Department Of Primary Industries

See next page for additional authors

Publication Details

Rees, M. J., Knott, N. A., Neilson, J., Linklater, M., Osterloh, I., Jordan, A. & Davis, A. R. (2018). Accounting for habitat structural complexity improves the assessment of performance in no-take marine reserves. *Biological Conservation*, 224 100-110.

Research Online is the open access institutional repository for the University of Wollongong. For further information contact the UOW Library:
research-pubs@uow.edu.au

Accounting for habitat structural complexity improves the assessment of performance in no-take marine reserves

Abstract

Seascape variability may confound assessments on the effectiveness of no-take marine reserves (NTMRs) in conserving biodiversity. In most cases baseline data are lacking, resulting in evaluations of NTMR effectiveness being Control Impact (CI) assessments. Even with independent replicate areas among management zones, this approach can make it difficult to detect zone effects if seascape attributes, such as habitat structural complexity varies among experimental areas. To determine the importance of structural complexity in evaluations of NTMR effectiveness we performed assessments on the abundance of a targeted fish, yellowtail kingfish (*Seriola lalandi*), in the Lord Howe Island Marine Park (LHIMP). We compared assessments which did and did not account for structural complexity, quantified using high resolution multibeam bathymetry. Despite almost 3 times more *S. lalandi* in NTMRs, the traditional CI assessment explained only 3% of the variation in the abundance of *S. lalandi* and revealed no clear effect of protection. Incorporating structural complexity into the assessment increased the deviance explained to 65% and uncovered an important interaction between zone and structural complexity. Greater abundances of *S. lalandi* were detected in NTMRs compared to fished zones but only on highly complex reefs. By accounting for structural complexity, we demonstrate that the precision and accuracy of NTMR assessments can be improved, leading to a better understanding of ecological change in response to this conservation strategy. Consequently, where marine park zones vary greatly in structural complexity, we strongly advocate for quantifying and accounting for such variability in assessments of NTMR performance.

Publication Details

Rees, M. J., Knott, N. A., Neilson, J., Linklater, M., Osterloh, I., Jordan, A. & Davis, A. R. (2018). Accounting for habitat structural complexity improves the assessment of performance in no-take marine reserves. *Biological Conservation*, 224 100-110.

Authors

Matthew Rees, Nathan A. Knott, Joseph M. Neilson, Michelle Linklater, Ian Osterloh, Alan Jordan, and Andrew R. Davis

ACCOUNTING FOR HABITAT STRUCTURAL COMPLEXITY IMPROVES THE
ASSESSMENT OF PERFORMANCE IN NO-TAKE MARINE RESERVES

Matthew J. Rees^{a,b,*}

mj.rees@aims.gov.au

Nathan A. Knott^c

Joseph Neilson^c

Michelle Linklater^d

Ian Osterloh^c

Alan Jordan^c

Andrew R. Davis^a

^aCentre for Sustainable Ecosystem Solutions (CSES), School of Biological Sciences,
University of Wollongong, NSW 2522, Australia

^bAustralian Institute of Marine Science, Indian Ocean Marine Research Centre, UWA
(MO96), 35 Stirling Hwy, Crawley, Western Australia 6009, Australia

^cNSW Department of Primary Industries, Port Stephens Fisheries Institute, Locked Bag 1,
Nelson Bay, NSW 2315, Australia

^dSchool of Earth and Environmental Sciences, University of Wollongong, NSW 2522,
Australia

*Corresponding author

HIGHLIGHTS

- No-take marine reserve assessments were compared with and without habitat structure
- Abundances of yellowtail kingfish were greater in NTMRs but only on complex reef
- Including habitat structure increased deviance explained from 3% to 65%
- This reduced the standard error of mean abundances in NTMRs by 40%
- Assessment precision & accuracy improved, providing robust outcomes for management

ABSTRACT

Seascape variability may confound assessments on the effectiveness of no-take marine reserves (NTMRs) in conserving biodiversity. In most cases baseline data are lacking, resulting in evaluations of NTMR effectiveness being Control Impact (CI) assessments. Even with independent replicate areas among management zones, this approach can make it difficult to detect zone effects if seascape attributes, such as habitat structural complexity varies among experimental areas. To determine the importance of structural complexity in evaluations of NTMR effectiveness we performed assessments on the abundance of a targeted fish, yellowtail kingfish (*Seriola lalandi*), in the Lord Howe Island Marine Park (LHIMP). We compared assessments which did and did not account for structural complexity, quantified using high resolution multibeam bathymetry. Despite almost 3 times more *S. lalandi* in NTMRs, the traditional CI assessment explained only 3% of the variation in the abundance of *S. lalandi* and revealed no clear effect of protection. Incorporating structural complexity into the assessment increased the deviance explained to 65% and uncovered an important interaction between zone and structural complexity. Greater abundances of *S. lalandi* were detected in NTMRs compared to fished zones but only on highly complex reefs. By accounting for structural complexity, we demonstrate that the precision and accuracy of NTMR assessments can be improved, leading to a better understanding of ecological change in response to this conservation

strategy. Consequently, where marine park zones vary greatly in structural complexity, we strongly advocate for quantifying and accounting for such variability in assessments of NTMR performance.

KEY WORDS

marine reserves, marine protected areas, remote sensing, seascape ecology, habitat structural complexity, multibeam

INTRODUCTION

Highlighted as an effective strategy to address a number of human pressures that contribute to changes in marine ecosystems, no-take marine reserves (NTMRs) have increased steadily on a global scale in the last two decades (Halpern et al., 2010; Costello and Ballantine, 2015). To evaluate whether this form of spatial management is providing beneficial conservation outcomes, it is essential that no-take marine reserves are accurately assessed (McCook et al., 2010). Robust assessments of ecological change related to marine reserve zoning relies upon sampling designs capable of teasing apart the effects of protection. This entails disentangling specific ecological attributes from underlying temporal and spatial variability (García-Chartron and Pérez-Ruzafa, 1999; García-Chartron et al., 2000). If natural variability is not accounted for, assessments of no-take marine reserve effectiveness may be confounded, potentially leading to misleading conclusions (Claudet and Guidetti, 2010). A popular approach to date has been Before After Control Impact (BACI) experimental designs, which allow zone effects to be separated from underlying natural variability (Underwood, 1992). This methodology however, requires sampling multiple times prior to NTMR establishment which rarely occurs (Halpern and Warner, 2003). Instead, most studies use a Control Impact (CI) approach where biological assemblages within protected areas (preferably replicated areas) are compared to those in adjacent, or nearby, partially protected or unprotected areas (Lester et al., 2009; Sciberras et al., 2013; Miller and Russ, 2014). Differences observed in biological assemblages among management zones are then inferred as evidence of a reserve effect.

