Geographic coupling of juvenile and adult habitat shapes spatial population dynamics of a coral reef fish

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Abstract. Marine spatial population dynamics are often addressed with a focus on larval dispersal, without taking into account movement behavior of individuals in later life stages. Processes occurring during demersal life stages may also drive spatial population dynamics if habitat quality is perceived differently by animals belonging to different life stages. In this study, we used a dual approach to understand how stage-structured habitat use and dispersal ability of adults shape the population of a marine fish species. Our study area and focal species provided us with the unique opportunity to study a closed island population. A spatial simulation model was used to estimate dispersal distances along a coral reef that surrounds the island, while contributions of different nursery bays were determined based on otolith stable isotope signatures of adult reef fish. The model showed that adult dispersal away from reef areas near nursery bays is limited. The results further show that different bays contributed unequally to the adult population on the coral reef, with productivity of juveniles in bay nursery habitat determining the degree of mixing among local populations on the reef and with one highly productive area contributing most to the island's reef fish population. The contribution of the coral reef as a nursery habitat was minimal, even though it had a much larger surface area. These findings indicate that the geographic distribution of nursery areas and their productivity are important drivers for the spatial distribution patterns of adults on coral reefs. We suggest that limited dispersal of adults on reefs can lead to a source–sink structure in the adult stage, where reefs close to nurseries replenish more isolated reef areas. Understanding these spatial population dynamics of the demersal phase of marine animals is of major importance for the design and placement of marine reserves, as nursery areas contribute differently to maintain adult populations.

Key words: Curaçao; dispersal; Ocyurus chrysurus; otolith chemistry; population connectivity; sea grass; source contribution; spatial simulation model; stable isotopes; yellowtail snapper.

Introduction

Animal movement between and within habitats is a key driver of spatial population dynamics. These movement patterns are often caused by changes in an animal's needs, leading to ontogenetic habitat shifts (Werner and Gilliam 1984, Dahlgren and Eggleston 2000). However, a dependence on multiple habitats increases the vulnerability of species when habitats are increasingly lost or fragmented due to increasing urban development and overexploitation (Munday 2004). This also implies that processes occurring in one area may influence individuals elsewhere. Knowledge of spatial population dynamics is thus essential for management of single species as well as for determining boundaries for protected areas at the ecosystem level (Sale 2004).

Habitat heterogeneity creates the potential for source–sink dynamics within a population, a concept in which some patches (sources) yield a demographic excess and export individuals to sink patches (Dias 1996). This theory has predominantly been applied to understand terrestrial population dynamics (e.g., Boughton 1999, Kreuzer and Huntly 2003, Auestad et al. 2010). More recently, source–sink dynamics have been used to understand marine metapopulations (Kritzer and Sale 2006), but mainly focused on differences in larval supply to distinct but connected populations due to ocean current patterns (James et al. 2002, Bode et al. 2006, Figueira 2009, White and Samhouri 2011) or habitat heterogeneity (Shima et al. 2010). Although larval influx might determine the initial productivity of a habitat

patch, little understanding has been gained on how movement patterns during consecutive demersal life stages could influence spatial population dynamics.

Ontogenetic habitat shifts can be induced when habitat quality is perceived differently by the juvenile life stages of a species compared to their adults, resulting in stage-structured habitat use (Mumby 2006, Grol et al. 2011). This life history strategy leads to spatial separation between adults and juveniles within a population. A variety of terrestrial and marine species show a stage-structured life cycle, for example, juveniles and adults that occur in aquatic vs. terrestrial habitats, respectively (e.g., hermit crabs, Brodie 1999; frogs, Altwegg 2003), or that are separated by thousands of kilometers (e.g., salmon, Dittman and Quinn 1996; anguillid eels, Tsukamoto et al. 2002). In tropical coastal ecosystems, species occur that consecutively utilize different vegetated habitats throughout their life cycle (Beck et al. 2001). Juveniles of these species utilize sea grass beds and mangrove habitats before finally joining adult populations on coral reefs. In absence of these inshore nursery habitats, many species show diminished adult populations (Nagelkerken 2009) including several threatened species (Dorenbosch et al. 2006). As such, these nursery habitats may act as principal areas that locally replenish reef populations. When nursery habitats are spatially isolated from one another, multiple local adult populations may be sustained on the reefs adjacent to those nursery habitats. Consecutively, these local reef populations could act as sources for distant adult habitats, depending on the dispersal ability of the adults. The main problem for understanding such source–sink dynamics along reefs lies in tracking movement of fish across ecosystems and subsequent adult dispersal (Pittman and McAlpine 2003). The determination of the nursery origin of reef fish adds an additional level of complexity to understanding their population dynamics. Ontogenetic movements occur on relatively long time scales (multiple years), and therefore artificial tagging techniques are not always appropriate to detect such movements.

Natural chemical tags in fish ear bones (otoliths) are extremely valuable tools to study ontogenetic fish movement because otoliths grow continuously throughout the life of a fish, and remain chemically inert. Therefore, they preserve a lifelong record of the fish's environment (Campana 1999). Several studies have investigated the spatial differences in chemical otolith signatures to discriminate among coastal habitats or locations (e.g., Chittaro et al. 2004, Clarke et al. 2009, Tobin et al. 2010), or have determined movement patterns among different habitats (Rooker et al. 2008, Verweij et al. 2008). Dissolved inorganic carbon (DIC) typically contributes 70–80% to otolith carbon and varies among water bodies around major vegetation types, while oxygen isotopes are often related to variability in water temperature and salinity (Campana 1999). Stable carbon isotope ratios are usually more enriched in sea grass beds compared to coral reefs (Cocheret de la Morinière et al. 2003), and are thus a valuable tracer for movement among these habitats.

