



# Highly localized replenishment of coral reef fish populations near nursery habitats

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**ABSTRACT:** Connectivity is essential for ecosystem functioning, and in particular for the population dynamics of species that use different habitats during consecutive life stages. Mangrove and seagrass habitats serve to replenish populations of a range of species that live on coral reefs, but we know little about the fate of these early stages and the spatial scale at which adult populations benefit from this enhancement effect. We examined densities of 12 ecologically important Caribbean fish species across 3 nursery-dependency categories (high, low, none). We tested the hypotheses that for nursery species, (1) densities and (2) biomass in the adult habitat decrease with distance from nurseries as the enhancement effect is progressively diluted, and (3) densities in the adult habitat are positively correlated with total juvenile abundance in nurseries. Reef density and biomass of the high- and low-dependence species declined rapidly within ~4 km from nurseries, while at a distance of ~14 km densities of most species were close to zero. These patterns were not confounded by local habitat complexity. Density and biomass of the no-dependence species remained unchanged with distance. Total abundance of juvenile fishes in nurseries was a good predictor of total adult abundance on adjacent reefs for the high-dependence species. Our results demonstrate that for several species, enhancement of adult reef populations by mangrove and seagrass nurseries is highly localized (less than ~4 km) in terms of abundance and biomass, and the magnitude of this enhancement is highly correlated with juvenile population abundances within the nursery habitats.

**KEY WORDS:** Mangroves · Seagrass · Nursery function · Population replenishment · Dispersal · Caribbean

## INTRODUCTION

Ecosystems are functionally linked by the movement of organisms across their boundaries (Webster et al. 2002, Baguette et al. 2013). Whereas many species have recurring migrations across landscapes, the uni-directional movement from natal to adult habitats by species with a stage-structured life cycle has

received much less attention (Werner & Gilliam 1984). Such dispersal across ecosystem boundaries can be driven by bet-hedging against environmental disturbances, avoiding intraspecific competition, or avoiding inbreeding (Johnson & Gaines 1990). Alternatively, dispersal to adult habitats is not necessarily a part of a life-history strategy, but can be merely a function of movement capacity, and related to traits

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such as body size (Field et al. 2005, Benard & McCauley 2008). Dispersing individuals influence many ecological processes in recipient habitats, such as food web structure, organic matter/energy/nutrient exchange between habitat patches, species' population replenishment, and ecosystem resilience (Polis et al. 1997, Mumby & Hastings 2008, Hyndes et al. 2014, Allgeier et al. 2014). Therefore, an understanding of how far animals disperse from their natal habitats is vital in determining the strength of inter-habitat connectivity and the importance of different habitats in maintaining populations and ecological processes. Such insights provide the basis for planning and management of corridors and stepping stones that maintain connectivity between populations in heterogeneous landscapes (Pittman et al. 2011, Baguette et al. 2013).

Ontogenetic niche shifts, which include habitat or ecosystem shifts (depending on the spatial scale at which this occurs) with changing life phase, are pervasive and found in ~80% of animal taxa (Werner 1988). In freshwater and marine environments, many species show ontogenetic movements across different habitats and ecosystems (Werner & Gilliam 1984). Such movements typically occur at scales of 10s to 100s of m between 'habitat' patches (Dorenbosch et al. 2004, Verweij & Nagelkerken 2007, Luo et al. 2009) and at scales of km to 100s of km across 'ecosystems' (Gillanders et al. 2003). One well-studied example of ontogenetic niche shifts in tropical marine organisms is that of coral reef fishes that use spatially segregated, non-reef ecosystems such as mangroves and seagrasses as juveniles (Nagelkerken 2009). The common presence of juvenile fish and crustaceans in inshore vegetated ecosystems has led to the formulation of the 'nursery hypothesis', which postulates that inshore juvenile ecosystems replenish adult populations in adjacent deeper ecosystems (Beck et al. 2001, Adams et al. 2006). Possible advantages of such a strategy include lowered predation risk and/or faster relative growth rates in juvenile compared to adult ecosystems, postulated to be the result of better food availability and/or quality (Dahlgren & Eggleston 2000, Grol et al. 2011).

Ontogenetic niche shifts alter community structures in recipient ecosystems, and coral reef fish populations differ in their density and community structure in the presence of nearby nurseries such as mangroves and/or seagrasses (Nagelkerken et al. 2002, Halpern 2004, Mumby et al. 2004, Dorenbosch et al. 2005). However, there have been few formal tests of the hypothesis that the influence of nurseries on coral reef population replenishment decreases

with distance from nurseries (Mumby 2006, Huijbers et al. 2013). There is still a lack of understanding of how far young animals disperse and up to what distances nurseries affect adult community structure.

We therefore tested the following hypotheses: for fish species with a stage-structured life history, (1) densities and (2) biomass in the adult habitat decrease with distance from nurseries as the enhancement effect is progressively diluted. Such insights are essential to predict the ecological implications of ecosystem connectivity on population sizes and community structure, and therefore represent a test of the nursery hypothesis. Because it is likely that populations of species with such a stage-structured life cycle are primarily driven by the positioning of nursery habitats within the marine landscape, these insights are relevant to fisheries management, design of marine protected areas, and marine spatial planning (Beger et al. 2010, Grüss et al. 2011).

Adult population sizes can also be influenced by the size of nurseries and/or propagule densities (Halpern et al. 2005, Grober-Dunsmore et al. 2007, Jones et al. 2010, Paillon et al. 2014, Serafy et al. 2015). Some studies have therefore examined the correlation of variables such as total nursery surface area to the size of offshore fish or shrimp populations (see reviews by Manson et al. 2005, Nagelkerken et al. 2008a, Blaber 2009). However, not all habitat patches within a seascape are equally productive nurseries, and the variability of fish densities within habitats at various spatial scales can be complex (Nagelkerken et al. 2015, Sheaves et al. 2015). In addition, the surface area of nurseries and juvenile densities may be inversely correlated, resulting in 'crowding' when juveniles are abundant and ideal habitat is sparse, or in patchy fish distributions in the opposite case. Total juvenile abundance in nurseries, rather than mean density or habitat surface area, might therefore be a more meaningful or powerful predictor of adult population enhancement, but this has not been considered previously in studies on nursery function. Accordingly, we tested a third hypothesis: that for fish species with stage-structured life histories, (3) densities in the adult (reef) habitat are positively correlated with total juvenile abundance in the nearest nurseries. Because nursery species typically show cross-ecosystem movement driven by increasing body size and/or maturity stage rather than by density-dependent overflow from nurseries onto adjacent reefs (Kimirei et al. 2013a, Grol et al. 2014), we investigated how higher juvenile abundances might enhance adult abundances on reefs through ontogenetic shifts rather than density-dependent processes.