A potential issue for CI studies testing no-take marine reserve effectiveness is that they may be confounded by seascape variability (Claudet and Guidetti, 2010; Huntington et al., 2010; Osenberg et al., 2011). For example, in coral reef environments numerous studies have demonstrated the importance of habitat structural complexity as an important driver of the diversity and abundance of fishes (Friedlander and Parrish, 1998; Almany, 2004; Gratwicke and Speight, 2005). Previous research has demonstrated that coral reef habitats of greater structural complexity generally harbour a greater diversity and biomass of fishes compared to reefs of low structural complexity. This relationship is likely to be a result of structurally complex habitats providing increased abiotic variability, niches and resources (Bell and Mushinsky, 1991; Friedlander and Parrish, 1998). Therefore, if structural complexity varies among management zones and is not accounted for in CI assessments on marine reserve effectiveness, there is a risk that incorrect conclusions may be drawn from such assessments (Young et al., 2016).

A possible solution to this issue is to include a measure of structural complexity as a co-variate in statistical tests of no-take marine reserve effectiveness, thereby improving the accuracy and precision of the assessment (Claudet and Guidetti, 2010). In the past however, this has been problematic due to the difficulties and costs associated with collecting seascape data over the broad spatial scales that NTMRs and multi-use marine protected areas (MPAs) encompass. Recent advances in remote-sensing technologies now allow seafloor habitats to be mapped in high resolution over a range of spatial scales (Mellin et al., 2009; Brown et al., 2011). Consequently, marine ecologists have employed this technology to explore relationships between remotely-sensed seascape measures, such as structural complexity and biological assemblages in both coral and temperate rocky reef environments (Kuffner et al., 2007; Purkis et al., 2008; Pittman et al., 2009; Rees et al., 2014; Ferrari et al., 2017). As strong relationships between remotely-sensed measures and biological assemblages have been observed; habitat mapping has become increasingly used in guiding the design of zones within MPAs (Pittman and Brown, 2011; Rees et al., 2014). Despite the applicability of this technology, the use of remote-sensing to account for potential seascape confounding in CI assessments is still in its infancy. This is most likely a result of the relatively high costs and limited

availability of this technology throughout many regions of the world. However, as remote-sensing technologies become more cost effective and readily available (Mellin et al., 2009; Brown et al., 2011; Ierodiaconou et al., 2011), the application of this approach to aid no-take marine reserve assessments is likely to become more feasible.

In this study, we tested the effectiveness of no-take marine reserves in the Lord Howe Island Marine Park (LHIMP) with and without accounting for underlying differences in structural complexity. The LHIMP is located 610 km off the east coast of Australia in the subtropical region of the South Pacific Ocean. For many reasons the LHIMP provides an ideal system to test marine reserve performance while accounting for differences in structural complexity. First, Lord Howe Island and its surrounding waters have significant biological value, comprising the world's southernmost coral reef and a diversity of both tropical and temperate taxa that includes a suite of endemic species (Edgar et al., 2010). Consequently, Lord Howe Island received World Heritage Listing in 1982 (Environment Australia, 2000). Second, the LHIMP is positioned in the subtropics; a region prone to the effects of climate change, and the marine park's remoteness makes it vulnerable to ongoing and increasing anthropogenic pressures (Edgar et al., 2010). Therefore, it is critical that conservation efforts are adequately and accurately assessed. Finally, the Lord Howe Island shelf has been extensively mapped with high resolution sonar (~5 m resolution) to understand the distribution and structure of shelf habitats, particularly relict coral reefs formed 7000 to 9000 years ago (Woodroffe et al., 2010). As a result, quantification of structural complexity across the majority of the LHIMP shelf habitat is possible.

To determine the importance of accounting for structural complexity in CI assessments of no-take marine reserves, we performed two tests on the effectiveness of the LHIMP. The first, a traditional CI assessment and the second, a series of CI assessments including a measure of structural complexity. Both tests compared the effect of NTMR protection on the abundance of yellowtail kingfish (*Seriola lalandi*), a heavily exploited species of bony fish in the LHIMP (Figueira and Hunt, 2012). We predicted that remotely-sensed structural complexity and reserve protection would influence the abundance of *S. lalandi*. Consequently, we predicted that the model including structural

complexity would explain more of the variation in *S. lalandi* abundance, therefore leading to a more accurate and precise assessment of NTMR effectiveness on this targeted species compared to the model excluding structural complexity.

MATERIALS AND METHODS

The Lord Howe Island Marine Park is a 3470 km² multi-use marine park located 610 km off NSW, Australia, at latitude 31°50'S. The marine park contains two separate shelf areas adjacent to Lord Howe Island and Balls Pyramid, which are separated by a 4 - 8 km wide trench reaching depths of approximately 500 m. The marine park covers the State waters (proclaimed in 1999) and Commonwealth waters (proclaimed in 2000) which surround Lord Howe Island and Balls Pyramid. State waters are from the mean high water mark to 3 nautical miles (nm) surrounding the islands while Commonwealth waters extend from 3 nm to 12 nm offshore. The study was undertaken on the Lord Howe Island and Balls Pyramid shelves between depths of 25 – 50 m. At this depth, 2 different management zones are present within federal and state waters. Zones are either, sanctuary zones which are strictly no-take marine reserves (referred to as NTMRs in this study) that prohibit extractive activities, or habitat protection zones which are partially protected areas allowing some forms of fishing, such as charter boat operations and recreational line fishing (referred to as fished zones in this study) (Fig. 1). Spearfishing and commercial fishing in the park is prohibited.

