

Understanding community–habitat associations of temperate reef fishes using fine-resolution bathymetric measures of physical structure

Matthew J. Cameron*, Vanessa Lucieer, Neville S. Barrett, Craig R. Johnson, Graham J. Edgar

Institute for Marine and Antarctic Studies (IMAS), University of Tasmania, 20 Castray Esplanade, Battery Point, TAS 7004, Australia

ABSTRACT: Multibeam sonar (MBS) hydro-acoustic technology allows for inexpensive, broad-scale, fine-resolution assessment of marine fish habitats. Parallel advancements in geographic information systems and new analytical techniques are providing researchers with the ability to generate informative surrogate predictors of biodiversity and species responses. The aim of this study was to determine whether fine-scale bathymetric derivatives of MBS survey data could be effectively applied as surrogates to explain spatial patterns in reef fish diversity and species–habitat relationships. In the absence of direct metrics of habitat, these derivatives might prove to be effective tools for marine spatial planning. Species–habitat relationships were examined across a marine reserve on the south-eastern coast of Tasmania at fine spatial scales using boosted regression tree analyses. The most important explanatory variables of community diversity were those describing the degree of reef aspect deviation from east and south (seemingly as a proxy for swell exposure), reef bathymetry (depth), plane and slope. Models could account for up to 30 % of the spatial variability in measures of species diversity. Responses in species abundance and occurrence to habitat structure appeared to be largely species-specific at the scales investigated. Models accounted for up to 67 % and 58 % of the abundance and occurrence, respectively, for the southern hulafish *Trachinops caudimaculatus*. Our results demonstrate that multibeam-derived metrics of reef habitat structure, employed in combination with modern modelling approaches, have the potential to explain and predict fine-resolution patterns in temperate reef fish community structure. This knowledge is urgently required to effectively manage marine ecosystems and conserve biodiversity and fisheries resources.

KEY WORDS: Temperate reefs · Remote sensing · Bathymetric derivatives · Physical structure · Fish–habitat relationships

—Resale or republication not permitted without written consent of the publisher—

INTRODUCTION

Apparent failures in traditional single-species fisheries management have led to an increasing impetus towards ecosystem-based approaches, requiring a quantitative understanding of community responses to changing environments at scales relevant to marine management (Garcia et al. 2003). The collection of biological and habitat data across these scales is

often labour intensive, financially expensive, incomplete and spatially or temporally biased (Anderson et al. 2009). However, understanding community-habitat associations of temperate reef fishes is vital for effective ecosystem management because of the potential of habitat type and structure to drive broad-scale patterns of biodiversity (Ward et al. 1999). One of the major problems faced by policy makers and managers with the task of implementing effective

*Corresponding author: matthew.cameron@utas.edu.au

marine protected areas (MPAs) is targeting suitable habitat structure and types which will maximise conservation value and safeguard over-exploited and threatened species, communities and systems (Babcock et al. 1999). Quantifying fish community responses to habitat structure is crucial for applied aspects of MPA management, particularly if the goals of management approaches are to maximise biodiversity (Garcia-Charton & Perez-Ruzafa 1998). The feasibility of identifying cost-effective predictive surrogates of reef fish biodiversity where associations between communities, species and habitats can be accurately modelled, needs to be established in order to aid ecosystem management and conservation planning (Anderson et al. 2009).

Studies focussing on fish have revealed that physical habitat can influence fish community structure through varying recruitment and post-recruitment survival (Connell & Jones 1991, Tupper & Boutilier 1997), prey availability (Warfe & Barmuta 2004), predation and competition (Hixon & Beets 1993, Johnson 2006) home range size, morphology and behaviour (Shumway 2008). Few studies have considered the community and species-specific relationships of reef fish with habitats at ecologically realistic resolutions at which they are directly interacting with their environments.

With the recent technological advancement of acoustic remote sensing tools, physical habitat data are becoming increasingly obtainable from the marine environment. Technological advances in multi-beam hydro-acoustics now allow relatively inexpensive, broad-scale, continuous lateral assessment of marine habitats at fine resolutions (i.e. across metre and sub-metre scales; Brown et al. 2011). This information is considerably cheaper and easier to acquire than direct diver assessments of reef habitat structure over equivalent spatial scales. Concurrent advances and developments in geographic information systems (GIS) and other analysis tools have enabled various derivative metrics of habitat structure to be calculated from bathymetric digital elevation models (DEMs), providing researchers with a variety of potentially informative surrogate measures of biodiversity and species-specific environmental responses (Guisan & Zimmermann 2000, Lucieer et al. 2013).

Recent studies have investigated the effectiveness of using bathymetric DEM-derived metrics of habitat structure to model patterns in the distribution of various benthic biota and habitat types (Rattray et al. 2009, Ierodiaconou et al. 2011) but studies using similar metrics to model reef fish distributions are less

common and generally focus on broad-scale habitat differences (Kracker et al. 2008, Knudby et al. 2010). Recently, a number of studies have attempted to apply fine-resolution multibeam sonar-derived measures of habitat structure to model reef fish community diversity and species distributions; Monk et al. (2011) successfully modelled blue-throated wrasse habitat suitability using seafloor variables derived from hydro-acoustic survey data at varying spatial scales.

Guisan & Zimmermann (2000) reviewed a wide variety of modelling approaches available for predicting the distribution and abundances of species and communities. Boosted regression trees (BRTs) are a newly emerging statistical approach to modelling species distributions; the approach is gaining favour with ecologists attempting to model species distribution patterns because of its strong predictive ability to identify ecologically meaningful interactions between species and environments and because model outputs can be summarised intuitively to give clear ecological insight into relationships between response and predictor variables (Elith et al. 2008). BRTs are being increasingly applied to ecological modelling of fish responses to the physical nature of their environments (Leathwick et al. 2006, 2008, Pittman et al. 2009, Knudby et al. 2010, Richards et al. 2012) and have been shown to out-perform and provide superior flexibility over other common methods of modelling, such as generalized linear models (GLMs) and generalized additive models (GAMs) (Elith & Leathwick 2011). They possess many of the advantages of traditional tree-based methods in their ability to handle different types of predictor variables, accommodate missing data, fit non-linear relationships and automatically handle interaction effects between predictors, and they require no dependency on prior data transformation or removal of outliers, while simultaneously they are able to overcome the main problem of poor predictive performance inherent in traditional tree-based methods, through fitting multiple tree models (Elith et al. 2008).

Here we used high-resolution, multibeam acoustic data and BRT modelling approaches to explain reef fish community responses to their environments at fine spatial scales across a coastal Tasmanian reef system and evaluated whether bathymetrically derived measures of habitat structure can be effectively applied as surrogates of direct physical measures to model temperate reef fish community diversity, occurrence and abundance. Multi-species relationships with habitat were examined at scales at which fish directly interact with their environments. Fine-scale bathymetric derivatives were tested to identify

whether they could be feasibly applied as surrogates to understanding biodiversity and the specific habitat associations of fish in the absence of direct metrics of habitat and in so doing identify an effective tool for managing the marine environment.

MATERIALS AND METHODS

Surveys

Fish surveys were carried out at 11 sites within the Tinderbox Marine Reserve (43° 2' S, 147° 20' E) situated at the northern end of the D'Entrecasteaux Channel on the south-eastern coast of Tasmania, Australia (Fig. 1). The Tinderbox reserve covers an area of 1.44 km², extending approximately 200 m offshore. A mix of sandstone outcrops and fractured dolerite reef extends almost continuously around the Tinderbox headland to a depth of approximately 10 m, where the substratum then becomes sand and broken shell and is interspersed in places with small embayments and channels. The surrounding seabed is formed of soft sediment shoals out to a depth of approximately 50 m (Nichol et al. 2009). The reef in this area is dominated by high densities of the canopy-forming laminarian alga *Ecklonia radiata*

along with a diverse algal understory and communities of sessile invertebrates including hydrozoans, bryozoans, ascidians and sponges, typical of the broader region of eastern Tasmania (Andrew 1999).

Non-cryptic reef fish species and abundances were surveyed on 5 separate occasions between May and December 2011 by a 2-person dive team using open-circuit SCUBA. Each survey occasion was considered as a survey replicate at each site in subsequent analysis. All surveys were conducted in reasonably benign weather during daylight between 10:00 and 15:00 h. Sites were located on sub-littoral rocky reef at intervals of approximately 300 m parallel to the coastline. All sites were positioned less than 100 m from shore, within and parallel to the 5–10 m depth contour. At each site, a single 50 × 10 m (500 m²) transect was positioned across the reef, and the beginning and end were marked with fixed subsurface buoys to allow accurate GPS location fixes from a surface vessel. Each transect was divided into 20 blocks (25 m² each) on either side of the transect centre line, by marking 5 m intervals along the centre line and visually estimating 5 m out from either side. Reef fish species identity and abundance were recorded within each 25 m² block by a single observer swimming approximately 2.5 m to one side of the transect centre line and approximately 2 m above the reef surface.

