Transferability of predictive models of coral reef fish species richness

Ana M. M. Sequeira¹, Camille Mellin^{2,3}, Hector M. Lozano-Montes⁴, Mathew A. Vanderklift⁴,
Russ C. Babcock⁴, Michael Haywood⁵, Jessica J. Meeuwig¹, M. Julian Caley²

¹ UWA Oceans Institute and Centre for Marine Futures, University of Western Australia, School of
Animal Biology, University of Western Australia M470, 35 Stirling Highway, Crawley, Western
Australia 6009, Australia.

² Australian Institute of Marine Science, PMB No. 3, Townsville MC, Townsville, Queensland 4810,
Australia

³ The Environment Institute and School of Earth and Environmental Sciences, The University of
Adelaide, South Australia 5005, Australia

⁴ CSIRO, Oceans and Atmosphere Flagship, Underwood Avenue, Floreat, Western Australia 6014,
Australia.

⁵ CSIRO, Marine and Atmospheric Research, Dutton Park, Brisbane, Queensland 4001, Australia.

Corresponding Author (ana.sequeira@uwa.edu.au)

Tel: +61 (0)8 6488 2219

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Summary

1. Understanding biodiversity patterns depends on data collection, which in marine environments can be prohibitively expensive. Transferable predictive models could therefore provide time- and cost-effective tools for understanding biodiversity - environment relationships.
2. We used fish species counts and spatial and environmental predictors to develop predictive models of fish species richness (S) for two major coral reefs located in separate ocean basins: Australia's Great Barrier Reef (GBR; Queensland) and Ningaloo Reef (NR; Western Australia). We tested the ability of the GBR model to predict S at NR (its transferability) under various scenarios using different sampling durations, years sampled and transect sizes.
3. Based on R^2 , the GBR model poorly predicted S at NR ($R^2 < 16\%$) with few predicted values strongly correlated with observations. However, comparable spatial patterns in S across NR were predicted by both the NR and the GBR models when calibrated at similar spatio-temporal scales.
4. This result suggests that poor validation of the transferred models may indicate low deviance explained by the predictors in the new system (where other, not included, predictors might have a more direct effect on the response), and that in some situations, model transferability may be considerably improved by using datasets of similar spatio-temporal scales. Therefore, data filtering by time and space may be required prior to transferring models.

5. *Policy implications*: Transferable models can provide initial estimates of fish species richness patterns in poorly sampled systems, and thereby guide the design of better and more efficient sampling programs. Further improvements in model transferability will increase their predictive power and utility in conservation planning and management.

KEYWORDS generalized linear mixed-effects modelling, Great Barrier Reef, Ningaloo Reef, prediction, spatial autocorrelation, biodiversity distribution models, macroecology.

Introduction

Anthropogenic impacts on global biodiversity are rapidly increasing (Worm *et al.* 2006), making the need for efficient management tools urgent. One option is to improve the predictive ability of biodiversity distribution models (a.k.a. species distribution, habitat suitability, resource selection and ecological niche models). Such models codify our understanding of relationships between biodiversity metrics (e.g., species occurrence, richness or abundance) and the environment, and are commonly used to predict spatial patterns of biodiversity in aid of conservation planning and management (Guisan & Thuiller 2005). Following the surge of application of these models in terrestrial contexts (refer to Lehmann, Overton & Austin 2002), they have now also been widely applied to marine environments (e.g., Kelly, Fonseca & Whitfield 2001; Sequeira *et al.* 2014a), and specifically to coral reef systems (Mellin *et al.* 2010; Tittensor *et al.* 2010) where the influence of both fine- and broad-scale patterns of environmental variation (i.e., assumption of spatial stationarity) has also been tested (Mellin *et al.* 2010). A major strength of these models is their ability to predict species occurrence patterns in areas

where no data are available (Robertson *et al.* 2003), whether by (i) interpolating results and providing predictions for unsampled sites within the sampled area (e.g., Mellin *et al.* 2010), or by (ii) forecasting results under expected future environments (Araújo & New 2006; Sequeira *et al.* 2014a) or to new geographical areas (Sequeira *et al.* 2014a; Sequeira *et al.* 2014b), as defined by Elith & Leathwick (2009). The application of such models to unsampled areas is termed transferability (Phillips 2008). Therefore, improving transferability of existing biodiversity distribution models could provide cost-effective tools for understanding biodiversity-environment relationships in support of conservation and management.

Previous studies of model transferability have focused largely on terrestrial ecosystems (Graf *et al.* 2006; Randin *et al.* 2006), and have generated highly variable results ranging from “zero” (Fielding & Haworth 1995) to “highly accurate” transferability (Vanreusel, Maes & Van Dyck 2008). In aquatic environments, however, model transferability remains poorly studied, having been examined for only a few anadromous and freshwater fish species (Sundblad *et al.* 2009; Wenger & Olden 2012). Because geographical ranges of marine species are often larger than those of terrestrial and freshwater species, marine systems may provide better possibilities for building transferable biodiversity models as there will be more opportunities to fit models using subsets of species’ ranges, and testing their transferability to other parts of their ranges (Robinson *et al.* 2011).

Among marine ecosystems, coral reefs are the most biodiverse and are globally threatened (Knowlton *et al.* 2010; Plaisance *et al.* 2011). On coral reefs, biodiversity can be predicted from a range of environmental factors, including depth, slope, sediment type, coastline length or distances to shore or shelf, water temperature, chlorophyll *a*, and oxygen concentration (e.g., Mellin *et al.* 2010; Tittensor *et al.* 2010). Of these, broad scale covariates are likely to be

more appropriate for explaining variation at the ecosystem scale (Mellin *et al.* 2014). Transferability of biodiversity models built around such broad-scale predictors could therefore be particularly useful in assisting the management and conservation of coral reefs. Also, because some coral reefs are relatively well sampled (Fisher *et al.* 2011), they present a good opportunity to build predictive models of biodiversity patterns (e.g., Mellin *et al.* 2010) and then test their transferability to other reef systems.

Here we begin the task of understanding how to improve transferability of predictive models of fish species richness (S) on coral reefs. We examine how well a model developed for a well-studied reef system, the Great Barrier Reef (GBR), predicts S at the ecologically distinct and geographically distant Ningaloo Reef (NR), for which there is currently far less information available (Fisher *et al.* 2011). We also tested whether transferability could be improved by using different subsets of data (scenarios hereafter) during calibration of the GBR model, and then compared each GBR scenario result with the results from an analogous predictive model developed for NR using data collected at NR. From these comparisons, we identify key aspects of predictive models that support transferability.

Materials and methods

The GBR, off NE Australia, is the world's largest coral reef ecosystem (~2300 km long, 60 to 250 km wide, ~3000 individual reefs) (Fig. S1). NR, off NW Australia, is the world's largest fringing reef (~300 km long, <3 km wide) (Fig. S1). These two fundamentally different reef systems are separated by thousands of kilometres and are located in the Pacific and Indian Ocean basins, respectively.

Fish data

We used reef fish data for the GBR from the Long Term Monitoring Program (Sweatman *et al.* 2008) of the Australian Institute of Marine Science (AIMS). A minimum of 137 sites from 46 reefs within six sectors of the GBR (Cooktown/Lizard Island, Cairns, Townsville, Whitsunday, Swain, Capricorn Bunkers; Fig. S1) were surveyed during 2003-2005, and every second year thereafter, until 2013. Species of the following ten fish families were counted: Acanthuridae, Chaetodontidae, Labridae, Lethrinidae, Lutjanidae, Pomacentridae, Scaridae, Serranidae, Siganidae, and Zaclidae (see Supporting Information species list). Counts were made using 5x50-m long transects per site across three shelf positions (inner, mid and outer) (for details, see Halford & Thompson 1996).

For NR, we used reef fish data from the Commonwealth Scientific and Industrial Research Organisation (CSIRO) collected in 2013 (Fig. S1). A total of 88 sites were sampled using 3x25-m long transects per site. Species from 46 families, including the 10 sampled on the GBR, were counted. We modelled fish species richness (S) for both the GBR and NR by pooling S across transects within sites, i.e., summing the total number of different species observed

across transects sampled for each site. When data from multiple years were available for the GBR, we also pooled *S* across years within sites.

Environmental and spatial predictors

We used environmental data (see Table S1) with 0.01° resolution, collated at a national scale (Huang *et al.* 2010; www.marinehub.org) ensuring that environmental data used for both the GBR and the NR were similar. This dataset (Table S1) includes bathymetric variables, percentage cover of sediment characteristics such as carbonates, sand, gravel and mud, and averaged mean annual estimates and seasonal ranges for nutrients (nitrate, silicate, phosphate), oxygen, salinity, temperature and chlorophyll *a*. Because the ‘annual mean estimates’ and ‘seasonal ranges’ of the variables were mostly correlated, we only used ‘annual mean estimates’ (Table S1). For NR, we also used hyperspectral bathymetric data (Heyward 2006).

