Benthic biodiversity changes due to the opening of an artificial channel in a tropical coastal lagoon (Mexican Caribbean)

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The construction of an artificial channel to a small embayment in the Chetumal Bay coastal lagoon complex, located on the Caribbean coast of Mexico, provided an opportunity to evaluate how large environmental changes influenced the structure of a low diversity benthic system. The objective of this study was to demonstrate that despite the absence of previous baseline information, the artificial channel has induced measurable changes in the biodiversity patterns of a hard substrata benthic community. The experimental design took into account the environmental setting influencing local benthic community structure and the sources of variability as a result of different substrate types and water depth. Four localities with ten replicates each were surveyed, and the presence/absence of macrobenthic biota species recorded during the rainy season. Our analysis using permutational multivariate analysis of variance indicated a significant increase in species richness in locations adjacent to the artificial channel. The highest species richness (66 species) was observed in the immediate area adjacent to the artificial channel and where exclusive species density was three to six times (18 exclusive species) than those present in other localities (6, 5 and 3 species) away from the channel. The presence of six species of hard corals indicated that the artificial channel offers a more suitable habitat for marine organisms colonizing the area than the natural channel. This study indicates the relative significance of confinement in structuring coastal lagoon benthic assemblages in tropical systems. Our results are similar to other findings underscoring the rate of colonization of marine organisms as a relevant process to explain benthic assemblage gradients and the importance of spatial–temporal interactions. The changes in species diversity caused by the artificial channel were clearly identified based on a sampling design that incorporated the main sources of environmental variability (distance to channels, substrate type and depth). Our study further demonstrates that changes in benthic community structure in the Chetumal Bay lagoon complex, as a result of human impacts, can be assessed even when community structure data before impact are absent.

Keywords: benthos, environmental impact, corals, coastal lagoons, multivariate analysis, variability

Submitted 29 July 2010; accepted 5 November 2010; first published online 23 December 2010

INTRODUCTION

Coastal lagoon assemblages are characterized by high spatial–temporal variability in community composition and distribution patterns (Benedetti-Cecchi *et al.*, 2001; Esteves *et al.*, 2008). Sources of variability affecting biodiversity patterns in coastal lagoons are: degree of confinement (i.e. water circulation patterns and residence time, *sensu* Guelorget & Perthuisot, 1983; cited in Guelorget *et al.*, 1990); geomorphological features e.g. lagoon size, coastal development and inlet dimensions (Franco *et al.*, 2008), hydrological variability and productivity (Pérez-Ruzafa *et al.*, 2005, 2007a); and substrate type and depth (Pérez-Ruzafa *et al.*, 2008). These characteristics define boundaries with strong physical and ecological gradients (Duarte *et al.*, 2006; Pérez-Ruzafa *et al.*, 2007b). The degree of confinement is a measure of the interaction between lagoon and coastal waters and is considered as a critical variable for explaining species distribution in brackish ecosystems (Frénod & Goubert, 2007). The degree of confinement is modified by direct human intervention through the construction of artificial channels that increase connectivity between coastal lagoons and the sea (Pérez-Ruzafa *et al.*, 2006). An increase in connectivity may have detrimental impacts due to the displacement of coastal lagoons biota by the rapid colonization of marine organisms, shifting community structure and function (Pérez-Ruzafa *et al.*, 1991; Sfriso *et al.*, 2003; Young & Potter, 2003). However, beneficial effects can be obtained when restoring connectivity, particularly after human impact isolates portions of coastal lagoons, by allowing the entrance of marine biota (Griffiths, 1999; Layman, 2003; Lai *et al.*, 2007).

The importance of physical connectivity between coastal lagoons and reef lagoons has been widely recognized, especially for fish that use coastal environments during their ontogenetic changes (Sale & Kritzer, 2003; Mumby, 2006). However, sessile fauna cannot migrate and might be more susceptible, than mobile fauna, to subtle and permanent changes derived from the increase in connectivity between coastal lagoons and the sea. Thus, sessile organisms respond directly to the abiotic and biotic aquatic environment and could be used as sensitive indicators of environmental change

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(Guelorget *et al.*, 1990; Warwick, 1993). The colonization rate of marine organisms is one of the main factors explaining lagoon assemblage structure along a confinement gradient (Pérez-Ruzafa *et al.*, 1992 cited in Pérez-Ruzafa *et al.*, 2007a). The presence of marine benthic biota is an indicator of the suitability of the environment for settling and survival, particularly for slow growth long-lived organism (Strathmann *et al.*, 2002; Harrington *et al.*, 2004).

The main challenge in environmental impact assessment studies is to isolate the effect of interest from natural variability. Therefore these types of studies require a statistical framework defining proper spatial–temporal replication for comparison of differences in temporal changes of ecologically meaningful variables before and after disturbance (either natural or human) and several control locations (Underwood, 1994, 2000; Queiroz *et al.*, 2006). It is recognized that the lack of data previous to disturbance, particularly the absence of properly designed sampling programmes, hinders the assessment of actual ecological changes in coastal ecosystems (Underwood, 1993; Wiens & Parker, 1995; Underwood *et al.*, 2003).