Here, we examined the spatial scale at which marine nurseries might affect recipient adult habitats and how this relates to the abundance of young fish. This work builds on several previous studies which focused on (and answered) questions surrounding the influence of adjacent nursery habitat presence/absence on adult densities on nearby reefs. We do not seek to revisit these important 'first order' questions. Rather, we focus on quantifying the rate of adult density decrease as the distance between juvenile and adult habitats increases — what we consider a logical 'second order' question from which we can gain insight into the extent of adult fish enhancement. We used a mangrove–seagrass–coral reef seascape mosaic as a model system because it is found in tropical areas around the globe and because they are widely studied as fish habitats, with good evidence supporting their importance for juvenile fish. We predict that the response of fish populations to increasing isolation from nursery habitats is driven by the life-history strategy of the species in question, i.e. the strength of their association with nurseries during the juvenile life stage. We therefore selected species that belong to 3 functional groups, ranging from high, to low, to no dependency on nurseries. Together, our results provide a model of the subsidy magnitude of reef populations by nurseries, the variables that best explain this enhancement effect, and a quantification of the dilution effect.

## MATERIALS AND METHODS

### Study area

We collected fish density and biomass data in 2005 and 2006 off 4 islands: 3 in the Caribbean Sea (Aruba, Curaçao, Grand Cayman) and 1 far north of the Caribbean (Bermuda) (Fig. 1). Aruba, Curaçao, and Grand Cayman are surrounded by continuous fringing reefs, with a slowly sloping 100 to 400 m wide shelf, after which the reef drops off steeply. Bermuda has a large shallow shelf of <10 m depth that ranges ~1.5 to 16 km in width, with many small reef patches. Mangroves and seagrass beds at the 4 islands are largely confined to semi-enclosed embayments and lagoons (Fig. 1). Off Aruba and Bermuda, seagrass beds occur on some parts of the shelf, but these exposed beds are largely devoid of fish (I. Nagelkerken & M. G. G. Grol pers. obs.), in contrast to the wave-protected seagrass beds within the embayments. For a more detailed description of the reef, mangrove, and seagrass habitats at these islands, see

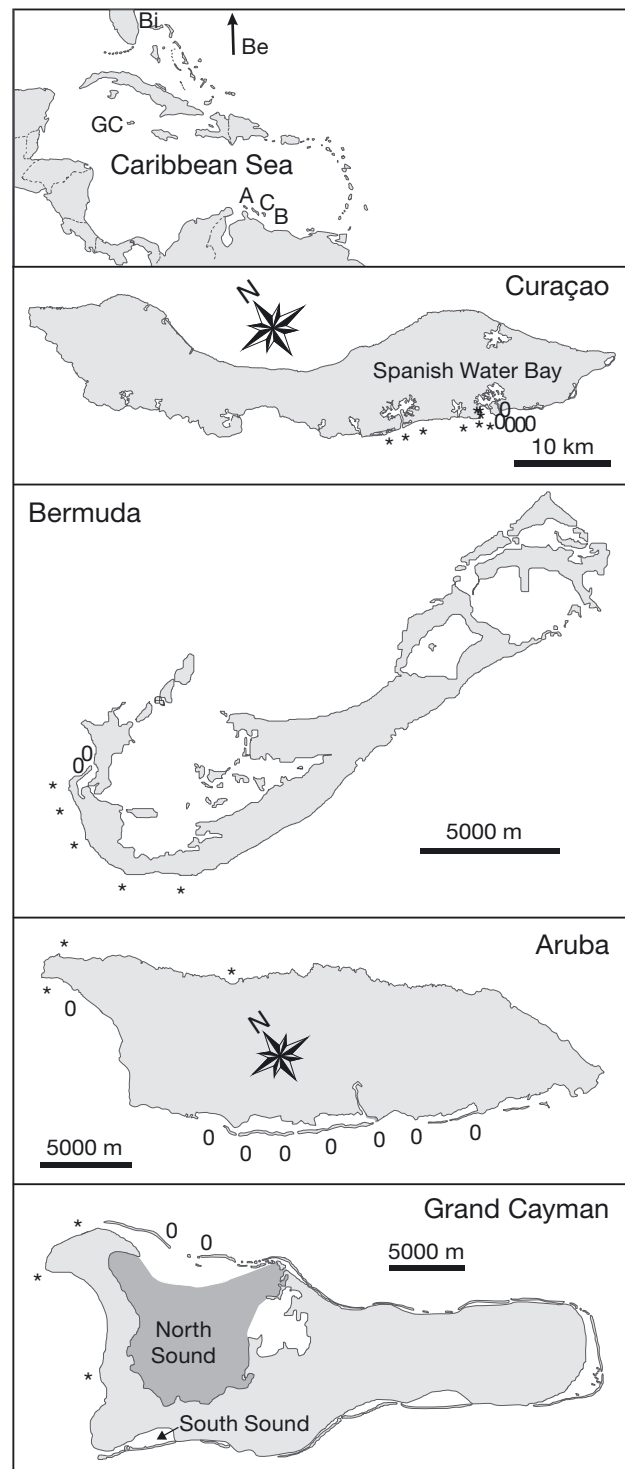


Fig. 1. Study area showing island locations and the surveyed reef sites at each island. In the top panel, A: Aruba; Bi: Bimini; Be: Bermuda; B: Bonaire; C: Curaçao; GC: Grand Cayman. In lower panels, (\*) indicates reef sites in the gradient with increasing distance from nursery habitats; 0: reefs in front of nursery habitats at '0 km' distance. North is indicated by a compass rose for Aruba and Curaçao, while for the other locations, north is straight up

Nagelkerken et al. (2008b). Furthermore, we used previously published data from Bonaire (Nagelkerken et al. 2000b) and Curaçao (Nagelkerken et al. 2000a) to correlate total juvenile fish abundance with those of adults on coral reefs.