We assigned to each fish sampling site the environmental values on for the closest grid-cell, and calculated the spatial predictors shortest distance to coast (*coast*) and to the outer limit of the reefs (*barrier*). We calculated these distances using the *Near* tool in ArcGIS10.1 (ESRI, Redlands, CA) and the Equidistant Cylindrical projection from the spherical geographical coordinate system.

We selected our models predictors according to their multicollinearity estimated by Spearman’s correlation coefficient (ρ) from the *pairs.panels* function from the *psych* package in R (R Core Team 2014). Our final model set (Table 1) considered different categories of predictors in different models, and by including only non-collinear variables (i.e., $\rho < 0.5$) within each model in the model set. To account for non-linear dependencies with bathymetry, distances to domain boundaries and sea surface temperature, we included the respective

predictors (*depth*, *coast* and *barrier*, and SST_{av}) as a second order polynomial using the *poly* function from the *stats* package in R. This was done after comparing models including the quadratic terms and models including only the linear term for each predictor.

Modelling approach

Our modelling approach is summarised in Fig. 1. After predictor selection, we developed two NR models for S (hereafter NR models) using: (i) species data from the ten families sampled on the GBR (S_{10}) and (ii) all species data collected at NR (S_{All}).

For the GBR, we used different data subsets for developing a set of modelling scenarios (i.e., scenarios A to G; Table 2) to explore the influence of different calibration datasets on model transferability. Scenario A was based on Mellin *et al* (2010), where spatial patterns of fish species richness was successfully predicted using four years of data (2003 – 2007, except 2006) collected using 50 m transects and a similar environmental dataset (Appendix S1, Table S2, Fig. S2). We then built the other scenarios (i.e., B-G) using updated environmental data, with scenario B repeating scenario A but using these updated data. For the remaining scenarios we changed the (i) sampling years to cover four years of data collected more recently (2007 – 2013 odd years only; scenario C), (ii) transect size to 25 m (scenario D), and (iii) length of the dataset used to a single year: 2007 for scenarios E and F, and 2013 for scenario G, where downscaling was also tested in F and G (Table 2). We downscaled the GBR transect data (length = 50 m) to match the transect size sampled at NR (length = 25 m) by: (i) calculating the average increase in the number of species added per transect (50-m long) within each site (first transect selected randomly, and iterated 100 times) to account for differences in S among sites, then (ii) dividing

the resulting average by 2 (the ratio between 50 and 25 m), and then (iii) subtracting this amount from the totals observed on each transect within the same site on the GBR.

We started by developing generalized linear models (GLM) using a Poisson distribution and log link function, following Mellin *et al.* (2010). We then calculated Moran's *I* (Diggle & Ribeiro 2007) to test for spatial autocorrelation in model residuals using the *sp.correlogram* function from the *spdep* library (Bivand 2013) in R. If significant spatial autocorrelation was present, we developed generalised linear mixed-effects models (GLMM) by including a spatial random effect for reef to account for relationships among sites within each reef. We did this using the *lmer* function from the *lme4* package in R (Bates *et al.* 2013). For model assessment, we used Akaike's (corrected for small sample sizes; AIC_c) and the Bayesian (BIC) information criteria (Burnham & Anderson 2004) and their weights ($wAIC_c$, $wBIC$, respectively) to (i) compare model probabilities, and to (ii) assess each model's strength of evidence relative to the entire model set. To assess the model's goodness-of-fit and draw comparisons between models from the same model set, we used the percentage of deviance explained (%De; a pseudo- R^2 referring to a likelihood ratio between each model and the null model) for GLM, and the marginal and conditional R^2 (Nakagawa & Schielzeth 2013) for GLMM. We first used each model to predict *S* in the respective reef system, and validated the results by calculating the mean 10-fold cross-validation error (Davison & Hinkley 1997) for each model and across the model set. We validated our predicted patterns of *S* for NR by examining the correlation between the observed and predicted values on sampled sites when developing a linear model (LM) using field observations as the response and the corresponding *S* predictions as predictor (Piñeiro *et al.* 2008). We then compared the goodness-of-fit of these LM models using the resulting *p-values* and R^2 . We also calculated mean effect sizes for each predictor following Sequeira *et al.* (2014b).

Testing model transferability

Because the GBR is a diverse reef system, the calibration of the GBR models includes a series of different habitats and/or reef regions (sensu Graf *et al.* 2006) potentially allowing estimation of a more general relationship between S and the environmental variables considered, which might also be transferable to other reef ecosystems (sensu Vanreusel, Maes & Van Dyck 2008; Wenger & Olden 2012). The NR model, on the other hand, was calibrated using comparatively limited data specific to NR's ecological and biogeographical settings. Therefore, we tested model transferability from the GBR to NR by predicting S patterns at NR using the GBR models, but not the reverse.

To test the influence of different calibration datasets on model transferability (Fielding & Haworth 1995), we used each model scenario for the GBR to predict S at NR and then assessed transferability in two ways (Fig. 1). First, we validated our cross-system predictions with data collected at NR. We did this by comparing the goodness-of-fit (i.e., R^2 and p -values) of a LM of the S predictions for NR from each GBR scenario as a function of the observed values at NR. When transferred models from the GBR failed to predict low S (< 30 species), we also tested the LM using only locations at NR where > 30 species were observed. Second, we compared the results from our GBR scenarios predicting to NR and those from the NR(S_{10}) model by calculating differences in estimated means, and by comparing maps of predicted S for NR by both the GBR scenarios (i.e., transferred models) and the NR(S_{10}) model. We did the latter in four ways: (i) we compared the mean direct validation errors (observed *versus* predicted values from LM) obtained for both procedures to estimate differences in accuracy by both models ; (ii) we calculated the mean absolute difference between values predicted by both models on a grid-cell basis to compare the precision of the resulting predictions; (iii) we estimated the percentage

of grid-cells with absolute values differing $\leq 15\%$ (i.e., by $\leq 5.4 \pm 0.9$ species) between both models to quantify how comparable both predictions were; and finally, (iv) we rescaled the predictions from the GBR scenarios to the same maximum and minimum value of S predicted by the NR(S_{10}) model to directly compare the high-*versus*-low S patterns predicted for NR by both procedures.

Results

Our model set, including 17 environmental predictors, was similar for both reef ecosystems (Table 1). Occasional differences (models 1 and 4; Table 1) were needed to avoid strong collinearity between variables (Spearman's $\rho > 0.5$) observed at NR, but not for the GBR. We also observed little spatial autocorrelation in the residuals of the NR models (first lag only and Moran's $I < 0.2$). Therefore, we modelled S at NR using GLM. For both NR models (S_{All} and S_{10}), the full model (model 1) explained the greatest deviance (23.6 % and 27.8 %, respectively) in S , while the 'nutrient' model (model 7) had the strongest support ($wAICc = 0.984$ and 0.953 , respectively; $wBIC = 1$ for both models). Model 7 also had the lowest cross validation error in both NR models (8.8 ± 2.7 and 7.6 ± 2.3 species, respectively). The predictors with greatest effect size were: nitrate ($NO3_{av}$) and oxygen concentration ($O2_{av}$) followed by chlorophyll a ($Chla$) and the coefficient of light attenuation ($K490$) (Fig. S3 – NR). The NR model-averaged predictions of S were correlated with the observed values ($R^2 = 0.396$ and 0.437 for S_{All} and S_{10} , respectively, $p < 0.001$; Fig. S4). The models predicted higher S in the northern central sections of NR, and lower S in the south and northernmost sections of NR (Fig. 2a).

For most GBR scenarios (A – E, except B) the light attenuation model (model 11) received the strongest $wAIC_c$ and $wBIC$ support. For scenarios F and G, a different set of two models received equally high $wAIC_c$ (model 11 and 4, and model 10 and 1, respectively; Table S3). Scenario F had the lowest cross-validation error (7.8 ± 1.5 species), and scenario G had the highest R^2_c (31.6 and 57.5, respectively for model 10 and 1) and R^2_m (83.0 and 83.85, respectively for model 10 and 1) (Table S3). Both scenarios F and G used GBR data downsampled to 25 m from one year only (2007 and 2013, respectively) (Table 2). The predictors with greatest effect sizes were similar for all GBR scenarios (Fig. S3), except scenario G for which salinity had the largest effect size, and the effect of some other predictors was also closer to that obtained for the NR model (e.g., quadratic terms for *coast* and *SST_{av}*) (Fig. S3). The predicted patterns of *S* for the GBR were also similar for all GBR scenarios (Fig. 2b) however, the predicted range was always narrower than the observed values (cf Tables 2 and 3).