The construction of an artificial channel used as a second entrance to a small embayment, located within Chetumal Bay on the Caribbean coast of Mexico, provided an opportunity to assess how large environmental changes impacted a low diversity benthic system (Quan-Young *et al.*, 2006) as the connectivity between the embayment and a reef lagoon increased. Indeed the artificial channel provided alternative access to fishermen and tourist services around the region. Moreover, this channel is part of a wider tourist development plan in Chetumal Bay, which includes the construction of resort facilities, marinas and a golf course. Thus, it is expected that given the spatial footprint of this resort development, the population dynamics of sessile organisms will be modified as connectivity between the small embayment and reef lagoon increases in comparison to the connectivity provided by a natural narrower channel. The objective of this study is to demonstrate that despite the absence of previous baseline information, the artificial channel has induced measurable changes in the biodiversity patterns of a hard substrata benthic community present in a localized region in Chetumal Bay. Our study also allows us to assess the degree of implementation of environmental impact studies for coastal development plans on the Caribbean coast of Mexico.

MATERIALS AND METHODS

Study area

The study area is a shallow embayment located on the southeast of the Caribbean coast of the Yucatan Peninsula (18°12′12″N 87°51′43″W and 18°10′16″N 87°53′34″W). Water depth ranges from 0.5 to 2.5 m and benthic environment is a mosaic of hard and soft substrate that varies at scales of metres to hundreds of metres. A unique feature is the presence of sinkholes conducting marine water into the lagoon; the sink holes' diameter range from few metres (5–9 m) to tens of metres (20–30 m). The study area comprises an interaction zone between a coastal lagoon, The Sanctuary of the Manatee or Chetumal Bay, and the reef lagoon of The National Park Xcalak Reefs via two channels: (a) Bacalar

Chico a natural channel 30 m width, borderline between Belize and Mexico, that meanders among mangroves for about 3 km length; and (b) Canal de Zaragoza an artificial channel, first built in 1909 silted to a very narrow and shallow creek and re-opened between 1999 and 2004. It is a straight-line 50 m width, 1300 m length and 2.5 m deep and it has modified intensively the local hydrology. To the south, the area is connected to the main Chetumal Bay (Figure 1). Previous to the re-opening of the artificial channel local hydrology was similar to the main Chetumal Bay: brackish water with salinity around 20 psu and increasing to marine water at the area of influence of the natural channel. At present, local hydrology has changed becoming more marine, with salinity ranging from 26 to 32 psu (unpublished data).

Approach and sampling design

Optimal sampling designs to detect changes in spatial and temporal biodiversity patterns due to human and natural disturbances require information before and after impact (Eberhardt & Thomas, 1991; Underwood, 1994; Hewitt *et al.*, 2001). Yet, there is no legal requirement in Mexico for the design of appropriate sampling programmes to detect environmental impact derived from human activities before, during and after impact. For example, an environmental impact study for the construction of the artificial channel in the study area concluded 'no projected impact is expected on the benthic biota in the long term' (HP-Consultores-Ambientales, 1999). Yet no information was offered to support this statement. To assess if any change occurred as result of the channel construction on the benthic biota biodiversity, we used a crossed-sampling design where time (three levels) and locality (four levels) were considered as fixed factors. The factor time included the rainy season and samples were collected in May (T1), July (T2) and September (T3) 2006. Our sampling schedule was selected to detect small-scale temporal variation, since in the rainy season there is an increase in underground and surface freshwater discharge significantly reducing salinity values from 22 to 16 psu at the south-eastern portion of Chetumal Bay (Carrillo *et al.*, 2009). We expected that due to changes in salinity, benthic marine species would either migrate, withstand salinity changes or die, depending on the degree of confinement controlled by the structural features of the artificial channel. The factor locality included the degree of spatial influence by the artificial channel (L1), the area of influence of the natural channel (L2) and two localities (L3 and L4) representing environmental conditions typical of Chetumal Bay (Figure 1). Substrate type and water depth are key variables controlling benthic assemblages (Sfriso *et al.*, 2003; Pérez-Ruzafa *et al.*, 2007a); thus, to experimentally assess their influence on benthic density and species composition, the field sampling was performed on hard bottom habitats at depths ranging from 0.8 to 1.5 m. Distances among localities were from 3 to 5 km. Ten replicates of 10 m² areas (30 to 50 m apart) of hard substrate were haphazardly selected at each sampling time and visually censed to record presence/absence of all the sessile macrobenthic biota at each locality. A photographic record was used to assist organisms' identification in the laboratory. Taxonomic identification was to species level or at least to operational species using distinct morphological features.
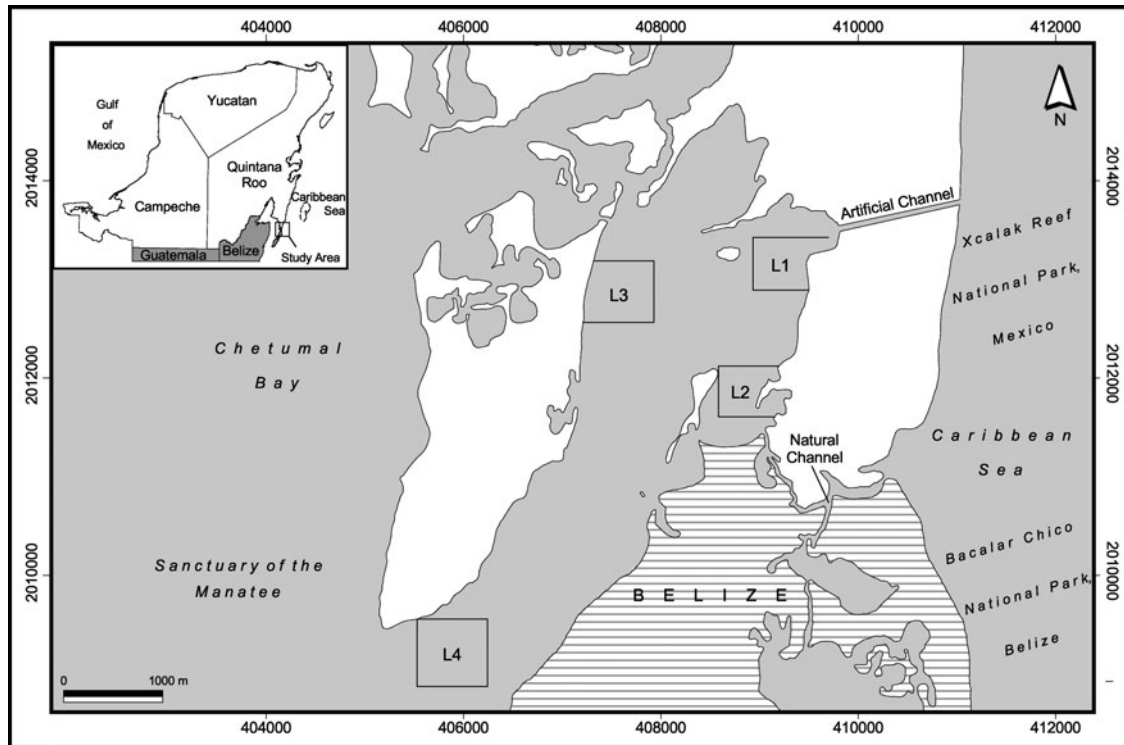
Fig. 1. Study area of Chetumal Bay showing localities L1 to L4, the natural and artificial channels and the connections with the main Chatumal Bay and the Caribbean Sea.