### Fish densities and biomass

Nursery species (sensu Nagelkerken et al. 2000a) are defined as reef fish species that show highest juvenile densities in mangrove and/or seagrass habitats; in the Caribbean they include at least 17 species. Adults of these species live on coral reefs and vary in their nursery dependency, as demonstrated by a comparison among reefs with and without the presence of nursery habitats (Nagelkerken et al. 2002). From these 17 nursery species, we selected 4 showing high dependence and 4 showing low dependence on nursery habitats (sensu Nagelkerken et al. 2002), respectively (see Supplement 4 at [www.int-res.com/articles/suppl/m568p137\\_supp.pdf](http://www.int-res.com/articles/suppl/m568p137_supp.pdf)). A third category consisted of 4 species that were congeners of the nursery species and that were abundant on coral reefs, but had no apparent dependence on these nurseries based on the absence or low abundance of their juveniles in nursery habitats versus coral reefs (Nagelkerken & van der Velde 2002); we specifically selected congeners because they resemble the nursery species more closely in their phylogeny and ecology than unrelated reef species. Due to their dependency class, the fish we counted on the reefs consisted almost entirely of adults for the high-dependence group, mainly adults but also some juveniles for the low-dependency group, and a mix of adult and juvenile fishes for the no-dependence group. To examine how nursery presence also altered the broader reef fish community structure, we included an additional 39 reef fish species. These 39 species, together with the 12 species belonging to the 3 dependency groups, covered all species within the families Acanthuridae, Chaetodontidae, Gerreidae, Haemulidae, Lutjanidae, Mullidae, Scaridae, and Sphyraenidae. Each of these families contains species that are associated as well as not associated with mangrove/seagrass nurseries. We excluded other families from the surveys because they only had no-dependence representatives.

We visually surveyed our target species (all size classes included, but predominantly adults) on coral reefs during daytime using a point-count method, estimating the number and size (to nearest cm) of each fish in an imaginary quadrat of 10 × 10 m for

10 min (see full details of the methodology in Dorenbosch et al. 2005). We transformed fish lengths to biomass using regression equations from Bohnsack & Harper (1988). The same 3 observers, all of whom were highly experienced with the method and continuously practiced size estimation underwater, did all surveys. Surveys on Curaçao, Aruba, and Grand Cayman covered a depth range of 5 to 15 m, while the patch reefs of Bermuda covered a 3 to 6 m depth range. Within islands, surveys were done at the same depth range on similar reef types to avoid introduction of confounding factors that might explain differences in fish densities. Because the Caribbean has predominant trade winds blowing from the northeast, sites had different wave exposure, but because the study sites were oriented differently relative to the wind direction for the different islands, we considered this condition to be random across islands.

At each island, we selected 3 to 9 coral reef sites (Table 1) at increasing distances from semi-enclosed lagoons or bays harbouring extensive seagrass beds and mangroves, up to a maximum distance of 14 km (Fig. 1). In addition to the sites along this distance gradient, we surveyed 2 to 8 reef sites directly adjacent to the nursery habitats to obtain a mean '0 km' distance value (Table 1). We averaged these 0 km sites to obtain one value because the other distances along the gradient were also represented by a single value (per island). Sites along the distance gradient were not close to any mangroves or seagrass areas

Table 1. Number of sites at which fish surveys were conducted for each of the main 4 islands and 3 habitats. Numbers in brackets show how many of the total number of reef sites were at 0 km distance (i.e. in front of nurseries). Numbers of sites are also shown for the additional islands that were included for the nursery habitat–coral reef correlations

	No. of sites		
	Coral reef	Mangrove	Seagrass
<b>Coral reef sites for fish density as function of distance from nursery</b>			
Aruba	11 (8)	4	3
Bermuda	7 (2)	2	2
Curaçao	14 (5)	12	11
Grand Cayman (North Sound)	5 (2)	4	7
<b>Additional sites for correlation between nursery and reef populations</b>			
Bimini	5	5	10
Bonaire (1981)	2	6	3
Curaçao (1998)	3	12	11
Grand Cayman (South Sound)	3	–	5

other than those at 0 km. The reason for lack of mangroves and seagrasses at distances >0 km were (1) lack of suitable embayments where these nursery habitats typically occur (Aruba, Bermuda, Grand Cayman), or (2) presence of embayments along the gradient that did not harbour any nursery habitats due to high water turbidity within the embayment. We surveyed at least 10 replicate quadrats at each reef site off each island. The sequence of site surveys was random for all islands.

To test whether the fish distribution patterns were driven by nursery presence or local habitat complexity, we made 4 visual estimates of live benthic cover (% cover of all living sessile organisms) and 1 estimate of average coral (dead and alive combined) elevation above the substratum (as a proxy for reef rugosity) for each fish census quadrat on the reef. Both of these structural complexity variables can have a strong effect on fish communities (Gratwicke & Speight 2005) and were included in the statistical models (see 'Analysis').

At each of the 4 study locations we also quantified daytime juvenile abundances of the selected fish species within the nearest mangrove and seagrass nursery habitats. Replicate sites were spread throughout the embayments, and we surveyed 2 to 12 seagrass or mangrove sites per island (Table 1), depending on the size of the bays. At each site, we visually surveyed 3 to 18 replicate belt transects (2 m wide) of at least 10 m<sup>2</sup> in the mangroves and 20 m<sup>2</sup> in the seagrass beds.

To correlate total juvenile fish abundance (calculated as habitat surface area × mean fish density) within nurseries with those of adults on coral reefs (see Supplement 4), we used the above juvenile and adult fish data from our 4 principal study locations, but also added Bimini and South Sound at Grand Cayman as study locations (Fig. 1), and added data from previously published studies, i.e. data for Bonaire in 1981 (Nagelkerken et al. 2000b) and Curaçao in 1998 (Nagelkerken et al. 2000a) (Table 1). Density data for juveniles within nurseries and adults on reefs for these additional studies were also based on visual daytime surveys of fish communities, and were collected either in quadrats of the same size (Bimini and South Sound) as for our 4 principal study locations, or in quadrats of different sizes (Bonaire 1981 and Curaçao 1998). For Bonaire and Curaçao, we used belt transects of 300 and 150 m<sup>2</sup> on coral reefs and 900 and 150 m<sup>2</sup> on seagrass beds, respectively, while transects in mangroves were 300 m<sup>2</sup> versus 2 m wide along the entire length of each mangrove stand, respectively; for further details see

Nagelkerken et al. (2000a,b). As only reef populations were surveyed at Curaçao in 2005, we used the 1998 Curaçao data for the correlation analyses examining mangrove, seagrass, and reef populations. We did not include these additional datasets in our analysis of fish communities as a function of distance from nurseries, because we only had reef fish density data from reefs directly in front of nurseries at these additional locations, and no data along a distance gradient.