For GBR scenarios transferred to NR, the range of predicted *S* (Table 3) was also always narrower than the observed range at NR (8 – 67 species). The transferred GBR models failed to predict observed values < 30 species resulting in weaker correlations between the predictions from the GBR scenarios and NR observations ($R^2 < 20.7\%$) (Table 3). R^2 was lowest for scenarios F and G ($p > 0.05$) despite the range of *S* predicted by scenario G (32.2 – 53.3 species) being the closest to that observed at NR. To confirm that poor validation was associated with lack of prediction for *S* < 30, we validated these two scenarios using LM at locations at NR where > 30 species were observed. This restriction resulted in a higher R^2 for scenario G (13.1%; $p < 0.05$) (Table 3). The mean predicted estimates of *S* for NR by the transferred GBR scenarios were also greater than those predicted by the NR models, except for scenarios E, F and G, which included GBR data from one year only (i.e., similar to NR data). Similar results were

obtained for the direct validation error, which was generally high for most scenarios (~ 40 %; Table 3), but again, lower for scenarios E, F and G (< 28 %). The prediction maps for NR from the GBR scenarios A – D mostly over-predicted *S* for all NR locations (Fig. 3a). Prediction maps from scenarios F and G resulted in the lowest absolute mean differences (8.2 ± 7.9 and 6.1 ± 6.7 species, respectively; Table 3), and highest % of the grid-cells with predicted *S* differing ≤ 15 % (i.e., $\leq 5.4 \pm 0.9$ species; Table 3) to that predicted by the NR model. When comparing the high-*versus*-low *S* patterns predicted for NR by the transferred GBR scenarios, predictions from scenario G were the most similar (~ 35 % replicated) to those obtained by the NR model (Fig. 3b). Differences in the maps obtained by the GBR scenario G and the NR model included greater than expected *S* predicted around Mangrove Reef, in the northernmost section of NR, and in the Cloates area, higher *S* was predicted only towards the reef but not in the lagoon (Fig. 3c).

Predictions from the transferred GBR scenarios E, F and G (one year of GBR data) were most comparable to those obtained from the NR model (Table 3). Among these, predictions from scenario F (2007 data, downscaled to 25 m) resulted in a lower mean absolute difference compared to those from the NR model (6.1 ± 6.7 species) and the highest % grid-cells with predicted *S* values differing $\leq 15\%$ from the predictions obtained with the NR models. Scenario G, however, calibrated with downscaled GBR data collected in the same year (2013) as the data from NR, resulted in the most comparable high-*versus*-low patterns predicted (Fig. 3c).

Discussion

Transferability is an important utility of ecological models for conservation planning and management (Murray *et al.* 2011), but what confers transferability upon these models remain

poorly understood. To help address this knowledge gap, we tested the transferability of *S* models between two fundamentally different reef ecosystems located in separate ocean basins, and demonstrate that comparable patterns of *S* can be predicted either by applying a model developed for the GBR to NR, or by developing a new model calibrated for NR. Our results suggest that both data and models developed for a well-studied reef ecosystem (e.g., GBR) can provide useful information for understanding other coral reefs. Further research is needed, however, to improve model transferability.

Transferability of our GBR models was better when the spatio-temporal scales of the calibration data matched the scales of the data observed in the other reef system (NR). This included matched (i) temporal range (one year only), (ii) sampling year (same year for both systems), and (iii) transect size. Consistent with Fielding and Haworth (1995), our results from transferring each GBR scenario supports the idea that model transferability is affected by the data used to develop the model to be transferred. During model development, we also adopted existing recommendations for improving transferability, including the use of GLMs, which may be better suited for transferability than e.g., GAMs due to data overfitting (Randin *et al.* 2006). We also developed models with non-site specific predictors (Fielding & Haworth 1995; Graf *et al.* 2006; Vanreusel, Maes & Van Dyck 2008; Heinänen, Erola & von Numers 2012) by using environmental variables available for both reefs and by testing transferability from a diverse system with different habitat types and/or reef regions (GBR) to a fringing reef system (NR). The vastness of the GBR also allowed the GBR model to incorporate a large range of predictor values mostly encompassing those observed for NR, which is essential for reducing extrapolation when predicting to a new location (Thuiller *et al.* 2004; Randin *et al.* 2006; Sundblad *et al.* 2009). The

more extensive data from the GBR also likely facilitated better estimation of relationships between S and the environmental variables considered.

For both NR models (S_{10} and S_{All}), environmental predictors explained relatively little deviance in observed S ($< 28\%$). Therefore, we expected a low R^2 ($< 20.7\%$) using LM to compare predictions from the GBR scenarios with those from NR indicating poor model transferability. Indeed, direct validation showed poor transferability for scenario G ($R^2 \sim 2\%$, $p > 0.05$) even though the most similar patterns of S were predicted by this scenario and by the NR model (Fig. 3). We attribute this result mostly to the lack of predictions < 30 species; our LM for observations of > 30 species resulted in a significant R^2 of 13.1% . The general over-prediction of S at NR by the GBR models may stem from differences among sampled sites at both reefs. GBR sampling included locations with greater coral cover (Sweatman *et al.* 2008) than those at NR, which were mostly on reef flats where lower fish density is expected (Gratwicke & Speight 2005). Direct validation of the NR model predictions resulted in R^2 values of $\sim 40\%$, which were slightly higher than the highest deviance explained by the NR models ($< 28\%$, Table S3). These results suggest that poor direct validation of transferred models may be indicative of low deviance explained by the predictors in the new system rather than poor model transferability *per se*. If so, the environmental predictors in our models might only be reflecting indirect effects on S patterns in NR while other factors not accounted for, such as system-specific constraints like fishing pressure, may be influencing the number species observed per unit area (Vanderklift, Babcock & Cook 2013). As fishing pressure is typically species and size selective (Zhou *et al.* 2010), differential fishing pressure among locations may condition relationships between environmental predictors by changing species abundance distributions. Accounting for

differences in fishing pressure among reefs where predictive models are built and those to which they are transferred may help improve our understanding of model transferability.

Most GBR scenarios (A – E) resulted in similar model rankings based on weights of the information criteria, importance of predictors, and general spatial patterns of *S* on the GBR (Fig. 2b), indicating that models developed for the GBR are potentially stable and robust even when using shorter time series. For scenarios F and G, the results were the most dissimilar, with effect sizes of some predictors becoming more comparable to those obtained with the NR model. Differences in effect sizes, and the importance of predictors have previously been associated with different discriminative ability of transferred models (Murray *et al.* 2011). Therefore, the effect size changes of some predictors for scenario G might have contributed to the similarities in the resulting high-*versus*-low spatial patterns of *S* predicted for NR by this scenario and those from the NR model. As observed for model transferability in terrestrial ecosystems (Heinänen, Erola & von Numers 2012), our results focused on fish species richness also suggest that the most transferable model might not be the most robust model for the reef system from which it is transferred.

When comparing the predicted patterns of *S* for the GBR from the GBR scenarios F and G (Fig. 2b) which used GBR data from 2007 and 2013, respectively, the map for the more recent scenario shows a slightly reduced area of higher *S* and higher prediction uncertainty. Such change in predicted patterns indicates that other factors not accounted for in the models may be influencing *S* patterns on the GBR as well, possibly reducing species richness. When transferred to NR, GBR Scenario G was the only one not to predict high *S* in the southern sections of NR (Fig. 3b) and therefore predicted the most comparable *S* patterns at NR (Fig. 3c). However, GBR scenario G predicted higher *S* in the northernmost sections of NR (around Mangrove) as well,

where more shore-based recreational activities (including fishing) occur year round (Smallwood *et al.* 2011). Similarly to the NR model, the GBR scenario G also predicted slightly higher S between Point Cloates and Coral Bay but only towards the reef and not in the lagoon. This difference in predictions may be associated with non-stationarity or simply with differences in the way data were collected in each reef ecosystem as highlighted above. The downscaling procedure used to match the GBR and NR data also had a large effect on predictions (cf E and F, both calibrated with data from 2007, Table 3). While validation error and high-*versus*-low patterns obtained by scenarios D and F are similar, the downscaling procedure used in scenario F greatly reduced absolute mean difference in predicted values from 11.9 ± 7.2 to 6.1 ± 6.7 species, and increased by 40% the percentage of grid-cells with predicted S differing $\leq 15\%$ from the predictions of the NR model. The high-*versus*-low patterns most comparable to those obtained from the NR model were, however, obtained for the transferred GBR scenario G which used data from the same year as the observations at NR. This result suggests a temporal association between patterns of S between reef ecosystems separated by thousands of kilometres. Potential causes of such synchrony are not yet understood but may be worth pursuing in future research.