Data analyses

A multivariate approach was used to evaluate the environmental spatial and temporal effect on sessile macrobenthic community structure. Two hypotheses of differences in community structure were tested corresponding to locality and time using permutational multivariate analyses of variance (PERMANOVA; Anderson, 2001). This technique allows the testing of the simultaneous response of a community to a number of factors considered in a structured sampling design. It is based on distance measures using permutation methods, following a linear model of additive partitioning of variation for complex sampling designs (Anderson, 2001). Based on the strategy proposed by Warwick (1993), Anderson (2001) and Anderson *et al.* (2005) the biological matrix of species presence/absence data at each replicate/locality/time was used to build a triangular similarity matrix based on the Bray–Curtis similarity measure. We use a presence–absence matrix because our purpose was to incorporate the widest possible species richness of sessile biota including macrophytes and fauna. Due to the macrophytes growth patterns and variable densities, they are difficult to measure quantitatively under the same sampling unit used for benthic organisms. By using presence–absence records we were able to increase sample size and coverage at each sampling locality.

A crossed PERMANOVA model was run to test the response of the benthic assemblage for differences among localities across time and among time across locality. Planned pairwise comparisons were made for the interaction term time × locality. The spatial pattern was displayed in two-dimensional canonical analysis of principal coordinates (CAP), which produces a constrained ordination to separate samples based on an *a priori* hypothesis by looking for group differences along other dimensions. CAP also takes into account the correlation structure among the variables (i.e. species) in the presence/absence matrix (Anderson & Willis, 2003). A natural extension to this approach is to find the smallest subset of species, which account for the whole spatial and temporal pattern of influence of the natural and artificial channels within the area of interest. In order to identify this subset of species, we follow the procedure described by Clarke & Warwick (1998). This approach uses a matching set of samples and measures how closely related two sets of multivariate data are by calculating a rank-correlation coefficient among all the elements of their respective similarity matrices to a set criterion of Rho = 0.95. This matching process is achieved by a stepwise algorithm, which searches at several different random starts of a randomly selected set of 10% of the species. The selected smallest subset can be considered influential species (*sensu* Clarke & Warwick, 1998) in explaining the full pattern from the whole set of species. All statistical analyses were run using the PRIMER software routines BEST and PERMANOVA plus (Clarke & Gorley, 2006; Anderson *et al.*, 2008).