### Habitat dimensions

Island mangroves were all of the fringing-mangrove type (Faunce & Layman 2009), located along the shoreline, continuously inundated by seawater, and had sufficiently clear water for visual surveys. Using Google Earth™, we manually measured mangrove fringe length at a virtual altitude of ~3.6 km. We only included inundated mangroves based on our own extensive field surveys in all embayments. In addition, we measured the width of inundated mangrove habitat *in situ* every 5 m along the mangrove fringe for each mangrove stand surveyed for juvenile fish abundance. We calculated total inundated mangrove surface area by multiplying mean inundated mangrove width by total mangrove fringe length. We obtained seagrass surface areas from aerial photographs or satellite imagery from Google Earth™.

We determined shelf width of coral reefs located near nurseries using Google Earth™. We calculated total 2-dimensional reef surface area adjacent to nurseries by taking a fixed coastline distance directly adjacent to the nurseries and multiplying this by the mean shelf width (see Supplement 1). There was no *a priori* assumption of the distance at which nurseries affected reef fish densities, so we used 2 different distances of 1.2 and 5.2 km from nurseries, respectively, to calculate total shelf/reef surface areas. We chose these distances because each of the islands had a fish census site located at or close to these 2 distances from nurseries. We multiplied each of the 2 coastline distances by 2 (i.e. 2.4 and 10.4 km coastline lengths, respectively) to combine the up-current as well as down-current direction along the fringing reefs that fish could migrate to when exiting from a nursery bay mouth onto the reef. Based on extensive diving on reefs close to nurseries, we observed that within islands, the reef structures at <1.2 and <5.2 km from nurseries were similar.



## Analysis

We developed a series of general linear mixed-effects models to examine the relationship between reef fish density (or biomass) and distance (non-centring scaled and  $\log_{10}[x + 1]$  transformed) to nursery for each of the 4 study islands. We calculated the median for both density and biomass for each site across all transects because of the zero-inflated distribution of both responses, then transformed both median variables using a non-centring scale function and a  $\log_{10}(x + 1)$  function. For each response, we constructed 5 models (see Table 2) with various combinations of distance and dependency class (high, low, or none), including the distance  $\times$  dependency interaction using a Gaussian error distribution (on transformed data) and an identity link function. We set a nested random effect of species within islands to account for the non-independence of site-level values within species and island. Residual and quantile–quantile (QQ) plots indicated only slight departure from Gaussian error distribution assumptions, and no other error distribution performed better. The top-ranked model in both sets was identical, so we are satisfied that slight departure from the error-distribution assumption did not bias model ranking for either model set. We compared and ranked models using Akaike's information criterion corrected for small samples ( $AIC_c$ ), which measures their weight of evidence relative to other models (Burnham & Anderson 2002). We assessed each model's relative probability using  $AIC$  weights ( $wAIC_c$ ) and its structural goodness-of-fit via the marginal  $R^2$  ( $R_m$ ) as a measure of the variance explained by the model's fixed effects (Nakagawa & Schielzeth 2013). We also separated the dataset for each density and biomass test (as above) for high-, low-, and no-dependency species to determine the change in  $R_m$  among groups, thus testing the hypothesis that the models' explanatory power declines from high to no dependency.

We then repeated all analyses described above, to test for the influence of local habitat complexity on fish distribution patterns. We added the 2 coral reef complexity variables (cover and height, respectively) to the model set to test the hypotheses that coral characteristics further influenced the distance relationships. This increased the total number of models for each response variable to 20 (see Supplement 2). To normalize these variables, we applied a logit transform to the  $x/100$  median % coral cover, and a non-centre scaled  $\log_{10}(x + 1)$  transform to the median coral height among transects.

To test whether distance to nurseries also altered the broader fish community structure, we constructed a multivariate analysis on densities of the 51 species identified above. Per species and island, we averaged fish density at sites above and below a range of cut-off distances (i.e. 1, 2, 3, 4, 5 km from nurseries). We calculated Bray-Curtis similarity coefficients among sites using log-transformed mean density per species. We used the similarity matrix to generate a non-metric multi-dimensional scaling plot. We tested the importance of nursery proximity (close vs. isolated) and island (4 levels) using a 2-way ANOSIM with replication (Clarke 1993), followed by SIMPER analysis to identify the species driving any non-random patterns.

To examine the relationships between juvenile nursery fish abundance and adult reef fish density and abundance, respectively, we used non-parametric Spearman's rank correlations (for non-Gaussian distributions) or parametric Pearson product-moment correlations (for Gaussian distributions), on a per-species basis and combining data from our 4 study locations as well as previous studies (i.e. Aruba, Bermuda, Bimini, Bonaire, Curaçao, and North and South Sound at Grand Cayman). We applied a Shapiro-Wilk test to determine which distributions were approximately Gaussian. Predictor variables were total juvenile fish abundance (i.e. calculated as habitat surface area  $\times$  mean fish density in the respective habitat) in (1) mangroves, (2) seagrasses, and (3) mangroves and seagrasses combined (abundances summed), respectively. The dependent variables were mean fish density and total fish abundance, respectively, on coral reefs adjacent to nurseries. For mean fish density adjacent to nurseries, we averaged fish densities of all sites located between 0 and 1.2 or 5.2 km from nurseries, respectively. For total reef fish abundance adjacent to nurseries, we averaged fish densities of all sites located between 0 and 1.2 or 5.2 km from nurseries, respectively, and multiplied this by total coral reef surface area (see 'Habitat dimensions' above) at these distances. We also did the same analyses with habitat surface area of (1) mangroves, (2) seagrasses, and (3) mangroves and seagrasses combined, respectively, as the predictor variables to examine the relationships between nursery habitat surface area and adult reef fish density/abundance.

