**Predictive mapping of reproductive fish habitats to aid
marine conservation planning**

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1 **Title:** Predictive mapping of reproductive fish habitats to aid marine conservation planning

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22 **Keywords:** fecundity, spawning biomass, larval subsidy, marine protected area, GAMLSS

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24 **Abstract**

25 Post-settlement spillover from marine protected areas (MPAs) can support adjacent fished
26 populations and has been subject of many scientific studies. The larval subsidy effect, on the
27 contrary, is more challenging to study and less demonstrated although it, arguably, provides
28 key benefits for fisheries. We modeled and predicted the spatial distribution of fish spawning
29 biomass and fecundity across a temperate insular MPA network (Azores archipelago,
30 Northeast Atlantic) and identified potential single and multi-species reproductive habitats
31 (RHs) in shallow reefs. Reproductive strategies or skewed sex ratios influenced spatial
32 patterns of potential spawning biomass and fecundity. Predicted multi-species RHs covered
33 5-20% of the studied reef habitat. Given their potentially high reproductive output we argue
34 that such sites should be considered in marine conservation planning to increase chances of
35 achieving fisheries and conservation benefits. Spatial patterns of the reproductive output may
36 function as surrogates for larval subsidy when limited or no larval connectivity information is
37 available and assist in identifying potential larval sources and priority sites for conservation.

38 Introduction

39 Well planned marine protected areas (MPAs) and especially marine reserves (MRs) can
40 replenish fish populations by enhancing fish abundance, size, and biodiversity within their
41 boundaries (Halpern 2003; McCook et al. 2010; Kelaher et al. 2014). Fisheries then may
42 benefit from a subsequent spillover of juvenile or adult fish (spillover effect), and from larval
43 dispersal (larval subsidy effect) to adjacent, fished areas (Goñi et al. 2008; Planes et al. 2009;
44 Pelc et al. 2010). The dispersal of early life history stages of fishes, pelagic eggs and larvae,
45 is affected by a variety of biotic, abiotic and physical factors, such as pelagic larval duration
46 (PLD), food availability, predation, swimming abilities, and transport by ocean currents (e.g.,
47 Pineda et al. 2007; Di Franco et al. 2012; Andrello et al. 2015; Koeck et al. 2015). Larvae can
48 be retained locally, close to the natal population, or are dispersed to more distant locations, up
49 to several hundred kilometers (Berumen et al. 2012; Di Franco et al. 2012; Trembl et al. 2012;
50 Thomas et al. 2014). Various factors then affect the recruitment success, such as larval
51 behavior, habitat choice (and availability) at settlement, and post-settlement survival (Pineda
52 et al. 2007; White and Caselle 2008; Felix-Hackradt et al. 2013; Soeparno et al. 2013).

53 Larval subsidy and settler abundance, however, will depend on the reproductive potential of
54 the adult fish population in the first place. This, in turn, is determined by the magnitude of the
55 reproductive output or the spawning biomass, with older, large-sized specimens generally
56 producing more and better eggs (Berkeley et al. 2004). Protecting mature adults may enhance
57 the reproductive output and the potential larval subsidy to adjacent habitats (Birkeland and
58 Dayton 2005; Pelc et al. 2010; Trembl et al. 2012). The extent of realized larval dispersal and
59 the degree of connectivity in fish populations will largely determine if a MPA network can
60 effectively promote fishery yields and sustainability (Sale et al. 2005; Botsford et al. 2009;
61 D'Aloia et al. 2015).

62 Most empirical studies focus on adult or juvenile spillover and migration across MPA
63 boundaries (e.g., Goñi et al. 2008, Harmelin-Vivien et al. 2008, Afonso et al. 2009), whereas
64 measuring larval connectivity and integrating it into MPA design remains challenging (Sale
65 et al. 2005; Lagabriele et al. 2014; D'Aloia et al. 2015). Nevertheless, different methods exist
66 to estimate connectivity, and progress in recent years has shown local and large-scale larval
67 seeding between MPAs and unprotected sites (e.g., Planes et al. 2009; Christie et al. 2010; Di
68 Franco et al. 2012; Harrison et al. 2012). The use of 'connectivity surrogates' has been
69 proposed as alternative for incorporating connectivity in conservation planning when other
70 information or direct measurements on larval dispersal patterns are absent (Bode et al. 2012).
71 Surrogates reflect easy measurable characteristics of reef communities, such as the spawning
72 biomass of fishes that outperformed surrogates based on physical dimensions of reefs (Bode
73 et al. 2012). Considering habitats with a great amount of a given surrogate in MPA site
74 selection processes may support connectivity, although using surrogates will never be as
75 accurate as incorporating measured connectivity patterns.

76 An effective spatial management requires solid information about the spatial distribution of
77 species, habitats and other ecological/biological/socio-economic features (Klein et al. 2008;
78 Green et al. 2009; Costello et al. 2010). Often such information only exists for a few sampled
79 locations and statistical modelling techniques are applied to predict the distribution also in
80 non-surveyed areas. Resulting predictive maps can then be used to evaluate existing MPA
81 networks and assist site selection (Sundblad et al. 2011; Schmiing et al. 2015), if modelling
82 techniques are thoroughly implemented and in concordance with statistical assumptions
83 (Schmiing et al. 2014b).

84 MPAs have been established worldwide, for example to preserve biodiversity, prevent
85 ecosystem degradation, and as additional fisheries management tool (Russ 2002; Botsford et
86 al. 2009; McCook et al. 2010). First MPAs were established in the 1980's to manage marine

resources in the Azores, the most isolated archipelago of nine islands in the Northeast Atlantic (Santos et al. 1995; Abecasis et al. 2015b). Since then, several advances in marine conservation took place, including EU-driven initiatives, and today exists 1) a network of nine Island Natural Parks (INPs) that include all terrestrial and coastal MPAs within the territorial sea (12 NM), and 2) the Azorean Marine Park, including all MPAs outside territorial waters (Calado et al. 2009, 2011; Abecasis et al. 2015b). Although these MPAs have strengths (e.g. establishment considered pioneer, involvement of scientific community, and legal requirement for stakeholder consultation), their design is largely inadequate, very few no-take areas exist, management plans are missing, low recourses for enforcement are available, and community involvement and public outreach is weak (Calado et al. 2011; Abecasis et al. 2015b).