RESULTS

Description of community structure

We recorded 86 species, belonging to nine major groups of organisms, of macrobenthic biota on hard substrate. Total number of species per locality increased from locality 4 to localities 2 and 1, the area of influence of the natural and artificial channels. The cnidarians (including hard corals),

macroalgae and sponges had large differences in number of species between localities (Table 1A). The number of exclusive species at locality 1, the artificial channel, was three to six times larger than those exclusively present at the other localities. Localities 1–2 shared more species, followed by localities 2–3, 1–3, 1–4, 2–4 and 3–4, that represented 56%, 57%, 46%, 30%, 33% and 37%, respectively, of the total number of species. Finally, there were more species shared exclusively by localities 1–2 compared to any other pair of localities (Table 1B).

Multivariate test of differences

The multivariate analysis approach allowed direct comparisons among time and locality to identify differences at the spatial and temporal scales considered. Table 2 shows the results of PERMANOVA; significant differences were detected in community composition among time and locality. However, the interaction term was also significant indicating dependence in the effect of the main factors. The component of variation explained by each of the tested terms showed that the highest variation corresponds to the residuals, the spatial scale of replicated areas, followed by locality which explains nearly the same amount of variation indicating a strong spatial pattern of differences. We estimated pair-wise comparisons in order to better describe the interaction term time × locality. Fixing each level of time, the locality effect remains the same indicating a strong spatial pattern of differences, all pairs of localities showed significant differences ($P <$ 0.05, alpha = 0.05). However, when looking at the time effect at each level of locality its effect varied, the temporal pattern of differences changed in relation to what locality is considered. Table 3 shows the interaction between time and locality when the level of locality is fixed. For example, L1 and L3 showed differences in community structure between T1–T2 and T1–T3, L2 presented temporal differences in all pairs of times and L4 showed differences only between T2–T3.

Table 1. (A) Number of species of macrobenthic biota from hard substrate in each locality distributed within nine major groups of organisms; (B) abundance/commonality matrix. Diagonal (bold figures) are species present exclusively at a particular locality, upper diagonals (italic figures) are total number of species for each pair of localities, lower diagonals are number of species shared by a given pair of localities and in parentheses are the number of species shared exclusively by that pair.

Group	Locality 1	Locality 2	Locality 3	Locality 4
(A)				
Arthropoda	3	4	3	4
Ascideacea	1	2	2	2
Cnidaria	12	6	5	1
Echinodermata		1		
Macroalgae	16	10	11	5
Mollusca	13	11	11	8
Polychaeta	5	2	2	2
Porifera	15	16	10	4
Seagrasses	1	2	1	2
Total	66	54	45	28
(B)				
Locality 1	**18**	*77*	*76*	*72*
Locality 2	43 (7)	**6**	*63*	*60*
Locality 3	35 (3)	36 (3)	**5**	*53*
Locality 4	22 (2)	20 (1)	20 (1)	**3**

Table 2. PERMANOVA results of significant differences in community structure for main factors and interaction term for a structured two factor crossed design, with components of variation (CV) in percentage explained by each factor design. Bold figures are statistically significant.

Source	df	SS	MS	Pseudo-F	P (perm)	CV%
Time	2	13115	6557.7	5.7974	**0.001**	5.24
Locality	3	1.014×10^5	33797	29.8175	**0.001**	42.03
Time × locality	6	20883	3480.5	3.0769	**0.001**	9.07
Residual	108	1.222×10^5	1131.1			43.66
Total	119	2.576×10^5				100.00

Therefore, it would not make much sense to consider a time effect without taking in to account on what locality this effect is taking place.

The graphical representation of the spatial and temporal pattern of community structure differences showed a strong spatial pattern, consistent with the percentage of component of variation explained only by factor locality. The locality effect is noticeable, all four localities separated out, and locality one (the artificial channel) is grouped out of the evident gradient of community composition differences from the area of influence of the natural channel (L2) towards L3 and L4. The depicted gradient corresponds with the degree of marine influence, its direction and the relative magnitude of change are similar in all the observed times. In contrast, despite significant differences between times its effect is dependent on the particular locality, as can be observed from the graph where there is no clear time pattern within localities as pointed out from the pair-wise comparisons (Figure 2).

Influential species

In order to identify a group of influential species, indicative of the structural pattern observed between localities, a structural redundancy analysis was performed to find out one or more subsets of species that produce a nearly perfect match with

Table 3. Pairwise comparisons for the interaction term time × locality, when level of locality is fixed. Permutation test used was the Monte Carlo due to the number of permutations (999) allowed by the degrees of freedom (bold figures are statistically significant at $P < 0.05$).