## RESULTS

The general linear mixed-effects models supported the full model (~distance + dependence + interaction)

as the most likely ( $>0.999$  model probabilities as measured by  $AIC_c$  weights) for both density and biomass (Table 2). The marginal  $R^2$  ( $R_m$ ) was low for both density and biomass (5.6 and 7.7%, respectively) despite a high total variance explained (63 to 72%) over all fixed effects and random factors as indicated by the conditional  $R_c$  (i.e. most of the variance was explained by the random effects of species nested within island) (Table 2). The variance explained by the factors coral reef cover and coral reef height was consistently low (all  $R_m \leq 0.4\%$ ; see Supplement 2), so

we present only the simpler (coral reef variables excluded) models in the main text henceforth.

When we split the species into high-, low-, and no-dependence groups, the greatest  $R_m$  was for the high-dependence group for both density and biomass (9.9 and 19.2%, respectively), as predicted (Table 2). The decline in density and biomass with increasing isolation from nursery habitats was strongest for the high-dependence group, supported for the low-dependence group, and weak or non-existent for the no-dependence group (Fig. 2, Supplement 3). For the

high-dependence group, the sharpest drop in density occurred within ~2 to 4 km from nurseries, with densities approaching 0 at a distance of ~14 km. Three species belonging to the low-dependence group also showed a decrease in reef density with distance. For this group, 2 species (French grunt *Haemulon flavolineatum* and mahogany snapper *Lutjanus mahogoni*) showed the same strong decline in density with distance as observed for the high-dependence species, while 1 species (four-eye butterflyfish *Chaetodon capistratus*) declined for the first few km, after which densities stabilised. Fish species biomass showed a similar trend as a function of distance from nurseries as density (Supplement 3).

The broader fish community structure (i.e. 51 species) also varied as a function of distance from nurseries. Multivariate analysis showed that the fish community structure at 0 to 4 km from nurseries differed non-randomly from that at  $>4$  km distance (Fig. 3; ANOSIM, global  $R = 0.38$ ,  $p = 0.007$ ), with island also having an effect ( $R = 0.85$ ,  $p < 0.001$ ). At cut-offs of 2 and 3 km, the fish community structure also differed ( $R = 0.30$ ,  $p = 0.021$ ;  $R = 0.38$ ,  $p = 0.007$ , respectively) between areas close versus distant to nurseries, but not at a cut-off distance of 1 or 5 km ( $R = -0.06$ ,  $p = 0.614$ ;  $R = 0.26$ ,  $p = 0.067$ , respectively). Across islands, striped parrotfish *Scarus iseri* (high dependence), French grunt (low dependence), tomtate *Haemulon aurolineatum* (unknown dependence), yellowtail snapper *Ocyurus chrysurus* (high dependence), yellow goatfish *Mulloidichthys martinicus* (unknown dependence), and four-eye butterflyfish *C. capistratus* (low dependence) contributed most (SIMPER analysis, cumulative contribu-

Table 2. General linear mixed-effects models (GLMMs) for reef fish density and biomass as a function of distance to nursery (dist) and nursery dependence class (dep: high, low, none). All models include the species/island nested random effect. We calculated the median of density and biomass over transects per site as the response variables. Included for each model is maximum log-likelihood (LL), number of parameters ( $k$ ), change in Akaike's information criterion corrected for small samples relative to the top-ranked model ( $\Delta AIC_c$ ), their weights ( $wAIC_c$ ), the marginal  $R^2$  of each resampled GLMM ( $R_m$ ) as a measure of the variance explained by the fixed terms, and the conditional  $R^2$  ( $R_c$ ) of each resampled GLMM ( $R_m$ ) as a measure of the variance explained by both the fixed effects and the random factors (Nakagawa & Schielzeth 2013)

Model	LL	$k$	$\Delta AIC_c$	$wAIC_c$	$R_m$	$R_c$
<b>(i) Density</b>						
~dist + dep + dist $\times$ dep	-312.714	9	0	$>0.999$	5.6	71.9
~dist	-329.727	5	33.489	$<0.001$	3.0	64.6
~dist + dep	-329.751	7	37.471	$<0.001$	2.7	68.5
~1 (intercept only)	-344.017	4	65.263	$<0.001$	-	61.1
~dep	-344.045	6	69.245	$<0.001$	0.1	65.3
(a) high dependency						
~dist	-112.586	5	0	$>0.999$	9.9	75.5
~1 (intercept only)	-133.920	4	44.781	$<0.001$	-	64.3
(b) low dependency						
~dist	-113.225	5	0	0.999	4.7	60.0
~1 (intercept only)	-118.709	4	12.987	0.001	-	53.5
(c) no dependency						
~dist	-79.261	5	0	0.604	0.5	77.8
~1 (intercept only)	-78.418	4	0.845	0.396	-	77.4
<b>(ii) Biomass</b>						
~dist + dep + dist $\times$ dep	-322.242	9	0	$>0.999$	7.7	63.2
~dist	-339.424	5	34.657	$<0.001$	4.1	55.1
~dist + dep	-339.907	7	38.639	$<0.001$	3.8	58.9
~1 (intercept only)	-355.279	4	69.511	$<0.001$	-	50.8
~dep	-355.762	6	73.493	$<0.001$	0.1	55.0
(a) high dependency						
~dist	-124.140	5	0	$>0.999$	19.2	56.3
~1 (intercept only)	-147.399	4	48.443	$<0.001$	-	35.6
(b) low dependency						
~dist	-108.520	5	0	0.980	3.1	56.3
~1 (intercept only)	-111.329	4	7.730	0.020	-	52.8
(c) no dependency						
~1 (intercept only)	-79.555	4	0	0.666	-	75.7
~dist	-81.5001	5	1.383	0.334	0.1	75.8