In the present study we quantify spatial patterns of the reproductive potential of eight common reef fish species through predictive modeling of spawning biomass and potential fecundity, using the Azores archipelago as case study. We focus on species with no known movements between habitats during the reproductive season. In particular, we (1) produce predictive maps of both reproductive metrics, (2) compare single- and multi-species spatial patterns, (3) identify sites with potentially high reproductive output, (4) analyze the significance of these potential reproductive habitats (RHs) for the existing MPA network, and (5) discuss the use of both metrics as ‘conservation surrogates’ in marine spatial management if data on connectivity patterns are absent. Results are expected to deliver new strategies in support of marine conservation planning.

108

109 **Material and Methods**

110 *Study site and fish counts*

The study area comprises shallow coastal habitats down to the 40m isobath around Faial and West Pico Islands, Azores, Northeast Atlantic (Fig. 1). Despite the limited geographic extent the study area encompasses a wide range of environmental conditions, such as sheltered bays, exposed coasts, offshore reefs, sandy bottoms, and a large variety of rocky substratum, including bedrock reefs, boulder fields, cliffs, and submerged volcanic cones, that covers more than half of the area (59%, 34 km²) (Tempera et al. 2012). Detailed descriptions, habitat maps, environmental, and ecological information are available from previous studies (Santos et al. 1995; Tempera 2008; Tempera et al. 2012; Schmiing et al. 2013, 2014b).

Faial and Pico have designated Island Natural Parks (INPs), comprising terrestrial and marine protected areas (Calado et al. 2009) of which six coastal MPAs lie (partly) in the study area. These MPAs cover about 60% of the study area and encompass most of the rocky substrate (22 km² out of 34 km²). Regulations regarding extractive activities are not uniform and vary from no limitations to prohibition of a certain fishing activity. Only a single, small no-take reserve exists (8 ha) at the south-east tip of Faial. However, MPA compliance and enforcement are poor (Abecasis et al. 2015b, Diogo et al. 2015), and positive MPA effects are widely missing (Schmiing et al. 2014a; Afonso et al., unpubl. data), thus no differentiation is made between the protection levels of the MPAs for the purpose of the present study.

Reef fish assemblages were surveyed between 1997 and 2004 with a total of 462 underwater visual fish censuses (UVCs) along 50 x 5 m SCUBA dive transects, using a random stratified sampling design. Transects were parallel to the coast to stay within the same depth and habitat strata (i.e. 10m depth increments, and rock or sediment) (see Schmiing et al. 2013 for a detailed description). Fish were identified, counted, grouped into species-specific size classes (small, medium, large, very large; Morato et al. 2001), and the sex was determined whenever possible. A mean length in cm was assigned to the individual size classes of each

species, using data from local populations (Morato et al. 2001). For the purpose of the present study, all individuals of the size classes medium to very large were defined as mature. In a next step, spawning biomasses (W_s , i.e. total biomass of mature individuals) of *Abudefduf luridus*, *Coris julis*, *Diplodus sargus*, *Labrus bergylta*, *Sarpa salpa*, *Serranus atricauda*, *Sparisoma cretense* and *Symphodus caeruleus* were estimated via species-specific length-weight relationships (Morato et al. 2001). Furthermore, the total potential fecundity (i.e. number of oocytes; F_p) of mature females of *D. sargus*, *L. bergylta*, *S. atricauda*, *S. cretense* were calculated per transect, using published fecundity equations (Table 1). For this purpose, the number of females of species with unidentified sex was estimated via sex ratios from local populations, whenever possible per size class (Morato et al. 2003; unpubl. data). Study species were chosen based on their ecological and/or commercial importance for rocky reefs in the Azores (Schmiing et al. 2013) and their contrasting reproductive strategies. *D. sargus* is a digynic hermaphrodite (Morato et al. 2003), *S. atricauda* is a simultaneous hermaphrodite (García-Díaz et al. 2002), *S. cretense* is essentially gonochoristic with a prematurational sex-change (de Girolamo et al. 1999), and *L. bergylta* is a protogynous hermaphrodite (Dipper and Pullin 1979) and the only of the four species used for F_p estimations that lays its demersal eggs into algae nests (Artüz 2005) (Table 1). Spawning periods are typically in summer, except for *L. bergylta* (winter; Villegas-Ríos et al. 2014) and *D. sargus* (spring/beginning of summer; Morato et al. 2003). No large scale migrations across reefs for aggregating in high numbers at a given place and time (i.e. spawning aggregations) are known for any of the species. They all are benthic fishes, have small to medium home ranges/yearly displacement, and the majority is territorial (Claudet et al. 2010).

158

159 *Predictive models*

Only fish counts from the main sampling period ('summer' months, June to November, 354 transects) were used for model building (i.e. model fitting data set) to account for an unequal seasonal sampling effort. Eleven environmental variables were available for modeling the spawning biomass and potential fecundity of reef fishes, including depth, slope, slope of the slope (Pittman et al. 2009), distance to coast, main bottom type (sediment or rock), distance to nearest sediment, distance to nearest rock, ruggedness, exposure to currents, exposure to ocean swell, and concentration of Chlorophyll a (see Table 2 in Schmiing et al. 2013). Accurate data exploration, following Zuur et al. (2007, 2010), was applied to the model fitting data set and included analyses of homogeneity, potential outliers, Cleveland dotplots, pairplots, boxplots and frequency plots. Spatial independency was evaluated with variograms but only for shorter distances (<1000 m) to avoid possible land intersections. Variance Inflation Factor (VIF) analysis and Spearman rank correlations were used to test (multi)collinearity, while (stepwise) removing variables with a VIF higher than 3 and pairwise correlations of $\rho < -0.5$ and > 0.5 . Data exploration resulted in a final set of five explanatory variables: 1) depth - mean transect depth in meters, measured *in situ*; 2) slope - mean seafloor steepness in degrees, estimated via a bathymetric grid in a geographic information system (GIS); 3) distance to sediment - mean distance in meters to the nearest soft bottom as estimated in a GIS; (4) exposure to current - relative exposure derived from a shallow-water oceanographic current model (percentage of the maximum; Tempera 2008; Tempera et al. 2012); and 5) exposure to swell - relative exposure derived from a GIS-based fetch analysis (percentage of the maximum; Tempera 2008; Tempera et al. 2012). Distance to sediment was log transformed (base 10, adding the constant 1 because of zero values) and exposure to current square root transformed because data exploration revealed extreme observations and non-normality. A detailed description of the environmental variables and the data exploration is given in Schmiing et al. (2013).