A Kongsberg EM3002(D) 300 kHz multibeam sonar was employed during shipboard surveys carried out in collaboration with Geoscience Australia to collect bathymetric data for selected areas of the Tinderbox Marine Reserve inclusive of all 11 survey sites. The multibeam bathymetric data were resolved to 2 m resolution and output as an *x-y-z* grid using Caris HIPS/SIPS v.6.1 software to remove vessel movement and tide-related artefacts. Reef habitat structure metrics were derived from a 2 × 2 m resolution bathymetric DEM using a number of toolbox applications in the ArcGIS 9.3 software package. From the DEM, 11 derivative variables used to characterise seafloor structure and topography were generated using commonly obtainable toolbox extensions in ArcGIS 9.2 and ArcView 3.2. Derivatives were selected based on their ease of interpretation and a perception of their likely ecological importance. For instance, measures of aspect deviation from east and south were included, as they were likely to act as proxies for the dominant wave exposure influencing sites from those directions. Measures of habitat complexity and heterogeneity such as rugosity, topographic position index (TPI), channel, ridge and plane morphometry were included for their ability to

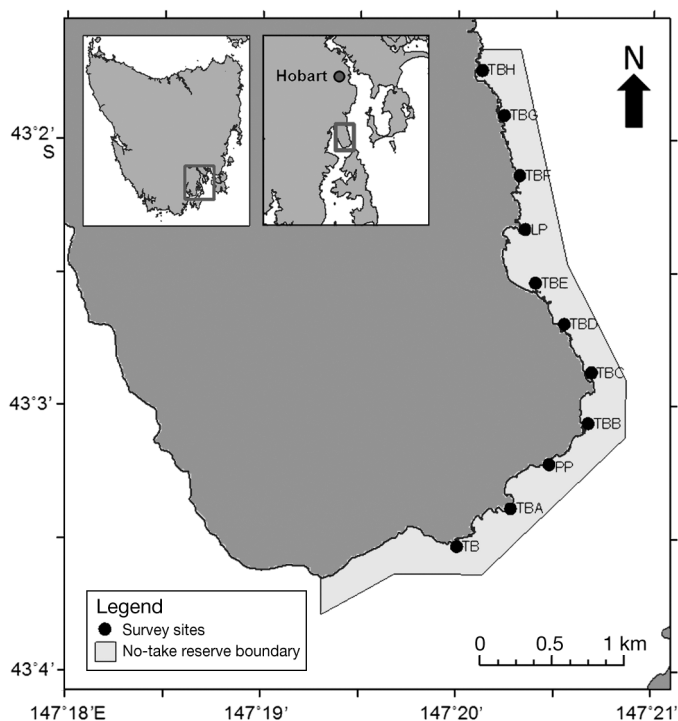


Fig. 1. Tinderbox Marine Reserve boundary and study site locations in the southeast of the Tinderbox Peninsula (northern end of the D'Entrecasteaux Channel, Tasmania)

quantitatively describe habitat structure. The 11 bathymetric derivatives are listed in Table A1 in the Appendix along with a description of the variable and the software and relevant toolboxes used to generate each.

Geo-referenced polygon shape files were constructed in ArcGIS 9.3 to delineate the block outlines of each transect at each site and then overlaid onto separate raster layers of the 11 physical derivatives. From these layers, average derivative values were calculated for each 25 m² block (using the zonal statistics tool in ArcGIS 9.3). These averaged derivative variables (per block) were considered as the predictor variables in all subsequent model analyses. A draftsman plot of the individual predictor variables was consulted prior to analysis to identify extreme bi-variate correlations and redundant predictors from the models, but there were insufficient correlations between any pair of variables to warrant any removals.

Data analysis

Occurrence, mean abundance and 3 indices of community diversity (calculated from observed abundance and occurrence) were used to model reef fish community response against physical habitat structure. The abundance for each species surveyed was averaged across replicate surveys for each of the 25 m² blocks ($n = 220$) and $\log(x+1)$ transformed to reduce differences in scale among the species variables, reduce the contribution of highly abundant species and ensure the contribution of rarer species. Species occurrence (i.e. presence/absence), was determined for each of the 220 blocks. For community level analyses, 3 measures of diversity, viz. the total number of species (S), Margalef's index (d) and the Shannon-Wiener index (H'), were calculated from the mean species abundance data for each of the 220 blocks to reduce the complexity of the multispecies assemblage data into easily interpretable univariate response variables.

Individual species abundances and occurrence along with the 3 measures of diversity were modelled in relation to the 11 bathymetric derived reef-habitat metrics using BRTs. BRT models were fitted with crossvalidation using the `gbm` and `gbm.step` packages (Elith et al. 2008) in the R statistics software, version 2.13.1. Construction of optimal BRT models for each response variable was achieved through selecting the appropriate values of 3 parameters, i.e. learning rate, tree complexity and bag fraction, to minimise residual deviance in the resulting models.

The learning rate is a shrinkage parameter which determines the contribution of each tree to the growing model; tree complexity refers to the number of nodes permitted within each tree and controls the level of predictor interactions fitted; and the bag fraction is the proportion of the full data selected at each iteration. Together, these 3 parameters determine the number of trees required for optimal prediction (see Elith et al. 2008 for further explanation). Loop coding was written in R to perform parameter selection and arrive at an 'optimum' model with the minimum residual deviance for each response variable investigated. Abundance of individual species and measures of diversity were modelled using a Gaussian error distribution, and species occurrences (i.e. presence or absence) were modelled using a Bernoulli (binomial) error distribution. Measures of relative influence of each predictor term in the regression tree models were calculated using script functions included in the `gbm.step` package in R (Elith et al. 2008). Where a model explained a relatively high proportion of the deviance, partial dependency plots were used to understand the individual relationships between response and predictor variables with the highest relative influence in the model after accounting for the average effects of all other variables in the model. Interactions between predictor variables influencing a particular response variable were identified using the `gbm.interactions` package (Elith & Leathwick 2011) in R and plotted. For each of the fitted models, D^2 values were calculated as a measure of explained deviance, where: $D^2 = 1 - (\text{residual deviance}/\text{total deviance})$.

RESULTS

In total, we recorded 10026 individual reef fish observations throughout the total survey period comprising 31 species from 21 families (see Table A2 in the Appendix for a full list of the observed species). The southern hulafish *Trachinops caudimaculatus* was the most numerically abundant species encountered, comprising 67.5% of the total abundance of reef fishes surveyed, followed by blue-throated wrasse *Notolabrus tetricus* (9.3%), long fin pike *Dinolestes lewini* (8.7%), small scale bullseye *Pempheris multiradiata* (8.0%) plus all other species combined (6.5%). The blue-throated wrasse had the highest proportion of occurrence, occurring in 97.7% of blocks surveyed, followed by the southern hulafish (40.0%), senator wrasse *Pictilabrus laticlavius* (36.8%), bastard trumpeter *Latri-*

dopsis forsteri (26.8%) and purple wrasse *N. fusicola* (26.4%). The remaining 26 species all occurred in less than 15% of the blocks surveyed.

Community diversity

BRTs explained notable proportions for each of the diversity response variables modelled (Table 1). Margalef's index was the best explained diversity response variable modelled, with a D^2 of 30.1% (Table 1), largely influenced by a combination of average bathymetry (20.9%), slope (16.7%) and rugosity (16%) (Fig. 2). The remaining BRT models of number of species and Shannon-Wiener index explained 19.7 and 19.1% of the deviance, respectively. Fig. 2 displays the specific relationships between each diversity response variable and the 4 most influential predictor variables identified by BRT analysis as plots of fitted functions versus the observed values. East and south deviation were identified as the most important model terms explaining the number of species, plane (i.e. areas of low reef complexity) as the most important term explaining Shannon-Wiener index and bathymetry, slope and rugosity as the most important variables explaining Margalef's index.

Notable interactions were identified by the BRT analysis between model terms for 2 of the 3 diversity response variables. Interactions were identified for the total number of species between average south deviation and TPI, with higher species richness expected on more southerly facing, higher TPI value reef (Fig. 3). Interactions were identified for Margalef's index between bathymetry and profile, with higher values of d expected on shallower, lower profile reef areas (Fig. 4).

Species abundance

Eight species of reef fish had sufficient numbers of observations to allow BRT modelling of abundance. BRT models were used to investigate the relative influence of each of the 11 predictor variables on

individual reef fish species $\log(x+1)$ -transformed abundance. Table 2 displays the BRT model results for species abundance. The southern hulafish *T. caudimaculatus* was the best explained species response variable investigated, with an explained deviance of 66.9% (Table 2), largely influenced by a combination of average bathymetry (19.8%), slope (14.6%), plane (14.6%) and south deviation (13.6%; Fig. 5). The abundance of *T. caudimaculatus* showed a general positive relationship with bathymetry, slope and plane.