While we suggest here a path for improving model transferability, better understanding is still required about how to maximize and assess it, and about how inter-reef differences may affect transferability. In summary, to assist in understanding what confers transferability to biodiversity models, we suggest that (i) data of the same spatio-temporal range, (ii) general environmental predictors, and (iii) models that do not over fit data be used. Where some data from the system to which the model is transferred exists, comparison of model results will be enhanced. We also suggest that other modelling frameworks, such as Bayesian approaches that

can make use of prior information, be tested in a model transferability context. Our work illustrates initial steps towards improved model transferability among coral reefs, and demonstrates that transferred models can provide useful information even for fundamentally different and geographically distant reef systems. The more model transferability can be improved, the more useful will these tools be for conservation and management.

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 501

502 **Tables**

503 ***Table 1***

504 Models relating coral reef fish species richness (*S*) to environmental factors of the Great Barrier Reef (GBR) and Ningaloo Reef (NR).
505 *Coast*: distance to coast; *barrier*: distance to the reef's outer limit; *crbnt*: percent carbonates; percent *gravel*, *sand*, and *mud*;
506 concentrations of *NO3*: nitrate, *PO4*: phosphate, *SI*: silicate, *O2*: dissolved oxygen, *Chla*: chlorophyll *a*; *Sal*: salinity; *SST*: annual sea
507 surface temperature; *K490*: coefficient of light attenuation at 490 nm; subscript *av*: average. All predictors were mean centred, and
508 *coast*, *barrier*, *depth*, and *SST_{av}* were included as quadratic terms. Sediment variables were mostly collinear and therefore were
509 included in separate models (4 – 6). Bold face indicates predictors not included in both systems due to collinearity between variables
510 observed at NR.

Model	Predictor category	GBR model	NR model
1	Full model	<i>coast + barrier + depth + slope + O2_{av} + SST_{av} + K490_{av} + aspect + gravel + sand + NO3_{av} + PO4_{av} + SI_{av}</i>	<i>coast + barrier + depth + slope + O2_{av} + SST_{av} + K490_{av} + Chla_{av}</i>
2	Distance to domain boundaries	<i>coast + barrier</i>	
3	Physical predictors including range of depths	<i>depth + aspect + slope</i>	
4	Sediment characteristics	<i>crbnt + gravel</i>	<i>gravel</i>
5	Sediment characteristics	<i>sand</i>	
6	Sediment characteristics	<i>mud</i>	
7	Nutrients	<i>NO3_{av} + PO4_{av} + SI_{av}</i>	
8	Oxygen and salinity	<i>O2_{av} + Sal_{av}</i>	
9	Productivity	<i>Chla_{av}</i>	
10	Temperature	<i>SST_{av}</i>	
11	Light availability	<i>K490_{av}</i>	
12	Null model	<i>1</i>	

Table 2

Data included in each Great Barrier Reef (GBR) modelling scenario. Temporal range: sampling year (odd years only after 2005); sources of environmental data: NERP (National Environment Research Program) updated from CERF (Commonwealth of Australia's Environment Research Facility); *S* range: species richness observed per site averaged across transects. Scenario A is reproduced from Mellin *et al.* (2010) (details in Appendix 1).
*denotes downscaled transect size (see Methods for details).

Scenario	Temporal range	Environmental data	<i>S</i> range	Transect length (m)*
A	2003-2007	CERF	32 – 100	50
B	2003-2007	NERP	32 – 100	50
C	2007-2013	NERP	32 – 107	50
D	2007-2013	NERP	32 – 102	25*
E	2007	NERP	9 – 73	50
F	2007	NERP	8 – 66	25*
G	2013	NERP	5 – 80	25*

Table 3

Model-averaged predictions of fish species richness (S) for Ningaloo Reef (NR) and the Great Barrier Reef (GBR). Results are for the NR model using all species sampled (S_{All}), and only the species from the 10 families sampled on the GBR (S_{10}), and for the GBR scenarios A to G (see Table 2 for description). R^2 and p -value: results from linear models using prediction results as a function of the observed values at NR (* indicates p -values < 0.05). Val_{error} : validation error from comparing predictions with values observed at NR. Abs diff from S_{10} : the absolute mean differences between the predicted S from each GBR scenario and S_{10} (also shown in percentage). % grid-cell $\leq 15\%$: the percentage of grid-cells from the GBR scenario predictions differing only $\leq 15\%$ (i.e., 5.4 ± 0.9 species) from those obtained with S_{10} within the same grid-cells. High-versus-low: the percentage of grid-cells from the GBR scenarios predicting relative high-versus-low S in NR similar to the predictions obtained from S_{10} . Observed S range at NR was 8 –74 species. *Italic font* show results considering only observed $S > 30$ (applicable to scenarios F and G only).

		Predicted S range	Direct validation		Prediction results				
			R^2	p -value	Mean S predicted	Val_{error}	Abs diff from S_{10}	% grid-cell $\leq 15\%$	high- <i>versus</i> - low (%)
NR	S_{All}	6.7 – 55	39.6	< 0.001	42	7.3 ± 5.6 (17.8 ± 13.9 %)	-	-	-
	S_{10}	4.7 – 47.8	43.7	< 0.001	36	8.5 ± 2.2	-	-	-

					(27.6 ± 1.3 %)				
GBR	A	57.7 – 77.4	19.6	0.003*	70	29.5 ± 13.8 (42.4 ± 20.0 %)	33.9 ± 8.7 (107.7 ± 95.9 %)	0.2	9.8
	B	61.6 – 76.0	14.8	0.012*	70	30.98 ± 14.52 (43.4 ± 20.4 %)	33.9 ± 8.2 (107.9 ± 96.7 %)	0.2	14.3
	C	60.9 – 81.1	20.2	0.003*	72	32.9 ± 13.9 (45.1 ± 19.1 %)	36.5 ± 8.5 (116.6 ± 104.4 %)	0	2.5
	D	58.2 – 77.2	20.7	0.002*	69	29.5 ± 13.9 (42.4 ± 20.1 %)	33.2 ± 8.4 (106.6 ± 99.6 %)	0	4.0
	E	40.9 – 52.5	18.8	0.004*	48	12.8 ± 9.7 (26.5 ± 20.3 %)	11.9 ± 7.2 (42.6 ± 66.8 %)	18.8	18.6
	F	37.0 – 44.6	0.0	0.912	42	8.3 ± 6.7 (19.3 ± 15.6 %)	6.1 ± 6.7 (25.0 ± 56.8 %)	58.8	16.8
			2.0	0.371		6.7 ± 4.5 (15.4 ± 4.5 %)			
	G	32.2 – 53.3	2.1	0.357	44	12.8 ± 10.3 (26.8 ± 21.1 %)	8.2 ± 7.9 (32.1 ± 69.0 %)	40.3	34.5
			13.1	0.027*		8.4 ± 6.1 (17.5 ± 12.4 %)

531 Figure 1: The approach used to develop and test transferability of predictive models of fish
532 species richness (S) for the Great Barrier Reef (GBR) to Ningaloo Reef (NR). Two models
533 for NR are included: S_{10} includes the 10 fish families sampled on the GBR and S_{All} includes
534 all fish families sampled at NR (Appendix 2 in Supplementary Information). We modelled
535 seven GBR scenarios (A to G) each considering a subset of the fish data sampled for the
536 GBR (Table 2).

537 Figure 2: Prediction maps of fish species richness (S) for: a) Ningaloo Reef using all fish data
 538 (S_{All}) and the 10 fish families (S_{10}) sampled on the Great Barrier Reef (GBR); b) the GBR
 539 when using different subsets of the fish data sampled in that system (A-G; see Table 2).

540 Figure 3: Prediction maps of fish species richness (S) at Ningaloo Reef (NR) obtained from GBR scenarios A to G (Table 2) and the NR models
 541 (S_{All} : all species sampled and S_{10} : species of the 10 families sampled on the GBR). Panel a) highlights differences in prediction ranges from each
 542 model. Panel b) allows comparison of areas where greater S was predicted by each model. Panel c) compares prediction results for NR from both
 543 the GBR scenario G and the NR model highlighting: (i) the low predictions of S in the southernmost section of NR by both models, (ii) the
 544 prediction of higher S in the northernmost section of NR by the GBR scenario G, and (iii) the prediction of greater S in the central (circled) area
 545 of NR, with the GBR scenario G predicting higher S towards the reef but not in the lagoon around Cloates.