185 We used generalized additive models for location, scale and shape (GAMLSS, gamlss
186 package, version 4.1-2; Rigby and Stasinopoulos 2005) with a zero adjusted gamma
187 distribution (ZAGA) to model the (non-linear) relationship between the response and
188 environmental variables. This distribution is appropriate for modeling response variables with
189 positive values but also admits zeros. It is a three parameter distribution (μ , σ , ν) for
190 which we first modeled μ (mean of the response variable) and then ν (probabilities at zero)
191 as a function of the environmental variables while applying stepwise backward model
192 selection based on the minimization of the Aikake's Information Criterion (AIC) and
193 Schwarz Bayesian Criterion (SBC). As a result, the μ and ν parameter may have different
194 combinations of environmental variables. It was not necessary to model the σ parameter
195 for any response variable. We used penalized b-splines (Eilers and Marx 1996) that
196 automatically estimated the smoothing parameter and thus the degrees of freedom via
197 Maximum Likelihood. Variable selection and smoother estimates were confirmed with
198 graphical analyses and smoothers that constantly included zero in the confidence interval
199 were excluded (Wood and Augustin 2002). If smoothers indicated a straight line, parametric
200 terms were used in the GAMLSS instead of smoothing functions.

201 No GAMLSS could be produced for the spawning biomass of *L. bergylta*, *S. atricauda*, and
202 *S. caeruleus* because model validation revealed violation of underlying statistical
203 assumptions (i.e. residual patterns and heterogeneity, see below). Consequently, data were
204 transformed to presence-absence of mature individuals and generalized additive models
205 (GAMs) with a binomial error distribution, thin plate regression splines and automatic
206 smoothness selection were applied (mgcv package, version 1.5-5; Wood 2004). To avoid
207 potential overfitting, the upper limit of the degrees of freedom associated with a smooth term
208 was fixed, if applicable (i.e. explanatory variable current in GAMs of *L. bergylta* and *S.*
209 *cretense*).

Model validation considered i) the graphical analyses of residuals, including density plots, normal Q-Q plots, worm plots (detrended QQ plots; van Buuren and Fredriks 2001), detrended transformed Owen's plot (dtop; Owen 1995), and plots of residuals *versus* fitted values, each predictor, and spatial coordinates; ii) summary statistics of residuals (mean, variance, skewness, kurtosis, and Filliben correlation coefficient; Rigby and Stasinopoulos 2005; Stasinopoulos and Rigby 2007); and iii) calculation of receiver operating characteristic (ROC) curves and the area under the curve (AUC) for binomial models. Potential outliers, as revealed by model validation, were removed and the modeling process was repeated, if applicable. In addition, winter data (December to May, 108 transects) from the same study area and sampling period were used as validation data set to test the model generality, after applying a Mann-Whitney-test to examine differences between winter and summer data (Schmiing et al. 2013). The Spearman's rank correlation (Rho) between predicted and observed values was calculated for the model fitting and validation data set. All analyses were performed with the software R (version 2.14.1; R Development Core Team 2011).

Spatial patterns of the reproductive potential

Validation of the final models was positive and thus results were used to predict the spawning biomass (Ws) and potential fecundity (Fp) over the entire study area on a 5m grid for each species. Results were imported into a GIS (ArcGIS 10 ©ESRI) for visualization and further analyses. Predicted values of continuous response variables (ZAGA GAMLSS) were set i) equal to the maximum observed value of biomass or fecundity if this was exceeded (i.e. to mitigate possible overestimation), or ii) to zero if they were lower than the minimum observed fecundity or, respectively, the minimum weight of a single medium sized individual (i.e. to mitigate possible underestimation). Values were then converted to a relative scale (the ratio of a given predicted value to the maximum prediction) to compare individual species

with different reproductive strategies (adapted from Schmiing et al. 2013). Predictions of binomial models were on a logit scale from 0 to 1. There are different approaches for determining thresholds that convert the probabilities to presence/absence. We used the ‘equal sensitivity and specificity’ approach that has been shown to achieve good results (Liu et al. 2005), acknowledging that the choice is essentially arbitrary. This approach finds the threshold where positive observations are just as likely to be wrong as negative observations. We 1) identified areas containing a minimum of 1%, 10%, 25% and 50% of the maximum predicted spawning biomass (Ws_1 , Ws_{10} , Ws_{25} , Ws_{50}) or potential fecundity (Fp_1 , Fp_{10} , Fp_{25} , Fp_{50}) of each species (adapted from Schmiing et al. 2013), and 2) calculated the percentage of rocky reef habitat that was potentially suitable for these four different target levels of Ws and Fp (‘single-species reproductive habitats’, RH). Results of binomial models (GAM) were integrated in this analysis by identifying areas where the probability of occurrence was higher than the species-specific threshold. Finally, we calculated the representativeness of these areas in the existing MPA network (i.e. percentage integrated).

In addition, we identified ‘multi-species RHs’ as areas where the reproductive metrics had overlapping high-values: $Ws_{com/all}$ RHs have a minimum of 10% relative spawning biomass only of commercial species (‘com’) or commercial and non-commercial species (‘all’), respectively. Fp_{com} RHs consider areas with a minimum of 10% relative potential fecundity of commercial species (adapted from Schmiing et al. 2013). Multi-species RHs were either fisheries related and considered the spawning biomass and potential fecundity of the four commercial species (*D. sargus*, *L. bergylta*, *S. atricauda*, *S. cretense*) (Ws_{com} and Fp_{com} RHs) or considered the predicted spawning biomass of all eight species to analyze the protection of (fish) biodiversity (Ws_{all} RHs). Predictions for binomial models (the occurrence of mature *L. bergylta* and *S. cretense*) were included by selecting all sites with a predicted probability above the species-specific identified threshold that overlapped with Ws_{10} . We calculated the

amount of rocky reef habitat potentially suitable as multi-species RH and evaluated the representativeness of these sites by calculating their percentage inside the existing MPA network. We acknowledge that any definition of potential RHs is arbitrary and other criteria or thresholds may be reasonable too.