Our study area and focal species provided us with a unique opportunity to study spatial population dynamics through stage-structured habitat use and dispersal ability of a tropical reef fish. Our focal fish species is largely dependent on sea grass nurseries which in our study area only occur in a number of semi-enclosed lagoons, separated from adult habitats on the coral reef. However, the coral reef supports low juvenile densities as well (Nagelkerken 2007), and due to its much larger surface area compared to sea grass nurseries it may therefore prove to subsidize a significant number of juveniles to local adult populations. The island of Curaçao is an oceanic pinnacle, separated from other islands by deep waters (>1.5 km), which provides a true opportunity to study an enclosed demersal population, something that is extremely difficult in the marine environment where sedentary animals can move over hundreds of kilometers along continental shelves (Clarke et al. 2010).

Here, we argue that nursery bays contribute differently to local adult populations on reefs due to differences in nursery habitat quality (using juvenile fish densities as a proxy) and surface area. Additionally, we postulate that dispersal along reefs away from nursery bay mouths is limited as movement often increases risk of predation. If these two factors are important drivers of adult spatial population dynamics, we expect them to cause source–sink dynamics along island coastlines. Using a spatial model based on recruitment and survival, we simulated the contribution of different nursery bays to local adult reef populations and the degree of subsequent dispersal along the reef. Additionally, stable carbon and oxygen isotope signatures in fish otoliths provided empirical data to determine the contribution of juvenile to adult habitats, and the degree of mixing among local populations on the reef. This combined approach provides us for the first time with an understanding of how dispersal shapes spatial population dynamics of reef fish species that show a strongly stage-structured life cycle.

MATERIALS AND METHODS

Species and study area

The Caribbean island of Curaçao (12°07′ N, 68°55′ W) has seven inland bays that harbor sea grass beds (Fig. 1). Juvenile (up to 15 cm in fork length, FL) yellowtail snappers (Ocyurus chrysurus) live predominantly in these sea grass beds, although coral reefs sometimes support small numbers of juvenile fish (review by Nagelkerken 2007). Yellowtail snappers are believed to spawn year-round, with highest peaks between March and September, and possibly form offshore spawning aggregations (Munro et al. 1973). After a pelagic larval stage, early juveniles settle predominantly in coastal embayments with sea grass
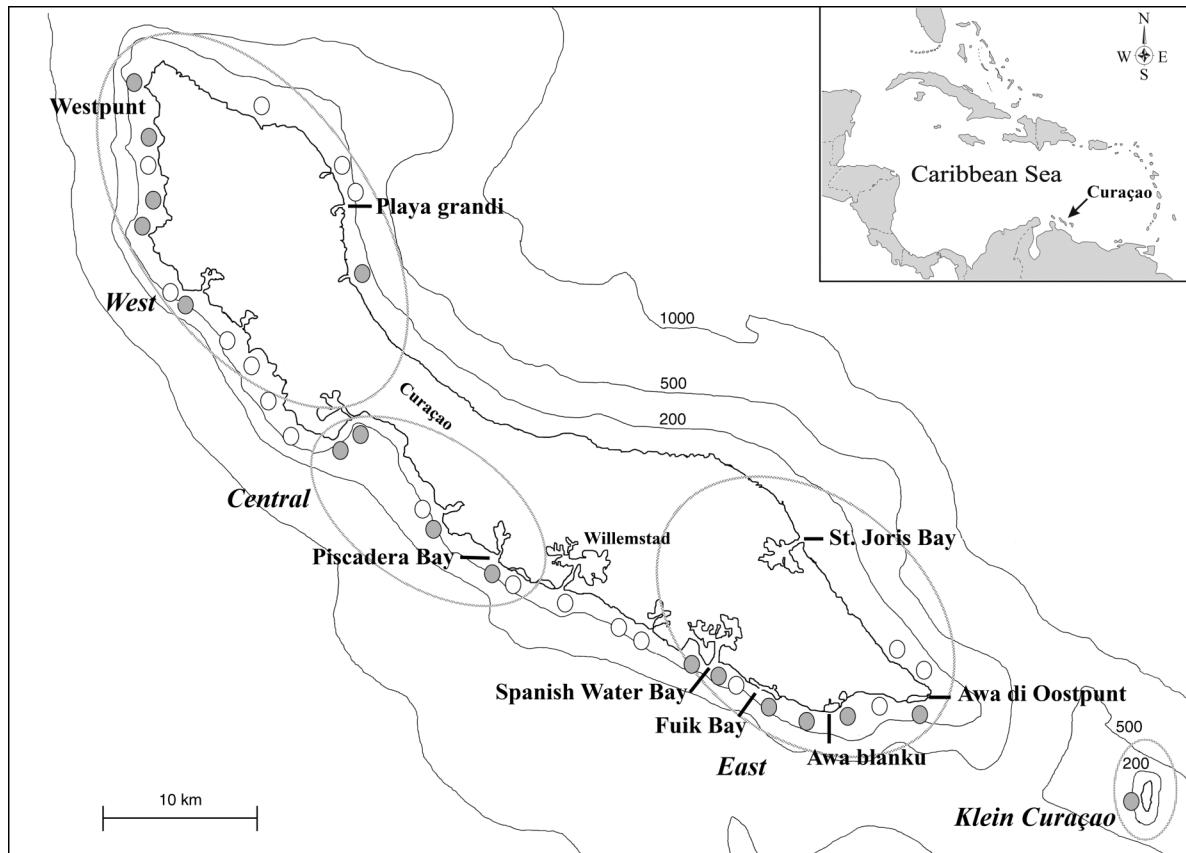
FIG. 1. Overview of the study area with the seven bays that harbor major sea grass areas, and bathymetry lines (depth in meters) around Curaçao. Gray-outlined ovals indicate the four designated destination areas on the coral reef (in italics). Circles along the coastline show reef sites for visual census and collection sites of adult yellowtail snappers *Ocyurus chrysurus* (white circles represent sites for visual census only; gray circles represent sites for both visual census and fish collection).

beds and mangroves (Pollux et al. 2007). Migration from sea grass nurseries to coral reefs takes place when fish range between 15 and 25 cm in length (Nagelkerken et al. 2000). Previous research has shown that 98% of the adult fish collected on the reef directly adjacent to two bays on Curaçao originated from sea grass nurseries (Verweij et al. 2008). Spatially separated adults on the reef adjacent to each nursery bay are here referred to as local adult populations, which combined form the entire island's demersal population.