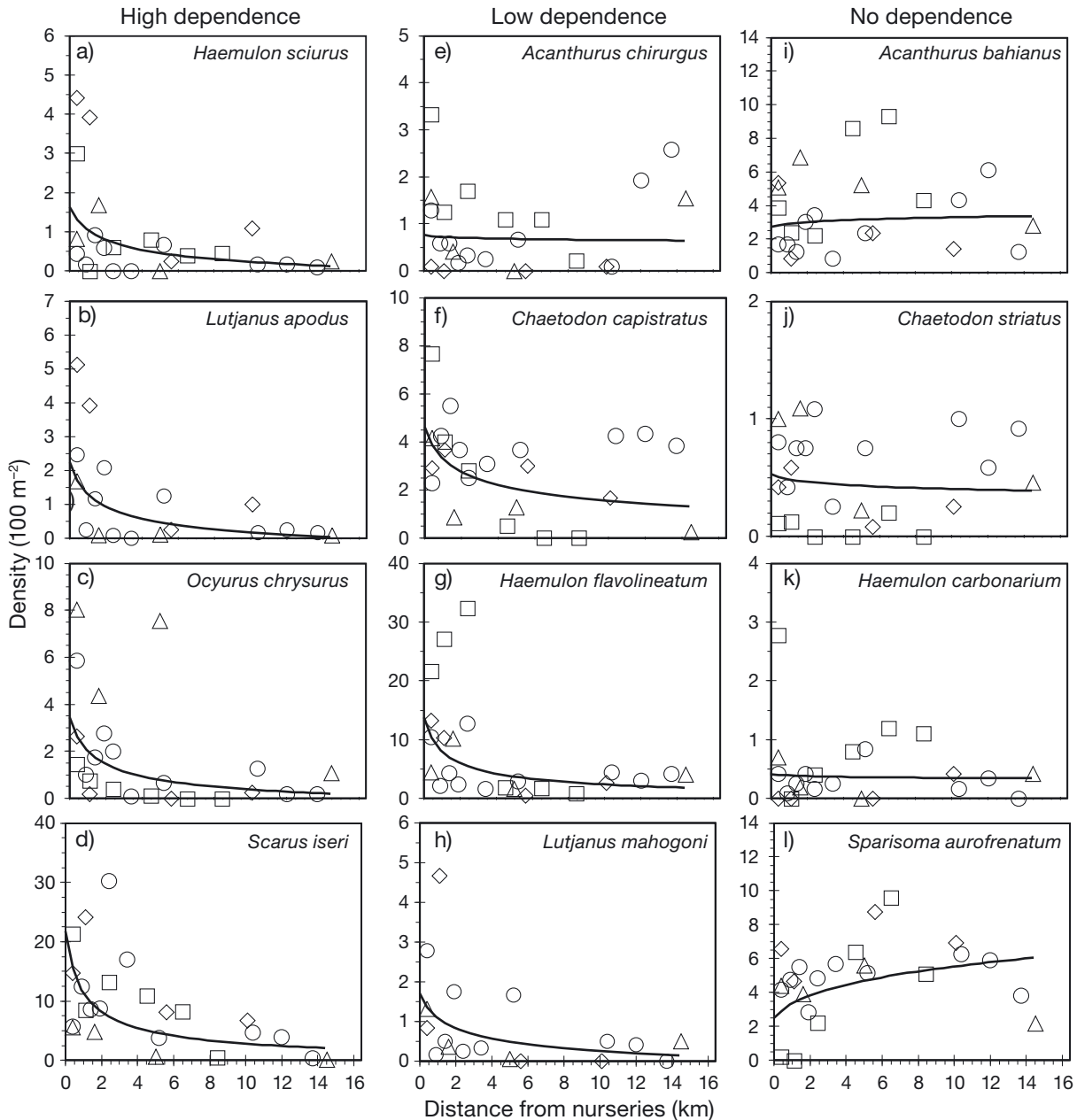


Fig. 2. Adult fish densities on coral reefs as a function of isolation from nursery habitats for species with (a–d) high dependence on nursery habitats, (e–h) low dependence on nursery habitats, and (i–l) no dependence on nursery habitats. Symbols represent data from Aruba ( $\Delta$ ), Bermuda ( $\square$ ), Curaçao ( $\circ$ ), and Grand Cayman ( $\diamond$ ). Logarithmic regression lines are fitted to the combined island data as an indication of the pattern at species level, independent of locality. For species' common names, see Supplement 4

tion: 38%) to the differences in community structure at 0 to 4 km vs. >4 km from nurseries, with their densities higher at sites closer to the nurseries. The no-dependence species, blue tang *Acanthurus coeruleus*, ocean surgeon *Acanthurus bahianus* and redband parrotfish *Sparisoma aurofrenatum* contributed another 15% to the difference (higher densities far from nurseries), and the remainder of the

high/low-dependence species, bluestriped grunt *Haemulon sciurus*, schoolmaster *Lutjanus apodus*, doctorfish *Acanthurus chirurgus*, and mahogany snapper contributed a total of 13% to the community differences (with higher densities close to nurseries). The high abundance of tomtate only at Bermuda at <4 km distance was the main reason for the separate cluster of its sites (Fig. 3). A separate cluster was also



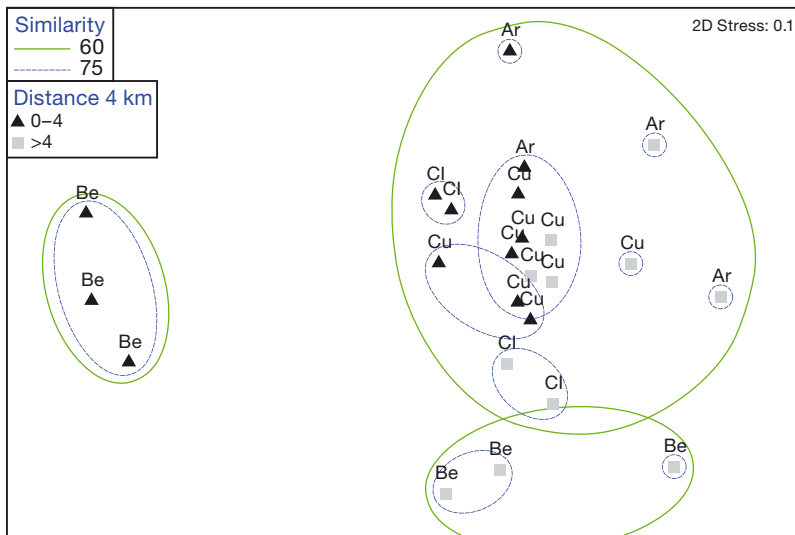


Fig. 3. Non-metric multi-dimensional scaling (nMDS) plot showing differences in the broader coral reef fish community structure (51 species) at distances of 0–4 versus >4 km from mangrove/seagrass nurseries at 4 Caribbean islands (Ar: Aruba; Be: Bermuda; Cl: Cayman Islands; Cu: Curaçao). The plot is a 2-dimensional representation of species abundances across reefs in a multivariate space. Included are clusters at 60 and 75% similarity, respectively

present for Bermuda at >4 km distance that was largely due to the unique presence of emerald parrotfish *Nicholsina usta* and midnight parrotfish *Scarus coelestinus*, and the absence of schoolmaster *L. apodus* and yellowtail snapper *O. chrysurus* compared to all other islands. At 75% similarity, communities at <4 and >4 km distance were generally separated, except for a few sites at Curaçao (Fig. 3).