Supporting Information

The following additional supporting information may be found in the online version of this article:

Appendix S1 Replication of existing GBR models (scenario A) from Mellin *et al.* (2010)

Appendix S2 Supplementary tables

Table S1 List of environmental predictors available around Australia with a resolution of 0.01 degrees used in our models and data sources

Table S2 Summary of models predicting fish species richness (S ; generalized linear models – GLM and generalized linear mixed-effect models – GLMM) to spatial and environmental properties for the Great Barrier Reef for the period: 2003 to 2007 as per Mellin *et al.* (2010).

Table S3 Summary of the best performing generalized linear mixed-effect models (GLMMs) for the GBR and model-averaged predictions of reef fish species richness (S) for the Great Barrier Reef (GBR).

Appendix S3: Supplementary figures

Figure S1 Location of the sampling sites where fish data were collected at Ningaloo Reef and the Great Barrier Reef.

Figure S2 Prediction maps of fish species richness (S) for the Great Barrier Reef and the period 2003 – 2007 obtained using our model replicating Mellin *et al.* (2010) and reproduced from Mellin *et al.* (2010)

Figure S3 Model-averaged effect sizes for each predictor included in the generalized linear model (GLM) developed for Ningaloo Reef (NR) and in the generalized linear mixed-effects models (GLMM) developed for each scenario using data collected from the Great Barrier Reef.

570 **Figure S4** Linear model of predicted fish species richness from the NR models versus
571 observed values for Ningaloo Reef.

572 **Appendix S4: References in supplementary material**

573 **Appendix S5: List of fish species sampled in Ningaloo Reef and the Great Barrier Reef**

574 **Appendix S6: Zipped folder with R script and data used from Ningaloo Reef**

575

Appendix S1: Replication of existing GBR models

We replicated the models of fish species richness (referred to as “fish species richness in the reference) developed for the GBR by Mellin *et al.* (2010) using a similar dataset to that used in the original publication: (i) fish data collected on the GBR from 2003 to 2007, and (ii) environmental data extracted from the CERF (Commonwealth of Australia’s Environment Research Facility) dataset. However, while Mellin *et al.* (2010) selected predictors using a multi-step procedure involving both a principal component and a correlation analysis followed by a series of GLM models using, at a time, each predictor and its quadratic term to predict *S* (Mellin *et al.* 2010), we simplified the variable selection procedure to be mostly based on non-collinearity of predictors, as described in the main body of the text.

Our reproduced GLM models resulted in a similar ranking (Table S2) to that presented in Mellin *et al.* (2010): the full model got the highest weights for both AICc and BIC, and also explained the greatest deviance (~ 60 %). The cross-validation error obtained for this model was 8.6 ± 1.6 species. Because we observed strong spatial autocorrelation in the GLM residuals (mostly in the first three lags), we developed GLMM by including a spatial random effect for reef in each model to account for spatial relationships among sites within each reef. No spatial autocorrelation was evident in the GLMM residuals. For these GLMM models comparison with the original publication was not possible as Mellin *et al.* (2010) used a penalized quasi-likelihood approach (Venables & Ripley 2002) which does not allow calculation of the likelihood, and therefore no AIC and BIC were computed.

We obtained the highest ranks from both information criteria weights (w_{AICc} and w_{BIC}) for the GLMM model including only the coefficient of light attenuation (*K490*; model 11), but these weights were equivalent to those obtained for model 9 (chlorophyll *a*: *Chla*) and model 2 (including distances to *coast* and *barrier*) (Table S2). The R^2_m obtained for these three models ranged from 23.1 to 29.9 but the full GLMM model resulted in the highest R^2_m

601 (53.1). All R^2_c values ranged between 70.9 and 73.7. The predictor with the greatest effect
602 was the linear term for *barrier* (Fig. S3 – scenario A, as per figure legend), followed by
603 *K490*, *Chla* and the percentage of carbonates in the sediment (*crbnt*). Similar to maps shown
604 in Mellin *et al.* (2010), the resulting spatial patterns we obtained showed higher *S* mostly in
605 the northern sections and towards the outer limits of the GBR (Fig. S2).

606 **Appendix S2: Supplementary Tables**

607 Table S1: List of environmental predictors available around Australia with a resolution of
608 0.01 degrees and used in our models (except predictors highlighted in grey): 1) Australian
609 Bathymetry and Topography Grid Geoscience Australia Record 2005/12 (Webster &
610 Petkovic, 2005) available at: www.ga.gov.au/products; 2) GEological and Oceanographic
611 Model of Australia's Continental Shelf (GEOMACS, Hemer, 2006 REF); 3) MARine
612 Sediment Database (MARS; Matthews et al, 2007 REF; Passlow et al, 2005), available at:
613 www.ga.gov.au/oracle/mars; 4) Commonwealth and Scientific Industrial Research
614 Organisation Atlas of Regional Seas (CSIRO – CARS) (Ridgway et al, 2002; Dunn et al,
615 2002) available at: www.marine.csiro.au; 5) Ocean colour standard monthly data products
616 from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) and Moderate Resolution
617 Imaging Spectroradiometer satellite (MODIS) from the National Aeronautics and Space
618 Administration (NASA); 6) sourced from the Ocean Productivity Home Page, Oregon State
619 University, U.S. www.science.oregonstate.edu/ocean.productivity; 7) estimated from
620 monthly surface photosynthetic radiation (PAR; SeaWiFs): $PAR * \exp(K_{490} * \text{depth})$; 8)
621 NASA standard monthly data products from the Advanced Very High Resolution Radiometer
622 (AVHRR) Pathfinder V5 satellite; 9) calculated using an exponential decay model: $\text{flux}(\text{depth}) = 3.523 \times \text{NPP} \times \text{depth}^{-0.734}$ (Biggs et al, 2008; Pace et al, 1987). For more details
623 on the data and links for access refer to Huang *et al.* (2010) and Pitcher *et al.* (2012).

Variable	Description	Units	Reference
Bathy	Depth	m	1
Slope	Slope derived from bathymetry	°	1
Aspect	Aspect of slope derived from bathymetry	°T	1
StresSTMN	Trimmed mean of seabed current stress		2
StressIQR	Inter-quartile range of seabed current stress		2
Crbnt	Percentage of carbonates in sediment	%	3
Gravel	Percentage of gravel grainsize fraction in sediment	%	3
Sand	Percentage of sand grainsize fraction in sediment	%	3

Mud	Percentage of mud grainsize fraction in sediment	%	3
NO3 _{av}	Annual average of nitrate (bottom water)	μM	4
NO3 _{sr}	Seasonal range of nitrate (bottom water)		4
PO4 _{av}	Annual average of phosphate (bottom water)	μM	4
PO4 _{sr}	Seasonal range of phosphate (bottom water)		4
O2 _{av}	Annual average of oxygen (bottom water)	ml L ⁻¹	4
O2 _{sr}	Seasonal range of oxygen (bottom water)		4
S _{av}	Annual average of salinity (bottom water)	‰ (ppt)	4
S _{sr}	Seasonal range of salinity (bottom water)		4
T _{av}	Annual average of temperature (bottom water)	°C	4
T _{sr}	Seasonal range of temperature (bottom water)		4
SI _{av}	Annual average of silicate (bottom water)	μM	4
SI _{sr}	Seasonal range of silicates (bottom water)		4
Chla _{av}	Mean sea surface chlorophyll <i>a</i> concentration	mg .m ³	5
Chla _{sr}	Seasonal range of sea surface chlorophyll <i>a</i> concentration		5
K490 _{av}	Mean diffuse attenuation coefficient at wavelength 490nm	m ⁻¹	5
K490 _{sr}	Seasonal range of mean diffuse attenuation coefficient		5
PAR _{av}	Available surface of photosynthetic radiation	Einstein m ⁻² day ⁻¹	5
PAR _{sr}	Seasonal range of available surface photosynthetic radiation		5
VGPM _{av}	Annual average of net primary production	mg C m ⁻² d ⁻¹	6
VGPM _{sr}	Seasonal range of net primary production		6
BIR _{av}	Annual average of benthic irradiance		7
BIR _{sr}	Seasonal range of benthic irradiance		7
SST _{av}	Annual average of sea surface temperature	°C	8
SST _{sr}	Seasonal range of sea surface temperature		8
EPOC _{av}	Annual average of exported particulate organic carbon flux	mg C m ⁻² d ⁻¹	9
EPOC _{sr}	Seasonal range of exported particulate organic carbon flux		9

Table S2: Summary of models predicting fish species richness (S ; generalized linear models – GLM and generalized linear mixed-effect models – GLMM) to spatial and environmental properties for the Great Barrier Reef for the period: 2003 to 2007 as per Mellin *et al.* (2010). Note that in Mellin *et al.* (2010), S is referred to as “fish species richness”. Shown for each model are the biased-corrected model probabilities based on weights of Akaike’s information criterion corrected for small sample sizes ($wAIC_c$, only > 0.001 shown) and of the Bayesian information criteria ($wBIC$, only > 0.001 shown), the percentage of deviance explained (%De for GLM), the cross-validation error (CV_{error}), and both the marginal and conditional R^2 for GLMM (R^2_m and R^2_c) (Nakagawa & Schielzeth 2013). GLMM include reef as a random effect. Bold case indicates highest rankings from $wAIC_c$ for each model set.

