

# Spatial and demographic consequences of nursery-dependence in reef fishes: an empirical and simulation study

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**ABSTRACT:** The rainbow parrotfish *Scarus guacamaia* has an obligate dependence on mangroves at juvenile stages, and, as the largest herbivorous fish in the Caribbean region, its distribution has important implications for coral reefs. The effect of connectivity with mangroves on relative density, biomass and size of *S. guacamaia* was assessed from over 65 km of visual surveys from Bonaire, Caribbean Netherlands. In addition, an individual-based, age-structured, mechanistic model (IBM) was developed to explain dispersal patterns from nurseries for *S. guacamaia*. In the IBM, mortality was constant, growth was determined by a von Bertalanffy growth equation, and movement was modeled through a random walk process. Using the IBM, simulations were run to generate patterns of density, biomass, and size with distance from nurseries. Rainbow parrotfish were observed as far as 42 km away from the nearest mangroves on Bonaire. Relative density and biomass showed significant exponential declines with distance from the primary mangrove nursery and were significantly higher in high versus low complexity non-mangrove habitats. Mean size increased linearly with distance ( $r^2 = 0.74$ ), reflecting an absence of smaller individuals with greater distance. These results were closely mirrored by the simulation study: density and biomass declined exponentially with distance from nurseries, and size and age increased following saturating functions. The results suggest that mangroves may have the potential to supply individuals much further than previously thought. Both the empirical and simulation studies reaffirm calls to prioritise protection of reef habitats close to nurseries as well as the nurseries themselves.

**KEY WORDS:** Connectivity · Nursery · Ontogeny · Dispersal · Herbivore · Coral reef · Parrotfish · Individual based model

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## INTRODUCTION

In many animal species, adults and juveniles occupy different habitats. Changes in habitat with ontogeny can reduce intraspecific competition for resources (Branch 1984, Werner & Gilliam 1984), accommodate different requirements for food (Polis 1984), provide size-specific shelter from predation (Eggleston et al. 1990), and facilitate reproduction (Pinder 1986). In tropical seas, a number of fishes that typically occupy reefs as adults can be found as juve-

niles in mangrove (Kathiresan & Bingham 2001) and seagrass habitats (Heck et al. 2003). It has long been proposed that shallow areas serve as nurseries for adult populations on adjacent reefs and are therefore crucial for the species' success (see reviews in Beck et al. 2001, Heck et al. 2003, Sheridan & Hays 2003, Dahlgren et al. 2006).

The majority of research on connectivity with nurseries has focussed on the Caribbean region where a continuum of dependency on non-reef juvenile habitat has been identified (Nagelkerken et al. 2000,

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2002). The continuum ranges from species that are rarely found in non-reef habitats, completing their entire post-settlement lives on reefs, to species that have an obligate dependency on nurseries as juveniles. Along this continuum, 'nursery species' have been defined as those where juveniles are mainly observed in non-reef habitats and adults are mainly documented on reefs (Nagelkerken et al. 2000, Nagelkerken & van der Velde 2002). Whilst the majority of Caribbean reef fishes are not nursery species, many commercially or artisanally important species require specific nursery habitats. For example, the largest species of parrotfish, *Scarus guacamaia* (scarine Labridae; Nagelkerken et al. 2000, Mumby et al. 2004, Dorenbosch et al. 2006), snapper *Lutjanus cyanopterus* (Lutjanidae; Lindeman & DeMaria 2005), and grouper *Epinephelus itajara* (Serranidae; Frias-Torres 2006, Koenig et al. 2007) all appear to have an obligate dependency on non-reef habitats during their early stages.

A location's level of connectivity with nurseries should be reflected in the density, biomass, size and age distribution of the nursery species found therein. When individuals have outgrown nurseries, they enter adjacent habitats as young and small individuals. Over time, individuals may disperse further away. Thus, areas close to nurseries should have higher densities and a greater proportion of smaller individuals than those further away (Huijbers et al. 2013; Fig. 1). This does not preclude large individuals adjacent to nurseries, but does preclude small individuals at greater distances. In addition, a nursery should act as a source of individuals only to habitats within a limited radius (hereafter referred to as a nursery's dispersal radius,  $r_d$ ). This distance will be linked to the mobility of the species in question, the level of recruitment from the nursery, and the spatial

arrangement of adult habitat; therefore  $r_d$  is both species- and location-specific. However, few studies have addressed the dynamics of dispersal from nurseries, and clear patterns of size, density and biomass of reef fishes with distance have rarely been described (but see Huijbers et al. 2013).

The rainbow parrotfish *S. guacamaia* (Cuvier 1829) was chosen as the study species because it has an obligate association with mangroves in its juvenile stages whilst adults are predominantly found in reef habitats (Nagelkerken et al. 2000, Mumby et al. 2004, Dorenbosch et al. 2006; Fig. 1). *S. guacamaia* is the largest herbivorous reef fish in the Caribbean, with a maximum size ( $TL_{max}$ ) of 120 cm total length (TL; Choat et al. 2006) and maximum age of 16 yr (Choat pers. comm in Choat et al. 2012). Although it is commonly observed in the study location, Bonaire (REEF 2014), densities are generally low throughout the species' range, and it is considered conservation-dependent (Comeros-Raynal et al. 2012). On reefs, individuals roam widely within home ranges of at least 1600 m<sup>2</sup> (Mumby & Hastings 2008). Predominantly, congeners are protogynous hermaphrodites (Robertson & Warner 1978) that spawn pelagically within or near to their home ranges (Domeier & Colin 1997) but specific details for *S. guacamaia* are not available. Following larval settlement, juvenile *S. guacamaia* remain in mangrove habitats until they migrate to reefs at larger sizes (Mumby et al. 2004). Although age and size at first maturity remain unknown, it is assumed that juveniles are rarely observed outside of mangroves (Serafy et al. 2003, Mumby et al. 2004, Dorenbosch et al. 2006, but also see Jones et al. 2010, Machermer et al. 2012).

