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Temporal mangrove dynamics in relation to coastal development in Pacific Panama

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Abstract

This study assessed the changes in extent of fringing mangrove located in Punta Mala Bay, Panama in relation to coastal development over a period of two decades. Punta Mala Bay was chosen for this study, due to its social importance and its biological significance, as it is one of the few mangrove areas left around Panama City. Fieldwork confirmed the importance of *Laguncularia racemosa* in the bay, which formed nearly monospecific stands with a large number of seedlings indicating that the forest was rejuvenating. The mangrove was mapped from 1980 to 2002 using digitised aerial photographs and a GIS was used to determine the location and rates of mangrove growth and loss before and after the construction of a road and water treatment works in 1998. The land use maps were produced with an overall accuracy of 83.8%. The user's accuracy of the maps for *L. racemosa* dominated stands was 89.7%, although the producer's accuracy was lower due to the omission of seedlings on intertidal areas. It was found that the mangrove was spatially dynamic and had grown substantially in the bay at a rate ranging from 6 to 215% per year until the construction commenced. Between 1997 and 2002 there were 100% loss of mangrove in some areas due to the coastal development. The resilience of the dominant species *L. racemosa* at this locality was shown by the continued growth of two mangrove zones during the construction period 1997–2002, with one zone increasing in area by 61%. The pioneering ability of *L. racemosa* after disturbance was demonstrated by the development of two new mangrove zones of 498 and 1254 m^2 on bare intertidal areas after construction finished. Future mapping and fieldwork could provide information on the development of mangrove communities and their response to reoccurring human impacts.
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Mangroves serve several important functions, including the maintenance of coastal water quality, reduction in severity of storm, wave and flood damage, and as nursery and feeding areas for commercial and artisanal fishery species (English et al., 1997; Baran and Hambrey, 1998). They are highly productive and their woody stems provide habitat, food and breeding grounds for a variety of fauna including benthic and pelagic marine animals such as fish and shellfish (Baran and Hambrey, 1998). However, they are threatened by increasing human populations, food production, coastal developments and wood extraction

(Field, 1998) and hence, there is an increased need to assess and monitor these resources.

There is a need for a reliable, cost-effective means of mapping the extent of mangroves. This information is crucial in long-term mangrove monitoring and to ensure sustainable management. Mangrove management must often deal with instances of rapid change, e.g. from natural mangrove stands to clearing for land use in shrimp farming and information is crucial for policy development, implementing conservation programmes and for increasing public awareness of the mangrove resource (Aschbacher et al., 1995; Ramachandran et al., 1998). Maps can be used in reforestation procedures and by fishery managers in their decision-making process (Dahdouh-Guebas et al., 2000; Manson et al., 2001). Mapping mangrove by ground inventory is extremely difficult, time consuming and expensive due to the remote location of some areas and the nature of the mangrove environment. Therefore, a more

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cost-effective approach is required for gathering the necessary information (Dahdouh-Guebas et al., 2000).

Remote sensing is an attractive management tool to obtain data for defining mangrove areas because it allows quantitative and qualitative assessments of ground conditions over large and inaccessible areas (Aschbacher et al., 1995; Manson et al., 2001). Although, there have been numerous studies using images from satellite sensors to map mangroves, there have been few published accounts on aerial photographic techniques for mangrove assessment and their accuracy, despite their long-term use. However, as Green et al. (1998) point out, this deficiency is often due to a lack of publications by governments, agencies and consultancies rather than the quality and resolution of data obtained from the technique. As satellite data are relatively recent, the interpretation of aerial photographs from the past is often the only way to determine the history of vegetation change and previous mangrove spatial dynamics in areas that do not have any other scientific records (Dahdouh-Guebas et al., 2000; Dahdouh-Guebas and Koedam, 2002). Aerial photographs are advantageous due to their high spatial resolution compared to satellite images from Landsat and SPOT, making them suitable for surveying small areas of interest, and aerial photographs have been utilised by authors including Tam et al. (1997), Cardona and Botero (1998), Chauvaud et al. (1998), Dahdouh-Guebas et al. (2000) and Manson et al. (2001). Aerial photography can also in some cases be used to discriminate between stands of mangrove genera, as shown by Dahdouh-Guebas et al. (2000). Despite this tool being available, the precise aerial extents of mangroves are unknown in many regions, hence measuring loss and predicting sensitivity and recovery are difficult (Farnsworth and Ellison, 1997; Field, 1998).

Whilst there is a need to collect field data to ground truth remotely sensed information, there is also a need for more field studies and experiments to investigate mangrove regeneration, zonation and stand development. The dominance of studies in mature mangrove forests has resulted in a lack of field data on mangrove stand development from colonisation, through to early development and maturity (*sensu* Jiménez et al., 1985), and the effects of disturbance during this process. The study of spatio-temporal changes in mangrove stand extent, structure and composition has recently been defined by Dahdouh-Guebas and Koedam (2002) as mangrove vegetation structure dynamics. They also note that up to date field work on vegetation structure (measurements of adults, saplings and seedlings) in conjunction with historical records of spatial dynamics via remote sensing can be used to evaluate the status of the mangrove as being spatially static or dynamic and rejuvenating. This study will deal with vegetation structure dynamics in an almost monospecific stand and hence changes in mangrove extent are the focus of this study.