Results

Predictive models

We modeled the potential spawning biomass of five species (*A. luridus*, *C. julis*, *D. sargus*, *S. salpa*, *S. atricauda*), the probability of occurrence of mature individuals of three species (*L. bergylta*, *S. cretense*, *S. caeruleus*), and the potential fecundity of mature females of four commercial species (*D. sargus*, *L. bergylta*, *S. atricauda*, *S. cretense*) (see online supplementary material, Table S1¹). Final models complied with central statistical assumptions (i.e. model residuals did not show any patterns, heterogeneity, or dependence, and were approximately normally distributed) as indicated by plots and summary statistics (not shown). The average correlation between predicted and observed values of the model building and validation data set, respectively, was higher than 0.5, indicating reasonable robust model fitting and generalization (online supplementary material, Table S2¹). A significant difference between group medians of the model fitting and validation data set (i.e. lower values in winter) was only detected for the spawning biomass of *A. luridus*, *C. julis*, and *S. cretense*.

The minimum AUC value for binomial models was 0.84, indicating excellent model fitting (Table S2¹, $0.8 \leq AU^1C < 0.9$; Hosmer and Lemeshow 2000). Smoother estimates of GAMLSS and GAMs are provided in the supplementary material (Figs. S1-S3¹) and show species-specific patterns (Figs. S1-S3¹). The mu parameter estimate for the explanatory

¹Supplementary data are available with the article on the journal Web site at: XX

variable depth in the biomass model of *S. salpa* was not significant but the variable was retained in the model because zero was not continuously included in the confidence interval of the smoother (Fig. S2¹; Wood and Augustin 2002). Instead, the smoother was similar to significant smoothers of other models for this species (Schmiing et al. 2013) and the AIC/SBC statistic increased if the variable was removed. The threshold for the presence of mature individuals, as modeled by binomial GAMs, was 0.34 for *L. bergylta* and *S. caeruleus* and 0.55 for *S. cretense*, respectively (Table 2).

Spatial patterns of the reproductive potential – single species

Predictive distribution maps of the relative spawning biomass and relative potential fecundity show distinct spatial patterns across the study area (Figs. 2-3). Depth and distance to sediment significantly shaped patterns of all metrics (supplementary material, Table S1, Figs. S1-S3¹), whereas biomass and fecundity typically increased (non-linearly) with increasing depth and distance to sediment. (Figs. S1-S3¹). Mature individuals of *L. bergylta*, *S. caeruleus* and *S. cretense* were predicted to occur in about half of the available reef habitat (Table 2). Minimum levels of relative spawning biomass or fecundity of single species, i.e. presence, were predicted for almost the entire reef habitat, as expected (Ws_1 : 91-100% of the hard-bottom in the study area, Fp_1 : 80-100%; Figs. 2-4), but the amount of suitable habitat decreased steeply when considering higher targets of the reproductive potential (Ws_{10} to Ws_{50} , and Fp_{10} to Fp_{50} ; Fig. 4). Habitats with target level Ws_{10} or Fp_{10} were predicted to cover more than 50% of the reefs, except for the fecundity of *S. cretense*, whereas habitats with target Ws_{50} or Fp_{50} typically encompassed less than 10% (Fig. 4). 59-90% of these single species RHs, or reefs with predicted presence of mature individuals, were represented inside the existing MPA network (Table 2, Fig. 4).

Spatial patterns of the reproductive potential – multiple species

Potential RHs with high spawning biomass of commercial species (i.e. areas containing 10% of the predicted spawning biomass of all commercial species, W_{scom} RHs) were distributed across the entire study area and covered 18% of the reef habitat (Figs. 4-5). If all study species were considered, disregarding their commercial use (W_{sall}), RHs fell inside the W_{scom} RHs of commercial species and had about half their size (Fig. 4). Modeled RHs with high fecundity of multi-species, Fp_{com} RHs, covered only 5% of the reef habitat and concentrated at the north coast of Faial Island and north-west coast of Pico Island (Figs. 4-5). The only larger overlap between W_{scom} and Fp_{com} was at the north-west coast of Pico Island. The majority of $W_{scom/all}$ and Fp_{com} RHs were located in the existing MPA network (74-91%, Figs. 4-5), where they represented 21% (W_{scom}), 12% (W_{sall}), and 7% (Fp_{com}), respectively, of the total protected reef habitat down to 40 m.

Discussion*Predictive models*

We modeled spatial patterns of the spawning biomass and potential fecundity of eight reef fishes and identified reef areas that likely supported fish populations with high reproductive potential. Modeling results concord with other studies that show how bathymetry, exposure to oceanographic forces, and distance to habitat edges significantly affect the distribution of reef fishes (Friedlander et al. 2003; Beger and Possingham 2008; Schmiing et al. 2013). Fish biomass, for example, is positively related to depth (Krajewski and Floeter 2011) and negatively to exposure (Friedlander et al. 2003; Krajewski and Floeter 2011) or distance to reef edges (Friedlander and Parrish 1998). Distance to sediment was the only variable that significantly influenced reproductive patterns of all species, whereas all metrics typically increased with increasing distance to sediment.

Overall, models performed well in the validation, even with data from another season. Optimally, however, the validation data should be spatially independent (Araújo and Guisan 2006), but such information was not available. Spawning (reproductively active) periods of study species were typically included in the data used for modeling, except for *L. bergylta* which spawn earlier (Villegas-Ríos et al. 2014) and *D. sargus* for which only part of the spawning season (Morato et al. 2003) was integrated. No significant differences, however, were found between data from winter and summer for these species. More importantly, no seasonal changes in spatial patterns, such as large scale migrations during the spawning season are known for any of the modeled species. Only *D. sargus* expands its home range slightly and increases the frequency of forays during the reproductive season, yet no evidence for spawning aggregations exists (Abecasis et al. 2015a). However, it could be considered the only species for which a reproduction related spatial behavior may influence the outcomes of the modeled reproductive habitats.