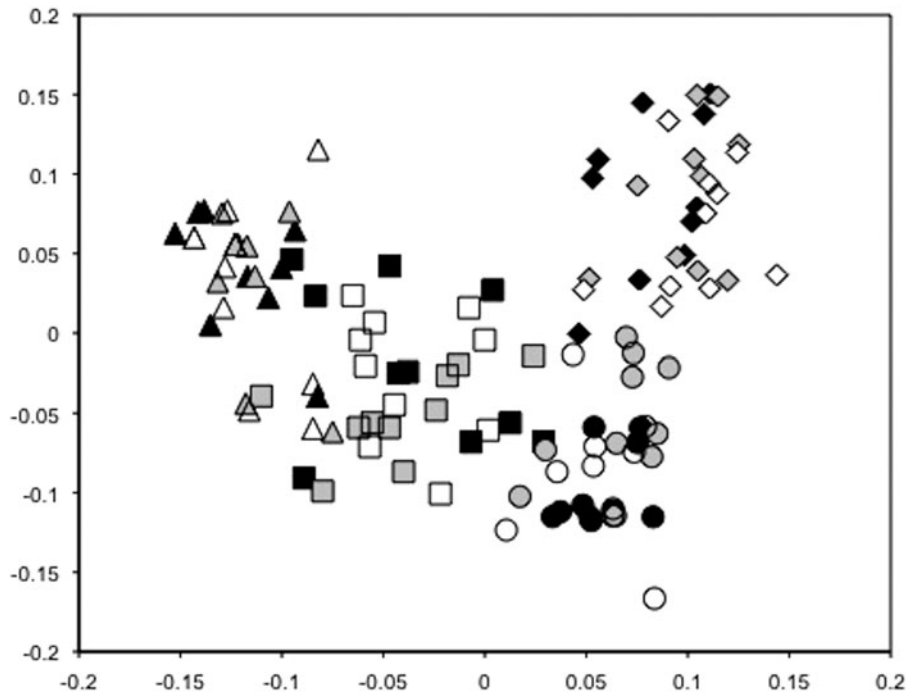| Groups	t-test	Unique permutations	P (Monte Carlo)
Locality	**L1**		
T1, T2	2.2331	994	**0.001**
T1, T3	2.4349	996	**0.001**
T2, T3	1.2555	991	0.152
Locality	**L2**		
T1, T2	1.6403	995	**0.014**
T1, T3	1.6679	991	**0.021**
T2, T3	1.5196	991	**0.048**
Locality	**L3**		
T1, T2	2.6479	993	**0.001**
T1, T3	2.9853	995	**0.001**
T2, T3	1.3335	991	0.13
Locality	**L4**		
T1, T2	1.4836	980	0.079
T1, T3	1.1058	984	0.292
T2, T3	1.8801	965	**0.011**

Fig. 2. Canonical analysis of principal coordinates ordination plot showing the spatial pattern of differences among localities. Differences among localities were statistically significant, with diversity (composition and abundance) increasing from the channels towards the main body of the bay (L1 – T1 ◆, L1 – T2 ◆, L1 – T3 ◇, L2 – T1 •, L2 – T2 ●, L2 – T3 ○, L3 – T1 ■, L3 – T2 ■, L3 – T3 □, L4 – T1 ▲, L4 – T2 ▲, L4 – T3 Δ)

the overall community structure displayed by the whole set. Following the procedure BEST of PRIMER routines, a subset of 22 species was extracted (Table 4) that reproduces practically the same strong spatial structural pattern (Figure 3A) with a correlation coefficient of 0.95 between its corresponding triangular similarity matrices. Following iterations of the BEST procedure no further subsets were identified that nearly match the criteria of correlation coefficient of 0.95, in fact, the second subset of 20 species identified had a correlation coefficient of 0.4 and the multivariate pattern, as displayed by the graphical interface used (Figure 3B), shows a very degraded pattern compared with the original one. Therefore, the first subset of 22 species might be considered a unique assemblage that maximizes the spatial differences in community composition, and a subset with a relative strong signal-to-noise ratio. In other words, the species listed in Table 4 are those that better summarize the environmental gradient from marine to lagoon – estuarine conditions.

Macrolgae like *Acetabularia crenulata* is present, preferably, under the area of influence of both the artificial and natural channel (L1 and L2) as well as the scleractinian coral *Siderastrea radians*. Other algae, like *Penicillus capitatus* dwell better on the area of direct influence of the artificial channel (L1). On the other hand, bivalves like *Brachidontes* sp. are limited to localities 3 and 4 characteristic of the local fauna of Chetumal Bay. Some sponges, like *Chondrilla nucula*, prefer the area of influence of the natural channel (L2). It is worth noticing that the structural redundancy analysis did not pick up on any of the exclusive species of any locality, except for *Dyctiosphaeria cavernosa* present only at locality 1 (see Discussion). Most of the exclusive species had low frequency of appearance, both spatially and temporally, including the various species of corals whose distribution is restricted on the area of influence of the artificial channel

(L1). Nevertheless, coral presence is a clear indication of the magnitude of influence that the artificial channel exerts on this particular area as a more efficient entrance of marine organisms into Chetumal Bay. Table 5 shows a list of hard coral species recorded in the artificial and natural channels compared with the presence and frequency of records of hard corals in 30 sampling units for the four study localities

Table 4. Results of redundancy analyses of influential species compared with their presence and frequency of records in 30 sampling units for the four study localities throughout the survey period.