Notable interactions existed between slope and plane, with higher abundances of *T. caudimaculatus* expected on higher plane, steep-sloped reef (Fig. 6). The remaining models of abundance for the other species explained between 48.1% and 4.9% of the deviance. Other notable model results were identified for the blue-throated wrasse *N. tetricus* ($D^2 = 48.1\%$), the senator wrasse *Pictilabrus laticlavus* ($D^2 = 34.6\%$) and the little weed whiting *Neoodax balteatus* ($D^2 = 26.7\%$). BRTs identified no notable interactions for any of the other species abundances modelled.

The most important explanatory physical variables of species abundances, commonly identified by BRTs, were bathymetry, south deviation and slope. Bathymetry was in the top 4 important model terms for 6 of the 10 species abundance response variables modelled and both south deviation and slope for 3 of the 10 response variables modelled.

Species occurrence

Eight species of reef fish had sufficient numbers of observations to allow BRT modelling of species occurrence. BRT models were used to investigate the relative influence of each of the 11 predictor variables on individual reef fish occurrence. Table 3 displays the BRT model results for species occurrence. As with abundance, *T. caudimaculatus* occurrence was the best explained response variable investigated with an explained deviance of 57.6% (Table 3), largely influenced by a combina-

Table 1. Boosted regression tree model analysis of community diversity with 'optimal' selected model parameters

Index	Tree complexity	Learning rate	Bag fraction	Number of trees	Residual deviance	Total deviance	Deviance explained (D^2), %
Total species (S)	5	0.0005	0.75	1350	1.676	2.087	19.7
Margalef's (d)	5	0.001	0.75	1100	3.664	5.241	30.1
Shannon-Wiener (H')	4	0.0005	0.75	1800	0.164	0.203	19.1

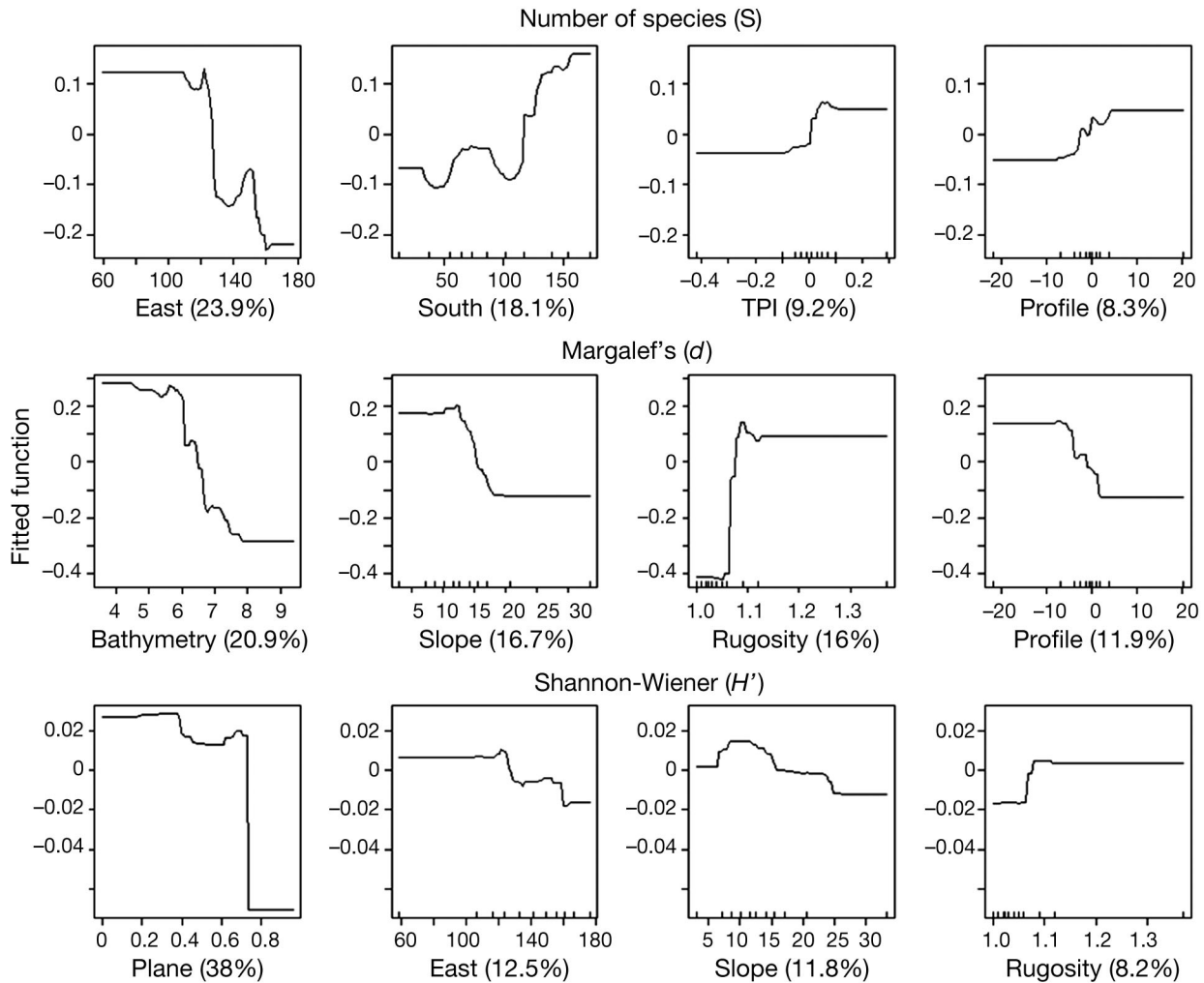


Fig. 2. Fitted functions versus observed values (indicated by ticks above the x-axis) for the top 4 terms (relative influence in parentheses) of the boosted regression tree model analysis for each diversity response variable. TPI: topographic position index

tion of average bathymetry (15.1%), east deviation (14.5%), south deviation (13.7%) and slope (13.1%) (Fig. 7). The occurrence of *T. caudimaculatus* showed a general positive relationship with depth and slope, a weak negative relationship from east deviation and a bi-modal relationship with south deviation.

Notable interactions existed between rugosity and slope with higher occurrences of *T. caudimaculatus* expected on steeper sloped, low-rugosity reef (Fig. 8). The remaining models of occurrence for the other species explained between 57% and 2.4% model deviance. Other notable model results were identified for *P. laticlavus* ($D^2 = 57\%$), *N. tetricus* ($D^2 = 42\%$), *M. australis* ($D^2 = 36.8\%$), *N. balteatus* ($D^2 = 31.1\%$) and *L. forsteri* ($D^2 = 26.7\%$). No notable interactions were identified for any of the other species occurrences modelled.

The most important explanatory physical variables of species occurrence, commonly identified by BRTs, were bathymetry, south deviation, east deviation and slope. BRTs identified bathymetry, south deviation and east deviation in the top 4 important model terms for 6 of the 10 species occurrence response variables and slope for 4 of the 10 response variables.

DISCUSSION

The extent to which derivative-based models were able to explain patterns in the reef fish community structure varied depending on the response variable being modelled, making it difficult to discern general patterns. This is perhaps unsurprising given that measures of community diversity represent the sum of the different species responses com-

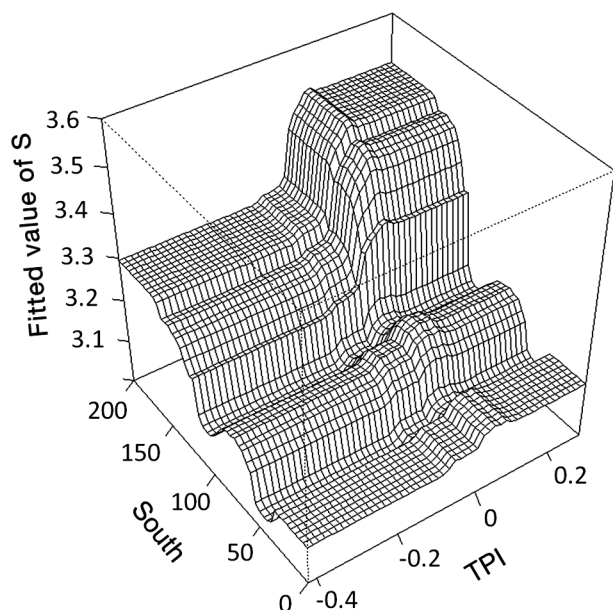


Fig. 3. Physical variable interaction of species richness (S) identified between south deviation and topographic position index (TPI) by boosted regression tree analysis