Spatial distribution of the reproductive potential

Predictive maps were used to identify sites with potentially high reproductive output. We argue that the spatial distribution of RHs is independent of the legal protection status in the present study, but rather influenced by environmental conditions. Studied MPAs are not effectively implemented: management plans are missing, only limited resources exist for enforcement and long-term monitoring, and compliance is low (Schmiing et al. 2014a; Abecasis et al. 2015b; Afonso et al., unpubl. data). No significant influences on exploited populations are observed (Schmiing et al. 2014a; Afonso et al., unpubl. data) and the single, small no-take area at the south-east tip of Faial Island is unlikely to achieve significant multi-species conservation goals because of its limitation (Abecasis et al. 2015b). Instead, highest fishing effort is even observed inside the protected areas (Diogo and Pereira 2013; Schmiing

et al. 2015). We thus argue that the present situation has to be distinguished from well-functioning MPAs that support denser fish populations with larger individuals ('reserve effect'; Lester et al. 2009) and, as consequence, most likely would encompass RHs. Instead, the present approach can be used as *a priori* study with the additional benefit of testing newly declared but yet unimplemented MPAs. It may also be used in support of a (potential) revision of a MPA network. In this context, predictive maps are a powerful and easy understandable tool for decision support and marine management (Sundblad et al. 2011; Schmiing et al. 2013).

In general, spatial patterns of fecundity and spawning biomass of most study species were similar (i.e. the location and size of areas with higher and lower values of both metrics were comparable for individual species). This contradicts the expectation that potential fecundity would be a refinement of spawning biomass (i.e. representing a narrower area) because it considers both the maturity and sex of a specimen. The situation appears reversed for *L. bergylta* where the probability of occurrence for spawning biomass seems narrower than for fecundity. Probably, this is an artefact of using presence/absence data instead of continuous biomass values, which turns direct comparisons between both reproductive metrics difficult. However, if true hermaphrodites (digynic, protogynous, simultaneous) have comparable spatial patterns for spawning biomass and potential fecundity, one of the two metrics can be chosen for analyzing the reproductive potential. The spawning biomass might be preferential for non-invasive methods such as UVCs. Identifying mature specimens, for example via size estimates, is more practicable than identifying mature females if sex-determination via distinct color morphs does not apply. Analyzing fecundity, however, seems advisable for male-dominated populations, such as *S. cretense*. Fecundity models are solely based on female counts and, as expected, all target levels of this reproductive metric ($F_{p10/25/50}$) are spatially more constrained than the distribution of mature males and females (i.e. spawning

biomass). The complex mating system of *S. cretense*, including territorial, harem males or multi-male groups (Afonso et al. 2008) and the highly skewed sex ratio (i.e. male dominated, average sex ratio $1:0.45 \pm 0.13$) are probably causing the observed precision of its Fp RHs. Predicted multi-species RHs of commercial species, W_{scom}/Fp_{com} , were much smaller than anticipated. The Fp_{com} RHs, for example, covered 5% of the rocky habitat, which probably is driven by the restricted distribution of Fp RHs of *S. cretense*. Reproductive habitats of spawning biomass that include all eight modeled species, W_{sall} , fall completely inside the W_{scom} RHs. This is a general consequence of the method used for RH identification (i.e. negative relation between the size of multi-species RHs and the number of integrated species), especially if species have small overlapping habitats and different life histories (Claudet et al. 2010; Schmiing et al. 2013). Alternatively, other methods than a simple spatial overlay of individual species maps may be used, such as an additive or complementarity approach (Schmiing et al. 2015). The presented approach for identifying RHs works well for reef fish with smaller home ranges and no significant movement between habitats for reproduction. If such seasonal movements occur, sampling design and modeling would have to be adjusted accordingly.

Implications for marine conservation planning

The reproductive output is the first of several processes for determining connectivity among populations (Cowen and Sponaugle 2009; Treml et al. 2012), whereas the likelihood of larval subsidy to adjacent (un)protected areas is low or insignificant if the reproductive output is low (or null). Although the opposite is not necessarily true, we argue that single- and multi-species RHs, either defined by spawning biomass or potential fecundity, are potentially good larval sources that, in addition to adult movement, may contribute to replenish and sustain

408 natal and neighboring areas and populations (Underwood et al. 2013). Such source habitats
409 are the ‘key’ to persisting, viable fish populations (Figueira and Crowder 2006).

410 The rate of successful larval settlement and recruitment to adjacent (or natal) populations,
411 however, is variable and also depends on a variety of biotic, abiotic and physical factors
412 (Christie et al. 2010). Larval behavior, larval survival, the availability of suitable settlement
413 habitat, and post-settlement survival contribute to connectivity patterns and can also modify
414 initial recruitment patterns after settlement (White and Caselle 2008; Cowen and Sponaugle
415 2009; Felix-Hackradt et al. 2013). Ocean circulations and currents shape connectivity
416 patterns between source and sink areas and determine the extent of local retention and self-
417 seeding (Cowen 2002; Di Franco et al. 2012). West and northwest swells predominate in the
418 study area, whereas the western tip of the Faial and the channel between Faial and Pico
419 Islands experience strongest swell and current (Carvalho 2003; Tempera 2008; Tempera et al.
420 2012). Hydrodynamic conditions might support distribution of potential recruits from the
421 RHs to sites with higher potential for larval retention, such as at the south coast of Faial
422 Island (Fontes et al. 2009a, 2009b). However, more research is needed to study larval
423 distribution and recruitment in the region. First studies from the same region confirmed
424 multiple natal signatures (i.e. different larval sources), even in sites where most signatures
425 were consistent with self-recruitment (i.e. south coast of Faial; Fontes et al. 2009b). Self-
426 recruitment, in general, probably is more common than previously perceived (e.g., Almany et
427 al. 2007; Berumen et al. 2012; Trembl et al. 2012). Some studies show that the success of
428 larval transport also depends on the PLD and typically decreases with longer PLDs (Koeck et
429 al. 2015). Other studies, on the contrary, highlight the importance of larval behavior,
430 swimming and sensory abilities (Lecchini et al. 2005; Cowen and Sponaugle 2009; Soeparno
431 et al. 2013). D’Aloia et al. (2015) estimated dispersal kernels based on genetic parentage
432 analyses, and showed that dispersal declines exponentially with distance but is unrelated to

433 PLD. Thus, small spacing distances between protected sites, such as in Faial Island, likely
434 promote larval connectivity (Almany et al. 2007; Fontes et al. 2009b; Green et al. 2014).
435 Nonetheless, MPA size rather than spacing between MPAs is likely to have a
436 disproportionate effect on densities of commercially targeted fish (Claudet et al. 2008;
437 Moffitt et al. 2011).