In addition to serving as a model species for investigating nursery function, *S. guacamaia* has the potential to enhance resilience of coral reefs. As reefs

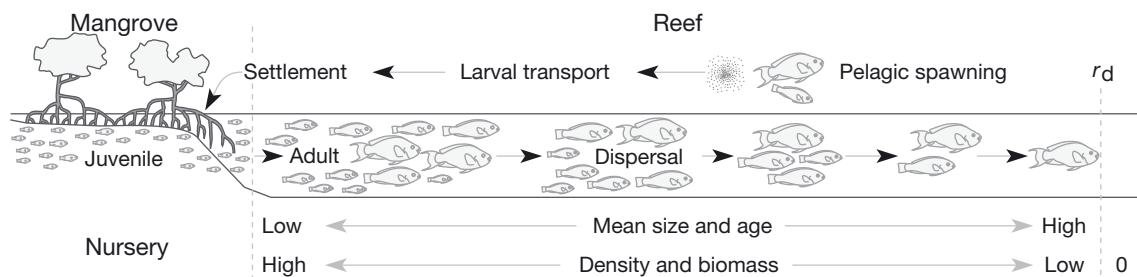


Fig. 1. *Scarus guacamaia* life cycle and hypothetical dynamics of nursery use. Adults spawn pelagic eggs from reef areas; larvae settle into mangrove habitats where they remain as juveniles; once old/large enough, individuals leave the nursery as adults and recruit to adjacent reef habitats. Over time, adults may disperse further away from the nursery. Thus, density and biomass are hypothesised to decrease with increasing distance, while mean size and age are predicted to increase. Beyond the dispersal radius ( $r_d$ ), reef habitats are no longer supplied with recruits from the nursery

around the world suffer declines in coral cover and increases in algae (Gardner et al. 2003, Pandolfi et al. 2003, Bellwood et al. 2004, McManus & Polsenberg 2004, Bruno et al. 2009, Norström et al. 2009), the role of herbivorous reef fishes in maintaining coral cover, reef integrity, and reef resilience has become increasingly recognised (Bellwood et al. 2004, 2012, Hughes et al. 2007, Ledlie et al. 2007, Mumby et al. 2007, Mumby 2009, Rasher et al. 2012, Graham et al. 2013). Although effects are species-specific (Burkepile & Hay 2010), in general, grazing by herbivores limits macroalgal growth which would otherwise outcompete or overgrow corals and provides substrate for coral recruitment (see review in Birrell et al. 2008). Despite a multi-familial assemblage of species contributing to overall grazing on a reef, in the Caribbean, levels of herbivory are estimated to increase by 16% on reefs adjacent to mangroves, and this is primarily attributable to the supply of *S. guacamaia* from these nurseries (Mumby & Hastings 2008). Therefore, a better understanding of the processes affecting populations of this species and its spatial distribution warrants further investigation.

The aims of this study were to assess how nursery-dependence affects local demographics of *S. guacamaia* over a contiguous expanse of habitat with a gradient of distance from a mangrove nursery. The study tested 4 specific hypotheses concerning rainbow parrotfish *S. guacamaia*: (1) fish density and biomass

decreases with increasing distance from mangroves; (2) fish mean size increases with increasing distance from mangroves; (3) fish density and biomass in non-mangrove habitats are higher around Bonaire, an island with mangroves, compared to Klein Bonaire, an island without; (4) fish are larger around Klein Bonaire than around Bonaire.

## MATERIALS AND METHODS

### Study site

The study was conducted on the islands of Bonaire and Klein Bonaire, Caribbean Netherlands ( $12^{\circ} 10' N$ ,  $68^{\circ} 17' W$ ). The islands lie on an oceanic platform in the southern Caribbean, ~85 km north of the coast of Venezuela (Fig. 2). Bonaire is 35 km long between its most distant points and a maximum of 10 km wide. Klein Bonaire is a small (4 km long) sister island that lies to the west of Bonaire's capital, Kralendijk. Although Klein is only 850 m away at its shortest distance, it is separated by depths of >100 m. Both islands are surrounded by a fringing reef system characterised by a shallow gently sloping terrace 10 to 300 m wide that stretches from the shoreline to the drop-off at a depth of 10 to 15 m.

The predominant easterly trade winds create a coastline with high wave exposure on the north and

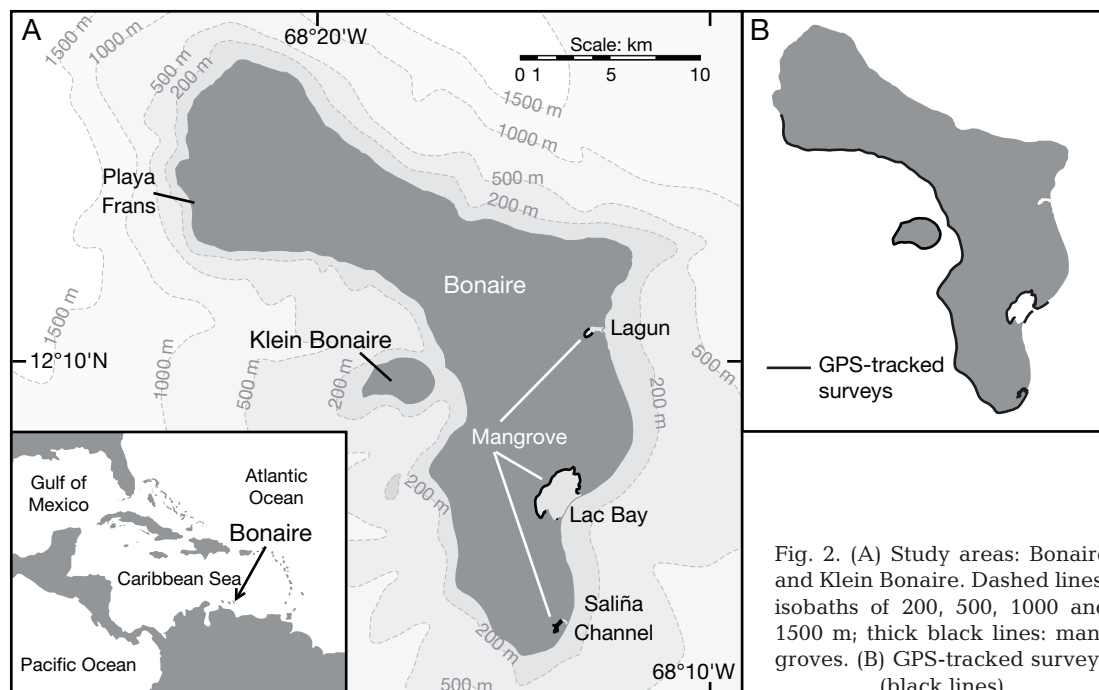


Fig. 2. (A) Study areas: Bonaire and Klein Bonaire. Dashed lines: isobaths of 200, 500, 1000 and 1500 m; thick black lines: mangroves. (B) GPS-tracked surveys (black lines)

east side of Bonaire, with more sheltered habitats to the west and around Klein Bonaire. The shallow terrace on the windward coast is dominated by sargassum, crustose coralline algae and gorgonians (IUCN 2011). Historically, the leeward coast was characterized by abundant *Acropora* spp. on the shallow terrace near to shore. However, the remnants of these communities can now be seen as large expanses of rubble, sand, and skeletal platforms that are mixed with massive corals and gorgonians.