Distribution, survival, and recruitment estimates

Underwater visual census surveys were conducted to estimate distribution, survival, and recruitment rates. Abundance and fork length of yellowtail snappers were visually estimated in transects on the coral reef along the entire southwestern coastline and parts of the highly wave-exposed northern and eastern coastlines (Fig. 1). Visual census was carried out during 2004–2005 at 28 different reef sites, by roving transects (range, 300–750 m length) during which two observers swam with the ocean current for 30 minutes parallel to the drop-off and coastline. All fish along the transects within a stretch 10

m wide between 10 and 20 m depth were counted and their size estimated. GPS was used to determine start and end points to be able to calculate transect length and survey area. An additional data set from 2005–2006 with some overlapping survey sites was used to fill in a data gap (13 km of coastline). To match these two data sets, the ratio between the fish counts at the overlapping reef sites was calculated, and this ratio was used to recalculate the number of fish counted at sites that were missing from the principal data set.

For all counted reef fish, the age of a fish at any given length was calculated with the von Bertalanffy equation ($L_t = L_\infty (1 - e^{-K(t-t0)})$) based on parameters calculated by Manooch and Drennon (1987). These age estimates were used to calculate the annual survival rate by fitting an exponential curve through the number of fish per age class (after dividing the counts per age class by the width of the age classes to obtain fish densities at the center of each age class).

To estimate recruitment rates for each possible nursery bay in one particular year, the total abundance of yellowtail snappers with FL <13 cm (fish <1 year old) in each of the seven bays was determined. Fish

TABLE 1. Overview of number and size range of fish collected at each location.

| | Fork length (cm) | | |
Location	Mean	Range	Number of otoliths analyzed per year
Eastern bays			
St. Joris Bay (SJ)	9.8	7.7–12.5	14 (1998)
Awa di Oostpunt (AO)	8.8	5.6–12.9	8 (2007); 8 (2008)
Awa blanku (AB)	11.9	10.1–15.7	7 (2007); 2 (2008)
Fuik Bay (FB)	12.0	6.9–16.2	2 (2008)
Spanish Water Bay (SW)	10.6	5.9–15.6	8 (2002); 9 (2006); 16 (2007); 4 (2008)
Piscadera Bay (PB)	12.0	7.2–16.0	26 (2002); 15 (2006); 7 (2007); 3 (2008)
Playa grandi (PG)	9.1	7.2–10.7	14 (2007)
Reef (fish >30 cm)	38.9	30.3–53.0	3 (2001); 4 (2002); 2 (2003); 1 (2005); 36 (2007); 26 (2008); 2 (2009); 16 (2010)

Notes: For each different region of juvenile origin (eastern bays combined), carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) stable isotope ratios (mean ± SD), and the amount of essential habitat are given (seagrass for the eastern bays, Piscadera Bay, and Playa grandi; coral reef for the reef region). The total contribution (mean ± SD) represents the number and percentage of fish that each region of juvenile origin contributes to the entire island's reef population.

communities of sea grass beds and sandy seabeds were sampled with a beach seine net (see Nagelkerken and van der Velde 2004 for detailed methods), providing an estimated density of fish per square meter. Total number of recruits for each bay was then calculated by multiplying the respective fish density per square meter with the total surface area of habitat.

Spatial simulation model

To study whether the distribution of yellowtail snappers on the reef along the coast of Curaçao can be predicted on the basis of a few straightforward demographic parameters, we built and analyzed a simple age-based spatial simulation model with a one-year time step (Appendix A). In this model the reef was represented as a one-dimensional habitat around the island, which is a reasonable assumption for Curaçao (distribution of the narrow fringing reef mapped by van Duyl 1985). The spatial resolution in the simulations was 100-m stretches of coastline. We used only two demographic rates: (1) a bay-specific number of 1-year-old recruits that entered the reef from each bay, and (2) a space- and age-independent annual survival rate of fish on the reef (averaged over the two time periods measured). Because dispersal of yellowtail snappers has not been studied before, we assumed that the kernel of annual dispersal distances (d) of a fish can be modeled with a continuously decreasing Weibull curve of which the cumulative distribution function is given by $1 - \exp(-d/\lambda)$. We optimized the scale parameter λ to best fit the simulated fish counts to the observed fish counts at various locations on the reef. As a measure of fit we used the R^2 of the correlation between the observed and simulated number of fishes in the 100-m stretches where fish abundances were determined.

We also studied the correlation of the simulated size distributions with the size distributions observed at the various locations. To obtain simulated size distribution from our age-based simulation model, we first translated the simulated age distributions into size distributions

using the size–age formulas described in *Distribution, survival, and recruitment estimates*. These local size distributions give the proportions of fish in each of the size classes.

Survival rate and number of recruits per year of yellowtail snapper were also calculated for two different Caribbean islands, Grand Cayman and Bermuda, using existing data sets of visual census surveys on the reef and potential source areas (I. Nagelkerken, *unpublished data*; see Huijbers et al. 2008 and Nagelkerken et al. 2012 for study sites and methodology). These parameters were used in the same model for direct comparison of the modeled dispersal rate between different Caribbean islands. Simulations and optimizations were done in R (R Development Core Team 2010).

