Environ Biol Fish (2010) 87:363–372
DOI 10.1007/s10641-010-9612-2

An experiment of fish spillover from a marine reserve in Cuba

**Fabián Pina Amargós · Gaspar González Sansón ·
Andrés Jiménez del Castillo · Abdel Zayas Fernández ·
Félix Martín Blanco · Wilbert Acosta de la Red**

Received: 28 November 2007 / Accepted: 1 February 2010 / Published online: 26 February 2010

Abstract Several studies on adult fish movement from marine protected areas to zones open to fishing activity conclude spillover is present, but most of these investigations use indirect evidence and small-sized species of little commercial importance. This paper reports the effects of manipulating a density gradient on movements of large-sized and commercially-important fish across "Jardines de la Reina" Marine Reserve boundaries, using tagging methods and visual census. Tagging was carried out using dart tags and modified spearguns at an experimental and a control site. Density of fish was experimentally manipulated on the unprotected side of the boundary. Before experimental manipulation, fish density was similar in both experimental and control sites and on both sides of the boundaries. After manipulation, fish density in the unprotected side of experimental site declined dramatically and a strong gradient was established through the boundary. One month later, this forced gradient disappeared, returning to the situation at the beginning of the study. This last result is due to spillover effect: the mean distance traveled by fish increased 1.5 times (mean from below 200 m to more than 300 m), the mean emigration rate doubled and the immigration rate decreased, allowing density levels to recover after manipulation.

Keywords Spillover · Movement · Adult fish · Coral reefs · Tagging

Introduction

Fish spillover is the net flow of fishes out of marine reserves produced by a density gradient across their boundaries due to fishing pressure. Evidence of adult fish spillover from protected areas is scarce and contradictory (Westera et al. 2003; Palumbi 2004; Sale et al. 2005). Rigorous studies about spillover are limited to a few sites (Russ et al. 2003; Alcala et al. 2005) and much of the remaining literature that endorses a spillover effect does so despite clear methodological weaknesses in the studies (i.e., Kelly et al. 2002; Maypa et al. 2002; Russ and Alcala 2003).

Only one study has manipulated a density gradient to assess spillover, convincingly discriminating between marine reserve related density dependent movement and other natural movements (Zeller et al. 2003). This research, however, indicates only an

---

F. P. Amargós (✉) · A. Z. Fernández · W. A. de la Red
Centro de Investigaciones de Ecosistemas Costeros,
Cayo Coco,
Morón, Ciego de Ávila CP 69 400, Cuba
e-mail: fabian@ciec.fica.inf.cu
e-mail: fabianpina1972@gmail.com

G. G. Sansón · F. M. Blanco
Centro de Investigaciones Marinas,
Ciudad de la Habana, Cuba

A. J. del Castillo
Centro de Investigaciones Medioambientales de Camagüey,
Ciudad de la Habana, Cuba

increase in movement trend. However, results were not significant and did not detect directional movements, apparently due to a lack of similarity between manipulated and control sites, the biased use of spearguns, and limited "natural" movement of target species. Sale et al. (2005) have highlighted the need of this kind of well-planned study.

In this paper, we report the results of a manipulative experiment aimed at corroborating the likelihood of spillover effects of adult fishes across the west boundary of the "Jardines de la Reina" Marine Reserve (JRMR), the largest of the Caribbean (Appeldoorn and Lindeman 2003). This is a limited take marine reserve. Fishermen do not fish close to the western boundary of the JRMR and there is no density gradient across that boundary. Fishermen fish ~10 km away of the western boundary where they find good fishing grounds closer to their ports. We used tagging (direct method) and visual censuses (for the estimation of density) to test the effects of artificially creating density gradients in the movement patterns of large-sized and commercially important fish species during a four-month period across a spatial scale of hundreds of meters.

Materials and methods

Study area

The "Jardines de la Reina" Archipelago stretches along 360 km, from the Gulf of Guacanayabo to Casilda Bay, south of Cuba (Fig. 1). Since 1996 about 950 km-2 were proclaimed as Zone Under Special Regime of Use and Protection, according to Resolution 562/96, from the Ministry of Fisheries. The protection is equivalent to the management practice internationally known as Marine Reserves, and so termed in this paper. The JRMR allows diving, boat traffic, gamefishing (catch and release) and lobster commercial fishing. Tourist operation and lobster boats take a small amount of fish for food. For these reasons, this is a limited take marine reserve.

We carried out sampling in two sites, one was manipulated and the other was a control. The manipulated site ("BG") crossed the west boundary of the JRMR, located south of Cayo Grande, west of Boca de Guano key and east of Boca Grande key (coordinates 20°58′ N–79°10′ W). The control site was in the area known as Los Pinos ("LP"), south of Caballones key and east of the Pasa de Caballones (coordinates 20°50′ N–78°59′ W) (Fig. 1). The reef slopes of the manipulated and control sites have similar features; their depths are from 8 to 20 m, with high structural complexity and similar fish density. Fieldwork was carried out daily between May and August, 2005.

Sampling methods

To study fish movement across the boundaries, we split both the manipulated site and the control site areas into eight zones, 200 m each, for a total of 1,600 m. In the case of the manipulated site, four zones were inside the marine protected area and four were outside (Fig. 2). In the case of the control site, we established an arbitrary boundary to consider one half (800 m) as "protected" and the other half (800 m) as "unprotected". This is a BACI design (before–after-control-impact) and is similar to that of Zeller et al. (2003).