Model	GLM				GLMM				
	$wAIC_c$	$wBIC$	%De/ R^2	CV_{error}	$wAIC_c$	$wBIC$	CV_{error}	R^2_m	R^2_c
1	1.000	1.000	58.1	8.6 ± 1.6	0.085	<0.001	15.5 ± 3.9	53.1	70.9
2	< 0.001	-	-	-	0.170	0.005	18.0 ± 4.1	29.9	72.3
4	< 0.001	-	-	-	0.027	0.010	11.3 ± 2.1	19.6	73.2
9	< 0.001	-	-	-	0.214	0.299	10.0 ± 2.0	23.1	73.3
10	< 0.001	-	-	-	0.021	0.008	16.8 ± 2.9	19.1	72.6
11	< 0.001	-	-	-	0.479	0.671	10.0 ± 2.1	25.0	73.6

Table S3: Summary of the best performing generalized linear mixed-effect models (GLMMs) and model-averaged predictions when predicting reef fish species richness (S) for the Great Barrier Reef (GBR). For each scenario (refer to Table 2 for details on each scenario), the biased-corrected model probabilities based on weights of Akaike's information criterion corrected for small sample sizes ($wAIC_c$), Bayesian information criteria ($wBIC$, only > 0.001 shown), marginal R^2 (R^2_m) and conditional R^2 (R^2_c) (Nakagawa, 2013), and the cross-validation error (CV_{error}) are reported. Model-averaged predictions obtained for each scenario when predicting to the GBR show the predicted range (Range) and the model-averaged cross-validation error (CV_{error_av}).

Scenario	Best model performance						Model-averaged predictions	
	Model	$wAIC_c$	$wBIC$	R^2_m	R^2_c	CV_{error}	Range (St Dev)	CV_{error_av}
A	11	0.479	0.671	25.0	73.6	10.0 ± 2.1	31.3 – 84.0 (0.98 – 6.16)	12.4 ± 2.6
B	2	0.636	0.049	32.7	72.4	18.4 ± 3.7	59.4 – 74.4 (1.49 – 3.37)	12.2 ± 2.4
C	11	0.654	0.871	27.4	77.1	11.6 ± 1.9	30.8 – 92.0 (0.71 – 2.00)	14.3 ± 2.6
D	11	0.615	0.858	26.6	76.4	11.3 ± 2.5	31.3 – 86.7 (0.75 – 1.84)	13.6 ± 2.5

E	11	0.681	0.841	23.1	71.0	8.5 ± 1.7	19.9 – 61.0 (0.50 – 1.29)	10.1 ± 2.1
	11	0.483	0.691	18.1	67.6	7.8 ± 1.5		
F	4	0.259	0.094	19.2	68.1	7.9 ± 1.5	21.2 – 50.5 (0.70 – 2.34)	8.9 ± 1.8
	10	0.398	0.510	31.6	83.0	10.1 ± 2.5		
G	1	0.366	< 0.001	57.5	83.8	20.9 ± 5.0	20.2 – 65.7 (1.76 – 17.9)	12.7 ± 2.6

Appendix S3: Supplementary Figures

Figure S1: Location of the sampling sites where fish data were collected at a) Ningaloo Reef (spanning $\sim 2^\circ$ latitude) and b) the Great Barrier Reef (spanning $\sim 15^\circ$ latitude) (from Mellin *et al.*, 2010). Numbers indicate locations for each latitudinal region; as per Mellin *et al.*, 2010).

645 Figure S2: Prediction maps of fish species richness (S) for the Great Barrier Reef and the period 2003 – 2007 obtained using our model
646 replicating Mellin *et al.* (2010) (i.e., scenario A) (left) and reproduced from Mellin *et al.* (2010) (right).

647 Figure S3: Model-averaged effect sizes for each predictor included in the generalized linear
648 model (GLM) developed for Ningaloo Reef (NR) and in the generalized linear mixed-effects
649 models (GLMM) developed for each scenario using data collected from the Great Barrier
650 Reef. For details on predictors and scenarios (A to G) refer to Table 1 and Table 2,
651 respectively.

652

Figure S4: Linear model of predicted fish species richness from the NR models versus observed values for Ningaloo Reef. Left: NR model using all species data sampled (S_{All}): $R^2=0.396$ and $p\text{-value} < 0.001$; Right: NR model using only species from the same 10 families sampled in the Great Barrier Reef (S_{10}): $R^2=0.437$ and $p\text{-value} < 0.001$.

657

658 **Appendix S4: References in supplementary information**

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684

685 **Appendix S5: List of fish species sampled on the Great Barrier Reef (GBR) and**
686 **Ningaloo Reef (NR). In the GBR only the following ten fish families were sampled:**
687 **Acanthuridae, Chaetodontidae, Labridae, Lethrinidae, Lutjanidae, Pomacentridae,**
688 **Scaridae, Serranidae, Siganidae, and Zaclidae. All rows including other families only**
689 **sampled in Ningaloo Reef are shown in grey.**

Family	Species	GBR	NR
Acanthuridae	<i>Acanthurus albipectoralis</i>	√	
	<i>Acanthurus auranticavus</i>	√	
	<i>Acanthurus bariene</i>	√	
	<i>Acanthurus blochii</i>	√	
	<i>Acanthurus dussumieri</i>	√	√
	<i>Acanthurus grammoptilus</i>	√	
	<i>Acanthurus lineatus</i>	√	
	<i>Acanthurus maculiceps</i>	√	
	<i>Acanthurus mata</i>	√	√
	<i>Acanthurus nigricans</i>	√	√
	<i>Acanthurus nigricauda</i>	√	
	<i>Acanthurus nigrofuscus</i>	√	
	<i>Acanthurus olivaceus</i>	√	√
	<i>Acanthurus pyroferus</i>	√	
	<i>Acanthurus thompsoni</i>	√	
	<i>Acanthurus triostegus</i>	√	√
	<i>Acanthurus xanthopterus</i>	√	
	<i>Ctenochaetus striatus</i>		√
	<i>Naso annulatus</i>		√
	<i>Naso fageni</i>		√
	<i>Naso lituratus</i>	√	√
	<i>Naso tuberosus</i>	√	
	<i>Naso unicornis</i>	√	√
	<i>Paracanthurus hepatus</i>	√	
	<i>Zebrasoma scopas</i>	√	√
	<i>Zebrasoma veliferum</i>	√	√
Apogonidae	<i>Apogon taeniophorus</i>		√
Aulostomidae	<i>Aulostomus chinensis</i>		√
Balistidae	<i>Pseudobalistes fuscus</i>		√
	<i>Rhinecanthus aculeatus</i>		√
	<i>Rhinecanthus rectangulus</i>		√
	<i>Sufflamen chrysopterum</i>		√
	<i>cf Platybelone argalus</i>		√
Belonidae	<i>Tylosurus crocodiles</i>		√
	<i>Aspidontus taeniatus</i>		√