The abundance of yellowtail kingfish; *Seriola lalandi*, was surveyed using baited remote underwater video systems (BRUVS) constructed by SeaGIS Pty Ltd with Canon HG21 video cameras. This species was chosen as they are the most common species targeted by fishers in the park. Catch by weight of *S. lalandi* based on landings by charter operators has ranged from 16,904 kg to 24,313 kg per year between 2006 and 2011 (Figueira and Hunt, 2012). Depredation of hooked and released individuals by the abundant galapagos whalers; *Carcharhinus galapagensis* is a common occurrence in the LHIMP, therefore fishing mortality is likely to be greater than reported (Figueira and Hunt, 2012). Although *S. lalandi* inhabit both demersal, mid-water and pelagic environments

(Heagney et al., 2007; Rees et al., 2015), the majority of charter boat fishing effort for *S. lalandi* occurs on or closely associated with seafloor habitats (NSW DPI unpublished data). This includes the Lord Howe Island and Balls Pyramid shelf; the habitat assessed in this study (Figueira and Hunt, 2012). In response to their high catch rates on the LHIMP shelf, *S. lalandi* are likely to show a positive response to the cessation of fishing (Claudet et al., 2010). In addition, the abundance and distribution of *S. lalandi* is likely to be influenced by structural complexity at the scale explored in this study. Reefs of high structural complexity are potentially optimal habitat for *S. lalandi* within the LHIMP, providing increased prey such as baitfish and macroinvertebrates as well as favourable abiotic conditions such as variability in current movements. Previous research has demonstrated increased catches of *S. lalandi* in areas of high structural complexity compared to areas of relatively low structural complexity (Hobday and Campbell, 2009). As a result, the response of *S. lalandi* to NTMR protection may well be influenced by the structural complexity of the reefs they inhabit.

To estimate the abundance of *Seriola lalandi*, BRUVS were deployed at 16 sites within the LHIMP in 2009. Eight of these sites were in fished zones and 8 sites in NTMRs where fishing is prohibited. These sites follow the design of a long-term fish monitoring program in the LHIMP and were originally selected to representatively sample no-take and fished zones. Consequently, sites were not stratified over areas of varying structural complexity raising the concern over potential habitat confounding in the no-take marine reserve assessment. Serendipitously, however, survey sites were representative of the structural complexity exhibited on the Lord Howe Island and Balls Pyramid shelf between depths of 25 – 50 m (Fig. A.1). In 2013 the same 16 sites were resampled and an additional 5 sites were surveyed (Fig. 1), of which 3 were in fished zones and 2 in NTMRs. The additional sites in 2013 were again chosen to representatively sample no-take and fished zones. At each site 4 BRUVS were deployed simultaneously (+/- 15 mins). We sought to position each deployment 200 m away from one another (average distance = 340 m). Due to difficult survey conditions there were 4 occasions where deployments were within this distance (160 m, 140 m, 120 m, 120 m). For the 2009 sampling period, bait consisted of 1 kg of crushed pilchards (*Sardinops sagax*) as there was a limited supply of bait on the island. As a result, the same kilogram of bait was re-used for each of the 4

BRUVS deployments within each site. Prior to deployment the bait was re-crushed in an attempt to keep bait plumes consistent. In 2013, bait bags were replenished for each deployment with a fresh 500 g of crushed pilchards (Wraith et al., 2013). Although inconsistencies in bait use between sampling years is not ideal, no significant difference in the abundance of *S. lalandi* was observed between years ($t = 0.77$, $df = 31$, $p = 0.45$) suggesting discrepancies in bait use had little influence on our estimates of abundance for *S. lalandi* (Fig A.2, A.3). In addition, previous research has reported that the quantity of bait has no effect on the abundance of fish recorded using BRUVS (Hardinge et al., 2013). All BRUVS were deployed for a minimum of 35 min to ensure a 30 min period was available for analysis. Previous research has demonstrated that a 30 min sample provides a representative sample of the fish at this latitude on the east coast of Australia (Harasti et al., 2015). Footage was analysed using Event Measure software (SeaGIS Pty). For each deployment, the relative abundance (Max N) of *Seriola lalandi* was recorded, which is the maximum number of individuals of *S. lalandi* viewed at any one time during the 30 minute sample. To determine the relative abundance of *S. lalandi* per site, the Max N of the four deployments was summed. Analyses were done at the site level as we sought to test the importance of structural complexity on the abundance of *S. lalandi* among sites, rather than its influence within sites.

Multibeam data acquired around the Lord Howe Island and Balls Pyramid shelves were collated from multiple surveys on the shelf platforms to form a high resolution (5 m cell size) seamless grid of the region (Brooke et al., 2010; Mleczko et al., 2010; Linklater et al., 2015; Linklater, 2016). Using the focal statistic function within *ArcGIS 10*, the bathymetric data were used to calculate two measures of structural complexity at a number of spatial scales surrounding each BRUVS deployment (25 m, 50 m, 100 m, 150 m and 200 m radii). The first measure, vertical relief (VR), was the range in bathymetry at a given scale. The second measure, bathymetric variance (BV), was the standard deviation in bathymetry at a given scale (Wilson et al., 2007; Rees et al., 2014). These measures were averaged across the four BRUVS deployment positions to estimate the vertical relief and bathymetric variance of each site. Larger values of vertical relief and bathymetric variance indicated reefs of greater structural complexity (Table A.1).

To determine the importance of accounting for structural complexity in no-take marine reserve assessments we constructed a series of Generalised Linear Models (GLMs) with Negative Binomial distributions. The first model simply tested the effect of zone (fixed: fished versus NTMR) on the abundance of *S. lalandi*. A second set of models tested the importance of accounting for underlying structural complexity by including an interaction between zone and a structural complexity measure (VR or BV) calculated at a particular spatial scale (20 m, 50 m, 100 m, 150 m or 200 m). Only one measure of structural complexity at a single spatial scale could be included in each model as strong multi-collinearity (Pearson Correlation >0.5) was identified among these variables (Graham, 2003). A third set of models were constructed to examine the importance of structural complexity in the absence of zone. This exploratory multi-scale approach was employed as the spatial scale that *S. lalandi* responds to structural complexity within the LHIMP was unknown. Sampling period; ‘year’ was not included as an explanatory variable as preliminary data exploration demonstrated that it had little influence on the abundance of *S. lalandi* (Fig. A.2). Models were ranked using Akaike’s Information Criterion corrected for small sample sizes (AICc) and AICc weights, whereby the model with the lowest AICc was considered to have the best fit (Burnham and Anderson, 2002; Wagenmakers and Farrell, 2004). Models within 2 AICc points of the model with the lowest AICc were also considered as plausible alternatives. Spatial autocorrelation in model residuals was assessed for the best fitting model using spline correlograms (Bjornstad and Falck, 2001). Positive spatial autocorrelation was apparent in model residuals up to approximately 2 km (Fig. A.4). As only 2 survey sites were within 2 km of one another, site 21 was removed from the analyses and spatial autocorrelation was no longer apparent in model residuals (Fig. A.4). To determine whether accounting for structural complexity had improved model fit and the assessment of NTMR performance we compared; i) variances of mean estimates of *S. lalandi* abundance within NTMRs and fished zones, and ii) the percentage deviance explained among models. All GLMs were run in R (R Core Development Team, 2014) using the package ‘MASS’ and the package ‘MuMIn’ was used to rank models (Bartoń, 2013).