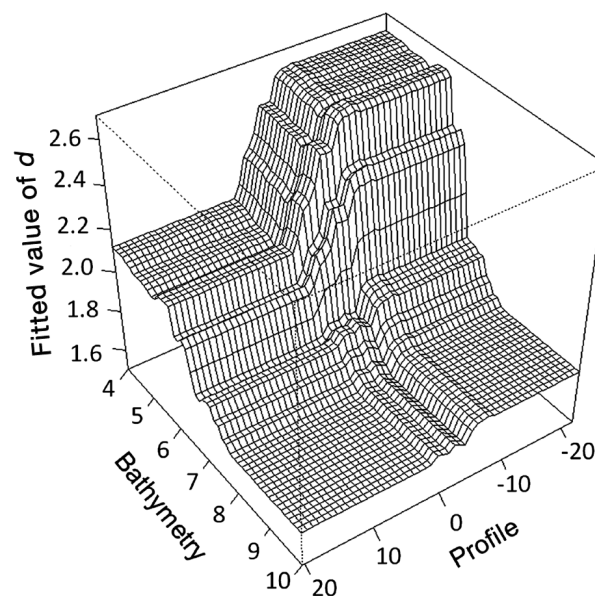


Fig. 4. Physical variable interactions of Margalef's diversity index (d) identified between bathymetry and profile by boosted regression tree analysis

bined and are unlikely to be the same across varying environmental gradients. Despite this, BRT approaches were able to explain a proportion of community diversity responses (up to 30% deviance explained) and the abundances and occurrence for some species (up to 67% deviance explained). These results compare well with other BRT model studies of species responses; 26% of total explained deviance for yellowfin tuna catch rates in the Gulf of Mexico (Abeare 2009), 64 to 72% of total explained deviance in fish and coral species richness and biomass across Puerto Rican reefs (Pittman et al. 2009), 7 to 29% of total explained deviance for the biomass of species of large-bodied reef fish in the Mariana Archipelago (Richards et al. 2012) and 5 to 73% of total explained deviance for the distri-

bution of sessile biota on temperate reefs in Tasmania (N. A. Hill et al. unpubl.).

The most important explanatory variables of community diversity identified in our study were generally east deviation, bathymetry and plane. The importance of bathymetry (i.e. depth) to community diversity, particularly Margalef's index, is probably a consequence of its importance to *Trachinops caudimaculatus*, which displayed far higher abundances towards the deeper areas of reef surveyed (8–9 m). *T. caudimaculatus* are small-bodied (up to 100 mm), shoaling zooplanktivores, highly abundant on sheltered to moderately exposed rocky reefs across southeast Australia (Edgar 2000). They are highly site attached after settlement (Ford & Swearer 2013) and often tend to aggregate in high densities (in

Table 2. Boosted regression tree model analysis results of $\log(x+1)$ -transformed species abundance with 'optimal' selected model parameters

Species	Tree complexity	Learning rate	Bag fraction	Number of trees	Residual deviance	Total deviance	Deviance explained (D^2), %
<i>Dotalabrus aurantiacus</i>	5	0.0001	0.75	3000	0.01	0.01	8.9
<i>Latridopsis forsteri</i>	5	0.0005	0.25	2500	0.06	0.07	11.2
<i>Meuschenia australis</i>	4	0.0005	0.25	1400	0.01	0.01	4.9
<i>Neodax balteatus</i>	3	0.001	0.75	1300	0.01	0.01	26.7
<i>Notolabrus fusicola</i>	4	0.0005	0.25	2700	0.04	0.04	13.4
<i>Notolabrus tetricus</i>	3	0.005	0.75	1000	0.07	0.13	48.1
<i>Pictilabrus laticlavus</i>	5	0.001	0.5	2200	0.01	0.01	34.6
<i>Trachinops caudimaculatus</i>	5	0.001	0.75	3350	0.66	1.99	66.9

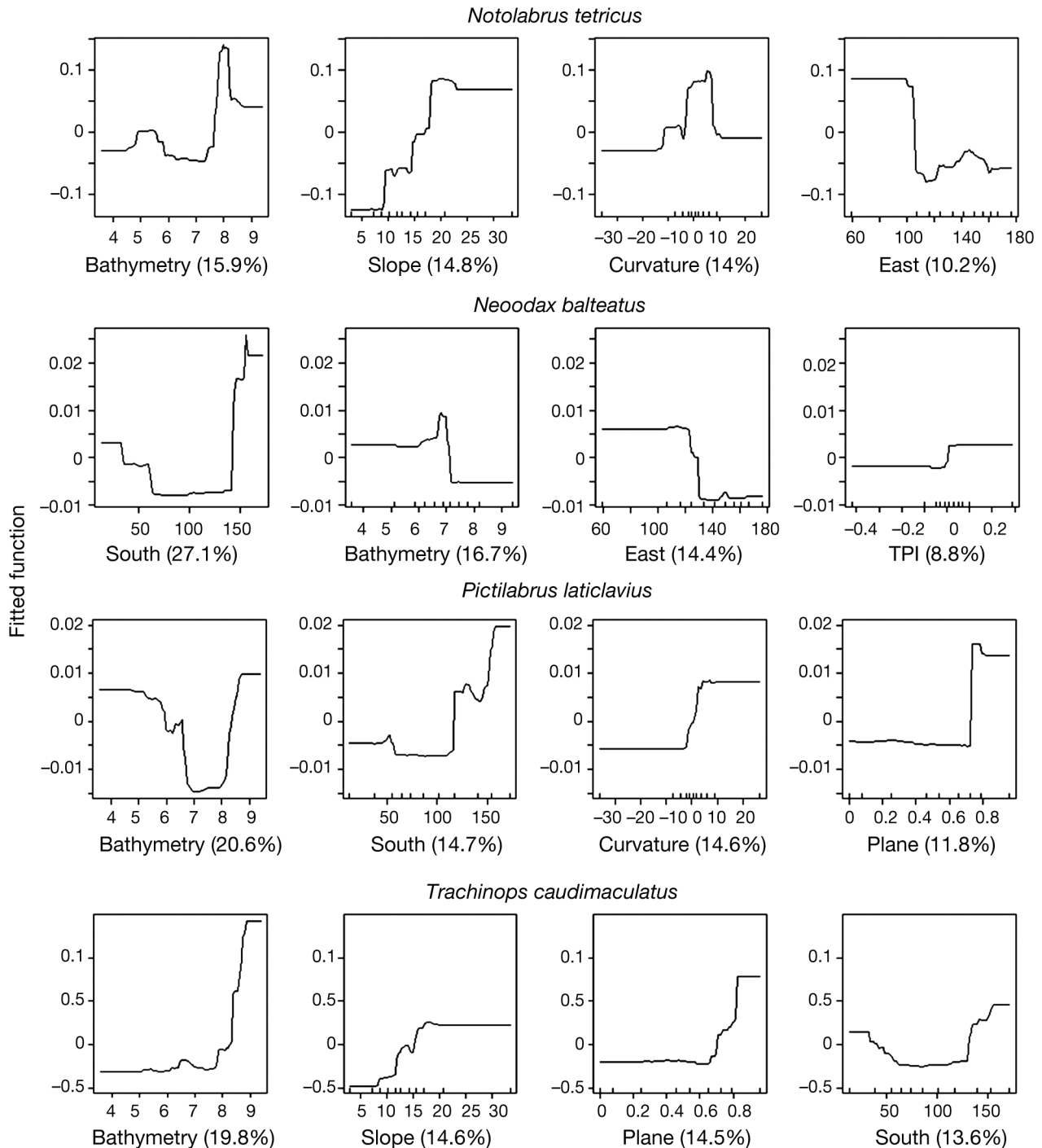


Fig. 5. Fitted functions versus observed values (indicated by ticks above the x-axis) for the top 4 terms (relative influence in parentheses) for the boosted regression tree model results of $\log(x+1)$ -transformed abundance for those response variables with notable proportions of deviance explained. TPI: topographic position index

excess of 100 ind. m^{-2}) over areas of reef (Hunt et al. 2011). Thus, they tend to contribute considerably to the total count of individuals in a survey. The relationship between east deviation and plane and community diversity is less clear and appears to be an emergent association specific to community diversity

and not clearly connected to any single species response. The specific mechanisms behind these identified patterns between habitat structure and community diversity are not clear but may be related to variability in swell exposure, refuge space availability, current flow and/or associated food availability.