438 The overall good representativeness of single and multi-species RHs inside the studied MPA
439 network largely supports the existing site selection. Representativeness is above commonly
440 recommended targets of 20 to 40% (World Parks Congress 2003; Green et al. 2014), but
441 more than half of the reef habitat is anyway integrated in the MPAs, relativizing this
442 percentage. Furthermore, multi-species RHs represent only 7% ($F_{p_{com}}$) to 21% ($W_{s_{com}}$) of the
443 entire protected reef habitat until 40m depth. Certain RHs, such as the $F_{p_{com}}$ RH on the north
444 coast of Faial, are mostly unprotected. Considering that often only a limited amount of
445 resources is available for marine conservation (Abecasis et al. 2015b), or only a limited
446 amount of habitat can be protected, this RH might be a strategic site for protection to enhance
447 population persistence and larval subsidy and, ultimately, fisheries. Further research is
448 needed to quantify the role for larval dispersal of this RH (and others). Nevertheless,
449 protection of potential source habitats instead of random or 'sink' habitats is more likely to
450 promote connectivity and support adjacent fisheries and, consequently, should be encouraged
451 (Crowder et al. 2000). For example, simulations showed that protecting 10-20% of the sites
452 with highest spawning biomass could lead to increased abundances and harvest of the coral
453 trout in the Great Barrier Reef, Australia (Bode et al. 2012). On the contrary, failing
454 protection and selective removal of large, mature individuals by fishing may alter genetic
455 variability and/or sex ratios, and reduce the reproductive potential of a population (e.g.,
456 Birkeland and Dayton 2005; Laugen et al. 2014). In summary, overall site selection of the
457 studied MPAs seems adequate if considering the distribution of RHs. It is, however, beyond

the scope of this study to deliver new conservation scenarios (but see Schmiing et al. (2015) who provide alternative solutions for site selection, integrating also the information of RHs). Nevertheless, certain conditions have yet to be met so that benefits for biodiversity and fisheries may arise by protecting RHs, including 1) efficient conservation measures (i.e., no-take reserves), 2) implementation of management plans, and 3) improved compliance of rules and appropriate enforcement (Abecasis et al. 2015b).

Despite the importance of other factors that influence larval subsidy and recruitment, we argue that analyzing connectivity surrogates, such as spawning biomass and potential fecundity, can be particularly useful when information about *in situ* larval sources, larval dispersal and connectivity is absent or the necessary information to model such processes is missing (this study; Bode et al. 2012). Nevertheless, gathering and incorporating accurate data of local connectivity patterns should be encouraged. Identifying RHs can be seen as a first step for site selection to identify key areas that potentially protect connectivity and benefit adjacent fisheries. In addition, a multitude of other factors have to be considered in marine spatial planning, including a diverse set of biological/ecological features, socio-economic aspects, conservation objectives, and climate change (Andrello et al. 2015; Beger et al. 2015; Schmiing et al. 2015).

In conclusion, the present study showed that spatial patterns of spawning biomass and potential fecundity are species-specific, heterogeneous, and influenced by distance to the habitat edge, bathymetry, and exposure to current or swell. Spatial patterns of the reproductive metrics seem to be similar for simultaneous hermaphrodites or female dominated populations. On the contrary, if females are underrepresented, considering the sex (i.e. fecundity) can refine predictions of reproductive spatial patterns based on the mature, spawning biomass of all specimens. Studied surrogates may assist site selection of MPAs.

We propose areas with increased reproductive output as potentially good larval sources and their protection should be encouraged to optimize MPA connectivity and ecologically functioning. The studied MPA network has potential to benefit fisheries/conservation but further progress is needed to ensure an effective implementation. The rather simple approach presented here works well for sedentary species and can support adaptive management and MPA design. Predictions and resulting maps of the reproductive potential are essential for systematic conservation planning, and can be used in stakeholder meetings, MPA evaluation and adaptive management (Sundblad et al. 2011; Schmiing et al. 2014b, 2015). We propose to integrate this or similar methods as a first step of a manifold process for identifying potential sources of recruitment subsidies and priority sites for conservation.

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Table 1: Summary of the (reproductive) ecology of four reef fishes, showing fecundity equations used to estimate the potential fecundity (number of oocytes) of mature females via the mean length (TL, in cm; Morato et al. 2001) of species-specific size classes (M- medium, L - large, XL - very large).

Species	Reproductive strategy	Fecundity	TL (cm)
<i>Diplodus</i>	Digynic	25398 TL – 484426	M: 17; L: 26, XL: 36
<i>sargus</i>	hermaphrodite	(Gonçalves and Erzini 2000) ^a	
<i>Serranus</i>	Simultaneous	63,648.435 * 1.1380 ^{TL}	M: 25; L: 32.5; XL: 40
<i>atricauda</i>	hermaphrodite	(García-Díaz et al. 2006) ^b	
<i>Sparisoma</i>	Gonochoristic,	9.158 * 10 ⁻⁸ * TL ^{5.0954}	M: 27.5; L: 37.5; XL: 47
<i>cretense</i>	prematurational sex-change	(González et al. 1993) ^c	
<i>Labrus</i>	Protogynous	1.4377 * TL ^{3.7276} (Villegas-	M: 24; L: 32.5; XL: 42.5
<i>bergylta</i>	hermaphrodite	Ríos et al. 2014)	

^aEquation for *Diplodus vulgaris*. ^bPublished equation was corrected (pers. com. V. Tuset).