RESULTS

The distribution of yellowtail kingfish; *Seriola lalandi* was patchy, with individuals only being observed on 35% of the BRUVS deployments across the two sampling periods. Summing the Max N's of *S. lalandi* across all deployments, a total of 164 individuals were observed during the study. Bathymetry of the Lord Howe Island and Balls Pyramid shelf revealed considerable variability in structural complexity (Fig. 2, Fig. A.5). For example, at the largest spatial scale examined (200 m radii), the vertical relief ranged from a minimum of 1.96 m to a maximum of 17.4 m across the survey sites (Table A.1).

On average, there were 2.7 times as many *Seriola lalandi* in no-take marine reserves compared to fished areas. Despite this, the model that excluded a measure of structural complexity revealed no clear evidence for an effect of zone on the abundance of *S. lalandi*. This was primarily due to substantial variability surrounding the mean abundance of *S. lalandi* in NTMRs; 6.8 ± 3.0 ($\pm$ SE) compared to fished zones; 2.4 ± 0.6 ($\pm$ SE).

All models accounting for structural complexity in the no-take marine reserve assessment were substantially better at explaining variation in the abundance of *Seriola lalandi* compared to the model containing just zone (Table 1). The model including the interaction between zone and bathymetric variance at the 100m scale provided the top-ranked fit (wAICc = 0.38) and explained the highest amount of deviance (D.E. = 65.47%). For these reasons, this model was preferred over the models including bathymetric variance at the 150m and 200m scale despite being within 2 AICc (Table 1).

Accounting for structural complexity in the assessment revealed an important interaction between zone and complexity on the abundance of *Seriola lalandi*. No-take marine reserves had a greater abundance of *S. lalandi*, but only at sites displaying high structural complexity (Fig. 3). There was no difference in the abundance of *S. lalandi* between NTMRs and fished zones in areas of low structural complexity (Fig. 3). Incorporating structural complexity into the model also substantially reduced the variance around the mean estimates of *S. lalandi* in NTMRs ($6.8 + 1.86$ and $- 1.43$, SE)

compared to the model containing just zone (6.8 ± 3.0 , SE). In contrast, variances remained similar in fished zones between the model accounting for structural complexity ($2.4 +0.56$ and -0.45 , SE) and the model containing just zone (2.4 ± 0.6 , SE). The model including structural complexity (BV 100m) in the assessment also explained a greater amount of the variance in the abundance of *S. lalandi* (D.E. 65.47 compared to 2.89). Notably, both NTMRs and fished zones displayed a relatively even spread of sites displaying low to high structural complexity (Fig. 3). There was no significant difference in average structural complexity (bathymetric variance) between the two zone types ($t = 0.42$, $df = 18$, $p = 0.68$), hence the initial CI assessment was not necessarily confounded.

The abundance of *Seriola lalandi* increased noticeably in no-take marine reserves where the underlying reef exhibited structural complexity (defined as bathymetric variance) greater than 2 m at a 100 m radii scale (Fig. 3). Areas displaying this level of structural complexity were well represented in no-take marine reserves and fished zones on the LHIMP shelf (Fig. 4).

DISCUSSION

Using high resolution bathymetric data, we have demonstrated that reef habitat on the Lord Howe Island Marine Park (LHIMP) shelf exhibits substantial variability in structural complexity. We were concerned that such variability may confound our Control Impact (CI) test on the response of a targeted species of fish to marine park zoning, leading to uncertainty in the assessment (Miller and Russ, 2014). This was not the case as sites of high and low structural complexities were well represented between the two management zones. The inclusion of structural complexity into the test, clearly resulted in a more complex and useful model, with greater explanatory power compared to the test without structural complexity. Although the initial CI assessment revealed almost 3 times greater abundance of *Seriola lalandi* inside no-take marine reserves compared to fished zones, this relationship was imprecise due to high variability surrounding mean estimates. Incorporating structural complexity into the assessment revealed a clear zone effect on the abundance of *S. lalandi*, but this effect was only apparent over suitable habitat (i.e. reefs of high structural complexity). By

accounting for differences in underlying structural complexity, we demonstrate a strong effect of the removal of fishing on the abundance of *S. lalandi*. This study probably represents the clearest example to date that accounting for habitat structural complexity, can lead to substantial improvements in the precision and accuracy of assessments on NTMR performance.

It is not surprising that the effectiveness of no-take marine reserve protection on the abundance of *Seriola lalandi* was dependent on underlying structural complexity. For *S. lalandi*, structurally complex reefs are likely to be optimal habitat, providing increased prey such as baitfish as well as favourable variability in abiotic conditions such as ocean currents. Strong links between biota, such as pelagic fishes and structural complexity has been observed previously (Bouchet et al., 2015). For example, Hobday and Campbell (2009) used a fine-scale scientific trolling method (km's), to explore the importance of seafloor structural complexity on the catch rates of three pelagic species including *S. lalandi*. They demonstrated that abundance of *S. lalandi* was significantly related to the structural complexity of the seafloor. Catch rates of *S. lalandi* were 26 times higher over structurally complex features compared to distances away from structurally complex features. Furthermore, *S. lalandi* is the most heavily targeted species by charter fishing operations in the waters of the LHIMP, with an average catch of approximately 20,000 kilograms per year (Figueira and Hunt, 2012). This is expected to result in a lower abundance of *S. lalandi* in preferred habitat (i.e. high structural complexity reef) open to fishing.