Total juvenile abundance in nursery habitats was a good predictor of total adult fish abundance and density on adjacent reefs for species with high nursery dependence, at distances of 1.2 as well as 5.2 km from nurseries (see Supplement 4). At the species level, adult reef abundances of 3 high-dependence species had the highest correlations with juvenile abundance in mangroves (bluestriped grunt,  $r = 0.71$ – $0.98$ ; schoolmaster snapper,  $0.86$ – $0.93$ ; striped parrotfish,  $0.10$ – $0.50$ ) rather than in seagrasses, or in mangroves and seagrasses combined. The high-dependence species yellowtail snapper had the highest correlations with juvenile abundance in seagrass beds ( $r = 0.68$ – $0.82$ ) and in mangroves and seagrasses combined ( $r = 0.68$ – $0.82$ ), rather than in mangroves alone. The above ranges in correlation coefficients decreased to  $0.43$ – $0.46$  (bluestriped grunt),  $0.18$ – $0.36$  (schoolmaster),  $-0.31$ – $0.14$  (striped parrotfish), and  $0.54$ – $0.68$  (yellowtail snapper), respectively, when total nursery habitat surface area rather than total juvenile abundance was the predictor vari-

able for the above species–habitat associations (see Supplement 5). However, the highest correlation coefficients for nursery habitat surface area had the opposite patterns than juvenile abundance in terms of habitat importance; correlations between nursery habitat surface area and adult reef density/abundance were highest in seagrasses (rather than mangrove) for bluestriped grunt, schoolmaster, and striped parrotfish, whereas they were highest for yellowtail snapper in mangroves (rather than seagrass). Correlation coefficients were approximately similar for seagrass habitats and for mangrove and seagrass habitats combined (Supplement 5), because the latter correlation was driven by the much larger surface area of seagrasses (factor 44 to 1198, depending on island) as opposed to that of mangroves. Compared to the high-dependence group,

correlation coefficients between juvenile abundance and adult reef density/abundance were much lower for the low-dependence group ( $r < 0.63$ ), although they increased (up to  $r = 0.96$ ) when nursery habitat surface area was considered instead of juvenile fish abundance (Supplement 5). We also found strong correlations (up to  $r = 0.89$ ) for some species/distance combinations of the no-dependence group (see Supplements 4 & 5), but this did not lead to enhanced reef populations (Fig. 2).

## DISCUSSION

We have identified a strong spatial enhancement of adult reef fishes close (less than ~4 km) to their nurseries, supporting our first hypothesis that densities in the adult habitat decrease with distance from nurseries as the enhancement effect becomes progressively diluted. This finding was not confounded by the effects of local structural complexity of reef habitat (see below). Previous studies have shown that with high connectivity, seagrass fish communities are altered by the presence of nearby mangroves (Nagelkerken et al. 2002, Dorenbosch et al. 2006) and reef fish communities are altered by the presence of nearby seagrass beds (Grober-Dunsmore et al. 2007) or nearby mangroves (Mumby et al. 2004, Olds et al. 2012). However, these studies focused solely on

changes in fish community structure on reefs close to nursery habitats (typically up to 1 km) and did not investigate how abundances of species with different nursery dependence changed across broader spatial scales as a function of nursery isolation, leading to a gap in understanding of the distance up to which cross-ecosystem reef enhancement is effective. Even though species identity, size of nursery habitat, and quality of adult reef habitat differed, we showed that fish densities of all high-dependence species and several low-dependence species dropped rapidly on reefs situated just a few km from the nearest nursery habitat, with population densities of some species approaching zero at ~14 km.

Our results revealed that for several species, the subsidy of reef populations by nurseries is largely localized to within ~4 km, with only little movement and spillover to more distant reef areas, and results in different reef fish community structures close to versus isolated (>4 km) from nurseries. Distant reefs still harboured low densities of species with high and low nursery dependence, and this could be due to local recruitment or long-distance dispersal of older individuals away from nurseries (Huijbers et al. 2013). Previous studies have confirmed that in the absence of nursery habitats, background densities of nursery species on reefs are low to zero, depending on the species (Nagelkerken et al. 2002, Dorenbosch et al. 2005), but our study provides new insights into density changes on reefs that lie on the gradient between connected and isolated reefs. Our study further shows that the majority of reef population enhancement of nursery species by nursery habitats occurs up to predictable distances from nurseries, and that presence of nursery habitats alters the broader reef fish community structure.

Our second hypothesis that biomass in the adult habitat decreases with distance from nurseries was also supported. Reef-fish biomass of the high-dependence species decreased in a pattern similar to fish density with distance from nurseries. Home range and dispersal probability usually increase with growing body size (Bradbury et al. 2008). This is especially true for large lutjanids (snappers) that have excellent swimming capabilities and are able to disperse 10s of km, and sometimes up to a few hundred km from their nursery sites (Nagelkerken 2009, Huijbers et al. 2013). Nevertheless, movement is risky (Turgeon et al. 2010) and fishes migrating from nurseries onto reefs would be expected to reduce (but not completely avoid) their dispersal to more isolated reefs as long as local resources and conditions remain favourable for survival and growth. As a result, the mature

individuals responsible for larval replenishment show strong spatial patterning. This is important for management because a spatially restricted distribution of reef fish on narrow island fringing-reef habitats makes them easier to manage due to the predictability of their distribution, but simultaneously more prone to overharvesting.