On Bonaire, the largest mangrove area is found in Lac Bay (comprising over 90% of the island's mangrove coverage), with a smaller area in Lagun and a still smaller area lining a man-made channel used (historically) to supply water to the salt production industry in the salina system (hereafter referred to as Saliña Channel; Fig. 2). The dominant red mangrove *Rhizophora mangle* creates a 0.5 to 5 m wide zone of subtidal prop root habitat above sand and silt sediments. Depths range from <1 to 3 m and seagrass and algae are abundant. The coverage of mangroves around Bonaire and the absence of mangroves around Klein Bonaire remained stable for over 16 yr prior to this study (confirmed through Google Earth satellite imagery; and see Hylkema et al. 2014). In 2010, fishing for all species of parrotfish (scarine Labridae) was banned around Bonaire and Klein Bonaire. Prior to this time, parrotfishes were not the target of fisheries (Hawkins & Roberts 2004a,b). Thus, the distribution of *Scarus guacamaia* observed in surveys was not affected by historical changes in mangrove coverage or fishing activity.

### GPS-tracked surveys

After establishing that *Scarus guacamaia* was predominantly observed at 1 m depth (see the Supplement at [www.int-res.com/articles/suppl/m525p171\\_supp.pdf](http://www.int-res.com/articles/suppl/m525p171_supp.pdf)) sampling was focused at this depth. In order to collect sufficient data on a species with a relatively low density and patchy distribution, it was necessary to cover as much area as logistically possible. Thus, conventional belt transects were not used. Instead, the entire coastline of interest was surveyed by 2 snorkellers swimming parallel along the 1 m isobath, and towing a handheld GPS (Garmin GPSMap 78s). Along this track, the location (GPS waypoint) and size of all *S. guacamaia* observed were recorded within a belt ~15 m wide in non-mangrove habitats and up to 5 m wide in mangroves.

A total of 65.25 km of surveys was conducted, with 1.25 and 4.5 km in mangroves of Saliña Channel and

Lac Bay, and 11.75 and 47.75 km in non-mangrove habitats of Klein Bonaire and Bonaire, respectively. In the mangrove study areas, all habitat was sampled where depth and visibility permitted observations on snorkel: i.e. >40 cm depth and >3 m visibility. Four non-mangrove areas were surveyed: (1) the coastline running clockwise from the entrance of Saliña Channel to Playa Frans (the furthest point on Bonaire from mangroves, 42 km away), (2) the reefs across Lac Bay, (3) the coastline running north of Lac Bay for 1.25 km, and (4) the entire coast of Klein Bonaire (Fig. 2). The coastline from Saliña Channel to Lac Bay was too exposed to waves to sample safely, and the mangrove area in Lagun was avoided due to its proximity to Bonaire's waste-disposal landfill site. In non-mangrove areas, the change in habitat was recorded on the GPS track, distinguishing high versus low complexity substratum at a landscape scale through visual assessment. High complexity substratum had abundant structures (i.e. at least one every 5 m of track) providing vertical relief >1 m tall, and was predominantly hard substratum habitat composed of live corals, their skeletal remains and rock. All other habitat encountered was categorised as low complexity substratum, which was predominantly hard substratum composed of limestone pavement, low-relief reef, and eroded coral skeletons, and also included rubble and sand (see the Supplement for further details). The track was considered to have changed habitat if an expanse of contrasting habitat >10 m long was encountered.

Sizes of *S. guacamaia* were estimated *in situ* on snorkel. For individuals <20 cm TL, size was estimated to the nearest cm. Sizes >20 cm TL were estimated in classes of 5 cm increments. Prior to data collection, observers were trained in estimating size underwater and achieved an accuracy of >90%. In addition, a scale marked with 5 cm increments was used *in situ* to assist in size estimation. Biomass of each individual ( $b_i$ ) in g was estimated from its length ( $TL_i$ ) using an allometric relationship established by Bohnsack & Harper (1988; cited in Froese & Pauly 2014):  $b_i = 0.0155 \times TL_i^{3.063}$ .

### Analysis of relative density and biomass with distance from mangroves

The track was divided into 1 m segments. Each segment was coded for habitat and the number and total biomass of *Scarus guacamaia* observed. It was then possible to sample the number of individuals and total biomass along this track within non-over-

lapping transects of either high or low complexity habitat. The track was divided into transects as close to 1.5 km long as possible, with the exact sizes determined by the lengths of contiguous sections of a single habitat type. For low complexity habitat, transect size ranged from 1484 to 1627 m ( $n = 22$ ), and because of the smaller contiguous expanses of high complexity substratum, this habitat included a 130 and 892 m long transect and the remainder ( $n = 9$ ) were from 1415 to 1902 m long.

Data for relative densities were fitted to a generalized linear model (GLM) using a Poisson framework, and biomass to a GLM with a Gamma distribution. Both models used habitat type as a factor (low versus high complexity) and distance from mangroves ( $m_{\text{dist}}$ , calculated as the mean of a transect's constituent 1 m segments) as a covariate. Different transect lengths were accounted for with an offset using the natural logarithm of transect length. Because of the negligible size of other mangrove areas,  $m_{\text{dist}}$  was calculated from mangroves in Lac Bay, and accounted for land so that  $m_{\text{dist}}$  represented the shortest distance an individual could swim over habitat <30 m deep. For transects on Klein Bonaire,  $m_{\text{dist}}$  was calculated incorporating the shortest distance to cross the channel from Bonaire. Although  $m_{\text{dist}}$  corresponds to distances from mangroves in Lac Bay, metrics describing the furthest distance from mangroves that *S. guacamaia* were observed in this study correspond to whichever area of mangroves was closest.

#### Analysis of size with distance from mangroves

It was necessary to calculate mean size ( $\overline{TL}$ ) from a standardised number of individuals, and because this number varied widely within transects (with the expected trend of decreasing with  $m_{\text{dist}}$ ), a different approach was used. Individuals were ranked with increasing  $m_{\text{dist}}$  and  $\overline{TL}$ s were calculated from non-overlapping groups of 50 (and one group of 49) adjacent individuals. Changes in  $\overline{TL}$  with  $m_{\text{dist}}$  were assessed with a linear regression. In addition, the sizes of individuals from mangrove habitats were compared to those from non-mangrove habitats around Bonaire using a Wilcoxon test.