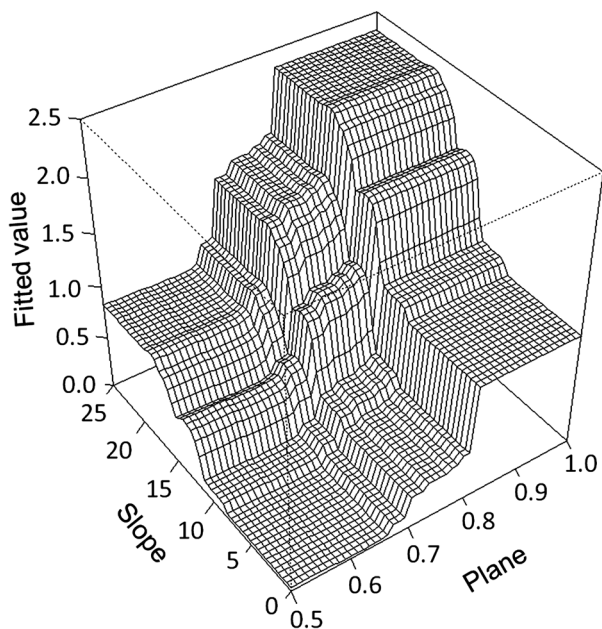


Fig. 6. Physical variable interaction identified between average slope and plane from boosted regression tree modelling of *Trachinops caudimaculatus* $\log(x+1)$ -transformed abundance

A major benefit of the BRT approach over other modelling approaches such as GAMs and GLMs is its ability to effectively identify interactions between predictor terms. Notable interactions were identified by BRT analysis between south deviation and TPI for species richness, which may have otherwise been overlooked when considering individual physical variables in isolation. This interaction suggests that the influence of TPI is enhanced in areas of reef with high aspect deviation from south (and vice versa). Notable interactions were also identified for Margalef's index between bathymetry and profile. These results hint at a more complex interplay between variability in aspect, reef depth and habitat heterogeneity in structuring reef fish community diversity at fine spatial scales. The majority of previous studies

have relied on more traditional methods of analysis without directly investigating potential interactions in fish community responses between differing physical variables. The relationships between fish community structure and the surrounding habitat are complex and to fully understand these requires investigation into how individual fish species respond to physical habitat variables in combination. Richards et al. (2012) applied similar analytical approaches to identify notable, varying interactions among reef depth, wave energy, distance to human population centres and water temperature to help explain the biomass of large-bodied coral reef fishes in the Mariana Archipelago.

The response in species abundances and occurrence to habitat structure appears to be largely species-specific at the scales investigated here. Fine-scale variability in bathymetry appears to be important in explaining the abundance and occurrence of a number of species, but particularly that of *T. caudimaculatus* and *Notolabrus tetricus*. Interestingly, the modelling results for occurrence appear to identify a stark contrast of habitat association with depth between *T. caudimaculatus* and *N. tetricus*. Slope was also identified as an important explanatory variable of *T. caudimaculatus* and *N. tetricus* abundance. Notable interactions were identified by BRT analysis for *T. caudimaculatus* abundance and occurrence between slope and plane and between slope and rugosity, indicating associations with steeper, low-complexity reef. These results are somewhat contrary to the findings of other research about this species. Hunt et al. (2011) identified the influence of additional aspects of reef habitat, such as the density of conspecifics and the accessibility of food in explaining the recruitment of *T. caudimaculatus*. These aspects of reef habitat were not considered in our study. They identified that 65% of the variation in recruitment of *T. caudimaculatus* could be explained by high adult abundance, prey density and physical

Table 3. Boosted regression tree model analysis results of species occurrence with 'optimal' selected model parameters

Species	Tree complexity	Learning rate	Bag fraction	Number of trees	Residual deviance	Total deviance	Deviance explained (D^2), %
<i>Dotalabrus aurantiacus</i>	3	0.001	0.5	550	0.65	0.73	11.1
<i>Latridopsis forsteri</i>	2	0.01	0.25	450	0.85	1.17	26.7
<i>Meuschenia australis</i>	5	0.001	0.5	1250	0.25	0.4	36.8
<i>Neodax balteatus</i>	5	0.0005	0.5	2300	0.56	0.82	31.1
<i>Notolabrus fusicola</i>	4	0.0005	0.75	1000	1.05	1.16	9.3
<i>Notolabrus tetricus</i>	2	0.005	0.25	600	0.13	0.22	42
<i>Pictilabrus laticlavus</i>	5	0.01	0.5	300	0.28	0.65	57
<i>Trachinops caudimaculatus</i>	4	0.01	0.75	500	0.57	1.34	57.6

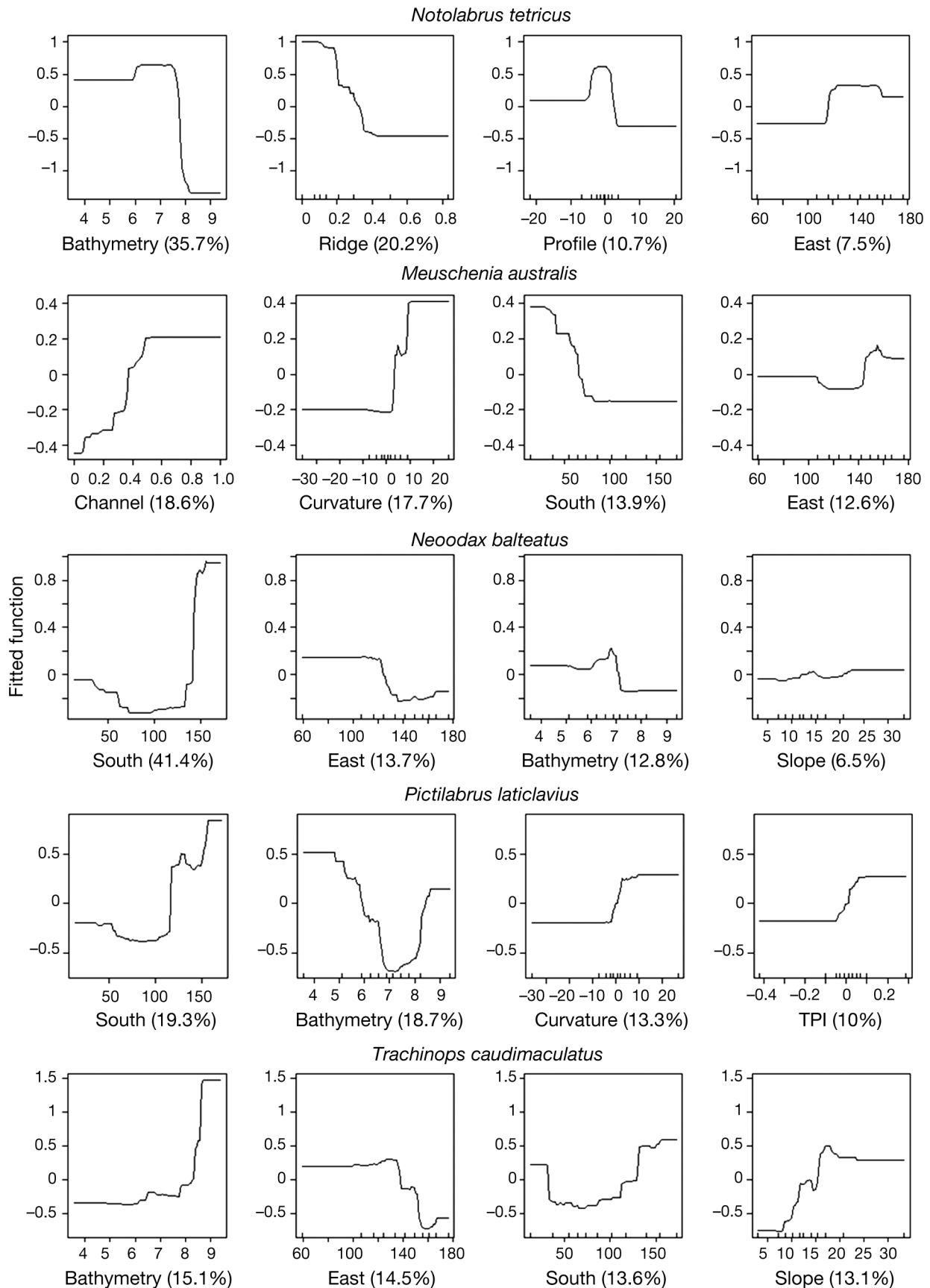


Fig. 7. Fitted functions versus observed values (indicated by ticks above the x-axis) for the top 4 terms (relative influence in parentheses) for the boosted regression tree model analysis of species occurrence for those species with notable proportions of deviance explained. TPI: topographic position index

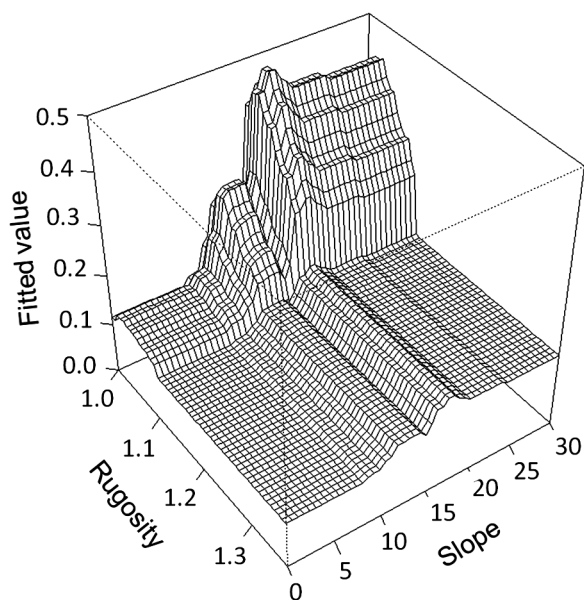


Fig. 8. Physical variable interaction identified between average rugosity and slope from boosted regression tree modelling of *Trachinops caudimaculatus* occurrence

shelter, suggesting enhanced survival through positive settlement cues of shoaling, higher growth rates and greater availability of refuges from predation. Additional predictor variables of conspecific density and prey availability may well have improved agreement between this and our own study results.