We used modified oleopneumatic spearguns for tagging fish with dart tags strengthened with steel wire (Floy Tag FT-1-94 tags) (Starr et al. 2007). We used tags with different colours in each zone and different colours were allocated to each month to be treated as independent replicates for comparisons before and after density experimental manipulation. Recaptures were performed visually while tagging and were based only on tag colours. We also used natural marks or tagging scars to complement tagging.

We targeted large-sized and commercially important fish species such as large species of groupers, snappers, jacks, parrotfish, rays and sharks for tagging and/or visual census. Experimental manipulation consisted of extracting individuals of targeted species on the unprotected side of the manipulated site. In early July a total of 266 individuals were removed, without affecting the protected side of the same site. Estimates of density made using visual census immediately before manipulation resulted in a mean of 300 individuals of the tagged species so it is assumed that density was drastically lowered by fishing to 11% of its original value.

To have an independent estimate of fish density, we visually observed six 800 m long × 10 m wide belt transects on both sides of the boundaries (the real one in the manipulated site and the arbitrary one in the control site). We made counts at the beginning of May, June and July (before and after manipulation) and twice in August.

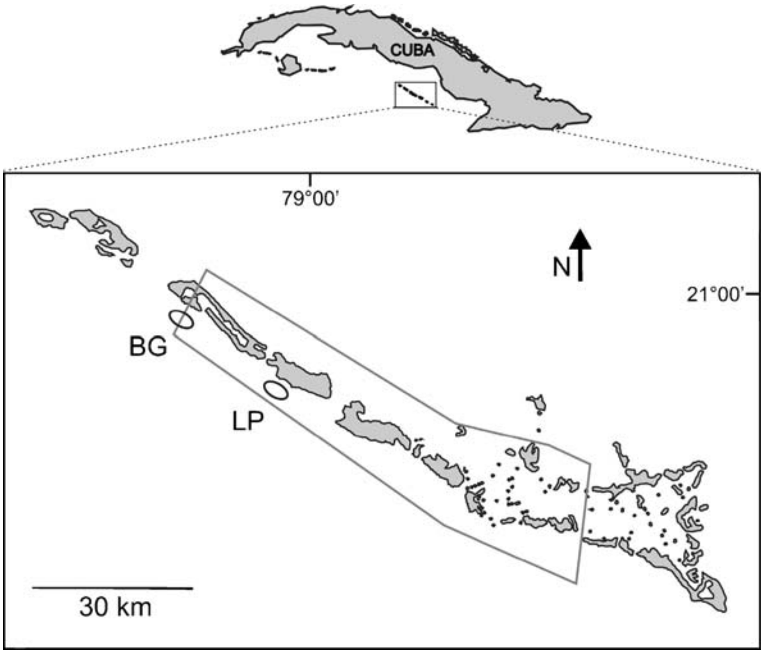

Fig. 1 Map of Jardines de la Reina archipelago and tagging sites. Ellipses are the tagging sites, to the northwest is the manipulated site (BG) and to the southeast is the control site (LP). The *continuous line* is the boundary of the JRMR

Data analysis

We analyzed spillover for all the species pooled and for each of seven species. We included the six species with more than 100 tagged individuals and more than 30% recapture and also Cubera Snapper because it showed the second biggest recapture rate. On the other hand, comparisons of density were carried out for all species pooled and the nine more abundant species separately. Movement variables were defined as follows:

- Immigration rate (I) = N_i/Tr
- Emigration rate (E) = N_o/Tr
- Crossing rate (C) = $(N_i + N_o)/Tr$ or I + E
- Distance (D) = mean distance traveled by all individuals of each species

Where N_i and N_o are the numbers of individuals that enter (i) or leave (o) the protected zone and Tr is the total number of individuals recaptured.

To assess mobility changes induced by manipulation in some species, D, I and E at both sites were calculated without manipulation (DC, IC, EC) and after manipulation in the manipulated site (DM, IM, EM). The ratios DM/DC, IM/IC and EC/EM were then calculated.

Statistical analyses were made by means of fixed effects factorial analysis of variance (ANOVA) and planned comparisons. Assumptions for the analyses

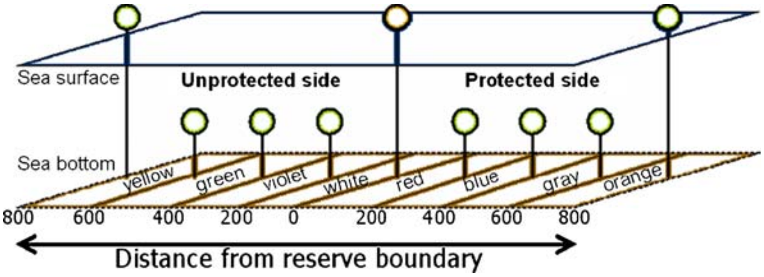

Fig. 2 Diagrammatic representation of the zones defined for tagging experiments (distances in meters). Color distribution by zones are shown. *Circles* are the buoys that marked sides and zones

were verified following the criteria of Underwood (1997) and Zar (1996). All ANOVAs were made at a level of significance of 0.05.