Given the breadth of literature indicating the importance of seascape variability in driving the spatial patterns in marine biological assemblages (Boström et al., 2011; Olds et al., 2016), we strongly recommend, if feasible, to quantify and account for such variability in NTMR and MPA zoning assessments. Previous studies have highlighted the need to standardize habitat type when assessing MPAs as differences in the diversity and composition of habitat types may confound comparisons between management zones (Friedlander et al., 2007; Harborne et al., 2008). To our knowledge only three studies have accounted for finer scale habitat variability (i.e. structural complexity, patch shape and size) when assessing NTMR effectiveness over a single habitat type such as coral reef or temperate rocky reef. The first by Huntington et al. (2010), assessed the Glover's Reef Atoll Marine

Reserve, offshore from Belize, excluding and including natural seascape variability derived from high resolution IKONOS imagery. They found no reserve effects on the abundance and diversity of coral and fish assemblages when seascape variation was omitted from the assessment. However, when analyses were performed accounting for each sites' seascape characteristics, significant reserve effects became apparent. The second study, by Young et al. (2016) tested the efficacy of a small marine reserve on southern rock lobster populations while using multibeam bathymetry to characterize and account for variability in seafloor structure. The third study, by Russ et al. (2005) reported that reserve effects were still apparent with the inclusion of structural complexity in the assessment as a co-variate. Our findings accord with the previous literature highlighting the benefit of accounting for seascape variability to better understand the complex responses of taxa to marine reserve protection. We encourage future studies assessing NTMR and MPA zoning performance to, wherever possible, account for seascape differences such as structural complexity as it may lead to improved assessments and ultimately better conservation outcomes

Not only did the inclusion of structural complexity improve the test on no-take marine reserve effectiveness, it also produced alternate findings, many of which have important conservation implications. As the abundance of *Seriola lalandi* exhibited a strong response to structural complexity, our results lend support to the use of remotely-sensed abiotic variables as surrogates for species of interest (Pittman and Brown, 2011; Rees et al., 2014). This information may be valuable in aiding the design of spatial conservation strategies, such as MPAs. Furthermore, the outcome that no-take zones are most effective for *S. lalandi* over reefs of high structural complexity provides valuable information for the ongoing management of this species in the LHIMP. High resolution mapping of habitats on the Lord Howe Island and Balls Pyramid shelf indicate that the current zoning arrangement of the LHIMP is adequately representing this seascape attributes within NTMRs. Therefore, a better understanding of the benefits and functioning of marine reserves in this region is important to effectively manage the LHIMP and surrounding Commonwealth waters into the future.

In conclusion, amid the growing concerns of increasing threats to marine biodiversity, globally there has been an unprecedented increase in the establishment of MPAs (Halpern et al., 2010;

Costello and Ballantine, 2015). As many MPAs need to consider socio-economic issues as well as ecological objectives there is a possibility that current MPAs and the zones within them (i.e. NTMRs) may not be effective in reaching stated conservation objectives (Roberts et al., 2003; Edgar et al., 2004). Therefore, it is critical that MPA zones are accurately assessed to ensure objectives are being met. Without biological data collected prior to MPA establishment, however, it is difficult to tease apart effects of protection from underlying natural variability such as structural complexity (Garcia-Charton et al., 2000). In this study, we present an approach to account for structural complexity using remote-sensing technologies, which allowed us to better assess no-take marine reserve performance within a multi-use MPA. We concur with Huntington et al. (2010), in that future CI assessments on marine reserve efficacy should incorporate measures of seascape variability, where the data are available. This will allow managers to better identify and understand the effects of the management strategies they have in place. The approach of incorporating habitat information with ecological data will provide a better understanding of the effects of marine reserves on marine biological assemblages, leading to improved conservation outcomes.

ACKNOWLEDGEMENTS

We thank Ian Kerr and Jimmy Maher for assistance with fieldwork and Sallyann Gudge and Rick Stuart-Smith for their help with fish identification. We also thank Sallyann Gudge and Hamish Malcolm for their comments on earlier drafts of the manuscript.

REFERENCES

- Almany, G.R., 2004. Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. *Oecol.* 141, 105-113.
- Bartoń, K., 2013. MuMIn: Multi-model Inference. R Package Version 1.9. 13. The Comprehensive R Archive Network (CRAN), Vienna, Austria.
- Bell, S., McCoy, E.D., Mushinsky, H.R., 1991.

365 Habitat structure: the physical arrangement of objects in space. Springer Science and Business
366 Media.

367 Bjornstad, O.N., Falck, W., 2001. Nonparametric spatial covariance functions: estimation and testing.
368 Environ. Ecol. Stat. 8, 53–70.

369 Boström, C., Pittman, S.J., Simenstad, C., Kneib, R.T., 2011. Seascape ecology of coastal biogenic
370 habitats: advances, gaps, and challenges. Mar. Ecol. Prog. Ser. 427, 191-217.

371 Bouchet, P.J., Meeuwig, J.J., Kent, S., Chandra, P., Letessier, T.B., Jenner, C.K., 2015. Topographic
372 determinants of mobile vertebrate predator hotspots: current knowledge and future directions.
373 Biol. Rev. Camb. Philos. Soc. 90, 699-728.

374 Brooke, B., Woodroffe, C., Linklater, M., McArthur, M., Nichol, S., Jones, B., Kennedy, D.,
375 Buchanan, C., Spinoccia, M., Mleczko, R., 2010. Geomorphology of the Lord Howe Island
376 shelf and submarine volcano. Geoscience Australia, Canberra.

377 Brown, C.J., Smith, S.J., Lawton, P., Anderson, J.T., 2011. Benthic habitat mapping: A review of
378 progress towards improved understanding of the spatial ecology of the seafloor using acoustic
379 techniques. Estuar. Coast. Shelf. Sci. 92, 502-520.

380 Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodal Inference: A Practical
381 Information-theoretic Approach, 2nd edn. Springer-Verlag, New York, USA.

382 Claudet, J., Guidetti, P., 2010. Improving assessments of marine protected areas. Aquat. Conserv.
383 Mar. Freshw. Ecosyst. 20, 239-242.