Carangidae	<i>Meiacanthus grammistes</i>	√
	<i>Carangoides ferdau</i>	√
	<i>Carangoides fulvoguttatus</i>	√
	<i>Caranx ignobilis</i>	√
Carcharhinidae	<i>Gnathanodon speciosus</i>	√
	<i>Carcharhinus amblyrhynchos</i>	√
	<i>Carcharhinus melanopterus</i>	√
	<i>Triaenodon obesus</i>	√
Chaetodontidae	<i>Chaetodon adiergastos</i>	√
	<i>Chaetodon andamanensis</i>	√
	<i>Chaetodon assarius</i>	√
	<i>Chaetodon aureofasciatus</i>	√ √
	<i>Chaetodon auriga</i>	√ √
	<i>Chaetodon baronessa</i>	√ √
	<i>Chaetodon bennetti</i>	√
	<i>Chaetodon citrinellus</i>	√ √
	<i>Chaetodon ephippium</i>	√ √
	<i>Chaetodon flavirostris</i>	√
	<i>Chaetodon interruptus</i>	√
	<i>Chaetodon kleinii</i>	√ √
	<i>Chaetodon lineolatus</i>	√ √
	<i>Chaetodon lunula</i>	√ √
	<i>Chaetodon melannotus</i>	√ √
	<i>Chaetodon mertensii</i>	√
	<i>Chaetodon meyeri</i>	√
	<i>Chaetodon ornatissimus</i>	√ √
	<i>Chaetodon oxycephalus</i>	√
	<i>Chaetodon pelewensis</i>	√ √
	<i>Chaetodon plebeius</i>	√ √
	<i>Chaetodon punctatofasciatus</i>	√ √
	<i>Chaetodon rafflesia</i>	√
	<i>Chaetodon rainfordi</i>	√
	<i>Chaetodon reticulatus</i>	√
	<i>Chaetodon speculum</i>	√ √
	<i>Chaetodon trifascialis</i>	√ √
	<i>Chaetodon trifasciatus</i>	√ √
	<i>Chaetodon ulietensis</i>	√ √
	<i>Chaetodon unimaculatus</i>	√ √
	<i>Chaetodon vagabundus</i>	√ √
	<i>Chelmon marginalis</i>	√
	<i>Chelmon rostratus</i>	√
	<i>Forcipiger flavissimus</i>	√
	<i>Forcipiger longirostris</i>	√
	<i>Hemitaurichthys polylepis</i>	√
	<i>Heniochus acuminatus</i>	√

Chanidae	<i>Chanos chanos</i>	✓
Cirrhitidae	<i>Cirrhitidae</i> spp	✓
Dasyatidae	<i>Taeniura lymma</i>	✓
Diodontidae	<i>Diodon hystrix</i>	✓
Echeneidae	<i>Remora</i> spp	✓
Ephippidae	<i>Platax teira</i>	✓
Fistulariidae	<i>Fistularia commersonnii</i>	✓
	<i>Fistularia petimba</i>	✓
Ginglymostomatidae	<i>Nebrius ferrugineus</i>	✓
Gobiidae	<i>Amblygobius phalaena</i>	✓
	<i>Valenciennesa longipinnis</i>	✓
Haemulidae	<i>Diagramma pictum</i>	✓
	<i>Plectorhinchus chaetodonoides</i>	✓
	<i>Plectorhinchus flavomaculatus</i>	✓
	<i>Plectorhinchus multivittatus</i>	✓
Hemiramphidae	<i>Hyporhamphus dussumieri</i>	✓
Hemiscylliidae	<i>Hemiscyllium ocellatum</i>	✓
Kyphosidae	<i>Kyphosus bigibbus</i>	✓
	<i>Kyphosus cornelii</i>	✓
	<i>Kyphosus sydneyanus</i>	✓
	<i>Kyphosus vaigiensis</i>	✓
Labridae	<i>Anampses caeruleopunctatus</i>	✓
	<i>Anampses geographicus</i>	✓
	<i>Anampses lennardi</i>	✓
	<i>Anampses meleagrides</i>	✓
	<i>Bodianus bilineatus</i>	✓
	<i>Bodianus bilunulatus</i>	✓
	<i>Cheilinus chlorourus</i>	✓
	<i>Cheilinus fasciatus</i>	✓ ✓
	<i>Cheilinus trilobatus</i>	✓
	<i>Cheilinus undulatus</i>	✓
	<i>Cheilio inermis</i>	✓
	<i>Choerodon cauteroma</i>	✓
	<i>Choerodon cyanodus</i>	✓
	<i>Choerodon fasciatus</i>	✓
	<i>Choerodon monostigma</i>	✓
	<i>Choerodon rubescens</i>	✓
	<i>Choerodon schoenleinii</i>	✓
	<i>Coris aygula</i>	✓
	<i>Coris caudimacula</i>	✓
	<i>Coris dorsomacula</i>	✓
	<i>Coris gaimard</i>	✓
	<i>Diproctacanthus xanthurus</i>	✓
	<i>Epibulus insidiator</i>	✓ ✓
	<i>Gomphosus varius</i>	✓ ✓

	<i>Halichoeres biocellatus</i>		✓
	<i>Halichoeres hortulanus</i>	✓	✓
	<i>Halichoeres lamarii</i>		✓
	<i>Halichoeres marginatus</i>		✓
	<i>Halichoeres nebulosus</i>		✓
	<i>Halichoeres richmondi</i>		✓
	<i>Halichoeres trimaculatus</i>		✓
	<i>Hemigymnus fasciatus</i>	✓	✓
	<i>Hemigymnus melapterus</i>	✓	✓
	<i>Hologymnosus annulatus</i>		✓
	<i>Labrichthys unilineatus</i>		✓
	<i>Labroides dimidiatus</i>		✓
	<i>Novaculichthys taeniourus</i>		✓
	<i>Stethojulis bandanensis</i>		✓
	<i>Thalassoma hardwicke</i>		✓
	<i>Thalassoma lunare</i>		✓
	<i>Thalassoma lutescens</i>		✓
	<i>Psammoperca waigiensis</i>		✓
Lethrinidae	<i>Lethrinus atkinsoni</i>	✓	✓
	<i>Lethrinus erythracanthus</i>	✓	
	<i>Lethrinus harak</i>	✓	
	<i>Lethrinus laticaudis</i>	✓	
	<i>Lethrinus lentjan</i>	✓	
	<i>Lethrinus miniatus</i>	✓	
	<i>Lethrinus nebulosus</i>	✓	✓
	<i>Lethrinus obsoletus</i>	✓	✓
	<i>Lethrinus olivaceus</i>	✓	
	<i>Lethrinus ornatus</i>	✓	
	<i>Lethrinus rubrioperculatus</i>	✓	
	<i>Lethrinus semicinctus</i>	✓	
	<i>Lethrinus xanthochilus</i>	✓	
	<i>Monotaxis grandoculis</i>	✓	
Lutjanidae	<i>Lutjanus adetii</i>	✓	
	<i>Lutjanus argentimaculatus</i>	✓	
	<i>Lutjanus biguttatus</i>	✓	
	<i>Lutjanus bohar</i>	✓	✓
	<i>Lutjanus bouton</i>	✓	
	<i>Lutjanus carponotatus</i>	✓	✓
	<i>Lutjanus decussatus</i>		✓
	<i>Lutjanus fulviflammus</i>	✓	✓
	<i>Lutjanus fulvus</i>	✓	✓
	<i>Lutjanus gibbus</i>	✓	✓
	<i>Lutjanus kasmira</i>	✓	
	<i>Lutjanus lemniscatus</i>	✓	✓
	<i>Lutjanus lutjanus</i>	✓	

	<i>Lutjanus monostigma</i>	√	
	<i>Lutjanus quinquelineatus</i>	√	
	<i>Lutjanus rivulatus</i>	√	
	<i>Lutjanus russellii</i>	√	
	<i>Lutjanus sebae</i>	√	
	<i>Lutjanus semicinctus</i>	√	
	<i>Lutjanus vitta</i>	√	√
	<i>Symphorus nematophorus</i>		√
Monacanthidae	<i>Aluterus scriptus</i>		√
	<i>Cantherhines fronticinctus</i>		√
	<i>Oxymonacanthus longirostris</i>		√
Mullidae	<i>Mulloidichthys flavolineatus</i>		√
	<i>Mulloidichthys vanicolensis</i>		√
	<i>Parupeneus barberinoides</i>		√
	<i>Parupeneus barberinus</i>		√
	<i>Parupeneus crassilabris</i>		√
	<i>Parupeneus cyclostomus</i>		√
	<i>Parupeneus indicus</i>		√
	<i>Parupeneus macronemus</i>		√
	<i>Parupeneus multifasciatus</i>		√
	<i>Parupeneus pleurostigma</i>		√
	<i>Parupeneus signatus</i>		√
	<i>Parupeneus spilurus</i>		√
	<i>Parupeneus trifasciatus</i>		√
	<i>Upeneus tragula</i>		√
Nemipteridae	<i>Pentapodus vitta</i>		√
	<i>Scolopsis bilineata</i>		√
Odontaspidae	<i>Carcharias taurus</i>		√
Orectolobidae	<i>Orectolobus wardi</i>		√
Ostraciidae	<i>Ostracion cubicus</i>		√
	<i>Ostracion meleagris</i>		√
Pempheridae	<i>Pempheris spp</i>		
Pinguipedidae	<i>Parapercis clathrata</i>		√
Plotosidae	<i>Paraplotosus butleri</i>		√
	<i>Plotosus lineatus</i>		√
Pomacanthidae	<i>Centropyge eibli</i>		√
	<i>Centropyge tibicen</i>		√
	<i>Pomacanthus semicirculatus</i>		√
	<i>Pomacanthus sexstriatus</i>		√
Pomacentridae	<i>Abudefduf bengalensis</i>		√
	<i>Abudefduf septemfasciatus</i>		√
	<i>Abudefduf sexfasciatus</i>		√
	<i>Abudefduf vaigiensis</i>		√
	<i>Acanthochromis polyacanthus</i>	√	
	<i>Amblyglyphidodon aureus</i>	√	