Results

Of the 2,254 tagged individuals, 957 individuals were recaptured (478 at the manipulated site and 479 at the control site), amounting to a 42% recapture rate. Of the total tagged individuals, dart tags accounted for 78%, while natural marks or tagging scars accounted for the rest.

Tagged individuals included three species of cartilaginous fish (Chondrichtyes) and 22 species of bony fish (Actinopterigii). Seven species (Dog Snapper, Cubera Snapper, Yellowfin Grouper, Tiger Grouper, Black Grouper, Hogfish and Great Barracuda) represented 63% of tagged individuals and 76 % of recaptured species (Table 1). No individuals of three species (Yellowmouth Grouper, Permit and Spanish Mackerel) were recaptured.

Before manipulation, fish density (all species pooled) was similar in both experimental and control sites and on both sides of the boundaries (real in experimental site and arbitrary in control site). After manipulation, fish density (all species pooled) in the unprotected side of manipulated site declined dramatically and a strong gradient was established through the real boundary. At the end of the study, this forced gradient disappeared, returning to the situation at the beginning of the spillover study. Similar results were found for the targeted species separately (Table 2, Fig. 3).

The relevance of the induced density gradients is strongly supported when the significance of first and

Table 1 Summary of species tagged and recaptured

Latin name	Common name	T	PR	RM	RC
Aetobatus narinari	Spotted Eagle Ray	27	11	1	2
Alectis ciliaris	African Pompano	6	100	3	3
Caranx bartholomaei	Yellow Jack	90	38	17	17
C. latus	Horse-eye Jack	40	15	3	3
C. ruber	Bar jack	42	12	2	3
C. hippos	Crevalle Jack	8	12	0	1
Dasyatis americana	Southern Stingray	21	43	5	4
Epinephelus striatus	Nassau Grouper	131	26	15	19
E. itajara	Goliath Grouper	3	100	2	1
Ginglymostoma cirratum	Nurse Shark	29	55	8	8
Haemulon album	Margate	15	20	2	1
Lachnolaimus maximus	Hogfish	503	39	111	85
Lutjanus jocu	Dog Snapper	117	113	61	71
L. cyanopterus	Cubera Snapper	93	84	34	44
L. analis	Mutton Snapper	321	13	24	18
Megalops atlanticus	Tarpon	49	55	12	15
Mycteroperca venenosa	Yellowfin Grouper	118	69	44	37
M. tigris	Tiger Grouper	135	62	45	39
M. bonaci	Black Grouper	114	52	33	26
M. interstitialis	Yellowmouth Grouper	6	0	0	0
Scarus guacamaia	Rainbow Parrotfish	43	72	10	21
S. coelestinus	Midnight Parrotfish	3	200	0	6
Scomberomorus cavalla	King Mackerel	3	0	0	0
Sphyraena barracuda	Great Barracuda	331	30	46	55
Trachinotus falcatus	Permit	6	0	0	0

T Number of tagged individuals, *PR* Percent recapture, *RM* Number of individuals recaptured at the manipulated site, *RC* Number of individuals recaptured at the control site

Table 2 Densities (individuals/8,000 m^2) and spillover variables for the species with higher number of tagged and recaptured individuals. Densities on months 1–3 were estimated before manipulation and on months 4–6 after it

Species	Density (by month)						DB	DA	EB	EA	IB	IA
	1	2	3	4	5	6						
Black Grouper	10.1±2.12	9.3±1.83	9.0±2.21	3.4±0.94	4.4±1.79	8.9±2.34	170±10.9	356±15.7	0.14±0.054	0.35±0.00	0.14±0.054	0.12±0.021
Yellowfin Grouper	9.9±2.33	8.4±1.58	8.0±1.82	2.4±1.17	5.8±1.49	9.0±2.09	129±21.2	246±24.6	0.11±0.015	0.31±0.024	0.11±0.015	0.09±0.020
Tiger Grouper	10.2±1.94	8.9±3.11	10.4±2.48	3.3±1.46	7.4±3.00	9.9±2.67	117±2.8	210±10.0	0.10±0.038	0.26±0.035	0.10±0.038	0.09±0.012
Cubera Snapper	10.0±2.22	8.4±1.99	10.4±2.51	3.9±2.15	8.1±2.52	11.9±2.44	201±38.2	342±17.5	0.14±0.054	0.40±0.100	0.19±0.009	0.11±0.012
Dog Snapper	14.9±3.25	9.9±2.19	10.1±3.00	3.8±1.43	5.4±2.11	10.4±1.73	98±7.5	237±5.6	0.07±0.016	0.18±0.027	0.10±0.135	0.06±0.003
Hogfish	20.4±4.51	16.9±3.82	16.4±4.39	6.1±3.76	15.4±3.97	18.0±3.91	263±3.6	330±24.8	0.30±0.114	0.61±0.025	0.22±0.030	0.11±0.054
Great Barracuda	10.8±2.99	7.4±3.03	11.9±4.08	4.8±2.55	4.5±1.97	5.5±2.48	348±37.8	609±33.9	0.16±0.044	0.43±0.062	0.21±0.011	0.10±0.027

DB distance before manipulation (m); *DA* distance after manipulation (m); *EB* emigration rate before manipulation; *EA* emigration rate after manipulation; *IB* immigration rate before manipulation; *IA* immigration rate after manipulation. Figures are means ± standard errors

second interaction terms of 3-ways ANOVAs was examined in detail (Table 3). In most cases (63%), the terms involving the date were significant. Only two species (Cubera Snapper and Hogfish) did not show significant interactions at any level. In these cases, it is apparent from the graphs (Fig. 3) that the change due to manipulation disappeared very fast. To get a better understanding of the progressive recovery of density, the analyses of density values in specific dates using planned comparisons was necessary.