^cTL in equation in mm.

Table 2: Modeled occurrences of mature individuals of three reef fishes, including the percentage of rocky reef habitat down to 40m depth (% Reef) with predicted presence ($\geq$ threshold) and the representativeness of these reef areas inside the existing marine protected area network (% MPA).

Species	Threshold ^a	% Reef	% MPA
<i>Labrus bergylta</i>	0.34	59.1	60.3
<i>Sparisoma cretense</i>	0.55	56.7	66.8
<i>Symphodus caeruleus</i>	0.34	57.1	66.2

^aThe 'equal sensitivity and specificity' approach was used for identifying species-specific thresholds of presence. **Note:** Occurrences were modeled with binomial generalized additive models.

Figure captions

Fig. 1: Map of the study area. 462 underwater visual censuses (dots; dots of neighboring transects overlap in the figure) were conducted down to the 40m isobath in the Azores archipelago. Rocky substrate (grey), 10m isobaths (grey lines) down to 40m, and the outline of the existing marine protected areas are shown (black squares; note that not all areas are visible at this spatial scale).

Fig. 2: Maps of the predictive relative spawning biomass (5m grid) of four reef fishes down to 40m in Faial and West Pico Island, Azores archipelago. Biomass predictions are represented i) as relative potential spawning biomass (ratio of a given predicted value to the maximum predicted biomass on a scale from 0-1, see common color code below maps; *Abudefduf luridus*, *Coris julis*, *Sarpa salpa*) or ii) as probability of occurrence of mature individuals (*Symphodus caeruleus*; note the individual scale bar). The outline of existing marine protected areas (black squares) and rocky substrate down to 40m is shown (black line). (Fish illustrations: L. Gallagher/fishpics/ImagDOP).

Fig. 3: Maps of the predictive spawning biomass (left column) and potential fecundity (right column) (5m grid) of four reef fishes down to 40m in Faial and West Pico Islands, Azores archipelago. Predictions are represented i) as relative potential spawning biomass (ratio of a given predicted value to the maximum predicted biomass on a scale from 0-1, see common color code below maps; *Diplodus sargus*, *Serranus atricauda*), ii) as probability of occurrence of mature individuals (*Labrus bergylta*, *Sparisoma cretense*; note the individual scale bars in the respective map), or iii) as relative potential fecundity (ratio of a given predicted value the predicted maximum fecundity on a scale from 0-1, see common color code below maps; all species). Other details as in Fig. 2.

818

819 **Fig. 4:** Summary of the percentage of available rocky reef habitat down to 40m depth,
820 suitable for different target levels of the reproductive potential. A) Predictive relative
821 spawning biomass ($> 1\%$, $> 10\%$, $> 25\%$, $> 50\%$ of the maximum), and B) predictive relative
822 potential fecundity ($> 1\%$, $> 10\%$, $> 25\%$, $> 50\%$ of the maximum). Potential multi-species
823 reproductive habitats combine either commercial (*) or all species (+), including results of
824 binomial models (see text for detail). Numbers indicate the representativeness (% included)
825 of the identified areas inside the existing MPA network.

826

827 **Fig. 5:** Predicted reproductive habitats (RHs) of commercial species (*Diplodus sargus*,
828 *Labrus bergylta*, *Sparisoma cretense*, *Serranus atricauda*). RHs consider a minimum of 10%
829 relative spawning biomass ($W_{s_{com}}$) or potential fecundity ($F_{p_{com}}$). Areas with overlapping
830 $F_{p_{com}}$ and $W_{s_{com}}$ are dark shaded. The threshold of occurrence was used as alternative
831 criterion for predictions of the spawning biomass of *L. bergylta* and *S. cretense* (see text for
832 more details). The outline of rocky bottom down to 40m (black line) and the marine protected
833 area network (black squares) of Faial and Pico Islands in the Azores archipelago are shown.

Fig. 1: Map of the study area. 462 underwater visual censuses (dots; dots of neighboring transects overlap in the figure) were conducted down to the 40m isobath in the Azores archipelago. Rocky substrate (grey), 10m isobaths (grey lines) down to 40m, and the outline of the existing marine protected areas are shown (black squares; note that not all areas are visible at this spatial scale).

Fig. 1
140x108mm (300 x 300 DPI)

Fig. 2: Maps of the predictive relative spawning biomass (5m grid) of four reef fishes down to 40m in Faial and West Pico Island, Azores archipelago. Biomass predictions are represented i) as relative potential spawning biomass (ratio of a given predicted value to the maximum predicted biomass on a scale from 0-1, see common color code below maps; *Abudedefduf luridus*, *Coris julis*, *Sarpa salpa*) or ii) as probability of occurrence of mature individuals (*Symphodus caeruleus*; note the individual scale bar). The outline of existing marine protected areas (black squares) and rocky substrate down to 40m is shown (black line). (Fish illustrations: L. Gallagher/fishpics/ImagDOP).

Fig. 2

142x119mm (300 x 300 DPI)

Fig. 3: Maps of the predictive spawning biomass (left column) and potential fecundity (right column) (5m grid) of four reef fishes down to 40m in Faial and West Pico Islands, Azores archipelago. Predictions are represented i) as relative potential spawning biomass (ratio of a given predicted value to the maximum predicted biomass on a scale from 0-1, see common color code below maps; *Diplodus sargus*, *Serranus atricauda*), ii) as probability of occurrence of mature individuals (*Labrus bergylta*, *Sparisoma cretense*; note the individual scale bars in the respective map), or iii) as relative potential fecundity (ratio of a given predicted value to the predicted maximum fecundity on a scale from 0-1, see common color code below maps; all species). Other details as in Fig. 2.

Fig. 3
264x413mm (300 x 300 DPI)

400x249mm (200 x 200 DPI)

Fig. 5: Predicted reproductive habitats (RHs) of commercial species (*Diplodus sargus*, *Labrus bergylta*, *Sparisoma cretense*, *Serranus atricauda*). RHs consider a minimum of 10% relative spawning biomass (Wscom) or potential fecundity (Fpcom). Areas with overlapping Fpcom and Wscom are dark shaded. The threshold of occurrence was used as alternative criterion for predictions of the spawning biomass of *L. bergylta* and *S. cretense* (see text for more details). The outline of rocky bottom down to 40m (black line) and the marine protected area network (black squares) of Faial and Pico Islands in the Azores archipelago are shown.