#### Klein Bonaire versus Bonaire

In order to test whether the deep channel between Klein Bonaire and Bonaire acts as an effective barrier to connectivity, the size, relative density, and bio-

mass of *Scarus guacamaia* from Klein Bonaire were compared to those from Bonaire using Wilcoxon tests. To eliminate the possible effects from a disparity in distance away from mangroves, separate comparisons were also made for size, relative density, and biomass from habitats around Bonaire at the same range of distances from mangroves as those found on Klein Bonaire.

#### Simulation study

A simple individual-based model (IBM) was used to present a parsimonious mechanism of dispersal from nursery habitats over time. The IBM was age-structured and accounted for growth, survival and movement along a continuous one-dimensional coastline that extended to both the east and west of a single mangrove nursery. The model was discretized in time steps of 0.1 yr. At each time step, a set number of age-1 individuals were recruited from the nursery, entering the reef at a distance of 0 m away from mangroves. At the end of each time step, a binomial function determined whether an individual survived ( $p = 0.96$ ), and a multinomial function determined whether individuals were assigned to high, medium or low quality reef habitats, with high being twice as likely as medium, which in turn was twice as likely as low ( $p_{\text{high}} = 0.5725$ ,  $p_{\text{medium}} = 0.285$ , and  $p_{\text{low}} = 0.1425$ ). The probability of survival was calculated as the average of estimates using methods by Jensen (1996), Ault et al. (1998), and Hewitt & Hoenig (2005), and reflects a population where the average longevity of individuals recruited from the nursery was 3.4 yr. However, varying the probability of survival had no effect on the general patterns produced through simulation (see the Supplement for further details).

In the IBM, individuals' movements were modeled through an uncorrelated and unbiased random walk process: at each time step, an individual moved a random distance (drawn from a uniform distribution) between zero and a fixed upper limit either to the east or west of its previous position (see the Supplement for further details). An individual's total length  $TL_i$  corresponded to its age and followed a von Bertalanffy growth function using the parameters estimated by Jones et al. (2010) for *Scarus guacamaia* ( $L_{\infty} = 123.06$ ,  $K = 0.293$  and  $t_0 = -0.385$ ). An individual's biomass ( $b_i$ ) in g was estimated from  $TL_i$  using the allometric relationship listed above.

Using the mechanistic IBM described above, simulations were run in order to investigate the

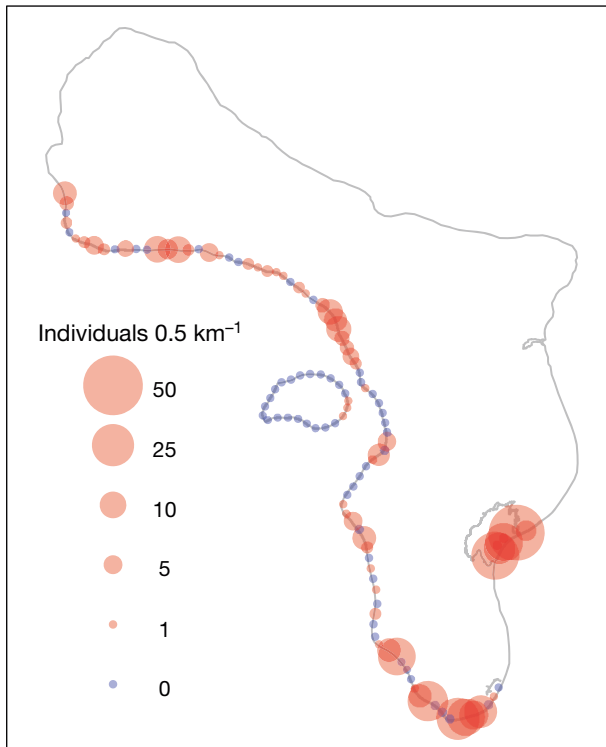


Fig. 3. Distribution of *Scarus guacamaia* in non-mangrove habitats from GPS-tracked surveys

manner in which size, age, density and biomass of *S. guacamaia* are likely to change with increasing distance from mangroves. Each simulation was run for 16 yr to cover the maximum longevity of *S. guacamaia*. The simulations were repeated 1000 times, and mean size, age, density and biomass were calculated from 2 km sections along the virtual reef habitat. These data were used to define curves representing the changes in these metrics with distance from mangrove nurseries.

Table 1. Wilcoxon test (*W*) results from comparisons in relative density, biomass and size of *Scarus guacamaia* observed in mangrove vs. non-mangrove habitats, and Klein vs. Bonaire on non-mangrove habitats. TL: total length. Bonaire2: data from surveys on Bonaire at the same range of distances from mangroves as surveys from Klein Bonaire.  $n_1/n_2$ : sample sizes

Comparison		$n_1$	$n_2$	<i>W</i>	<i>p</i>
Size (TL cm)	Mangrove vs. non-mangrove	475	399	4438.5	<0.05
	Klein vs. Bonaire	3	399	55.5	<0.05
	Klein vs. Bonaire2	3	41	115.5	<0.05
Relative density (ind. 1.5 km <sup>-1</sup> )	Klein vs. Bonaire	8	33	256	<0.05
	Klein vs. Bonaire2	8	6	1	<0.05
Biomass (kg 1.5 km <sup>-1</sup> )	Klein vs. Bonaire	8	33	232	<0.05
	Klein vs. Bonaire2	8	6	7	<0.05

representing the changes in these metrics with distance from mangrove nurseries. Levels of recruitment and dispersal are both unknown parameters for *S. guacamaia* in Bonaire and inestimable from survey data. Therefore, in order to investigate the effects of varying these parameters, the simulation exercise was repeated with yearly recruitment from nurseries to reef habitats at levels ranging from 10 to 10 000 individuals and with maximum step sizes in the random walk process ranging from 2 to 10 km.

All statistical analyses and simulations were performed using R (R Core Team 2014).

## RESULTS

### Mangrove versus non-mangrove habitats

During GPS-tracked surveys around Bonaire, 475 individuals were observed in mangroves (405 from Lac Bay and 70 from Saliña Channel) and 399 individuals were recorded in non-mangrove habitats (Fig. 3). Rainbow parrotfish found in mangroves were predominantly of juvenile sizes (mean  $\pm$  SD = 13.8  $\pm$  9.3 cm TL) and the majority of those in non-mangrove habitats around Bonaire were adult (49.5  $\pm$  16.3 cm) and significantly larger (Table 1, Fig. 4). Only 16% of *Scarus guacamaia* were found as solitary individuals, 11% as pairs and the remainder (73%) were found in close groups of up to 30 individuals.