384 Claudet, J., Osenberg, C., Domenici, P., Badalamenti, F., Milazzo, M., Falcón, J.M., Bertocci, I.,
385 Benedetti-Cecchi, L., García-Charton, J.A., Goñi, R., 2010. Marine reserves: fish life history
386 and ecological traits matter. Ecol. Appl. 20, 830-839.

387 Costello, M.J., Ballantine, B., 2015. Biodiversity conservation should focus on no-take Marine
388 Reserves 94% of Marine Protected Areas allow fishing. Trends Ecol. Evolut. 30, 507-509.

389 Edgar, G.J., Banks, S., Farina, J.M., Calvopina, M., Martinez, C., 2004. Regional biogeography of
 390 shallow reef fish and macro-invertebrate communities in the Galapagos archipelago. *J.*
 391 *Biogeography* 31, 1107-1124.

392 Edgar, G.J., Davey, A., Kelly, G., Mawbey, R.B., Parsons, K., 2010. Biogeographical and ecological
 393 context for managing threats to coral and rocky reef communities in the Lord Howe Island
 394 Marine Park, south-western Pacific. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 20, 378-396.

395 Environment Australia. 2000. Lord Howe Island Marine Park Proposal. Environment
 396 Australia, Marine Protected Area Section, Canberra.

397 Ferrari, R., Malcolm, H.A., Byrne, M., Friedman, A., Williams, S.B., Schultz, A., Jordan,
 398 A.R., Figueira, W.F. 2017. Habitat structural complexity metrics improve predictions of fish
 399 abundance and distribution. *Ecography*. In Press. doi:10.1111/ecog.02580

400 Figueira, W., Hunt, B., 2012. Lord Howe Island charter fisher report: 2004-2012.
 401 Prepared for the Lord Howe Island Marine Park.

402 Friedlander, A.M., Brown, E.K., Monaco, M.E., 2007. Coupling ecology and GIS to evaluate efficacy
 403 of marine protected areas in Hawaii. *Ecol. Appl.* 17, 715-730.

404 Friedlander, A.M., Parrish, J.D., 1998. Habitat characteristics affecting fish assemblages on a
 405 Hawaiian coral reef. *J. Exp. Mar. Bio. Ecol.* 224, 1-30.

406 Garcia-Charton, J.A., Perez-Ruzafa, A., 1999. Ecological heterogeneity and the evaluation of the
 407 effects of marine reserves. *Fish. Res.* 42, 1-20.

408 Garcia-Charton, J.A., Williams, I.D., Perez-Ruzafa, A., Milazzo, M., Chemello, R., Marcos, C.,
 409 Kitsos, M.S., Koukouras, A., Riggio, S., 2000. Evaluating the ecological effects of
 410 Mediterranean marine protected areas: habitat, scale and the natural variability of ecosystems.
 411 *Environ. Conserv.* 27, 159-178.

412 Graham, M.H., 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84,
 413 2809–2815.

414 Gratwicke, B., Speight, M.R., 2005. The relationship between fish species richness, abundance and
 415 habitat complexity in a range of shallow tropical marine habitats. *J. Fish Biol.* 66, 650-667.

416 Halpern, B.S., Lester, S.E., McLeod, K.L., 2010. Placing marine protected areas onto the ecosystem-
 417 based management seascape. *Proc. Natl. Acad. Sci. U.S.A.* 107, 18312-18317.

418 Halpern, B.S., Warner, R.R., 2003. Matching marine reserve design to reserve objectives. *Proc. Royal*
 419 *Soc. B* 270, 1871-1878.

420 Harasti, D., Malcolm, H., Gallen, C., Coleman, M.A., Jordan, A., Knott, N.A., 2015. Appropriate set
 421 times to represent patterns of rocky reef fishes using baited video. *J. Exp. Mar. Bio. Ecol.*
 422 463, 173-180.

423 Harborne, A.R., Mumby, P.J., Kappel, C.V., Dahlgren, C.P., Micheli, F., Holmes, K.E., Sanchirico,
 424 J.N., Broad, K., Elliott, I.A., Brumbaugh, D.R., 2008. Reserve effects and natural variation in
 425 coral reef communities. *J. Appl. Ecol.* 45, 1010-1018.

426 Hardinge, J., Harvey, E.S., Saunders, B.J. and Newman, S.J., 2013. A little bait goes a long way: the
 427 influence of bait quantity on a temperate fish assemblage sampled using stereo-BRUVs. *J.*
 428 *Exp. Mar. Bio. Ecol.* 449, 250-260.

429 Heagney, E.C., Lynch, T.P., Babcock, R.C., Suthers, I.M., 2007. Pelagic fish assemblages assessed
 430 using mid-water baited video: standardising fish counts using bait plume size. *Mar. Ecol.*
 431 *Prog. Ser.* 350, 255-266.

432 Hobday, A.J., Campbell, G., 2009. Topographic preferences and habitat partitioning by pelagic fishes
 433 off southern Western Australia. *Fish. Res.* 95, 332-340.

434 Huntington, B.E., Karnauskas, M., Babcock, E.A., Lirman, D., 2010. Untangling natural seascape
 435 variation from marine reserve effects using a landscape approach. *PLoS ONE*, 5, e12327.
 436 10.1371/journal.pone.0012327.

437 Ierodiaconou, D., Monk, J., Rattray, A., Laurenson, L., Versace, V., 2011. Comparison of automated
 438 classification techniques for predicting benthic biological communities using hydroacoustics
 439 and video observations. *Cont. Shelf Res.* 31, S28-S38.

440 Kuffner, I.B., Brock, J.C., Grober-Dunsmore, R., Bonito, V.E., Hickey, T.D., Wright, C.W., 2007.
 441 Relationships between reef fish communities and remotely sensed rugosity measurements in
 442 Biscayne National Park, Florida, USA. *Environ. Biol. Fishes* 78, 71-82.

443 Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D.,
 444 Airame, S., Warner, R.R., 2009. Biological effects within no-take marine reserves: a global
 445 synthesis. *Mar. Ecol. Prog. Ser.* 384, 33-46.

446 Linklater, M., 2016. Past and present coral distribution at the latitudinal limit of reef development,
 447 southwest Pacific Ocean. University of Wollongong.