| Group	Species	L1	L2	L3	L4
Arthropoda	Hermit crab sp. A	0.3	0.2	0.2	0.0
Ascideacea	Tunicate sp.	0.1	0.1	0.6	0.0
Cnidaria	*Siderastrea radians*	0.2	0.2	0.0	0.0
	Hydroid sp. C	0.4	0.3	0.1	0.0
Macroalgae	*Acetabularia crenulata*	0.9	0.9	0.1	0.0
	Anadyomene stellata	0.5	0.5	0.9	0.1
	Batophora oerstedii	0.9	1.0	1.0	1.0
	Dictyosphaeria cavernosa	0.5	0.0	1.0	0.0
	Dictyosphaeria ocellata	0.3	0.6	0.8	0.2
	Green filamentous algae	0.5	0.4	0.3	0.1
	Halimeda incrassata	0.3	0.1	0.0	0.0
	Jania capillacea	0.6	0.3	0.2	0.0
	Laurencia sp.	0.9	0.8	0.9	0.5
	Penicillus capitatus	0.6	0.1	0.5	0.0
Mollusca	*Anomalocardia* sp.	0.2	0.4	0.5	0.1
	Brachidontes sp.	0.0	0.1	0.8	1.0
	Marginella roscida	0.0	0.0	0.4	0.4
Polychaeta	Sabellid sp	0.6	0.2	0.1	0.0
Porifera	*Chondrilla nucula*	0.1	0.7	0.1	0.1
	Sponge sp. 3	0.4	0.1	0.4	0.0
	Sponge sp. 2	0.1	0.2	0.2	0.0
Seagrasses	*Thalassia testudinum*	0.7	1.0	0.6	0.1
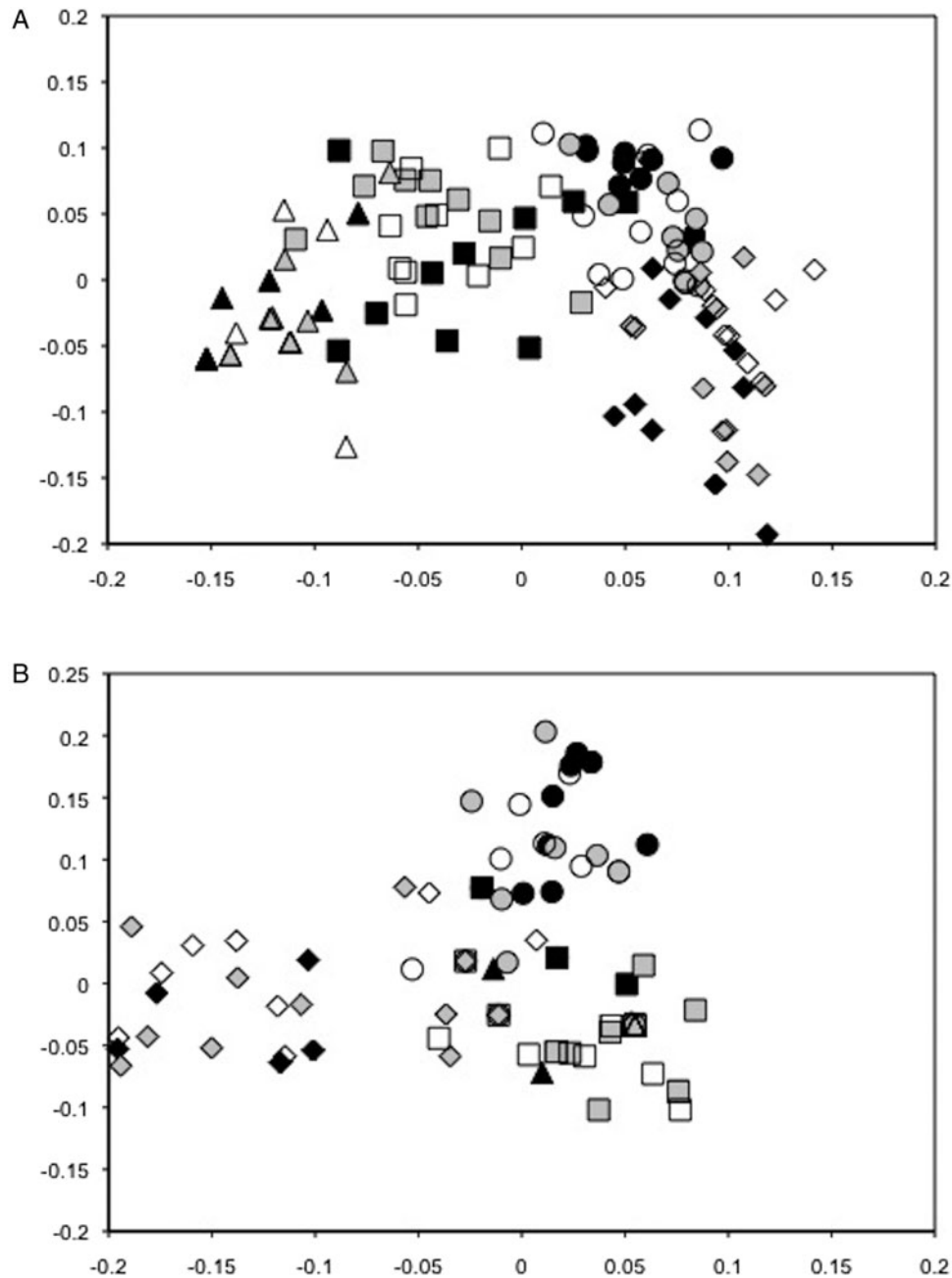
Fig. 3. Canonical analysis of principal coordinates ordination plot showing the spatial pattern of differences among localities of a subset of species extracted by the BEST procedure. (A) First subset of 22 species that reproduces practically the same strong spatial pattern of Figure 2 ($\rho = 0.95$); (B) second subset of species after removing the 22 species from the first subset ($\rho = 0.4$) (L1–T1 ◆, L1–T2 ◈, L1–T3 ◇, L2–T1 ●, L2–T2 ◉, L2–T3 ○, L3–T1 ■, L3–T2 ▦, L3–T3 □, L4–T1 ▲, L4–T2 ◮, L4–T3 △)