Limited dispersal by nursery-dependent species to reefs isolated more than a few km from nurseries is the most plausible explanation for the density dilution effects we observed (as shown in Fig. 2), but alternative explanations should also be considered. These include differences in (1) settlement, (2) survival, (3) fishing pressure, (4) habitat (coral reef) complexity, (5) food sources between reefs close to, and isolated from, nurseries, respectively, and (6) alternative source habitats that could act as nurseries. However, each of these alternatives are unlikely based on the following arguments. First, juvenile settlement of nursery species is low to absent on reefs and is mainly restricted to vegetated inshore habitats such as mangroves or seagrass beds (Nagelkerken et al. 2000a); this was also the case in our study (data not shown). Species of the no-dependence group with similar behaviour and requirements as nursery species had no changing trend for density with distance from nurseries. Second, while we did not measure survival, predation pressure is likely to be higher close to nurseries because estuaries and bays also enhance populations of local predators and regularly attract offshore predators (Sheaves et al. 2015, Harborne et al. 2016); therefore, differences in predation pressure cannot explain the decreasing abundance pattern with distance from nurseries. Third, although fishing pressure differed among islands (high: Curaçao; low: Aruba, Bermuda, Grand Cayman), all islands had the same pattern of decline. In Curaçao, fishers specifically target nursery species on reefs close to nurseries because fish densities are typically higher there (I. Nagelkerken pers. obs.). This is exacerbated because artisanal reef fishermen dock their boats within mangrove/seagrass embayments, and fish on nearby reefs to save time and fuel. Fourth, coral reef elevation and live benthic cover, both of which are conditions that strongly modify fish densities (Jones & Syms 1998, Gratwicke & Speight 2005), did not improve the fit of the models. In fact, the average values of coral cover and height were approximately stable with distance from nurseries. This suggests that the patterns of fish distribution were not confounded by local habitat complexity. This is further supported because the no-dependence group showed no change in density

or biomass distribution with distance from nurseries; if habitat complexity along the distance gradient was the main driver, then the no-dependence species group would also have shown a strong correlation between their density and distance from nurseries. Fifth, fishes might be attracted to bay/estuary mouths because of their higher food abundances (Sheaves et al. 2015). However, species of the no-dependence group did not show such an attraction, even though they were similar to the high/low-dependence groups in terms of family, genus, trophic guild, and ecological function. Sixth, different nurseries than the ones we examined probably did not contribute to the observed patterns. Only 3 habitats were present at our sites (reef, mangrove, seagrass), and we collected fish size-frequency data in each of these habitats. These data, as well as those from many other studies on Caribbean islands, consistently show that juveniles of nursery-dependent species are rarely found on coral reefs (see also meta-analysis by Igulu et al. 2014). Furthermore, we selected our sites in such a way that the gradient of reef sites was located close to only a single nursery area, to reduce possible influxes from other nursery patches that were not included. Although we did not tag the observed fishes to determine their origin, we have previously shown, using stable isotope signatures in otoliths and muscle tissue of the yellowtail snapper *Ocyurus chrysurus* (a high-dependence species) and French grunt *Haemulon flavolineatum* (a low-dependence species), that even though adults can disperse over long distances, most (but not all) of the dispersal from nurseries onto reefs is concentrated at their nearest nursery habitat in Curaçao and Bonaire (Verweij et al. 2008, Huijbers 2012, Huijbers et al. 2013), and a similar mechanism has been confirmed for several Indo-Pacific species (e.g. Nakamura et al. 2008, Kimirei et al. 2013b, Pailon et al. 2014). Hence, the best explanation for the spatially skewed distribution of nursery-dependent species is the enhancement of reef populations by nursery habitats in conjunction with high retention due to restricted dispersal from nurseries, with little effects of local habitat characteristics.

Our finding that for 3 of the 4 high-dependence species, total juvenile abundance in nursery habitats had a strong (i.e.  $r = 0.68$  to  $0.98$ ), positive relationship with adult density and abundance supported our third hypothesis that fish density and abundance in the adult (reef) habitat are directly related to juvenile fish abundance in the nearest nursery habitat. However, juvenile abundance in nursery habitats revealed an opposite outcome as a predictor variable (mangrove important for 3 species, seagrass for 1

species) than nursery habitat surface area as a predictor variable (mangrove important for 1 species, seagrass for 3 species) for reef density/abundance of high-dependence species. Both nursery habitat size (a proxy for quantity) and juvenile abundance (one of the proxies for quality because it reflects the abundance of fishes that have survived in the habitat) showed strong correlations with reef fish density and abundance, so it is likely that both conditions (in addition to others such as habitat structural complexity, regional diversity, hydrodynamic forcing, food and predator abundance) contribute to the magnitude of cross-ecosystem replenishment of reef populations, and underpins the complexity of various seascape metrics that drive nursery function (Mellin et al. 2009). Moreover, use of nursery habitats by juvenile fishes varies across space and time (Mellin et al. 2007a, Kimirei et al. 2011), and patterns of fish diversity and abundance and their link to nursery habitats can vary depending on the scale at which these variables are analysed (Grober-Dunsmore et al. 2007, Mellin et al. 2007b). Nevertheless, by combining studies from different years, seasons, locations, and spatial scales we still observed strong correlations between juvenile and adult populations, suggesting this connectivity has a strong imprint on coral reefs connected to nursery habitats, despite the important roles of other factors.

The restricted spatial distribution of ecologically important nursery species could have important implications for some species' population dynamics and reef functioning. Several of the species we examined have important ecological roles either as predators (snappers *Lutjanus* spp.) that structure local food webs (Stallings 2009, Lamb & Johnson 2010), as grazers (parrotfishes *Scarus* spp.) that keep fleshy reef algae in a cropped state (Mumby et al. 2006, Harborne et al. 2016), or as prey (grunts *Haemulon* spp.) for larger carnivores (Depczynski et al. 2007, Friedlander et al. 2010). The ongoing overfishing of coral reefs globally has diminished populations of many reef fish species, leading to loss of reef resilience, reef productivity, and ecosystem functioning (Newton et al. 2007). Coral reefs close to nurseries could therefore be important to maintain populations of essential reef species that can partially mitigate the increasing negative effects of humans on reef ecosystems. Furthermore, for species that depend on more than one habitat throughout their life cycle, a strong spatial enhancement of populations to areas close to their nurseries has implications for their management because it places their populations at higher risk of human impacts on and modification of coastal

seascapes. Species for which most individuals do not disperse far into adjacent ecosystems from their juvenile habitats might be easier to manage than species that disperse over larger areas because they are largely concentrated on small and spatially predictable adult habitat patches. However, this simultaneously makes them easier to target and more susceptible to overexploitation. Because population replenishment of these species depends on cross-habitat movements, their populations are also sensitive to negative impacts such as habitat fragmentation on dispersal corridors, while human pressure on a single habitat will indirectly affect populations in other connected habitats. Because of the strong nursery–reef connectivity and limited reef dispersal of several nursery species, preserving multiple, smaller, and spatially separated in-shore areas with nursery habitats is therefore likely to be a better approach than preserving a single or a few large nurseries that might have high local replenishment capacity, but restricted replenishment of more distant reefs.

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