As previously mentioned, bathymetry (depth) was also important in explaining the abundance and occurrence of *N. tetricus*. The distribution of this species across reef habitats is thought to vary between life stages, with larger adult individuals tending to live in relatively deep, exposed areas of reef, and juveniles occurring in larger numbers on shallower, seaweed-dominated reefs (Edgar 2000). Research considering the distribution of other species of temperate labrid fishes in relation to habitat depth and exposure suggests that there are general patterns of higher labrid diversity and abundance across deeper exposed or sheltered reefs, which in turn appears to be related to fish size and swimming performance (Fulton & Bellwood 2004). Similar influences of exposure may explain the patterns in abundance and occurrence of the labrid species *N. tetricus* and *Pictilabrus laticlavius* with reef bathymetry (depth) and aspect, respectively, identified in our study. Reef aspect (south and east deviation) as a proxy for exposure was important in explaining the abundance and occurrence of *Neodax balteatus*; however, other research has highlighted the importance of the proximity of surrounding habitat types and features in

influencing the distribution of this species (Shepherd et al. 2006). Our study did not consider other potentially important variables such as proximity to surrounding seagrass beds, even though these are habitats which are important to the recruitment of this and other species of fish (Jenkins & Wheatley 1998).

The specific aspects of physical habitat that influence the structure of reef fish communities appear varied and complex with no apparent dominance of a single variable beyond those influencing the exposure to the predominant swell direction. Other studies have identified the varying importance of physical habitat in structuring reef fish communities, identifying the specific influences of depth (Williams et al. 2008), complexity (Iampietro et al. 2008), swell exposure (Floeter et al. 2007), biogenic cover (Hirst 2008), and conspecifics and prey density (Hunt et al. 2011). Our study was ambitious in its attempt to relate variability in reef habitat structure to that of reef fish communities at such fine spatial scales. Most studies to date have considered multiple, widely differing habitats over large scales, identifying clear but largely coarse patterns in community-habitat associations. Monk et al. (2011) applied a similar approach at similar scales to our own, to investigate the habitat preferences of blue-throated wrasse *N. tetricus*, identifying shallow, high-rugosity, high-curvature areas as the species' preferred habitat. Our results did not identify rugosity or curvature as important variables in explaining the distribution of *N. tetricus*, but this may have been due to differences in the range of habitats considered between the 2 investigations or biases due to the different sampling approaches applied. For instance, our work only considered physical variables across areas of rocky reef habitat and therefore could not detect the large apparent differences in rugosity or curvature which would have existed between reef and surrounding sand habitats, identified as important in the study of Monk et al. (2011). However, our work did identify fine-scale variability in bathymetry as important, with deeper depths associated with higher abundances of *N. tetricus*. Slope was also identified as important, suggesting the importance of steep, high-profile reef to the fine-scale abundance of *N. tetricus*.

Other researchers have successfully explained fish species richness and biomass at relatively fine resolutions from 4 to 200 m (Wedding & Friedlander 2008, Pittman et al. 2009, Knudby et al. 2010) supporting a hypothesis that environmental gradients at these scales can be important for predicting local variations in reef fish communities, whereas coarser-scale environmental variables such as wave exposure or water

temperature are likely to have a more uniform impact on fish communities and are therefore less likely to be important in explaining differences in reef fish community structure at local scales (Knudby et al. 2010).

Our study has been able to provide some explanations of community and species–habitat associations using bathymetrically derived measures of physical habitat structure, and in the process has identified a number of shortfalls and possible improvements to assessing reef fish habitat associations at fine-scale resolutions in future studies. Given the differing habitat requirements of individual species, strong explanatory relationships were unlikely for every species in such a study.

Issues of scale and extent

Many of the species investigated in our study may have been too mobile at fine resolutions to identify clear relationships between distribution and habitat or may have been responding to their environments at different spatial scales or extents than those which were investigated. Organisms or communities often respond to environmental gradients in a spatially hierarchical fashion, resulting in different patterns at different spatial resolutions and extents (Guisan & Thuiller 2005). The type and scale of environmental gradients considered in an investigation are therefore important because they can limit the applicable geographical extent and resolution across which a model can be confidently applied without significant errors (Iampietro et al. 2008). Models based on gradients of direct ecological influence will likely be the most robust and widely applicable, but caution should still be applied when considering similar species and community responses across large regions exposed to differing climatic gradients. Paradoxically, direct ecological gradients, although often the more important in a predictive sense, are generally more difficult to understand and measure at the fine resolutions necessary, particularly using remote sensing methods. At present, many ecologically proximal gradients can only be measured accurately through direct field observations, making their use for predictive modelling of species distributions impractical. Our ability to measure these ecologically proximal gradients will likely improve in the near future as remote sensing technologies advance.

Similarly, studies can run into problems of modelling a truncated response to a subset of the full gradient of habitat structure available to a community.

Considering environmental predictors at the wrong extent can result in misinterpretation of the true response of an organism or community to its environment. The extent to which this was a problem in our study was largely unknown but was also largely unavoidable since the location and size of the survey were limited by financial and logistical constraints and the bathymetric data available at the time. Our study does, however, highlight the importance of obtaining fine-resolution remotely sensed data across large-scale, management-relevant extents to ensure accurate modelling of species and community responses to their physical environments if such predictive capacity is desired.

Ecological relevance of derivatives

It is doubtful whether the derivative measures included in this study were direct factors influencing community responses, and most may in fact have lacked real ecological relevance for many of the modelled species. Including additional direct ecologically influencing variables such as water temperature, predominant tidal currents, prey availability and the presence of conspecifics (which influence the requirements of fish to feed, breed and avoid predation) would likely have improved the explanatory power of the models. Unfortunately, during our study remotely sensed metrics of these variables were too technically challenging or expensive to obtain at relevant scales, as is often the problem in real world marine management situations. This study was also unable to consider biotic and ecological interactions, such as patchy recruitment and the abundances of known competitors and predators in the environment, which may have significantly influenced the spatial distribution of many species. Collecting biological and ecological information of this sort with remote sensing methods at the resolutions relevant to this study is particularly difficult at the current time; however, advancements in autonomous underwater vehicle and video technology are allowing improved survey capabilities to estimate algal, invertebrate and fish densities at depth and across large spatial extents. Autonomous underwater video (AUV) imagery and sonar are now beginning to emerge as potential tools for measuring physical habitat structure in the marine environment (Shumway et al. 2007) and will likely lead to the development of combined biological and physical survey capabilities in the near future. Future investigations should utilise methods such as AUV or towed underwater video

which are capable of imaging fish, benthic invertebrate and algal communities simultaneously. These survey technologies in combination with bathymetrically derived measures of the physical habitat probably represent the best current means of accurately and effectively modelling reef fish community structure across coastal reef habitats at relevant resource management scales.

Problems of ecological model assumptions

Unobserved influences such as disturbance (e.g. fishing pressure) can have an overriding effect on community structure and mask other natural associations with habitat. There are inherent limitations in the interpretations and application of spatial models across broad scales and locations due to the extent of unknown natural differences in the realised niches of separate communities. Ecological modelling implicitly assumes that pseudo-equilibrium exists between organisms and their environments (Austin 2002). This assumption risks inherent bias in model interpretation because what is being modelled in reality is the response observed as a result of biotic interactions and stochastic responses of an organism specific to a particular time and region (i.e. the realised niche) rather than the full response of a species occupying all of its suitable habitat (i.e. the fundamental niche) (Guisan & Zimmermann 2000, Guisan et al. 2002). Since it is very difficult to be certain that a statistical model represents a good approximation of the fundamental niche, caution is required when comparing models of a particular species or community response across different locations. The accuracy of a model based on environmental predictors will vary depending on the degree to which the dispersal and disturbance history have defined a particular community assemblage. It is therefore important that investigators are specific about the ecological assumptions underpinning any model and the appropriate extent and accompanying levels of uncertainty with which their predictions can be accurately applied. Accurate models of a species' fundamental niche require development based on a solid theoretical and empirically derived understanding of a species' response to its physical environment (Guisan & Thuiller 2005). Accurate models should also attempt to include quantitative measures of potential sources of community disturbance such as fishing pressure. Our study lacked quantitative measures of fishing disturbance but attempted to minimise its influence by surveying the reef fish community within an established MPA. For

this reason, MPAs perform a vital scientific function of controlling for the effects of various forms of human disturbance and should be utilised in similar modelling attempts of fish community structure.