Otolith analysis

To investigate empirically how spatially separated sea grass nursery bays contribute to the island's reef population, the otolith signatures of juveniles residing in the seven bays were used as baselines to be compared with the juvenile zone of otoliths from adults collected on the reef. During several years, juvenile yellowtail snappers (FL 10.5 ± 2.4 cm; mean ± SD) were collected from the bays, while adult fish (FL > 30 cm) were collected from the narrow (150–400 m wide) fringing reef of the island and from the offshore island of Klein Curaçao (Fig. 1, Table 1). Sagittal otoliths from the right side of the head of each fish were removed, cleaned, dried, and stored frozen, and subsequently mounted on glass plates, embedded in resin and then cross-sectioned in the transverse plane through the core. The outer otolith margin, which reflects the current habitat, was analyzed for juvenile bay and adult reef fish. Additionally, the juvenile zone of adult reef fish, which possibly reflects an earlier life stage in bay habitats, was analyzed. The mean width of juvenile otoliths was used to estimate the margins of the juvenile zone in adult otoliths. Otolith material (~20 µg) was drilled out by use of a micromill, collected and put into glass tubes. Subsequently, a few

TABLE 1. Extended.

$\delta^{13}C$ (‰)	$\delta^{18}O$ (‰)	Essential habitat area (m^2)	Total contribution (no. fish)	Total contribution (%)	Contribution per unit area
-2.4 ± 0.9	-1.2 ± 0.4	661 341	7293 ± 532	58.3 ± 4.3	0.01
-4.1 ± 0.8	-1.0 ± 0.3	13 133	4220 ± 626	33.7 ± 5.0	0.32
-4.3 ± 0.5	-1.4 ± 0.3	1 486	498 ± 128	4.0 ± 1.0	0.34
-5.2 ± 0.4	-0.6 ± 0.5	7 865 176	503 ± 220	4.0 ± 1.8	<0.01

drops of orthophosphoric acid were added at a temperature of 80°C to dissolve all CaCO$_3$. Stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope ratios of the released CO$_2$ were measured by a Finnigan MAT 252 mass spectrometer (Finnigan Instrument Corporation, San Jose, California, USA) equipped with an automated carbonate extraction line (Kiel device). All data are reported vs. VPDB (Vienna Pee Dee Belemnite). An in-house carbonate standard, calibrated to NBS18, NBS19, and NBS20, was routinely monitored during sample runs. Long-term reproducibility (±1 SD) of this in-house standard lies within 0.09‰ for $\delta^{18}O$ and 0.06‰ for $\delta^{13}C$.

Spatial and temporal variability in otolith $\delta^{13}C$ and $\delta^{18}O$ among the seven bays, complemented with the coral reef as an eighth possible juvenile origin, were tested with a multivariate analysis (MANOVA). The variance in $\delta^{13}C$ and $\delta^{18}O$ was first explained by fitting a MANOVA with all eight possible juvenile origins separately. We then tested whether grouping two origins at a time made the model fit significantly worse. This was not the case for the pairs SJ-AO, AO-AB, AO-FB, AO-SW, and AB-SW ($P > 0.150$; see Table 1 for identification of locations). This means that the combined $\delta^{13}C$ and $\delta^{18}O$ signatures of these bays were indistinguishable, and they were therefore pooled as a region of juvenile origin. Based on this analysis and the geographical distribution of the collection areas on the island, four different regions of juvenile origin were identified: three sea grass nursery regions located at the eastern, central, and western parts of the island, respectively (Fig. 1), and the coral reef (Appendix B). In three regions, otoliths were collected during several years (Table 1), yet the otolith $\delta^{13}C$ signature of fish did not differ significantly among years ($P > 0.1655$; Appendix B), indicating temporal stability. The $\delta^{18}O$ signature did differ significantly among years, possibly due to small temperature or salinity differences among years (Campana 1999). Additional analyses showed that these results did not change if years with small sample sizes (fewer than seven samples) from a bay were omitted from the analysis (Appendix B). Quadratic discriminant function analysis was used to assess the

degree to which otolith $\delta^{13}C$ and $\delta^{18}O$ signatures could be used to correctly classify juveniles to their known origin. This showed that combining all possible juvenile origins into four distinct regions increased the classification success based on otolith $\delta^{13}C$ and $\delta^{18}O$ considerably (82.8%), compared to eight different juvenile origins (65.2%).