Planned comparisons (Table 4) showed that density for all species pooled and the density of each species were significantly lower at the unprotected side of the manipulated site immediately after the manipulation (month 4). In month five, the density of six species and the pooled density were still significantly lower at the manipulated site. Exceptions were Mutton Snapper, Cubera Snapper and Hogfish. However, in month six, most species (except Great Barracuda) had recovered their former densities and no significant differences were found. The same result was obtained for the pooled density of all species (Fig. 3).

Spillover variables (D, E, I, C) showed a consistent pattern of change when analyzed for all species pooled (Fig. 4) and for each species separately (Table 2). In all cases the mean distance, emigration rate and crossing rate increased at the manipulated zone. The immigration rate decreased in all cases. The statistical significance of these changes was assessed by examination of the interaction terms' significance in bifactorial ANOVAs (Table 5).

Under control conditions (control site and protected side at the manipulated site before manipulation), 86% of the species tended to move less than 400 m (mean distance) in a four-month period, with great amount of recaptures right at the tagging zone (26% moved 0 m) or in the adjacent ones (41% moved 200 m). Immigration and emigration rates were the same in Tiger Grouper, Yellowfin Grouper, Black Grouper and therefore net balance was zero, while Dog Snapper, Cubera Snapper and Great Barracuda tended to import their biomass and Hogfish to export it (Table 2, Fig. 5).

Under manipulation condition (unprotected side at the manipulated site after manipulation), movement of all the species increased, each species exceeding a mean 200 m mark. The least mobile species, the Dog Snapper, almost tripled its mean distance after manipulation. This movement was essentially direc-

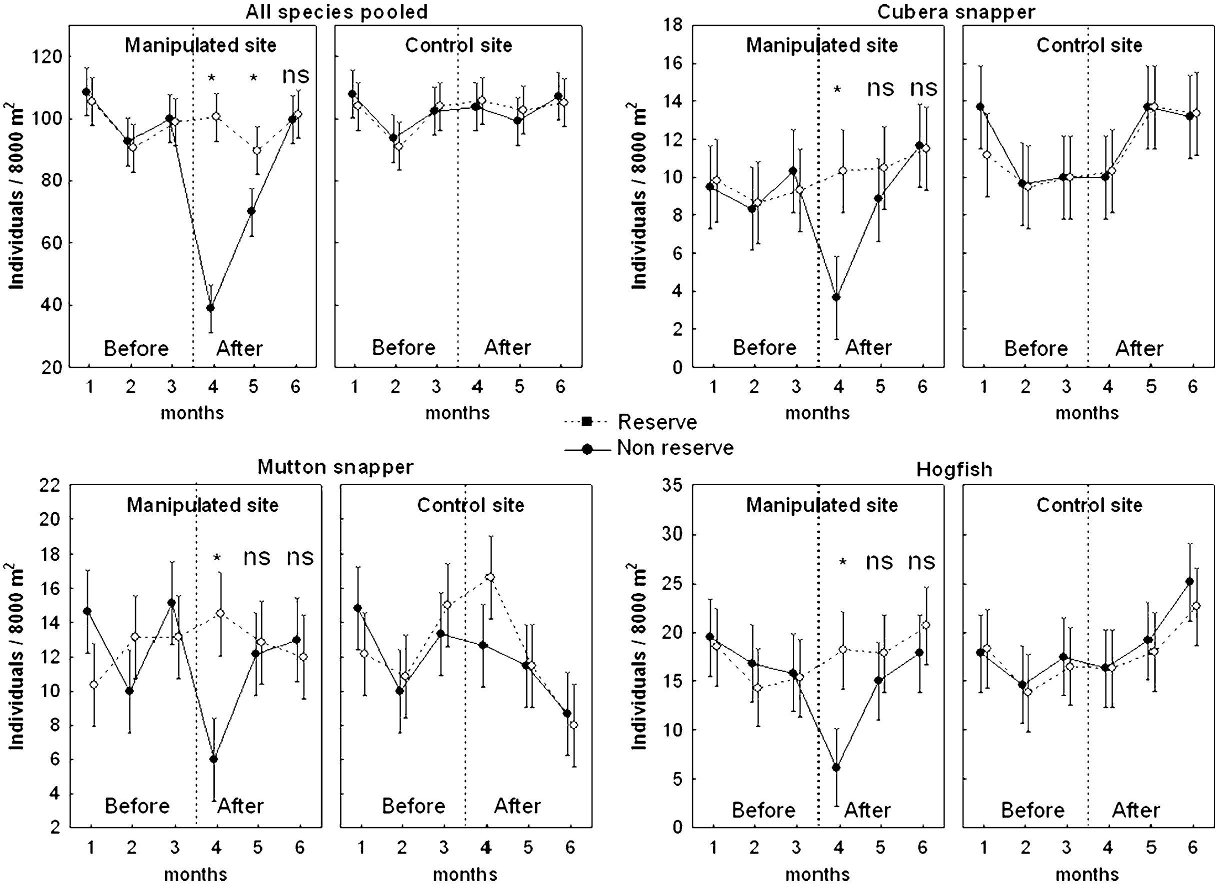

Fig. 3 Mean fish density estimated by visual censuses during the manipulative experiment. *Solid circles* and *solid lines* for unprotected side, *open circles* and *dotted lines* for protected side. Before and after refer to time of experimental removal on the unprotected side at the manipulated site. *Vertical bars* indicate 95% confidence intervals. *Stars* indicate that the means for that month in manipulated site were significantly lower after planned comparisons. No significance is indicated by ns

tional. In all the cases, emigration rate increased more than twice and immigration rate decreased, providing evidence that there is net spillover of all target species from the protected side to the unprotected side (Table 2, Fig. 5).