Fig. 5
209x148mm (300 x 300 DPI)

Supplementary material

Table S1: Summary of final generalised additive models for location, scale and shape (GAMLSS) for continuous response variables and generalised additive models (GAM) for binomial response variables. Environmental variables include depth, slope, distance to sediment (DistSed, log transformed), exposure to current (current, square root transformed) and exposure to swell. GAMLSS include separate formulas for the mu and nu parameters and, if applicable, penalised b-splines (pb) as smooth terms. GAMs used thin plate regression splines (s) and the upper limit of the degrees of freedom was fixed manually ($k = n$), if applicable. The model fitting data set comprised 354 underwater visual fish censuses.

Response	Spawning biomass	Potential fecundity
<i>Diplodus sargus</i>	$Mu: \sim pb(\text{Depth})^{***} + \text{Swell}^*$; $Nu: \sim pb(\text{DistSed})^{***}$	$Mu: \sim \text{Depth}^{***} + \text{DistSed}^{***} + \text{Swell}^{**}$; $Nu: \sim pb(\text{DistSed})^{***}$
<i>Labrus bergylta</i>	<i>Binomial model:</i> $\sim s(\text{Depth})^{***} + s(\text{Slope})^{***} + s(\text{DistSed})^* + s(\text{Current}, k=6)^{***}$	$Mu: 1$; $Nu: \sim pb(\text{Depth})^{***} + pb(\text{Slope})^{***} + pb(\text{DistSed})^{***} + pb(\text{Current})^{***}$
<i>Serranus atricauda</i>	$Mu: \sim pb(\text{Depth})^{***} + \text{DistSed}^{***}$; $Nu: \sim pb(\text{Depth})^{***} + pb(\text{DistSed})^{***} + pb(\text{Current})^{***}$	$Mu: \sim pb(\text{Depth})^{***} + pb(\text{DistSed})^{***}$; $Nu: \sim pb(\text{Depth})^{***} + pb(\text{DistSed})^{***} + \text{Current}^{2**}$
<i>Sparisome cretense</i>	<i>Binomial model:</i> $\sim s(\text{Depth})^{***} + s(\text{DistSed})^{***} + s(\text{Current}, k=6)^{***}$	$Mu: \sim pb(\text{Slope})^{***} + pb(\text{DistSed})^{***} + pb(\text{Swell})^*$; $Nu: \sim pb(\text{Depth})^{***} + pb(\text{DistSed})^{***} + \text{Current}^{**} + \text{Swell}^{***}$
<i>Abudefduf luridus</i>	$Mu: \sim pb(\text{Depth})^* + \text{DistSed}^* + pb(\text{Current})^*$; $Nu: \sim pb(\text{Depth})^{**} + pb(\text{DistSed})^{**} + \text{Swell}^{***}$	NA
<i>Coris julis</i>	$Mu: \sim pb(\text{Depth})^{***} + \text{Slope}^{***} + pb(\text{Swell})^{***}$; $Nu: \sim pb(\text{Depth})^{***} + pb(\text{DistSed})^{***}$	NA
<i>Sarpa salpa</i>	$Mu: \sim pb(\text{Depth})^{ns}$; $Nu: \sim pb(\text{Depth})^{**} + pb(\text{DistSed})^{***} +$	NA

	pb(Swell)***	
<i>Symphodus caeruleus</i>	Binomial model: ~ s(Depth)*** + s(Slope)*** + s(DistSed)** + s(Current)**	NA

10 Significance of environmental variables: ^{ns} = non significant; * = *p*-value <0.05; ** = *p*
11 <0.01; *** = *p* <0.001. NA= not applicable because no model was produced.

12
13

14 **Table S2:** Validation of model for the predictive spawning biomass and potential fecundity
15 of reef fishes in the Azores. The Spearman’s rank correlation coefficient, rho, between
16 predicted and observed values in the model fitting (Rho-fit, n= 354) and validation data set
17 (Rho-validate, n= 108) is given. All *p*-values are < 0.001. The validation of three binomial
18 models also includes the area under the curve (AUC). NA = not applicable.

Species	Spawning biomass			Potential fecundity	
	Rho-fit	Rho-validate	AUC	Rho-fit	Rho-validate
<i>Diplodus sargus</i>	0.58	0.55	NA	0.57	0.62
<i>Labrus bergylta</i>	0.55	0.58	0.85	0.57	0.57
<i>Serranus atricauda</i>	0.70	0.75	NA	0.72	0.70
<i>Sparisome cretense</i>	0.62	0.47	0.86	0.42	0.43
<i>Abudefduf luridus</i>	0.74	0.68	NA	NA	NA
<i>Coris julis</i>	0.69	0.62	NA	NA	NA
<i>Sarpa salpa</i>	0.54	0.50	NA	NA	NA
<i>Symphodus caeruleus</i>	0.52	0.34	0.84	NA	NA

19

Fig. S1: Smoother estimates (solid line, $s(x)$) for the environmental variables depth, slope, distance to sediment, and exposure to current obtained by generalised additive models (GAMs) for the occurrence of mature individuals of three reef fishes. Grey shaded areas indicate the approximate 95% confidence interval. Tick marks on the x-axis are sampled datapoints. NA= not applicable.

Fig. S2: Model results for the spawning biomass of mature individuals of four commercially valuable reef fishes. Smoother estimates (solid line, $pb(x)$) for up to five environmental

30 variables, as obtained for the μ (mean of the response variable) and ν (probabilities at
31 zero) parameters of generalised additive models for location, scale and shape (GAMLSS) are
32 given. Grey shaded areas indicate the approximate 95% confidence interval. NA= not
33 applicable. Tick marks above the x-axis are sampled datapoints.

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Fig. S3: Model results for the potential fecundity of four commercially valuable reef fishes. Smoother estimates (solid line, $pb(x)$) for up to five environmental variables, as obtained for the μ and ν parameter of generalised additive models for location, scale and shape (GAMLSS) are given. Other details as in Fig. S2.