Sampling reliability

Model accuracy is influenced by the reliability of occurrence data and distribution characteristic of the modelled species. Reliability of occurrence data to accurately predict species distributions will depend on the behaviour of a particular species in response to a chosen survey technique and the inherent ability of that technique to detect a species within its environment (Moore et al. 2009, Monk et al. 2012). Variability in the behaviour and habitat requirements between species means that survey techniques will often be biased in their capability to accurately sample the distribution of an individual species and will require tailoring towards the behaviour of individual species of interest (Connell et al. 1998). Species aggregating behaviour, range, habitat preference, behaviour in response to equipment or observers (i.e. avoidance or attraction), feeding behaviour (i.e. carnivorous or herbivorous), diurnal behaviour and body size in relation to refuge availability, amongst many other potentially biasing factors, will all determine how effective a particular survey technique may be for a particular species (Willis et al. 2000). The visual census methodologies applied in our study were based on established approaches of surveying reef fish assemblages similar to those employed in other studies considering comparable temperate reef fish communities (Barrett et al. 2007); however, such approaches may not be optimal in maximising modelling accuracy and sensitivity for individual species of fish. Appropriate survey techniques should be selected based on a good prior knowledge of their biases and drawbacks and the spatial extent across which they must be applied to accurately detect responses for individual species of interest.

CONCLUSIONS

Our results demonstrate that multibeam-derived metrics of reef habitat structure, employed in combination with modern modelling approaches, have the potential to explain and predict biologically meaningful patterns in the fine-resolution spatial variability of temperate reef fish communities. This know-

ledge is urgently required to improve the spatial management of marine ecosystems and more effectively conserve biodiversity and fisheries resources. The impetus behind this study was to identify the potential value of multibeam-derived metrics of reef habitat structure to accurately model temperate reef fish community structure at fine spatial resolutions with the intention that similar approaches could subsequently be applied in a predictive sense across larger spatial extents. With adequate model success and confidence, predictive maps of species diversity, occurrence and abundance could be generated, providing valuable tools for environmental management.

Our work highlights a number of practical considerations for successfully modelling communities of temperate reef fish using bathymetrically derived variables, including issues of scale, selection of appropriate predictors, awareness of ecological model assumptions and survey technique considerations. Future work in this field should focus on identifying suitable surrogate predictors and understanding their specific response relationships with communities and individual species. Improved understanding of the ecological relevance of predictors along with the increasing availability of fine-resolution bathymetry and biological data across larger extents should lead to the future development of robust and accurate models as tools for the prediction of reef fish community structure for marine resource and conservation management.

Acknowledgements. This work was undertaken for the Marine Biodiversity Hub, a collaborative partnership supported through funding from the Australian Government's National Environmental Research Program (NERP). NERP Marine Biodiversity Hub partners include the Institute for Marine and Antarctic Studies, University of Tasmania, CSIRO, Geoscience Australia, Australian Institute of Marine Science, Museum Victoria, Charles Darwin University and the University of Western Australia. Funding was provided in part by a Winifred Violet Scott trust fund research grant.

LITERATURE CITED

- Abeare S (2009) Comparisons of boosted regression tree, GLM and GAM performance in the standardization of yellowfin tuna catch-rate data from the Gulf of Mexico longline fishery. MSc thesis, Louisiana State University, Baton Rouge, LA
- Anderson TJ, Syms C, Roberts DA, Howard DF (2009) Multi-scale fish-habitat associations and the use of habitat surrogates to predict the organisation and abundance of deep-water fish assemblages. *J Exp Mar Biol Ecol* 379: 34–42
- Andrew N (1999) Under southern seas: the ecology of Australia's rocky reefs. UNSW Press, Sydney
- Austin MP (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecol Model* 157:101–118
- Babcock RC, Kelly S, Shears NT, Walker JW, Willis TJ (1999) Changes in community structure in temperate marine reserves. *Mar Ecol Prog Ser* 189:125–134
- Barrett NS, Edgar GJ, Buxton CD, Haddon M (2007) Changes in fish assemblages following 10 years of protection in Tasmanian marine protected areas. *J Exp Mar Biol Ecol* 345:141–157
- Brown CJ, Smith SJ, Lawton P, Anderson JT (2011) Benthic habitat mapping: a review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. *Estuar Coast Shelf Sci* 92:502–520
- Connell SD, Jones GP (1991) The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. *J Exp Mar Biol Ecol* 151:271–294
- Connell SD, Samoilys MA, Lincoln-Smith MP, Leqata J (1998) Comparisons of abundance of coral reef fish: catch and effort surveys vs visual census. *Aust J Ecol* 23:579–586
- Edgar GJ (2000) Australian marine life: the plants and animals of temperate waters. Reed New Holland, Sydney
- Elith J, Leathwick J (2011) Boosted regression trees for ecological modeling. Available at <http://cran.r-project.org/web/packages/dismo/vignettes/brt.pdf> (accessed 14 April 2013)
- Elith J, Leathwick J, Hastie T (2008) A working guide to boosted regression trees. *J Anim Ecol* 77:802–813
- Floeter SR, Krohling W, Gasparini JL, Ferreira CEL, Zalmon IR (2007) Reef fish community structure on coastal islands of the southeastern Brazil: the influence of exposure and benthic cover. *Environ Biol Fishes* 78:147–160
- Ford JR, Swearer SE (2013) Shoaling behaviour enhances risk of predation from multiple predator guilds in a marine fish. *Oecologia* 172:387–397
- Fulton C, Bellwood D (2004) Wave exposure, swimming performance, and the structure of tropical and temperate reef fish assemblages. *Mar Biol* 144:429–437
- Garcia SM, Zerbi A, Aliaume C, Do Chi T, Lasserre G (2003) The ecosystem approach to fisheries. Issues, terminology, principles, institutional foundations, implementation and outlook. Fisheries Technical Paper 443. Food and Agricultural Organization of the United Nations, Rome
- Garcia-Charton JA, Perez-Ruzafa AP (1998) Correlation between habitat structure and a rocky reef fish assemblage in the southwest Mediterranean. *Mar Ecol* 19: 111–128
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 8: 993–1009
- Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecol Model* 135:147–186
- Guisan A, Edwards TC, Hastie T (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecol Model* 157:89–100
- Hirst AJ (2008) Surrogate measures for assessing cryptic faunal biodiversity on macroalgal-dominated subtidal reefs. *Biol Conserv* 141:211–220
- Hixon MA, Beets JP (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecol Monogr* 63: 77–101
- Hunt TL, Ford JR, Swearer SE (2011) Ecological determinants of recruitment to populations of a temperate reef fish, *Trachinops caudimaculatus* (Plesiopidae). *Mar Freshw Res* 62:502–509