Discussion

The number and percentage of individuals tagged and recaptured obtained in this work are similar to those of the most comprehensive studies (Chapman and Kramer 2000; Zeller et al. 2003; Tupper 2007).

Few studies report emigration rates (Attwood and Bennett 1994; Zeller and Russ 1998; Zeller et al. 2003; Tupper 2007) and only three report the rates of bidirectional movement (Zeller and Russ 1998; Zeller et al. 2003; Tupper 2007). We followed the approach of Zeller et al. (2003), but unlike what is reported by these authors, our study detects an increase of the crossing rate and its directionality expressed as an increase of emigration due to manipulation of the density gradient. Our work is therefore one of the first that quantifies distance and movement direction due to a manufactured density gradient across marine reserve boundary. Since all targeted species exhibit similar movement trend (increase of distance and emigration rate and decrease of immigration rate after manipulation) our work convincingly discriminates spillover from natural movement of the species.

Most studies of movement on reef fish other than spawning migration report high site fidelity of studied

Table 3 Values of *F* ratios and associated probabilities (*p*) for the first and second order interaction terms in 3-ways ANOVAs of visual census data in the manipulative experiment

		Interaction terms			
		S × D	S × Z	D × Z	S × D × Z
	DF	5120	1120	5120	5120
Black Grouper	*F*	**2.86**	0.18	**2.35**	**3.66**
	p	**0.018**	0.676	**0.045**	**0.004**
Yellowfin Grouper	*F*	**2.32**	1.48	1.77	**3.56**
	p	**0.047**	0.226	0.125	**0.005**
Tiger Grouper	*F*	**4.16**	2.41	2.09	**2.81**
	p	**0.002**	0.123	0.072	**0.019**
Nassau Grouper	*F*	1.30	0.35	**4.39**	**3.61**
	p	0.267	0.556	**0.001**	**0.004**
Cubera Snapper	*F*	1.66	3.42	2.14	1.46
	p	0.149	0.067	0.065	0.207
Dog Snapper	*F*	**8.31**	0.86	**3.22**	**6.17**
	p	**<0.001**	0.356	**0.009**	**<0.001**
Mutton Snapper	*F*	**5.30**	0.09	**7.06**	1.39
	p	**<0.001**	0.761	**0.000**	0.235
Hogfish	*F*	1.54	3.58	1.83	1.67
	p	0.182	0.061	0.113	0.146
Great Barracuda	*F*	**2.87**	**5.75**	**3.67**	**2.93**
	p	**0.018**	**0.018**	**0.004**	**0.016**
Total	*F*	**13.34**	**16.80**	**12.32**	**9.32**
	p	**<0.001**	**<0.001**	**<0.001**	**<0.001**

S Site, *D* date of sampling, *Z* zone (reserve or no reserve), *DF* Degrees of freedom. Significant values in bold case

species regardless of size (Griffiths and Wilke 2002; Willis 2003; Zeller et al. 2003). Our results support these observations, since most of the species tended to move little, only two of the seven species moved more than 200 m, with most of recaptures recorded at the same or adjacent tagging area.

Most of the studies in the Caribbean target small- and medium-sized species, so little is known about the movement of large-sized reef species (Chapman and Kramer 2000; Meyer et al. 2000; Eristhee and Oxenford 2001). Only one of the seven species in our study, Black Grouper, has been previously tagged. Lindholm et al. (2005) found high site fidelity of this species, similar to our study.

The experimental design used in our study did not allow detection of movements beyond 1,400 m with 200 m precision. However, we assumed that the spatial scale used was appropriated and that movement detected in the present study correctly represents mobility of the species studied for the time and spatial scales used. These assumptions are supported by the high recapture rate, homogeneous tagging and recapture efforts, and the value of species mean distance far from the maximum possible value to be detected.

Tagging as a direct method for quantifying spillover was used in this study, avoiding undesirable biases of indirect methods such as fishing gears and visual censuses (Zeller and Russ 1998; Zeller et al. 2003). In addition, we carried out tagging inside and outside of the marine reserve with similar tagging and recapture effort on both sides of the boundaries, a procedure which has been recognized as essential for the reliability of the results (Attwood and Bennett 1994; Zeller and Russ 1998; Zeller et al. 2003). Other

Table 4 Results (Student's *t* and associated probability) for planned comparisons of mean density after manipulation at no protected side of the experimental site (BG) in each sampling date versus pooled mean density in all no-manipulated situations. Significant values are shown in bold case