448 Linklater, M., Brooke, B.P., Hamylton, S.M., Nichol, S.L., Woodroffe, C.D., 2015. Submerged fossil
 449 reefs discovered beyond the limit of modern reef growth in the Pacific Ocean.
 450 *Geomorphology* 246, 579-588.

451 McCook, L.J., Ayling, T., Cappel, M., Choat, J.H., Evans, R.D., De Freitas, D.M., Heupel, M.,
 452 Hughes, T.P., Jones, G.P., Mapstone, B., 2010. Adaptive management of the Great Barrier
 453 Reef: a globally significant demonstration of the benefits of networks of marine reserves.
 454 *Proc. Natl. Acad. Sci. U.S.A.* 107, 18278-18285.

455 Mellin, C., Andrefouet, S., Kulbicki, M., Dalleau, M., Vigliola, L., 2009. Remote sensing and fish-
 456 habitat relationships in coral reef ecosystems: review and pathways for systematic multi-scale
 457 hierarchical research. *Mar. Pollut. Bull.* 58, 11-19.

458 Miller, K.I., Russ, G.R., 2014. Studies of no-take marine reserves: methods for differentiating reserve
 459 and habitat effects. *Ocean Coast. Manag.* 96, 51-60.

460 Mleczko, R., Sagar, S., Spinoccia, M., Brooke, B., 2010. The creation of high resolution bathymetry
 461 grids for the Lord Howe Island region. Geoscience Australia, Canberra.

462 Olds, A.D., Connolly, R.M., Pitt, K.A., Pittman, S.J., Maxwell, P.S., Huijbers, C.M., Moore, B.R.,
 463 Albert, S., Rissik, D., Babcock, R.C., Schlacher, T.A., 2016. Quantifying the conservation
 464 value of seascape connectivity: a global synthesis. *Glob. Ecol. Biogeogr.* 25, 3-15.

465 Osenberg, C.W., Shima, J.S., Miller, S.L. and Stier, A.C., 2011. Ecology: assessing effects of marine
 466 protected areas: confounding in space and possible solutions. *Marine protected areas: a*
 467 *multidisciplinary approach*, 143-167.

468 Pittman, S.J., Brown, K.A., 2011. Multi-scale approach for predicting fish species distributions across
 469 coral reef seascapes. *Plos One* 6, e20583. 10.1371/journal.pone.0020583.

470 Pittman, S.J., Costa, B.M., Battista, T.A., 2009. Using lidar bathymetry and boosted regression trees
 471 to predict the diversity and abundance of fish and corals. *J. Coastal Res.* 25, 27-38.

472 Purkis, S.J., Graham, N.A.J., Riegl, B.M., 2008. Predictability of reef fish diversity and abundance
 473 using remote sensing data in Diego Garcia (Chagos Archipelago). *Coral Reefs* 27, 167-178.

474 R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for
 475 Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.

476 Rees, M.J., Knott, N.A., Fenech, G., Davis, A.R., 2015. Rules of attraction: enticing pelagic fish to
 477 mid-water remote underwater video systems (RUVS). *Mar. Ecol. Prog. Ser.* 529, 213-218.

478 Rees, M.J., Jordan, A., Price, O.F., Coleman, M.A., Davis, A.R., 2014. Abiotic surrogates for
 479 temperate rocky reef biodiversity: implications for marine protected areas. *Divers.*
 480 *Distributions* 20, 284-296.

481 Roberts, C.M., Andelman, S., Branch, G., Bustamante, R.H., Castilla, J.C., Dugan, J., Halpern, B.S.,
 482 Lafferty, K.D., Leslie, H., Lubchenco, J., McArdle, D., Possingham, H.P., Ruckelshaus, M.,
 483 Warner, R.R., 2003. Ecological criteria for evaluating candidate sites for marine reserves.
 484 *Ecol. Appl.* 13, S199-S214.

485 Russ, G.R., Stockwell, B., Alcala, A.C., 2005. Inferring versus measuring rates of recovery in no-take
 486 marine reserves. *Mar. Ecol. Prog. Ser.* 292, 1-12.

487 Sciberras, M., Jenkins, S.R., Kaiser, M.J., Hawkins, S.J., Pullin, A.S., 2013. Evaluating the biological
 488 effectiveness of fully and partially protected marine areas. *Environmental Evidence.* 2, 4.

489 Underwood, A., 1992. Beyond BACI: the detection of environmental impacts on populations in the
 490 real, but variable, world. *J. Exp. Mar. Bio. Ecol.* 161, 145-178.

491 Wagenmakers, E.J., Farrell, S., 2004. AIC model selection using Akaike weights. *Psychon. Bull. Rev.*
 492 11, 192-196.

- Wilson, M.F.J., O'Connell, B., Brown, C., Guinan, J.C., Grehan, A.J., 2007. Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. *Mar. Geod.* 30, 3-35.
- Woodroffe, C. D., Brooke, B.P. Linklater, M., Kennedy, D.M., Jones, B.G., Buchanan, C., Mleczko, R., Hua, Q., Zhao, J., 2010. Response of coral reefs to climate change: Expansion and demise of the southernmost Pacific coral reef. *Geophys. Res. Lett.* 37, L15602.
- Wraith, J., Lynch, T., Minchinton, T.E., Broad, A., Davis, A.R., 2013. Bait type affects fish assemblages and feeding guilds observed at baited remote underwater video stations. *Mar. Ecol. Prog. Ser.* 477, 189-199.
- Young, M.A., Ierodiaconou, D., Edmunds, M., Hulands, L., Schimel, A.C.G., 2016. Accounting for habitat and seafloor structure characteristics on southern rock lobster (*Jasus edwardsii*) assessment in a small marine reserve. *Mar. Biol.* 163, 1-13.

517 LIST OF TABLES

518 Table 1. Results of Negative Binomial Generalized Linear models used to compare the abundance of
 519 *Seriola lalandi* between management zones with and without accounting for structural complexity
 520 calculated at various spatial scales. Top ranked model is highlighted in bold font.