- Iampietro PJ, Young MA, Kvittek RG (2008) Multivariate prediction of rockfish habitat suitability in Cordell Bank National Marine Sanctuary and Del Monte Shalebeds, California, USA. *Mar Geod* 31:359–371
- Ierodiaconou D, Monk J, Rattray A, Laurenson L, Versace V (2011) Comparison of automated classification techniques for predicting benthic biological communities using hydroacoustics and video observations. *Cont Shelf Res* 31:S28–S38
- Jenkins GP, Wheatley MJ (1998) The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: comparison of shallow seagrass, reef-algal and unvegetated sand habitats, with emphasis on their importance to recruitment. *J Exp Mar Biol Ecol* 221:147–172
- Johnson DW (2006) Predation, habitat complexity, and variation in density-dependent mortality of temperate reef fishes. *Ecology* 87:1179–1188
- Knudby A, LeDrew E, Brenning A (2010) Predictive mapping of reef fish species richness, diversity and biomass in Zanzibar using IKONOS imagery and machine-learning techniques. *Remote Sens Environ* 114:1230–1241
- Kracker L, Kendall M, McFall G (2008) Benthic features as a determinant for fish biomass in Gray's Reef National Marine Sanctuary. *Mar Geod* 31:267–280
- Leathwick JR, Elith J, Francis MP, Hastie T, Taylor P (2006) Variation in demersal fish species richness in the oceans surrounding New Zealand: an analysis using boosted regression trees. *Mar Ecol Prog Ser* 321:267–281
- Leathwick JR, Elith J, Chadderton WL, Rowe D, Hastie T (2008) Dispersal, disturbance and the contrasting biogeographies of New Zealand's diadromous and non-diadromous fish species. *J Biogeogr* 35:1481–1497
- Lucieer V, Hill NA, Barrett NS, Nichol S (2013) Do marine substrates 'look' and 'sound' the same? Supervised classification of multibeam acoustic data using autonomous underwater vehicle images. *Estuar Coast Shelf Sci* 117:94–106
- Monk J, Ierodiaconou D, Bellgrove A, Harvey E, Laurenson L (2011) Remotely sensed hydroacoustics and observation data for predicting fish habitat suitability. *Cont Shelf Res* 31:S17–S27
- Monk J, Ierodiaconou D, Harvey E, Rattray A, Versace VL (2012) Are we predicting the actual or apparent distribution of temperate marine fishes? *PLoS ONE* 7:e34558
- Moore CH, Harvey ES, Van Niel KP (2009) Spatial prediction of demersal fish distributions: enhancing our understanding of species–environment relationships. *ICES J Mar Sci* 66:2068–2075
- Nichol S, Anderson T, McArthur M, Barrett N, Heap A, Siwabessy PJW, Brooke B (2009) Southeast Tasmania temperate reef survey post-survey report. Technical Report. Geosciences Australia, Canberra
- Pittman SJ, Costa BM, Battista TA (2009) Using lidar bathymetry and boosted regression trees to predict the diversity and abundance of fish and corals. *J Coast Res* 53(Spec Issue):27–38
- Rattray A, Ierodiaconou D, Laurenson L, Burq S, Reston M (2009) Hydro-acoustic remote sensing of benthic biological communities on the shallow South East Australian continental shelf. *Estuar Coast Shelf Sci* 84:237–245
- Richards BL, Williams ID, Vetter OJ, Williams GJ (2012) Environmental factors affecting large-bodied coral reef fish assemblages in the Mariana Archipelago. *PLoS ONE* 7:e31374
- Shepherd SA, Brook JB, Xiao Y (2010) Environmental and fishing effects on the abundance, size and sex ratio of the blue-throated wrasse, *Notolabrus tetricus*, on South Australian coastal reefs. *Fish Manag Ecol* 17:209–220
- Shumway CA (2008) Habitat complexity, brain, and behavior. *Brain Behav Evol* 72:123–134
- Shumway CA, Hofmann HA, Dobberfuhl AP (2007) Quantifying habitat complexity in aquatic ecosystems. *Freshw Biol* 52:1065–1076
- Tupper M, Boutilier RG (1997) Effects of habitat on settlement, growth, predation risk and survival of a temperate reef fish. *Mar Ecol Prog Ser* 151:225–236
- Ward T, Vanderklift M, Nicholls A, Kenchington R (1999) Selecting marine reserves using habitats and species assemblages as surrogates for biological diversity. *Ecol Appl* 9:691–698
- Warfe DM, Barmuta LA (2004) Habitat structural complexity mediates the foraging success of multiple predator species. *Oecologia* 141:171–178
- Wedding L, Friedlander A (2008) Determining the influence of seascape structure on coral reef fishes in Hawaii using a geospatial approach. *Mar Geod* 31:246–266
- Williams GJ, Cameron MJ, Turner JR, Ford RB (2008) Quantitative characterisation of reef fish diversity among nearshore habitats in a northeastern New Zealand marine reserve. *NZ J Mar Freshw Res* 42:33–45
- Willis TJ, Millar RB, Babcock RC (2000) Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. *Mar Ecol Prog Ser* 198:249–260

Appendix. Additional data

Table A1. Bathymetric derivative descriptions and software and toolboxes used to generate them

Derivative	Variable description (3×3 pixel analysis extent unless specified below)	Value range	Software/ toolbox
Bathymetry	Depth (negative elevation) of the grid cell. Bathymetric product generated from ascii output file into grid with 2 m resolution	3.6–9.4 m	Spatial Analyst-ArcGIS 9.3
Slope	Maximum change in depth between each cell and the cells in an analysis neighbourhood. Calculated in degrees from horizontal	0–33.3°	Spatial Analyst-ArcGIS 9.3
Curvature	Seabed curvature defined as the derivative of the rate of change of the seabed. It is a quantifiable measure of the shape of the seabed surface	–36.2 to 26.5	Spatial Analyst-ArcGIS 9.3
Profile curvature	Measure of the seabed in the direction of the slope of the seabed	–22.0 to 20.4	Spatial Analyst-ArcGIS 9.3
East deviation	Deviation from east is a value that reflects how much the aspect value deviates in degrees from East facing	0–176.6°	Jenness Grid Tools – ArcView Extension
South deviation	Deviation from south is a value that reflects how much the aspect value deviates in degrees from South facing	0–171.8°	Jenness Grid Tools – ArcView Extension
Topographic position index (TPI)	Measure of a location relative to the overall landscape, calculated by comparing the elevation of a cell with the mean elevation of surrounding cells by an analysis extent of 10. Locations that are higher than their surroundings will have positive values, whereas areas that are lower will have negative values. Flat areas have values closer to 0	–0.42 to 0.29	Benthic Terrain Modeller Tool for ArcGIS
Rugosity	Ratio of the surface area to the planar area across the neighbourhood of the central pixel in a 3×3 neighbourhood (Jenness 2002). By this method, flat areas will have a rugosity value near 1, whereas high-relief areas will exhibit higher values. This analysis is limited to a single scale, and whether it captures rugosity at a level relevant to the observed habitat is therefore sensitive to the initial raster resolution	0–1.37	Jenness Grid Tools – ArcView Extension
Channel morphometric	Proportion of cells within each survey block that lie in a local concavity that is orthogonal to a line with no concavity/convexity	0–1	LandSerf 2.3.1
Ridge morphometric	Proportion of cells within each survey block that lie on a local convexity that is orthogonal to a line with no convexity/concavity	0–0.83	LandSerf 2.3.1
Plane morphometric	Proportion of cells within each survey block that do not lie on any surface concavity or convexity	0–0.96	LandSerf 2.3.1

Table A2. Names, taxonomic membership, total numbers of observations (N) and survey block occurrence for reef fish species encountered across all survey within the Tinderbox Marine Reserve

Species	Common name	Family	N	Occurrence (%)
<i>Acanthaluteres spilomelanurus</i>	Bridled leatherjacket	Monacanthidae	5	0.5
<i>Acanthaluteres vittiger</i>	Toothbrush leatherjacket	Monacanthidae	11	4.1
<i>Aplodactylus arctidens</i>	Marblefish	Aplodactylidae	2	0.9
<i>Aracana aurita</i>	Shaw's cowfish	Aracnidae	20	8.6
<i>Caesioperca rasor</i>	Barber perch	Serranidae	10	2.7
<i>Cephaloscyllium laticeps</i>	Draughtboard shark	Scyliorhinidae	8	3.6
<i>Cheilodactylus nigripes</i>	Maggie perch	Cheilodactylidae	1	0.5
<i>Cheilodactylus spectabilis</i>	Banded morwong	Cheilodactylidae	2	0.9
<i>Dasyatis brevicaudata</i>	Smoothback ray	Dasyatidae	1	0.5
<i>Dinolestes lewini</i>	Longfin pike	Dinolestidae	601	1.4
<i>Diodon nichthemerus</i>	Porcupine fish	Diodontidae	8	3.6
<i>Dipturus whitleyi</i>	Whitley's skate	Rajidae	1	0.5
<i>Dotalabrus aurantiacus</i>	Pretty polly	Labridae	26	11.8
<i>Latridopsis forsteri</i>	Bastard trumpeter	Latridae	132	26.8
<i>Lotella rhacina</i>	Beardie cod	Moridae	2	0.9
<i>Meuschenia australis</i>	Brownstriped leatherjacket	Monacanthidae	12	5.0
<i>Meuschenia freycineti</i>	Six-spined leatherjacket	Monacanthidae	6	2.7
<i>Nemadactylus macropterus</i>	Jackass morwong	Cheilodactylidae	1	0.5
<i>Neoodax balteatus</i>	Little weed whiting	Odacidae	37	14.1
<i>Neosebastes scorpaenoides</i>	Gurnard perch	Neosebastidae	1	0.5
<i>Notolabrus fuscicola</i>	Purple wrasse	Labridae	87	26.4
<i>Notolabrus tetricus</i>	Blue-throated wrasse	Labridae	967	97.7
<i>Odax cyanomelas</i>	Herring cale	Odacidae	5	1.8
<i>Omegophora armilla</i>	Ringed toadfish	Tetraodontidae	1	0.5
<i>Pempheris multiradiata</i>	Bigscale bullseye	Pempheridae	18	3.6
<i>Pentaceropsis recurvirostris</i>	Longsnout boarfish	Pentacerotidae	4	1.4
<i>Pictilabrus laticlavus</i>	Senator wrasse	Labridae	136	36.8
<i>Scorpius lineolata</i>	Silver sweep	Kyphosidae	144	3.2
<i>Siphonognathus attenuatus</i>	Pencil weed whiting	Odacidae	7	2.7
<i>Trachinops caudimaculatus</i>	Southern hulafish	Plesiopidae	6665	40.0
<i>Urolophus cruciatus</i>	Banded stingaree	Urolophidae	1	0.5

Editorial responsibility: Janet Ley,
St. Petersburg, Florida, USA

Submitted: April 26, 2013; Accepted: March 16, 2014
Proofs received from author(s): May 28, 2014