		Contrast 1 Month 4	Contrast 2 Month 5	Contrast 3 Month 6
Black Grouper	*t*	**−6.180**	**−5.088**	−0.355
	p	**<0.001**	**<0.001**	0.723
Yellowfin Grouper	*t*	**−6.827**	**−2.637**	0.095
	p	**<0.001**	**0.010**	0.924
Tiger Grouper	*t*	**−7.731**	**−2.708**	−0.096
	p	**<0.001**	**0.008**	0.924
Nassau Grouper	*t*	**−6.335**	**−3.685**	−0.328
	p	**<0.001**	**<0.001**	0.743
Cubera Snapper	*t*	**−6.303**	−1.729	0.780
	p	**<0.001**	0.086	0.437
Dog Snapper	*t*	**−7.242**	**−5.893**	−0.110
	p	**<0.001**	**<0.001**	0.912
Mutton Snapper	*t*	**−5.107**	−0.208	0.454
	p	**<0.001**	0.836	0.651
Hogfish	*t*	**−5.634**	−1.348	0.027
	p	**<0.001**	0.180	0.979
Great Barracuda	*t*	**−4.646**	**−6.127**	**−4.091**
	p	**<0.001**	**<0.001**	**<0.001**
Total	*t*	**−15.512**	**−7.690**	−0.243
	p	**<0.001**	**<0.001**	0.808

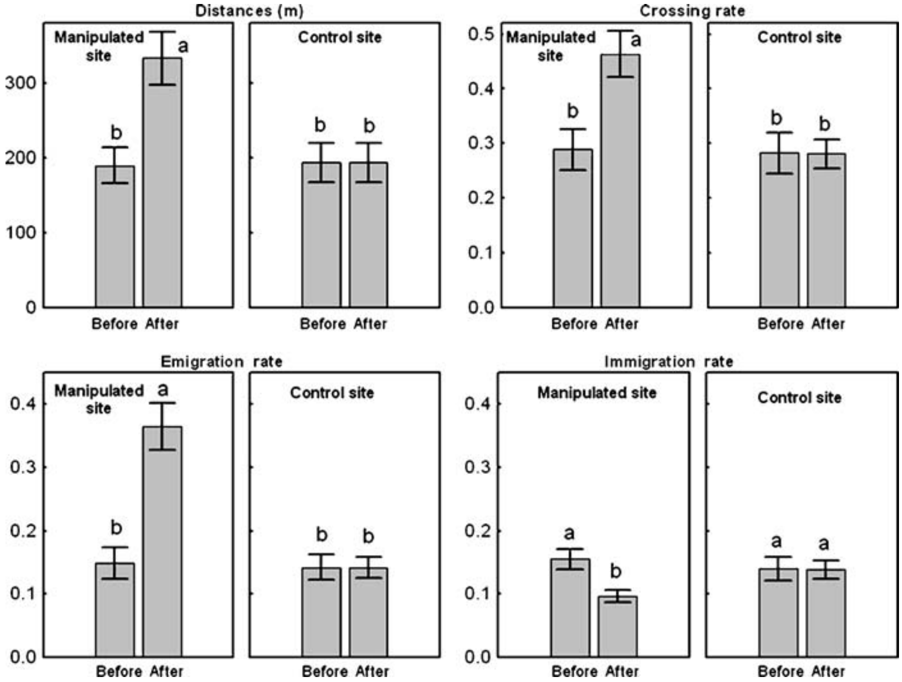

Fig. 4 Means and standard errors for spillover variables calculated for all species pooled during the manipulative experiment. Before and after refer to time of experimental removal in the unprotected side of the manipulated site. Means with different *letters* within each variable are significantly different after the Student Newman Keuls test

strengths of this study are the careful selection of experimental and control sites to ensure similar habitat type and fish density as well as forcing a density gradient using density reduction.

In summary, we were able to demonstrate a "spillover" effect by experimentally creating a density gradient. The "spillover" was evidenced by an increase in distance traveled by fish and emigration rate in comparison to "natural" movement of the studied species under control conditions. Detected mobility was species specific and variable but, in general terms, large-sized species tended to move hundreds of meters in the scale of months. These results suggest that in the case of a density gradient

Table 5 ANOVAs results for interaction term in comparisons of spillover variables calculated before and after the manipulation in control and manipulated sites. Degrees of freedom for *F* values were 1, 52 for all species pooled and 1, 4 for each species analysed separately

	D		C		I		E	
	F	*p*	F	*p*	F	*p*	F	*p*
All species	**6.52**	**0.014**	**5.83**	**0.019**	**4.22**	**0.045**	**17.48**	**<0.001**
Dog Snapper	**150.54**	**<0.001**	2.08	0.222	0.91	0.393	4.38	0.104
Tiger Grouper	**19.15**	**0.012**	1.88	0.241	0.05	0.829	7.22	0.055
Yellowfin Grouper	**12.28**	**0.025**	4.22	0.109	0.01	0.974	**16.64**	**0.015**
Black Grouper	**8.64**	**0.042**	**10.15**	**0.033**	0.15	0.713	**13.21**	**0.022**
Cubera Snapper	5.30	0.083	1.21	0.332	**11.55**	**0.027**	4.09	0.113
Hogfish	1.69	0.263	0.49	0.521	0.41	0.553	2.93	0.162
Great Barracuda	**13.91**	**0.020**	**9.40**	**0.037**	5.24	0.084	**11.28**	**0.028**