<i>Amblyglyphidodon curacao</i>	√	
<i>Amblyglyphidodon leucogaster</i>	√	
<i>Amphiprion akindynos</i>	√	
<i>Amphiprion chrysopterus</i>	√	
<i>Amphiprion clarkii</i>	√	
<i>Amphiprion melanopus</i>	√	
<i>Amphiprion percula</i>	√	
<i>Amphiprion perideraion</i>	√	
<i>Amphiprion rubrocinctus</i>		√
<i>Cheiloprion labiatus</i>	√	√
<i>Chromis acares</i>	√	
<i>Chromis agilis</i>	√	
<i>Chromis amboinensis</i>	√	
<i>Chromis atripectoralis</i>	√	√
<i>Chromis atripes</i>	√	
<i>Chromis chrysur</i>	√	
<i>Chromis cinerascens</i>		√
<i>Chromis flavomaculata</i>	√	
<i>Chromis iomelas</i>	√	
<i>Chromis lepidolepis</i>	√	
<i>Chromis lineata</i>	√	
<i>Chromis margaritifer</i>	√	
<i>Chromis nitida</i>	√	
<i>Chromis retrofasciata</i>	√	
<i>Chromis ternatensis</i>	√	
<i>Chromis vanderbilti</i>	√	
<i>Chromis viridis</i>	√	√
<i>Chromis weberi</i>	√	
<i>Chromis xanthochira</i>	√	
<i>Chromis xanthura</i>	√	
<i>Chrysiptera biocellata</i>	√	
<i>Chrysiptera flavipinnis</i>	√	
<i>Chrysiptera hemicyanea</i>		√
<i>Chrysiptera rex</i>	√	
<i>Chrysiptera rollandi</i>	√	
<i>Chrysiptera talboti</i>	√	
<i>Dascyllus aruanus</i>		√
<i>Dascyllus aruanus</i>	√	
<i>Dascyllus melanurus</i>	√	
<i>Dascyllus reticulatus</i>	√	√
<i>Dascyllus trimaculatus</i>	√	√
<i>Dischistodus melanotus</i>	√	
<i>Dischistodus perspicillatus</i>	√	√
<i>Dischistodus prosopotaenia</i>	√	√
<i>Dischistodus</i>	√	

	<i>pseudochrysopoecilus</i>		
	<i>Hemiglyphidodon plagiometopon</i>	√	√
	<i>Neoglyphidodon melas</i>	√	√
	<i>Neoglyphidodon nigroris</i>	√	√
	<i>Neoglyphidodon polyacanthus</i>	√	
	<i>Neopomacentrus azysron</i>	√	
	<i>Neopomacentrus bankieri</i>	√	
	<i>Neopomacentrus cyanomos</i>	√	
	<i>Neopomacentrus filamentosus</i>		√
	<i>Plectroglyphidodon lacrymatus</i>		√
	<i>Plectroglyphidodon dickii</i>	√	√
	<i>Plectroglyphidodon johnstonianus</i>	√	√
	<i>Plectroglyphidodon lacrymatus</i>	√	√
	<i>Plectroglyphidodon leucozonus</i>		√
	<i>Pomacentrus adelus</i>	√	√
	<i>Pomacentrus alexanderae</i>		√
	<i>Pomacentrus amboinensis</i>	√	√
	<i>Pomacentrus australis</i>	√	
	<i>Pomacentrus bankanensis</i>	√	
	<i>Pomacentrus brachialis</i>	√	
	<i>Pomacentrus chrysurus</i>	√	
	<i>Pomacentrus coelestis</i>	√	√
	<i>Pomacentrus grammorhynchus</i>	√	
	<i>Pomacentrus imitator</i>	√	
	<i>Pomacentrus lepidogenys</i>	√	
	<i>Pomacentrus moluccensis</i>	√	
	<i>Pomacentrus nagasakiensis</i>	√	
	<i>Pomacentrus nigromarginatus</i>	√	
	<i>Pomacentrus philippinus</i>	√	
	<i>Pomacentrus vaiuli</i>	√	√
	<i>Pomacentrus wardi</i>	√	
	<i>Pomachromis richardsoni</i>	√	
	<i>Premnas biaculeatus</i>	√	
	<i>Stegastes apicalis</i>	√	
	<i>Stegastes fasciolatus</i>	√	√
	<i>Stegastes gascoynei</i>	√	
	<i>Stegastes nigricans</i>	√	√
Pseudochromidae	<i>Labracinus lineatus</i>		√
	<i>Pseudochromis fuscus</i>		√
Rachycentridae	<i>Rachycentron canadum</i>		√
Scaridae	<i>Bolbometopon muricatum</i>	√	
	<i>Calotomus carolinus</i>	√	
	<i>Cetoscarus bicolor</i>	√	
	<i>Chlorurus bleekeri</i>	√	

	<i>Chlorurus frontalis</i>	√	
	<i>Chlorurus japanensis</i>	√	
	<i>Chlorurus microrhinos</i>	√	√
	<i>Chlorurus schlegeli</i>		√
	<i>Chlorurus sordidus</i>	√	√
	<i>Hipposcarus longiceps</i>	√	√
	<i>Leptoscarus vaigiensis</i>		√
	<i>Scarus altipinnis</i>	√	
	<i>Scarus chameleon</i>	√	√
	<i>Scarus dimidiatus</i>	√	√
	<i>Scarus flavipectoralis</i>	√	
	<i>Scarus forsteni</i>	√	
	<i>Scarus frenatus</i>	√	√
	<i>Scarus ghobban</i>	√	√
	<i>Scarus globiceps</i>	√	√
	<i>Scarus longipinnis</i>	√	
	<i>Scarus niger</i>	√	√
	<i>Scarus oviceps</i>	√	√
	<i>Scarus prasiognathos</i>		√
	<i>Scarus psittacus</i>	√	√
	<i>Scarus quoyi</i>		√
	<i>Scarus rivulatus</i>	√	√
	<i>Scarus rubroviolaceus</i>	√	√
	<i>Scarus schlegeli</i>	√	√
	<i>Scarus spinus</i>	√	
Scorpaenidae	<i>Pterois volitans</i>		√
Serranidae	<i>Cephalopholis argus</i>		√
	<i>Cephalopholis miniata</i>		√
	<i>Cromileptes altivelis</i>		√
	<i>Epinephelus bilobatus</i>		√
	<i>Epinephelus polyphekadion</i>		√
	<i>Epinephelus rivulatus</i>		√
	<i>Plectropomus areolatus</i>	√	
	<i>Plectropomus laevis</i>	√	
	<i>Plectropomus leopardus</i>	√	
	<i>Plectropomus maculatus</i>	√	√
	<i>Variola albimarginata</i>	√	
	<i>Variola louti</i>	√	
Siganidae	<i>Siganus argenteus</i>	√	√
	<i>Siganus canaliculatus</i>		√
	<i>Siganus corallinus</i>	√	
	<i>Siganus doliatus</i>	√	
	<i>Siganus fuscescens</i>	√	
	<i>Siganus guttatus</i>		√
	<i>Siganus javus</i>	√	

	<i>Siganus lineatus</i>	✓	✓
	<i>Siganus nebulosus</i>		✓
	<i>Siganus puellus</i>	✓	
	<i>Siganus punctatissimus</i>	✓	
	<i>Siganus punctatus</i>	✓	
	<i>Siganus spinus</i>	✓	
	<i>Siganus trispilos</i>		✓
	<i>Siganus virgatus</i>		✓
	<i>Siganus vulpinus</i>	✓	
Sphyraenidae	<i>Sphyraena jello</i>		✓
Synodontidae	<i>Saurida gracilis</i>		✓
Tetraodontidae	<i>Arothron hispidus</i>		✓
	<i>Arothron stellatus</i>		✓
	<i>Canthigaster coronata</i>		✓
	<i>Canthigaster rivulata</i>		✓
	<i>Canthigaster valentini</i>		✓
Zanclidae	<i>Zanclus cornutus</i>	✓	✓

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