Model	K	logLik	AICc	Δ AICc	wAICc	D.E.
Zone + BV 100m + Zone*BV 100m	5	-70.33	152.59	0.00	0.38	65.47
Zone + BV 200m + Zone*BV 200m	5	-70.70	153.33	0.74	0.26	62.79
Zone + BV 150m + Zone*BV 150m	5	-70.87	153.67	1.08	0.22	62.70
Zone + VR 50m + Zone*VR 50m	5	-72.14	156.22	3.63	0.06	61.13
Zone + VR 100m + Zone*VR 100m	5	-72.34	156.61	4.03	0.05	58.29
Zone + VR 200m + Zone*VR 200m	5	-74.05	160.03	7.44	0.01	53.22
Zone + BV 50m + Zone*BV 50m	5	-74.14	160.22	7.63	0.01	54.17
Zone + VR 150m + Zone*VR 150m	5	-74.74	161.41	8.83	0.00	51.19
Zone + VR 20m + Zone*VR 20m	5	-75.15	162.24	9.65	0.00	51.13
Zone + BV 20m + Zone*BV 20m	5	-76.57	165.07	12.48	0.00	46.19
BV 150m	3	-83.42	173.57	20.98	0.00	23.78
BV 200m	3	-83.44	173.62	21.03	0.00	23.66
VR 20m	3	-83.50	173.73	21.14	0.00	23.44
BV 100m	3	-83.75	174.23	21.64	0.00	22.36
BV 50m	3	-83.87	174.46	21.87	0.00	21.82
BV 20m	3	-84.06	174.84	22.25	0.00	20.98
VR 50m	3	-84.12	174.96	22.37	0.00	20.69
VR 200m	3	-84.17	175.07	22.48	0.00	20.44
VR 150m	3	-84.21	175.14	22.56	0.00	20.26
VR 100m	3	-84.43	175.58	22.99	0.00	19.27
Zone	3	-87.82	182.37	29.78	0.00	2.89
Intercept	2	-89.46	183.28	30.69	0.00	0.00

521

522

523

LIST OF FIGURES

Figure 1. A map of survey sites in the Lord Howe Island Marine Park. The Lord Howe Island shelf is in the north and the Balls Pyramid shelf to the south. Regions in pink represent no-take marine reserves while regions in blue, fished zones.

Figure 2. An image of the high resolution multibeam bathymetry at site 20 on the Balls Pyramid shelf in Lord Howe Island Marine Park. Below a bathymetric profile of the 1 km transect bisecting the site.

Figure 3. Relationship between the abundance of Yellowtail Kingfish (*Seriola lalandi*) and structural complexity in fished zones and no-take marine reserves across two sampling periods. Structural complexity is the bathymetric variance (standard deviation in depth) at a 100 m seascape scale. Trend lines constructed from the model using the ‘predict’ function in R. Shaded areas represent $\pm$ SE.

Figure 4. Map of the Lord Howe Island Marine Park and areas of shelf habitat (25 – 50 m) displaying structural complexity (bathymetric variance) greater than 2 m at a 100 m seascape scale. Regions in pink represent no-take marine reserves while regions in blue, fished zones.

Figure 1.

Figure 2.

Figure 3.

Figure 4.

572

573 Fig. A.1. Comparison of the mean bathymetric variance (100 m scale) of our study sites and the entire
574 shelf habitat between management zones (± 1 standard deviation). Similarity among means indicates
575 that study sites represented the structural complexity of the shelf habitat (25 – 50 m) within the Lord
576 Howe Island Marine Park.

577

578

579

580

581

582

583

584

Fig. A.2. There was no significant difference in the mean abundance of *Seriola lalandi* between years ($t = 0.77$, $df = 31$, $p = 0.45$). Error bars represent ± 1 standard error.

Fig.A.3. Counts of *Seriola lalandi* at each site between the two sampling periods. Only sites that were surveyed in both sampling periods are included.

Fig. A.4. Spline correlograms assessing spatial autocorrelation in the model residuals of the original analysis and b) after the removal of site 21 from the analysis.

Fig. A.5. Depth profiles along a 1 km transect bisecting each survey site.

602 TableA.1. Average vertical relief and bathymetric variance measures (m) at the various seascape radii
603 scales surrounding each survey site.

Site	Vertical Relief (VR)					Bathymetric Variance (BV)				
	20m	50m	100m	150m	200m	20m	50m	100m	150m	200m
1	0.78	1.74	2.67	3.11	3.65	0.21	0.41	0.61	0.66	0.74
2	0.23	0.62	1.19	1.62	1.96	0.05	0.14	0.25	0.34	0.42
3	0.42	0.89	1.96	3.22	4.20	0.11	0.21	0.44	0.68	0.91
4	0.62	2.03	4.51	7.08	8.76	0.16	0.43	0.91	1.46	1.91
5	1.23	2.81	4.72	6.12	6.80	0.34	0.70	1.09	1.36	1.46
6	0.76	2.14	4.68	6.58	8.25	0.20	0.50	1.03	1.47	1.89
7	1.18	2.79	4.94	7.40	9.28	0.34	0.68	1.21	1.71	2.17
8	1.04	1.70	2.44	3.24	3.96	0.27	0.47	0.59	0.69	0.84
9	1.99	4.56	6.57	9.85	11.19	0.49	1.30	1.86	2.48	2.79
10	3.27	5.60	7.05	8.80	10.40	0.96	1.77	2.28	2.52	2.80
11	0.71	2.07	4.83	6.84	8.67	0.18	0.48	0.97	1.36	1.77
12	1.17	3.20	4.75	5.68	6.36	0.30	0.76	1.20	1.31	1.39
13	0.99	2.01	2.67	3.10	3.60	0.23	0.48	0.58	0.72	0.78
14	0.51	1.16	2.41	3.88	4.57	0.12	0.23	0.47	0.80	1.06
15	1.89	3.99	5.59	7.07	8.43	0.53	1.08	1.43	1.66	1.91
16	2.54	6.42	9.44	10.60	11.25	0.65	1.60	2.34	2.85	3.22
17	1.20	2.52	3.65	5.41	6.51	0.30	0.62	0.79	1.02	1.25
18	2.46	5.80	8.52	11.15	13.75	0.66	1.45	2.14	2.56	2.87
19	0.58	1.41	2.76	3.58	4.61	0.15	0.35	0.59	0.77	1.02
20	2.14	5.42	10.36	14.94	17.44	0.53	1.28	2.20	3.16	3.78
21	1.44	3.76	7.25	9.35	10.56	0.37	0.83	1.69	2.36	2.68

604