The proportion of adult reef fish originating from each of the four identified regions of juvenile origin was predicted by use of a maximum likelihood-based mixed-stock analysis, "HISEA," developed by Millar (1990). Stable carbon and oxygen isotope signatures from bay juveniles from the different nursery regions were used as the baseline. To detect if fish had grown up on the reef as opposed to sea grass nurseries, we used otolith signatures from the adult margin of large (>30 cm FL) reef fish in the baseline, which are assumed to have lived on the reef for a significant amount of time. Because the composition of otoliths is determined by a complex mix of both physiological and environmental factors (Elsdon et al. 2008), a potential ontogenetic effect on $\delta^{13}C$ in adult otoliths cannot be completely ruled out. However, a linear regression analysis between fork length and otolith carbon isotope signature showed no significant metabolic effect for reef fish between 20 and 53 cm FL ($P = 0.10$, $R^2 = 0.01$). We only used reef fish >30 cm FL for our baseline reef signature, as smaller reef fish could include recent migrants with isotope signatures of their outer otolith margin still partly reflective of earlier sea grass nursery residence. Even though ontogenetic effects on $\delta^{13}C$ could not be teased apart from the effects of habitat on $\delta^{13}C$ for fish that had lived on the reef for their entire life cycle, the total contribution of the coral reef habitat as a juvenile source to the reef population was so low (4%) that this issue did not have an effect on the overall conclusion of this study. The $\delta^{13}C$ and $\delta^{18}O$ signatures of the juvenile otolith zone of (sub)adult reef fish were used as the unknown mixed data set for the estimation of the nursery origin of these fish. Based on distance among reef sampling sites and designated juvenile regions, the reef area was divided in four destination areas (Fig. 1), and the maximum likelihood analysis was run for fish
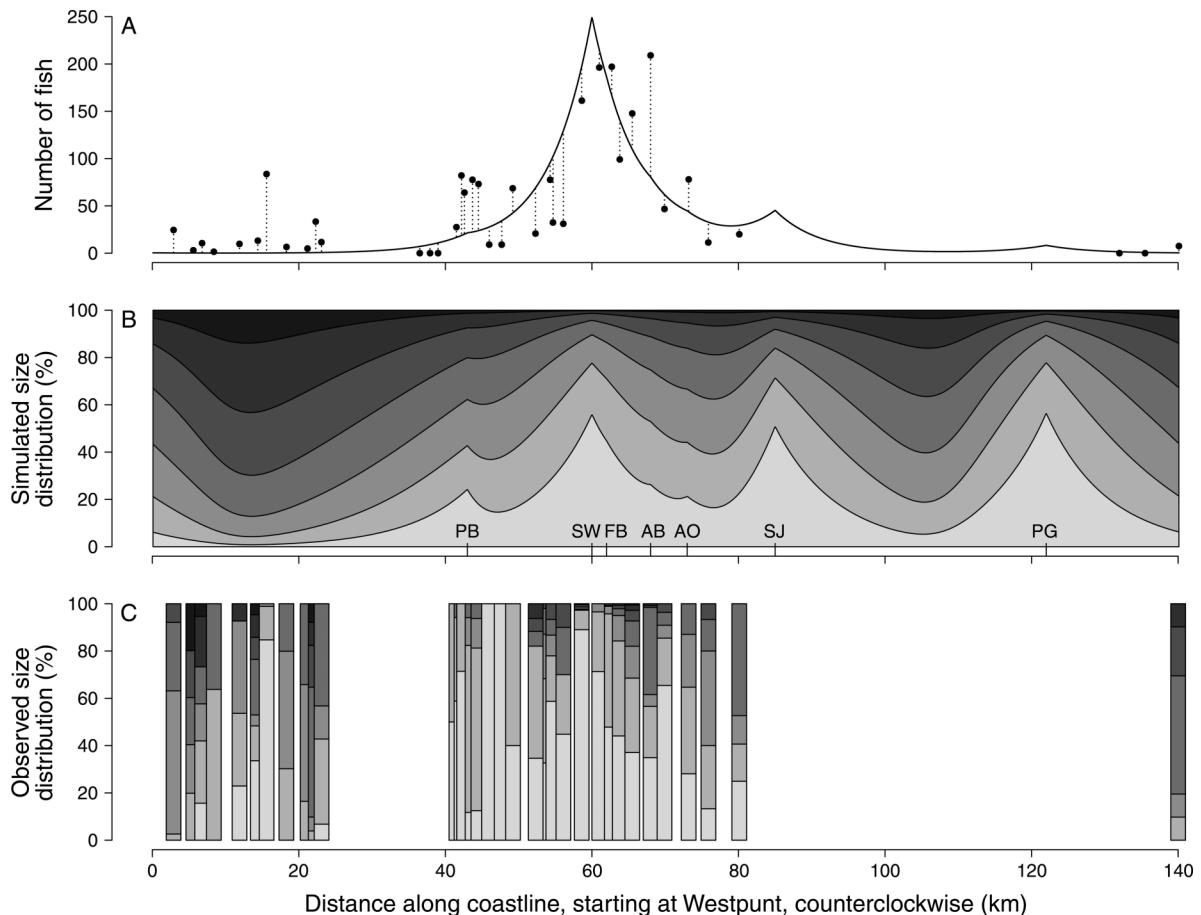
Fig. 2. Combined results from the spatial simulation model and the visual census survey for the best fit of the observed fish counts ($R^2 = 58.5\%$, corresponding to a 2.3 km/yr median dispersal rate). The 140 km along the x-axis represents the entire coastline counterclockwise around the island, starting and ending at Westpunt (see Fig. 1). (A) Observed reef fish counts from visual surveys along the coast of the island (solid dots). No surveys were conducted along the major part of the wave-exposed northern and eastern coast of the island (between 85 and 130 km). The solid line represents the simulated number of reef fish predicted by the model. (B) Simulated relative size distribution at a median dispersal rate of 2.3 km/yr. (C) Observed relative size distribution from visual surveys. The size distribution in panels (B) and (C) is divided into 5-cm size classes: 15–19.9 cm; 20–24.9 cm; 25–29.9 cm; 30–34.9 cm; 35–39.9 cm; and 45–49.9 cm (indicated by increasingly dark shading, from small to larger fish). Abbreviations for sea grass nursery bays in panel (B) are: PB, Piscadera Bay; SW, Spanish Water Bay; FB, Fuik Bay; AB, Awa blanku; AO, Awa di Oostpunt; SJ, St. Joris Bay; PG, Playa grandi. See Appendix F for a color version of Fig. 2.

caught in each area separately as reef fish densities differed considerably among destination areas (see *Results*). Maximum likelihood estimates and standard deviations were generated in HISEA by bootstrapping the baseline 500 times.

For each reef area, the quantitative contribution of each region of juvenile origin was calculated based on the actual density of reef fish. Because the reef areas were not of equal length, we calculated the total number of reef fish in each area by multiplying the fish density per square meter by the reef area in square meters. These numbers were then multiplied by the proportional contribution from each region of juvenile origin to ultimately derive an estimate for the actual number of fish that each juvenile origin contributed to a specific reef area in total. For each of the sampled reef areas, the

contribution of each juvenile origin was compared to the origin distribution resulting from the simulations previously described (in which we kept track of the bay of origin of fish).

RESULTS

Dispersal of reef fish

Data from the visual surveys showed that reef fish were not randomly distributed along the island's reefs (Fig. 2A; Appendix F). Yellowtail snappers were most abundant (~150–200 fish per 100-m length of coastline) on the reef at the southeastern side of the island that ran along the bays SW, FB, and AB (between 58 and 70 km from Westpunt). Another peak in abundance was found on the reef in front of PB (42 km from Westpunt), although numbers were lower here (60–80 fish per 100 m

of coastline) compared to those at the southeastern side. Considerably lower numbers of fish were found on reefs at the northern, western, and eastern sides of the island. Despite the fact that the island is surrounded by a continuous fringing coral reef, these results indicate that dispersal away from sea grass nurseries is limited.