throughout the survey period. The number of species of corals in the area of influence of both the artificial and natural channel is closely related to the number of species recorded within the channels. In the artificial channel we recorded eight species of hard corals, compared with two species of hard corals in the natural channel.

DISCUSSION

This study aimed to measure the influence of an artificial channel on the biodiversity pattern of a benthic community

on hard substrate, in a context of lack of previous information and where a natural channel maintained permanent connection to the sea. It is well known that coastal lagoon gradients in biodiversity composition relate to the proximity and characteristics of the channels communicating with the sea (Guelorget et al., 1990). For example, the degree of communication and channel characteristics determine differences in fish community structure in Mediterranean coastal lagoons (Pérez-Ruzafa et al., 2007a; Franco et al., 2008). Any change that alters the degree of communication between the coastal lagoon and the sea influences the turnover time of marine water and the replenishment of nutrients of marine origin,

Table 5. Hard coral species recorded in the artificial and natural channels compared with the presence and frequency of records of hard corals in 30 sampling units for the four study localities throughout the survey period.

Species	Artificial channel	L1	Natural channel	L2	L3	L4
Diploria strigosa	x					
Manicina areolata	x	0.03				
Porites astreoides	x	0.10				
Porites branneri	x	0.03				
Porites divaricata	x	0.27	x			
Porites furcata	x					
Porites porites	x	0.10				
Siderastrea radians	x	0.20	x	0.17		

i.e. changes the degree of confinement (*sensu* Guelorget & Perthuisot, 1982, cited in Guelorget *et al.*, 1990). Environmental changes caused by the opening of new inlets are: smoothing of extreme temperatures; modification of the salinity regime; changes in vegetation cover and organic matter content in sediment with concomitant changes in oxygen concentration; and increase in colonization rates from marine species (Pérez-Ruzafa *et al.*, 1991, Sfriso *et al.* 2003).

In the context of the confinement hypothesis, geomorphological variables are key factors explaining biological gradients in coastal lagoons (Mariani, 2001; Franco *et al.*, 2008). The channels' structural differences influenced the process of colonization of marine biota into the area of study. Species richness was highest at the direct area of influence of the artificial channel, and also the number of exclusive species was three-fold higher compared to the natural channel. The artificial channel is straight with no bordering vegetation, thus no dampening of water movement occurs and marine colonizers have, relatively, a high chance of reaching the interior of the embayment settling on suitable substrate. On the other hand, the natural channel is bordered by dense mangrove vegetation with a permeable root system that attenuates the water speed and acts as a barrier for particulate matter. Therefore, the natural channel has more restricted influence as it meanders among mangrove forest reducing the speed of inflow.

The artificial channel has become more relevant in terms of the degree of connectivity between the small embayment and the reef lagoon. The sequence of differences in community composition (see results in Figure 2) is from the artificial channel to the natural channel, followed by localities 3 and 4, indicating a strong spatial pattern of differences in community composition. The multivariate component of variation of factor locality (42%) implies a strong environmental gradient determined by the degree of marine influence. This is supported by the similar number of species shared between L1 and L3–L4, on the one hand, and between L2 and L3–L4 on the other. Considering a time span of 6 years since the opening of the new channel, the artificial channel's area of influence is comparable to the natural channel and its magnitude greater in terms of species richness. Our results confirmed previous findings where increases in colonization rates resulted in a gradient of diversity with the highest values near the communicating channels (Guelorget *et al.*,

1990; Pérez-Ruzafa *et al.*, 1991, 2004; Mariani, 2001). Here, both channels had a high number of species, the highest occurring at the direct area of influence of the artificial one.

The sampling design controlled for substrata type and depth, limiting the observations on hard substrata and at a depth-range of 0.8–1.5 m. Depth and substrata are a strong source of variability in lagoon benthic assemblages (Pérez-Ruzafa *et al.*, 2006, 2008) making them spatially heterogeneous at the scales at which substrata and depth change. The area of study is a karstic environment where limestone is covered by calcareous sediments and varies at scales of metres to tens of metres. Hence, the sampling size used attempted to cover only hard substrata. Unavoidably, there were small patches of soft sediment where some of the recorded macroalgae and seagrasses were present, but this condition occurred in all of the observed units. Thus, although some substrate effect may not have been effectively controlled, its contribution to the spatial differences in the benthic assemblage composition is contained in the large component of variation estimated by the residuals (see PERMANOVA results).