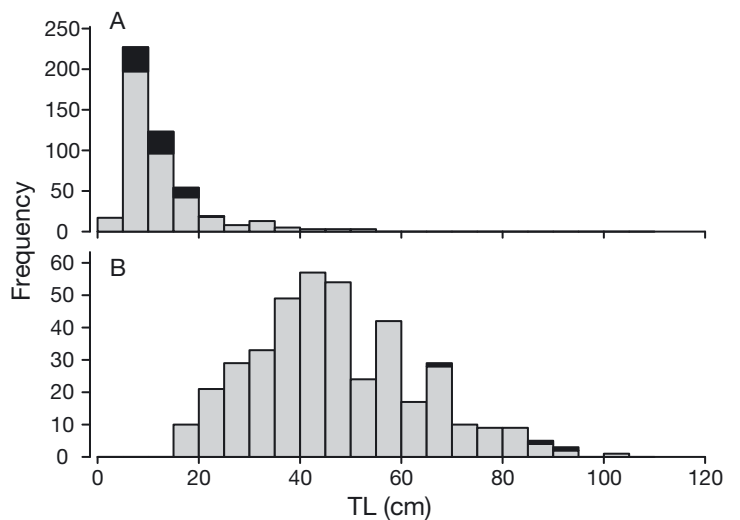


Fig. 4. Size-frequency distributions for total length (TL) of *Scarus guacamaia* in (A) mangrove and (B) non-mangrove habitats. Light grey bars: individuals observed in (A) Lac Bay and (B) around Bonaire; black bars: individuals from (A) Saliña Channel and (B) Klein Bonaire

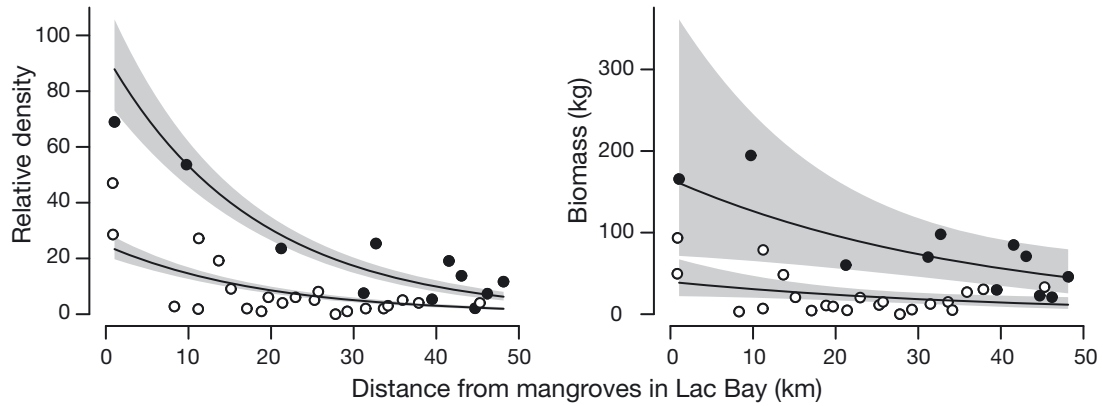


Fig. 5. Relative density (individuals  $1.5 \text{ km}^{-1}$ ) and biomass ( $\text{kg } 1.5 \text{ km}^{-1}$ ) of *Scarus guacamaia* with distance from mangroves in Lac Bay. Circles: transects from high (●) and low (○) complexity habitat. Curves: best-fit lines from generalized linear models (GLM) and their respective 95% CI (grey area)

**Relative density, biomass and size with distance from mangroves**

Individuals were observed as far as 42 km away from the closest area of mangroves, the furthest distances sampled. However, both relative density and biomass of *Scarus guacamaia* displayed significant exponential declines with  $m_{\text{dist}}$  and significantly higher values in high versus low complexity habitats that closely matched their respective GLMs (Fig. 5, Table 2).  $\overline{TL}$  increased significantly with  $m_{\text{dist}}$  with a strong regression ( $df = 1, 5; F = 14.18, p < 0.05, r^2 = 0.74$ ; Fig. 6).

**Klein Bonaire versus Bonaire**

Only 3 *Scarus guacamaia* were observed around Klein Bonaire. The relative density and biomass were

Table 2. Generalized linear model (GLM) results: coefficient estimates (Coef.  $\beta$ ), SE, associated Wald's z-score, and p-value for all predictors (intercept, distance from Lac Bay [ $m_{\text{dist}}$ ] and habitat type) from GLMs for both relative density and biomass of *Scarus guacamaia*. Both models use an offset of the natural log of the transect lengths

Comparison		$n_1$	$n_2$	W	p-value
Size (TL cm)	Mangrove vs. non-mangrove	475	399	4438.5	<0.05
	Klein vs. Bonaire	3	399	55.5	<0.05
	Klein vs. Bonaire	2	41	115.5	<0.05
Relative density (ind. $1.5 \text{ km}^{-1}$ )	Klein vs. Bonaire	8	33	256	<0.05
	Klein vs. Bonaire	2	8	6	<0.05
Biomass ( $\text{kg } 1.5 \text{ km}^{-1}$ )	Klein vs. Bonaire	8	33	232	<0.05
	Klein vs. Bonaire	2	8	7	<0.05

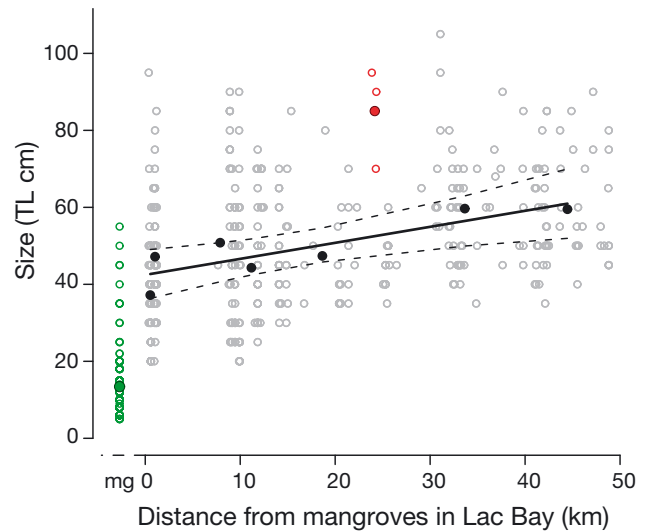


Fig. 6. Size (total length; TL cm) of *Scarus guacamaia* with distance from mangroves in Lac Bay ( $m_{\text{dist}}$ ). Open circles: sizes of individuals from mangrove habitats (mg, green); non-mangrove habitats around Bonaire (grey); and Klein Bonaire (red); filled green and red circles: means for respective habitat. Filled black circles: means of consecutive groups of 50 individuals from non-mangrove habitat around Bonaire. Solid line: resultant linear regression; dashed lines: 95% CI

significantly lower (by factors of 38 and 9 respectively) than in non-mangrove habitats around Bonaire (Table 1, Fig. 7). In addition, individuals were significantly larger on average by 35.4 cm around Klein (Table 1, Figs. 6 & 7). When comparisons were standardised for distance from mangroves (i.e. survey data from Bonaire at the same range of distances from mangroves as those in surveys from Klein), relative density and biomass remained signif-