Spatial simulation model

Our spatial simulation model contained only a few estimated vital rates: a 69.1% annual survival rate (the mean of 68.6% in 2004–2005 and 69.5% in 2005–2006) and an annual recruitment rate (number of young fish) migrating from the bays to the reef (2120 fish from SJ, 391 from AO, 532 from AB, 600 from FB, 12 541 from SW, 400 from PB, and 434 from PG). Calculations based on these immigration and death rates resulted in similar predicted fish densities on the reef to the observed in situ densities (Fig. 2A; Appendix F).

When the λ parameter of the Weibull dispersal function was optimized for the simulated fish distribution to best fit the observed fish counts along the coastline, the highest correlation ($R^2 = 58.5\%$) was found in correspondence with a median dispersal rate of 2.3 km/yr. However, at this dispersal rate the simulated (Fig. 2B; Appendix F) and observed (Fig. 2C; Appendix F) size distributions fitted less well ($R^2 = 17.6\%$). The opposite was true when we optimized λ for the best fit between the simulated and observed size distributions ($R^2 = 49.3\%$) resulting in a median dispersal rate of 10.7 km/yr. However, this improved fit for the size correlations corresponded with a somewhat poorer fit for the count patterns ($R^2 = 45.7\%$; Appendix C). This suggests that dispersal rates may well be size dependent. Optimization of a size-dependent dispersal model indeed resulted in an optimal model with increased median dispersal rates (20–25 km/yr) for the larger (>45 cm) fish, while the median dispersal rate remained low (2–3 km/yr) for the smaller (<20 cm) fish (Appendix D). The size-dependent dispersal simulations fitted better ($R^2 = 59.9\%$ for count distribution and $R^2 = 49.5\%$ for local size distribution correlations) than that of the size-independent simulation.

The annual survival rates estimated from the size distributions observed at Bermuda (68.7%) and Grand Cayman (69.0%) were identical to those found on Curaçao. While the number of recruits was much higher (Grand Cayman: 69 500 fish) or lower (Bermuda: 750 fish), on both islands the fish densities decreased more rapidly with increasing distance from the (single) bays from which juveniles join the adults on the reef, resulting in optimal fits for models with median dispersal rates of only 0.3 km/yr (Bermuda) and 0.1 km/yr (Grand Cayman), compared to >2.3 km/yr for Curaçao (Appendix E).

Juvenile origin contribution

Based on the predicted median dispersal rate of 2.3 km/yr derived from the spatial simulation model, the contribution of each bay to the fish population of the reef was calculated (Fig. 3A, B; Appendix G). Overall, due to the large number of recruits, SW contributed most to the number of adult reef fish along the greater part of the coastline. Only in more distant areas did local bays overrule this contribution (i.e., SJ on the eastern part of the island, and PG on the western part of the island).

The contribution per juvenile origin was also predicted with a maximum likelihood analysis (MLA), based on otolith isotope signatures from 180 (sub)adult reef fish (Table 2). The estimated proportion of fish originating from each region of juvenile origin was different for the four destination reef areas (Fig. 3C; Appendix G). Fish collected from reefs on the eastern side of the island (between 50 and 80 km from Westpunt) originated mainly (64.1%) from the nearby eastern bays. Nearly 50% of the fish collected from reefs close to PB ("Central" reef region, 25–50 km from Westpunt) originated from this bay, although some distant juvenile regions contributed fish to this reef area as well (Eastern bays contribution, 25%; PG contribution, 24.4%). Reef fish collected in areas distant from any sea grass bay (i.e., West and Klein Curaçao) had mixed origins from several regions. The bay PG contributed ~40% to the nearest populations along the southwestern coast (i.e., West and Central), but none to reef areas farther away.

Based on the MLA results, the total contribution of each region of juvenile origin to the entire island's reef was also calculated (i.e., actual number of fish observed per reef area multiplied by estimated proportion and summed per juvenile origin) (Table 1). Overall, these results showed that only 4% ± 1.8% of the (sub)adult yellowtail snappers collected on the entire coral reef spent their juvenile stage on the coral reef. Therefore, we can exclude the reef as a significant juvenile habitat. Of the three bay nursery regions, the eastern bays (58.3% ± 4.3%) appeared to be the most important region of juvenile origin for adult reef fish, compared to PB (33.7% ± 5.0%) and PG (4% ± 1.0%).