D distance; *C* crossing rate; *I* Immigration rate; *E* emigration rate. Significant values in bold case. See also Fig. 4

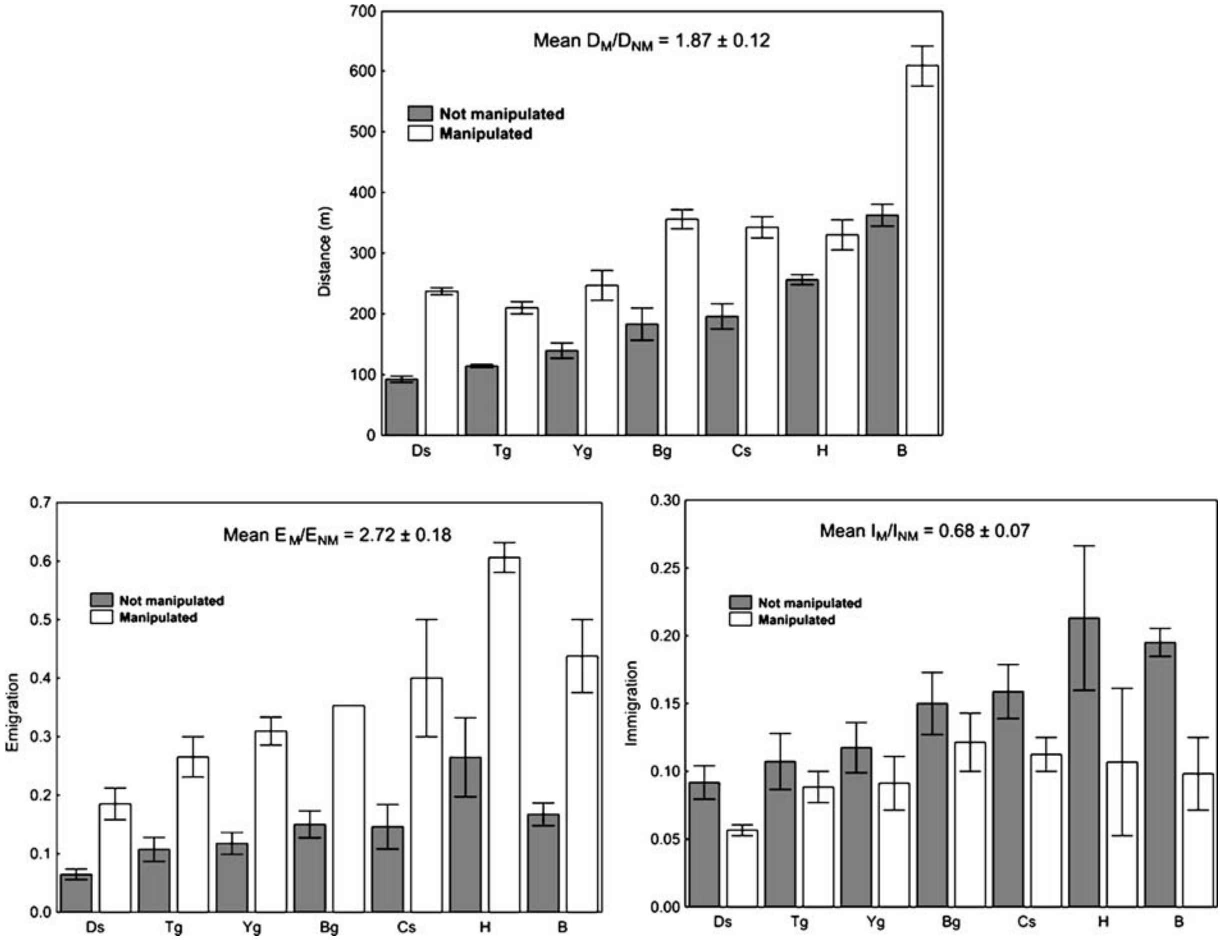

Fig. 5 Means and standard errors for spillover variables calculated for all species before and after the manipulation. *D* distance; *I* immigration rate; *E*, emigration rate. Species ordered from least to most mobile. *Ds* Dog Snapper; *Tg* Tiger Grouper; *Yg* Yellowfin Grouper; *Bg* Black Grouper; *Cs* Cubera Snapper; *H* Hogfish; *B* Barracuda

across a marine protected area boundary, adjacent areas might benefit from the spillover due to the greater density of fish inside the marine protected area. After our results, spillover could take place when a strong density gradient is present. Based in our experimental data, the zone with higher density should have at least twice the number of fish per unit area as the zone with lower density. In natural conditions the gradient could disappear just a month after the factors forcing it had ceased. Such a gradient could increase 1.5 times distances traveled by fish (increasing the mean from below 200 m to more than 300 m). Density differences could double the natural value of the emigration rate. However, these results could be only extrapolated to other marine protected areas and conditions similar to those at Jardines de la Reina Marine Reserve. Spillover experiments carried out in limited take marine protected areas which boundaries cross shallow reef slopes of the Caribbean region, could only be compared with our study as long as they are conducted from May to August and involving species such as Dog Snapper, Cubera Snapper, Yellowfin Grouper, Tiger Grouper, Black Grouper, Hogfish and Great Barracuda.

We strongly recommend that future efforts to assess spillover should do more replication, involve more habitats and other species and are carried out in other seasons. We also recommend the use of other tagging methods such as ultrasonic and satellite ones to extend research in time and space.