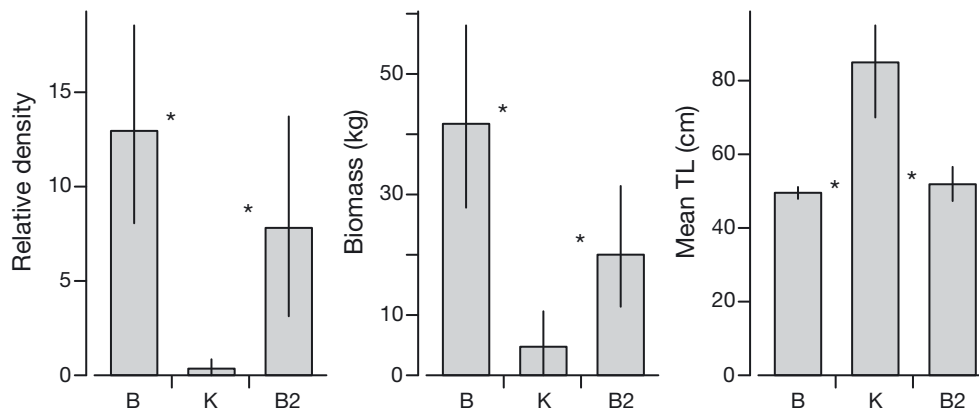


Fig. 7. Mean relative density (individuals 1.5 km<sup>-1</sup>), biomass (kg 1.5 km<sup>-1</sup>) and total length (TL cm) of *Scarus guacamaia* from Bonaire (B), Klein Bonaire (K), and Bonaire at the same range of distances from mangroves as habitats around Klein Bonaire (B2). Error bars: bootstrapped 95% CIs. \*p < 0.05

icantly lower around Klein (by factors of 23 and 4 respectively) and individuals remained significantly larger (by an average of 33.2 cm; Table 1, Fig. 7).

### Simulations

From the simulations, the mean size and age of *Scarus guacamaia* with distance from the mangrove nursery followed increasing saturating functions with intercepts shifted above zero and size approaching the asymptote more quickly than age (Fig. 8). The largest determinant of mean size and age was the increasing absence of smaller, younger individuals with distance from mangroves. For both size and age, the level of recruitment did not affect the curves, but did affect  $r_d$  (calculated as the mean of the furthest individual from each of the 1000 simulations at a single level of recruitment). As such,  $r_d$  increased linearly with the log of the corresponding recruitment level. Both density and biomass followed exponential declines with distance from mangroves. Because the mean size of individuals increased with distance, biomass declined at a proportionally slower rate than density. At any given distance, biomass and density were scaled to the level of recruitment (i.e. at 5 km away from mangroves, density was twice as high with 1000 individuals recruiting yr<sup>-1</sup> than with 500). The relationship with the level of dispersal was more complicated: at a constant level of recruitment, the asymptotic increases in size and age with distance from mangroves were more rapid at lower maximum step sizes; immediately adjacent to the nursery, density and biomass scaled logarithmically with the inverse of the maximum step size, but the exponential declines in density and biomass with distance

were more rapid at lower maximum step sizes, and  $r_d$  increased linearly with maximum step size. In addition, density and biomass scaled directly to the quality of the habitat: at any given distance from the mangrove nursery, density and biomass in low quality habitat were half the values of those in medium quality habitat and a quarter of the values from high quality habitat.

### DISCUSSION

All of this study's hypotheses were supported by the empirical data from Bonaire: (1) density and biomass of *Scarus guacamaia* decreased with increasing distance from mangroves, (2) mean size of *S. guacamaia* increased with increasing distance from mangroves, (3) density and biomass of *S. guacamaia* in non-mangrove habitats were higher around Bonaire than Klein Bonaire, and (4) *S. guacamaia* were larger around Klein Bonaire than around Bonaire. Thus, the level of connectivity between adult habitats and nurseries on Bonaire has a profound and predictable effect on the distribution of rainbow parrotfish. Furthermore, the simulation study using the parsimonious IBM closely replicated the patterns observed from empirical data.

While numerous studies have described higher densities of nursery species in habitats closer to nurseries than those further away (reviewed in Nagelkerken 2007), few displayed significant declines in density along gradients of connectivity with nurseries (Nagelkerken et al. 2000, Dorenbosch et al. 2007), and only one showed a change in size along this gradient (Huijbers et al. 2013). It is expected that such patterns underlie distributions of nursery species in