In the context of the multivariate analysis the implied hypothesis of independence of main factors effect was rejected, despite the significant effect of locality and time, similar to other studies. Seasonal change has been documented as a strong source of variability affecting hydrological conditions, nutrients and productivity (Pérez-Ruzafa *et al.*, 2005) which directly influences the degree of confinement producing changes on benthic macrophyte assemblage composition gradients (Sfriso *et al.*, 2003; Pérez-Ruzafa *et al.* 2008). Moreover, the latter authors identified a significant interaction between spatial and seasonal effects in the pelagic and benthic environments at the Mar Menor coastal lagoon, Spain. Our sampling design tried to control for seasonal effects fixing the seasonal factor for the most extreme condition, the rainy season, and looked at small temporal scale variability. In the region of the Yucatan Peninsula the rainy season has two peaks of precipitation, in June and August, and its effect on benthic assemblages in coastal lagoons may vary temporally as a result of the inertial effect of the previous dry season and the cumulative effect of rainfall throughout the rainy season. The interaction time × locality represented almost one-tenth of the overall variation in our design, and its contribution is considered relevant in structuring the benthic assemblage composition. Based on the pairwise comparisons, each locality presented a variable pattern of differences, i.e. the rainfall effect was not spatially homogeneous and had a larger effect at L2, the area of direct influence of the natural channel where benthic assemblage composition changed markedly showing a sequence of differences from T1–T2, T1–T3 and less different T2–T3 (see Figure 2). However, at the area of influence of the artificial channel the temporal differences occurred between T1–T2 and T1–T3.

This pattern of temporal differences may result from the displacement of marine species less tolerant to reductions in salinity, which we considered an indirect effect of the morphology of the channels as more strictly marine species are expected to reach coastal lagoon inner areas through the artificial channel compared to the natural one (see Table 1B for exclusive and shared species). Therefore, this temporal pattern of differences may reflect marine conditions at the beginning of the rainy season and the change on confinement after the two peaks of rainfall. This condition would first affect

the area of influence of the artificial channel followed by the natural one. The same pattern of temporal differences at L3 may be considered as indicative of the more active role of the artificial channel affecting inner sites. At L4 however, the changes in composition are detected only at the end of the rainy season, between T2 and T3, probably as a result of the inertial effect of the previous dry season.

The structural redundancy analysis for identifying influential species selected a unique subset of 22 species that reproduced nearly the same pattern as the overall data set. Analysis of structural redundancy in soft bottom benthos produces several sets (up to four) of influential species, interpreted as highly ecological redundant systems (Clarke & Warwick, 1998). However, under strong spatial environmental gradients, ecological structural redundancy is very low because few species characterize or respond uniquely to the gradient. This observation has been previously noted in soft benthic communities in other coastal lagoons (Mistri et al., 2001). It is worth noticing that the redundancy analysis did not pick up on any of the exclusive species, due to their low frequency of appearance within localities. The exception was the macroalga D. cavernosa, not recorded in previous studies of macroalgae biodiversity of Chetumal Bay (Quan-Young et al., 2006; Espinoza-Avalos et al., 2009). Nevertheless, it is important to point out the role of some of the exclusive species, for example hard corals as indicators of the degree of marine influence.

Hard corals are strictly marine organisms, with very limited tolerance to salinity changes and slow growth rate (Wells, 1956). Despite these limitations, some coral species, such as Siderastrea radians and Porites astreoides, can dwell in naturally suboptimal environments (Vermeij et al., 2007). The genera Porites and Siderastrea are dominant in the recruits' assemblages in the nearby reef system (Ruíz-Zarate & Arias-González, 2004). Moreover, P. astreoides is a dominant species in the adjacent reef lagoon with an average linear growth rate of 4.75 mm yr^{-1} (Highsmith et al., 1983), and direct field observations and measurements of specimens recorded at L1 were of small colonies no taller than 3 cm and 300 cm^2. Considering the growth rate, the largest colonies should be around five to six years, coincident with the opening of the channel in 1999. Although the natural channel also has corals, we recorded only two species, of which, S. radians dominated and this was the only species found in the direct area of influence of the natural channel on the coastal lagoon side. Siderastrea radians is a stress-tolerant and highly resilient coral species that can dwell under high sedimentation, fluctuating salinity and extreme temperatures, with the potential of growing back tissue after a large percentage of loss (Lirman et al., 2002). Colony size would therefore vary in relation to changing conditions more than on its actual rate of calcium deposition.

In summary, this study provides further evidence of the role of confinement in structuring coastal lagoon benthic assemblages in tropical systems, and reinforces previous findings on the colonization of marine organisms as a relevant process to explain benthic assemblages' gradients and the importance of spatial–temporal interactions occurring at various scales (Pérez-Ruzafa et al., 2005, 2008). We also add evidence that evaluating changes produced by human influence is feasible despite lack of previous information when considering the main sources of variability under an adequate sampling design. Although the ideal situation would be to have a pre and post-impact design, the lack of previous information should not be an impediment to finding suitable designs and relevant variables that allow evaluation of changes after the impact has occurred.

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