Acknowledgements The authors are thankful to the staff of Azulmar for logistical support on Jardines de la Reina, especially to Giuseppe Omegna (Pepe); to WWF Canada for funding this research and to E. Sala, Director of the Center for Marine Biodiversity and Conservation of the Scripps Institution of Oceanography for funding and logistics. We thank the Ministry of Science, Technology and Environment for funds and logistics, especially C. Pazos Alberdi, R. Gómez Fernández, A. Zúñiga Ríos and R. Estrada Estrada and the Ministry of Fisheries for logistics, specially J. Baisre, M. Iglesias (Gallega), Nachi and his crew. Infinite thanks to CIEC´s staff for supporting us in doing research on Jardines de la Reina, especially to T. Figueredo Martín, P. E. Cardoso Gómez and V.O. Rodríguez Cárdenas.

References

Alcala AC, Russ GR, Maypa AP, Calumpong HP (2005) A long-term, spatially replicated experimental test of the effect of marine reserves on local fish yields. Can J Fish Aquat Sci 62:98–108

Appeldoorn RS, Lindeman KC (2003) A Caribbean-wide survey of marine reserves: spatial coverage and attributes of effectiveness. Gulf Caribb Res 14(2):139–154

Attwood CG, Bennett BA (1994) Variation in dispersal of galjoen (Coracinus capensis) (Teleostei: Coracinidae) from a marine reserve. Can J Fish Aquat Sci 51:1247–1257

Chapman MR, Kramer DL (2000) Movements of fishes within and among fringing coral reefs in Barbados. Environ Biol Fishes 57(1):11–24

Eristhee N, Oxenford HA (2001) Home range size and use of space by Bermuda chub, Kyphosus sectatrix (L.) in two marine reserves in the Soufriere Marine Management Area, St Lucia, West Indies. J Fish Biol 59(Supplement A):129–151

Griffiths MH, Wilke CG (2002) Long-term movement patterns of five temperate-reef fishes (Pisces: Sparidae): implications for marine reserves. Mar Freshw Res 53:233–244

Kelly SD, Scott D, MacDiarmid AB (2002) The value of a spillover fishery for spiny lobsters around a marine reserve in northern New Zealand. Coast Manage 30:153–166

Lindholm J, Kaufman L, Miller S, Wagschal A, Newville M (2005) Movement of yellowtail snapper (Ocyurus chrysurus Block 1790) and Black Grouper (Mycteroperca bonaci Poey 1860) in the northern Florida Keys National Marine Sanctuary as determined by acoustic telemetry. Marine Sanctuaries Conservation Series MSD-05-4. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Marine Sanctuaries Division, Silver Spring, MD. 17 pp

Maypa AP, Russ GR, Alcala AC, Calumpong HP (2002) Long-term trends in yield and catch rates of the coral reef fishery at Apo Island, Central Philippines. Mar Freshw Res 53:207–213

Meyer CG, Holland KN, Wetherbee BM, Lowe CG (2000) Movement patterns, habitat utilization, home range size and size fidelity of whitesaddle goatfish, Parupeneus poryphyreus, in a marine reserve. Environ Biol Fishes 59:235–242

Palumbi SR (2004) Marine reserves and ocean neighborhoods: the spatial scale of marine populations and their management. Annu Rev Environ Resour 29:31–68

Russ GR, Alcala AC (2003) Marine reserves: rates and patterns of recovery and decline of predatory fish. 1983–2000. Ecol Appl 13:1553–1565

Russ GR, Alcala AC, Maypa AP (2003) Spillover from marine reserves: the case of Naso vlaminii at Apo Island, the Philippines. Mar Ecol Prog Ser 264:15–20

Sale PF, Cowen RK, Danilowicz BS, Jones GP, Kritzer JP, Lindeman KC, Planes S, Polunin NVC, Russ GR, Sadovy YS, Steneck RS (2005) Critical science gaps impede use of no-take fishery reserves. Trends Ecol Evol 20(2):74–80

Starr RM, Sala E, Ballesteros E, Zabala M (2007) Spatial dynamics of the Nassau grouper Epinephelus striatus in a Caribbean atoll. Mar Ecol Prog Ser 342:239–249

Tupper MH (2007) Spillover of commercially valuable reef fishes from marine protected areas in Guam. Micronesia Fish Bull 105:527–537

Underwood AJ (1997) Experiments in ecology. Their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge, 504 p

Westera M, Lavery P, Hyndes G (2003) Differences in recreationally targeted fishes between protected and fished areas of a coral reef marine park. J Exp Mar Biol Ecol 294:145–168

Willis TJ (2003) Protection of exploited fishes in temperate regions: high density and biomass of snapper Pagrus auratus (Sparidae) in northern New Zealand marine reserve. J Appl Ecol 40:214–227

Zar JH (1996) Biostatistical analysis, 3rd edn. Prentice Hall, New Jersey, 662p

Zeller DC, Russ GR (1998) Marine reserves: patterns of adult movement of the coral trout (Plectropomus leopardus (Serranidae). Can J Fish Aquat Sci 55:917–924

Zeller DC, Stoute SL, Russ GR (2003) Movements of reef fishes across marine reserve boundaries: effects of manipulating a densidad gradient. Mar Ecol Prog Series 254:269–280