DISCUSSION

This study demonstrates that the unequal contribution of spatially separated juvenile habitats can shape source–sink dynamics in the adult stage of a coral reef fish. We used a combination of empirical data from in situ size–frequency distributions of fish and from otolith chemistry, and modeled dispersal based on simple demographic parameters. Whereas the understanding of marine source–sink dynamics has mainly been based on larval dispersal through ocean current patterns (James et al. 2002, Bode et al. 2006, Figueira 2009), our study provides insight into processes occurring during the demersal phase of the juvenile and adult life stages, which is of vital importance to understand demographic connectivity among habitats.
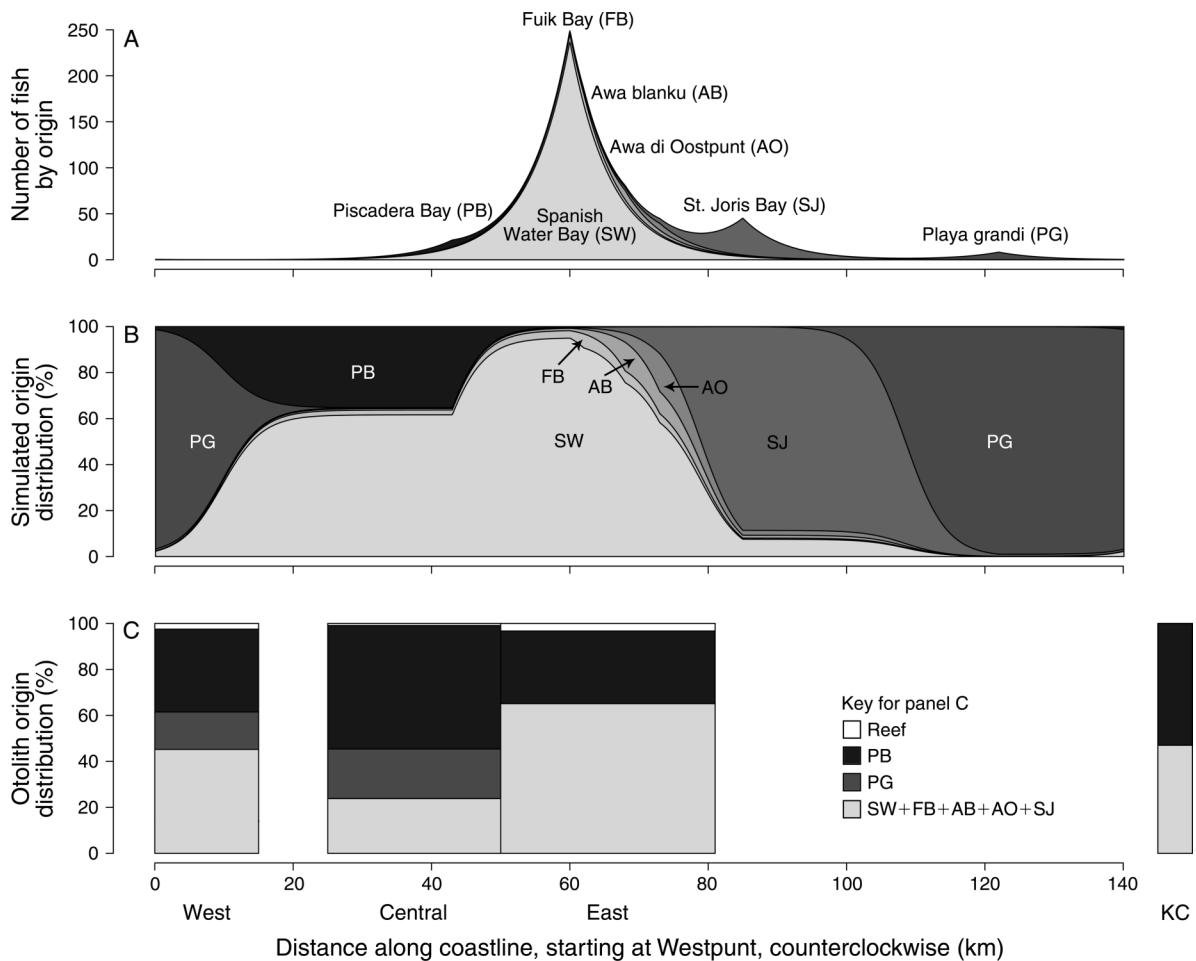
FIG. 3.   Contribution per region of juvenile origin as predicted by the spatial simulation model (median dispersal rate of 2.3 km/yr), and by otolith isotope signatures. (A) Total number of reef fish contributed by each juvenile nursery bay as predicted by the model. (B) Percentage contribution of fish by the same bays as in panel (A). (C) Predicted estimates of juvenile origin for adult fish collected from four different reef areas based on otolith isotope analysis; from left to right: West ($n = 37$ adult reef fish), Central ($n = 38$), East ($n = 85$); KC (Klein Curaçao; $n = 20$) is a small island located 10 km off the southeast coast of the main island of Curaçao. The narrow white areas at the top of the graph represent the contribution of the coral reef (in total) to the adult population. See Fig. 1 for area locations. Abbreviations and x-axis are as in Fig. 2. See Appendix G for a color version of Fig. 3

Although on continental shelves fish are able to move long distances away from juvenile habitats (Gillanders et al. 2003), our results show limited dispersal on the island level for a reef-associated fish. For individual organisms, movement may be risky due to predation (Almany

2004). Therefore, if local habitat quality is appropriate, there is no need for long-distance dispersal. Besides limited dispersal, our results also demonstrate that regions of juvenile origin contribute differently to the island's adult reef population. Based on a median

TABLE 2.   Results of the maximum likelihood analysis (MLA) in which the percentage of adults originating from each region of juvenile origin is predicted.

Region collected	Eastern bays		Piscadera Bay		Playa grandi		Reef	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
West ($n = 37$)	43.3	9.6	37.0	17.0	17.0	14.1	2.7	3.0
Central ($n = 38$)	25.0	10.2	48.1	17.1	24.4	16.7	2.5	3.8
East ($n = 85$)	64.1	7.0	31.5	7.5	0.0	0.1	4.4	3.0
Klein Curaçao ($n = 20$)	44.8	12.8	55.2	12.8	0.0	0.0	0.0	0.0

Notes: This table shows the percentages for each predicted origin for adult reef fish caught in four different reef areas ($n = $ number of fish). See Fig. 1 for locations.

dispersal rate of 2.3 km/yr, as predicted by the spatial simulation model, most nursery bays contributed only to local reef populations, except for one bay (SW) with a disproportional large standing stock of juvenile fish. The combined effect of limited dispersal and unequal contributions of different regions of juvenile origin leads to the conclusion that the geographic distribution of juvenile nursery areas is an important driver of the spatial distribution of adult reef populations.

In support of our model-based contribution estimates, otolith chemistry also revealed that not all juvenile regions of this closed demersal population contributed significantly to the adult reef population. A maximum likelihood analysis clearly indicated that the majority of the adult reef fish had spent their juvenile stage in sea grass nurseries on the eastern side of the island. Only 4% of the adults had recruited as juveniles on the coral reef itself, even though its surface area was an order of magnitude larger than that of all sea grass bays combined. These results indicate a strong and rather complex spatial structure in a closed demersal population of this fish species. In addition to spatially separated life stages distributed over habitat patches represented by different ecosystems, a source–sink structure might be present in the adult stage within a single ecosystem. The latter is demonstrated in the model by the disproportionate seeding of adults by SW to the adjacent reefs, resulting in consecutive seeding of adults by this "source" reef to more distant reef areas, which acted as "sinks."