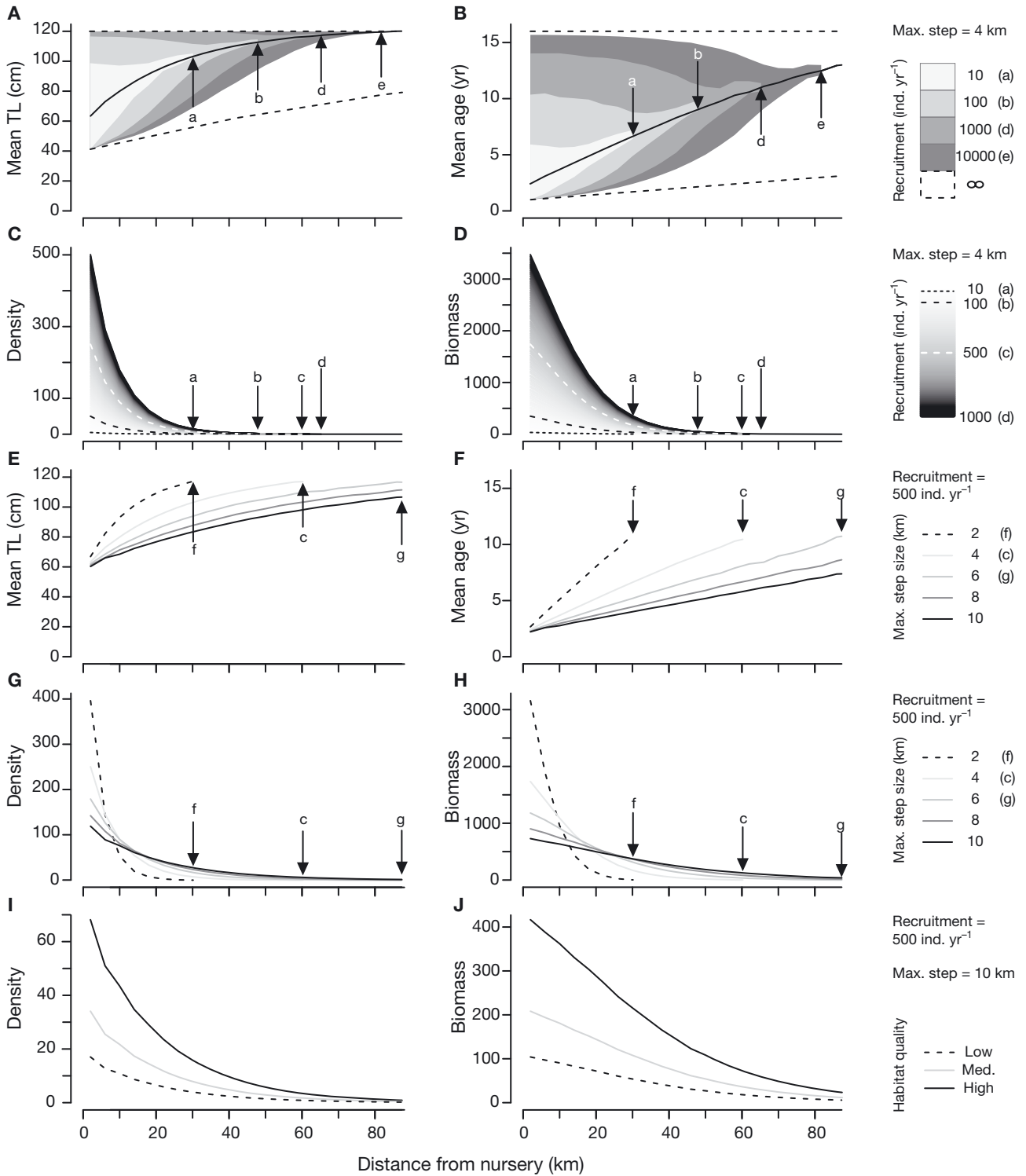


Fig. 8. Simulation results: (A,E) size, (B,F) age, (C,G,I) density and (D,H,J) biomass of *Scarus guacamaia* with distance from mangrove nursery. Curves: mean results at varying levels of (A–D) recruitment (# individuals  $\text{yr}^{-1}$  moving from nursery to reef habitat), (E–H) dispersal (i.e. maximum step size in random walk process), and (I,J) habitat quality (key to the right of each pair of graphs). At a fixed maximum step size, mean size (A) and age (B; black curves) are consistent among different levels of recruitment while the range in size and age (shaded areas) varies; their hypothetical maximum and minimum limits with recruitment at infinity (dashed lines) are displayed. Arrows: mean distance of furthest individual from mangroves ( $r_d$ ) at the combination of recruitment level and dispersal (lowercase letters). Units: # individuals  $2 \text{ km}^{-1}$  of one-dimensional reef (density);  $\text{kg } 2 \text{ km}^{-1}$  (biomass)

general, but may be obscured in locations where dispersal radii from multiple nurseries overlap and for species that also settle outside of nurseries. In addition, while distance is an appropriate proxy for connectivity for the relatively mobile *S. guacamaia* in the expanse of contiguous habitats of Bonaire, this proxy may be less suitable for other species or different locations where inhospitable habitats present barriers to movement (Turgeon et al. 2010). Furthermore, the current study accounted for the low abundance and patchiness of *S. guacamaia* by using sampling units covering areas far larger than is typical for underwater visual censuses of reef fishes. As a result, the target species was observed in all but one transect along the coast of Bonaire. Sampling in other studies may be insufficiently tailored to nursery species that are uncommon (e.g. larger Lutjanidae, scarine Labridae and Serranidae), form schools (e.g. Haemulidae and Lutjanidae), or are heavily fished, both currently (e.g. *Sphyraena barracuda* and *Ocyurus chrysurus*) or historically (e.g. *Epinephelus striatus* and *E. itajara*).

*S. guacamaia* was observed as far as 42 km away from the nearest mangroves, the furthest distance possible around Bonaire. This contrasts greatly with conclusions that this species is only found close to mangroves (Jones et al. 2010), and  $r_d$  is at least 3 times greater than the 13 km previously described for *S. guacamaia* in Aruba (Dorenbosch et al. 2006). Even in the furthest transect sampled, the presence of *S. guacamaia* was ecologically relevant, represented by 11 individuals with an estimated biomass of >43 kg, which respectively equate to 17 and 24% of the values from transects with the highest density and biomass. Dispersal on a similar scale to *S. guacamaia* in Bonaire has been documented for other species: stable isotope analyses have tracked adults to nurseries at least 30 km away for *Lutjanus ehrenbergii* (McMahon et al. 2012), and 9 km away for *Lutjanus fulviflamma* (Kimirei et al. 2013); dispersal over scales of 5 to 15 km has been inferred from successive years of demographic data for *Abudefduf saxatilis*, *Lutjanus apodus*, *Lutjanus griseus* and *S. barracuda* (Jones et al. 2010); and tagging studies have recorded movements of 10 km for *L. griseus* (Luo et al. 2009) and up to 400 km for *E. itajara* (Koenig et al. 2011) from nurseries. The manner in which individuals disperse is largely undescribed, but tracking of *L. apodus* revealed that individuals moved in steps both away from and back towards the nursery (Verweij et al. 2007) in a similar fashion to the random walk process in the IBM. However, dispersal may be more punctuated in species that have complex social sys-

tems or form large schools, and in such cases the limits of  $r_d$  are unlikely to be represented by solitary individuals. Other behaviours or more complex spatial arrangements of habitats may also affect movement in ways not reflected by the random walk process. Nonetheless, the parsimonious IBM used in the simulations closely replicated the patterns of *S. guacamaia* observed around Bonaire and expands upon the approach taken in Huijbers et al. (2013).

It is currently unclear whether the minimum limit for  $r_d$  from Bonaire (42 km) is applicable to *S. guacamaia* in alternative locations. Multiple local factors may affect dispersal. For example, Bonaire has a relatively one-dimensional arrangement of adult habitat forming a thin band around both the study islands. In locations where habitat is more 2-dimensional, densities may decline more rapidly with distance from mangroves. As dispersal requires suitable intermediate habitat through which an individual can travel, deep channels (such as in the current study) or a lack of habitat in which to forage or shelter may also reduce dispersal. Although Klein Bonaire is only 850 m away from Bonaire at its closest point, the >100 m deep channel separating these islands has a substantial effect on connectivity between Klein Bonaire and Bonaire. The density of individuals on Klein Bonaire is lower and their mean size is higher than those contained within the limits of the regression lines at the furthest distances from mangroves around Bonaire. Thus, the channel reduces connectivity with mangroves by the equivalent of at least 20 km of contiguous shallow habitat. In *E. itajara*, dispersal is thought to be density-dependent (Koenig et al. 2011), and the simulation study indicated that larger populations disperse further, which, amongst other factors, may be related to the size of the nursery habitat (Halpern 2004). Therefore, fishing and the removal of mangrove habitat may reduce  $r_d$  by decreasing population sizes. In addition, if  $r_d$  is a function of age and population size, as indicated by the simulation study, any reduction in average longevity through fishing pressure will also reduce  $r_d$ .

Although use of nursery habitats is thought to be adaptive with regards to access to food (Beck et al. 2003) or refuge from predators (Heck et al. 2003, Sheridan & Hays 2003), reef fishes with an obligate dependence on nursery habitats may be at a disadvantage with regards to the amount of adult habitat they can exploit: their distributions will be restricted to within a limited distance of nursery habitats (Kendall et al. 2003, Serafy et al. 2003, Adams et al. 2006). Therefore, it may be expected that obligate

use of nurseries is a trait found only in species that disperse widely across adult habitats. This may explain why *S. guacamaia* was found so far away from mangroves in the current study with no apparent density-dependent shortage of foraging habitat or shelter sites driving this dispersal. Conversely, nursery species with less widespread movements would be expected to settle directly into adult habitats as well as nurseries. This prediction is hard to judge based on our current understanding of the dynamics of reef fishes. However, in the Caribbean region, obligate use of nurseries has thus far been described for just 3 species of reef fish: *S. guacamaia*, *E. itajara* and *L. cyanopterus*. All 3 species use mangroves as nurseries (Mumby et al. 2004, Lindeman & DeMaria 2005, Frias-Torres 2006), and whilst long-distance dispersal from nurseries has only been documented in *E. itajara* (up to 400 km away, Koenig et al. 2011), widespread dispersal, albeit probably over more modest scales, is also feasible in *S. guacamaia* and *L. cyanopterus*. Size is an indication of mobility (Kramer & Chapman 1999), and although they are smaller than *E. itajara* (>200 cm, Bullock et al. 1992), these species have maximum sizes of at least 120 cm TL (Allen 1985, Choat et al. 2006). In addition, *S. guacamaia* moves within extensive home ranges (1600 m<sup>2</sup>, Mumby & Hastings 2008), and *L. cyanopterus* migrates to spawning sites (reviewed in Sadovy de Mitcheson et al. 2012).

The current study assumes that *S. guacamaia* does not settle into non-mangrove habitats, and therefore wherever a rainbow parrotfish was observed it must have first moved from mangroves to get there. An alternative interpretation is that *S. guacamaia* predominantly settles into mangroves, but also uses other habitats at a low level, undetected in previous studies (Mumby et al. 2004). In such a scenario, low (background) densities of *S. guacamaia* would be evident in locations not connected to nurseries (i.e. separated from nurseries by excessive distance or inhospitable habitat), and could therefore explain the 3 individuals found around Klein Bonaire and those far away from mangroves on Bonaire. However, the data do not support this hypothesis: while the mean size of individuals found in mangroves was <15 cm TL, no rainbow parrotfish <20 cm were found outside of mangroves. Although the sampling protocol could have been less effective at finding smaller sizes in non-mangrove habitat, this effect should have been consistent. However, the further the distance away from mangroves, the larger the minimum size of individuals observed, such that individuals <35 cm TL were all found at relatively close distances to man-

groves. In addition, even if background settlement outside of mangroves does occur in the study area and is the exclusive origin of individuals found on Klein Bonaire (which ignores the possibility of individuals crossing from Bonaire), this process does not adequately explain the relatively high density of individuals found up to 42 km away from mangroves on Bonaire: densities at this distance are >28 times higher than those around Klein. Thus, although settlement of *S. guacamaia* outside of mangroves cannot be completely excluded (see Robertson pers. comm. in Choat et al. 2012), its influence on patterns of density and size around Bonaire is likely to be negligible. However, a definitive understanding of the relative contribution to the population from settlement inside versus outside of nurseries may only be feasible through tracking juveniles tagged in the mangrove areas and stable isotope analysis of adults.

The importance of protecting nursery habitats is well recognised (Nagelkerken et al. 2002, 2012, Mumby et al. 2004, Dahlgren et al. 2006). More recently, in the Caribbean, coral reefs close to nurseries (i.e. adult habitat with high connectivity to nurseries) have also been identified as priority areas for protection: the higher levels of herbivory through greater densities of (mangrove-supplied) parrotfishes make these coral reefs more resilient (Mumby & Hastings 2008), and commercially exploited nursery species appear to benefit most from protecting these areas (Nagelkerken et al. 2012). The current study suggests that adult habitats close to nurseries are also important as sources of individuals to habitats further away, acting as the gateways through which fish pass to access more distant reefs. However, if fishing pressure is high (likely for such areas with predictably high densities of nursery species) then these reefs may be transformed from sources into sinks. Fishing could, therefore, close these gateways and restrict the connectivity of more distant habitats with nurseries, effectively reducing  $r_d$ . Thus, for multiple reasons, the protection of both nurseries and nearby adult habitats is crucial for the management of shallow tropical marine systems.

The patterns of density, biomass and size of *S. guacamaia* observed around Bonaire are supported by the hypothetical framework developed in the IBM and simulation study. Understanding whether such patterns exist in other nursery species and the scales over which they are manifested is important given these species' ecological roles as herbivores, predators and prey (Nagelkerken et al. 2012), and as targets of fisheries. Incorporating a more advanced appreciation of connectivity and nursery function

into the design and placement of marine protected areas (MPAs) would be of great benefit to the management and conservation of coral reefs.

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