Otolith chemistry previously indicated that different nursery areas might unequally contribute juveniles to adult populations (Gillanders 2005, Mateo et al. 2010, Rooker et al. 2010). Although most studies have aimed to determine connectivity between habitats on a population level, the calculated contribution from each putative nursery area is often not related to adult population densities at different collection sites, as was done in this study. In the case of skewed density distributions of fish in the adult habitat, such a density-independent approach leads to biased predictions of importance of individual regions of juvenile origin. Furthermore, in most study areas it is hard to sample all possible destination areas due to the existence of open populations. Our study area provided us with the excellent opportunity to study a closed demersal population. Although it was not possible to distinguish the origin of reef adults among the five bays in the eastern region, our results clearly show that the island's reef population can be maintained by a single distant region with high juvenile recruitment.

Quantifying the value of different juvenile origins is indispensable for effective management of coastal ecosystems, yet this quantification might vary depending upon which concept is used to define nurseries (Fodrie and Levin 2008). Based on the definition of Beck et al. (2001), a habitat can be regarded as a nursery if its contribution per unit area is larger compared to that of

other habitats. If we applied this theory to our results, the region of eastern bays would not be classified as an important nursery (contribution per unit area was 0.01; Table 1), while PB (0.32) and PG (0.34) would be classified in that way. However, based on the expanded nursery theory of Dahlgren et al. (2006), the eastern bays, which have a greater than average overall contribution (58.3%) to the adult population, would be regarded as the most important nurseries. Furthermore, at the ecosystem level the amount of available habitat appears to be less important than its quality, which is demonstrated by the fact that the total reef surface area is 12 times larger than that of sea grass in the eastern bays, yet the contribution is ~20 times lower. Hence, in trying to understand what drives replenishment of fish populations, life history strategy (in this case stage structure), habitat quality (in this case presence of sea grass vegetation for juveniles), and quantity of essential habitat (in this case surface area of sea grass beds) are critical factors to consider, in addition to differences in initial larval supply.

Marine spatial population dynamics are often primarily based on dispersing pelagic larvae, regarding juveniles and adults as nonmotile or incorporating juvenile or adult movement as a simple diffusion process (Botsford et al. 2001, Gerber et al. 2003). The results of our model show that the latter is not the case, as dispersal rates are probably size dependent, with larger fish dispersing farther away than small fish. The sometimes lower observed than modeled fish densities on the eastern side of the island might be a result of higher fishing pressure on the reefs in that area (between 50 and 70 km in Fig. 2; Appendix F). Furthermore, the significantly lower median dispersal rates of fish on Grand Cayman and Bermuda, with much higher and lower number of recruits, respectively, than on Curaçao, indicate that dispersal away from nursery bays is not density dependent, as is often assumed (Shepherd and Litvak 2004).

In addition to behaviorally driven dispersal of adult fish, early juveniles also show active orientation behavior to find suitable settlement habitats after their pelagic stage (Leis 2006). Previous studies showed that they can use olfactory cues to find sea grass nursery areas (Huijbers et al. 2012). Although the smallest reef fish were predominantly found on reefs close to nursery bays, we did observe a lower fit between the observed and simulated size distributions, which is probably due to a relatively large proportion of small fish at one reef site (15 km from Westpunt). On such reef areas that lie well away from tidal bay water plumes containing crucial olfactory cues of nursery habitat, settlement-stage fish larvae are probably forced to settle on the reef, as the time window for settlement is a few days at the most (Kaufman et al. 1992). Hence, neither adult nor juvenile movement can be regarded as passive behavior, and knowledge about this behavior can provide valuable spatially explicit information for management strategies.

In our case it shows that different life stages show specific behavior that results in spatially explicit distribution of specific stages.

Over the past 20 years, the number of both modeling and empirical studies incorporating fish movement has increased, especially for the design of marine reserves (Gerber et al. 2003, Grüss et al. 2011). The results of our spatial simulation model show that juvenile production and consecutive dispersal can be predicted based on easily acquired measures and few assumptions. The observed densities of yellowtail snappers and their spatial distribution on the reef matched very well with that predicted by the simulation model, as did the contribution of juvenile origins calculated from otolith chemistry and the simulation model. However, knowledge about juvenile and adult fish movement is still very limited and remains a critical science gap in understanding ecosystem connectivity (Sale et al. 2005). Dispersal of animals depends on connectivity between juvenile and adult habitats, and between adult source and sink habitat patches, but this dispersal might be impeded through habitat loss or fragmentation leading to barriers too large to cross for certain species (Turgeon et al. 2010). Corridors can increase movement among patches (Gilbert-Norton et al. 2010), but their effectiveness for demersal marine species has not been widely explored. According to Crowder et al. (2000), placement of reserves in sink areas alone might not be beneficial for sustaining reef fish populations. Especially when juvenile habitat is in short supply, which is the case in our study area where the surface area of sea grass beds is much lower compared to the total coral reef area, the identification and protection of these areas that produce juvenile recruits is critical for designating effective marine protected areas. Finally, to maintain movement of organisms from source to sink areas, management strategies should also preserve corridors between habitats that function as stepping stones for movement of organisms.

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SUPPLEMENTAL MATERIAL

Appendix A

Description of the spatial simulation model (*Ecological Archives* E094-168-A1).

Appendix B

Multivariate analysis of $\delta^{13}C$ and $\delta^{18}O$ signatures of fish otoliths (*Ecological Archives* E094-168-A2).

Appendix C

Combined results from the spatial simulation model and the visual census survey for the best fit of the observed fish size distributions in correspondence with a median dispersal distance of 10.7 km/yr (*Ecological Archives* E094-168-A3).

Appendix D

Optimization of the size-dependent dispersal model (*Ecological Archives* E094-168-A4).

Appendix E

Optimal fitted model for observed fish counts on Bermuda and Grand Cayman (*Ecological Archives* E094-168-A5).

Appendix F

A color version of Fig. 2 (*Ecological Archives* E094-168-A6).

Appendix G

A color version of Fig. 3 (*Ecological Archives* E094-168-A7).