This study aimed to use aerial photography to look at the growth and loss of mangrove at a site in Pacific Panama from 1980 to 2002. The area provides the opportunity to study the resilience and regeneration of mangrove after coastal development. Field data were collected to assess the mangrove's current forest structure and stand development and to provide ground truth data to assess the accuracy of mangrove classification from the photographs.

1. Method

1.1. Study site

The discontinuous fringing mangrove of Punta Mala Bay, Panama City within the Bay of Panama (08°56′45″N, 079°33′10″W) was the study site in this investigation. Punta Mala Bay is approximately 8.3 ha in size and is located to the west of the city, towards the entrance to the Panama Canal. The Gulf of Panama is characterised by wet and dry seasons, with the wet season lasting from May to December (average monthly rainfall 350 mm) and the dry season occurs between January and April (Glynn, 1972). Panama City is subject to semi-diurnal tides (Glynn, 1972), with the average range being approximately 3.76 m. The monthly maximum range was 4.97 m and the minimum range was approximately 2.2 m for June 2002 when the study was conducted.

Most of the mangrove of the Gulf of Panama is classified as either critical or endangered on the conservation status scale due to losses associated with shrimp pond construction, crops, cattle farming and tidally flooded land (D'Croz, 1993). The mangroves of Punta Mala Bay and the rest of Panama Bay are threatened by reclamation projects, urbanisation, tourism developments and pollution. Punta Mala Bay was subject to the construction of a road and wastewater treatment plant, and there is currently a marina being built in Amador, approximately 500 m to the south of the bay. There are also plans for a housing development within the bay. Punta Mala Bay was chosen for this study as it is locally important socially and biologically. It is used by local inhabitants from the nearby Chorillo district who collect bivalves from within the intertidal areas and palms that grow at the landward edges of the mangrove area. The motivation for small-scale clear cutting of mangroves by these people is due to economic incentives, with collectors selling the cuttings for firewood in their local community (*sensu* Farnsworth and Ellison, 1997). Those trees targeted generally had larger diameters, greater than 2.5 cm. It is estimated that approximately 20–30 people utilise the bay's mangrove associated produce, based on observations and informal discussions with local fishermen in the field (S. Benfield 2002, pers. comm.). The mangrove of the bay is also biologically important in the locality. It is one of the only areas of mangrove left in the Bay of Panama near to Panama City, a coastline that used to be fringed by mangrove forest before coastal development started. Additionally Punta Mala Bay is a useful site to investigate the application of aerial photography for mapping

and monitoring long-term mangrove regeneration, because the site is easily accessible by road and the forest is of low density.

1.2. Field survey

Field work was conducted during June 2002. Punta Mala Bay was visited twice before sampling plots were permanently established and data collected to assess the dominant species present and the forest structure throughout the bay. Those areas which would best represent the distribution, forest structure and incorporate areas which were altered due to coastal developments were chosen as sampling sites. Five sites were chosen for survey and at each site one 10 m by 10 m plot was marked out using four iron rods. Plot locations were haphazardly chosen within the five sites of interest (Fig. 1). The GPS location of each point was taken but the error was ± 30 m as DGPS was not available, and this subsequently meant positioning the plot locations on the image relied on ground features, e.g. roads, buildings (see Section 1.3). At each plot measuring tapes were laid between the iron rods to create x and y-axes for recording the coordinates of the trees. All live trees and saplings greater than 1 m in height were tagged with marking tape so they could be identified. This height restriction ensured the inclusion of saplings, defined as trees greater or equal to 1 m in height with a girth of less than 4 cm (English et al., 1997). For each individual, the species was noted, height above ground sediment measured and the x and y coordinates taken to allow future monitoring. The diameter of the tree was measured at 130 cm from the ground (D_{130}) (Brokaw and Thompson, 2000) and was recorded using a pre-calibrated tape measure when D_{130} was greater or equal to 2.5 cm. In circumstances when the tree branched below this height standardised rules were followed (English et al., 1997). Trees measured for D_{130} were marked with a numbered stainless steel tag to assist future relocation for monitoring. As the bay had many seedlings compared to mature mangrove forest the number of 1 m by 1 m subplots (within the 10 m by 10 m plot) for surveying seedlings was increased to 25 from the standard 5 (*sensu* CARICOMP, 2001) to allow a greater percentage of the population to be surveyed. For all subplots the species and height of every seedling was recorded and five subplots were haphazardly chosen and marked using four PVC poles so they could be monitored. Coordinates of the seedlings in these five subplots were also recorded.

The importance value of each species in each plot for the adult/sapling population was calculated using the equations given by Cintrón and Schaeffer Novelli (1984). This was to ascertain the contribution of each species to the mangrove forest and the importance value was used as an indicator of the degree of monospecificity (Cintrón and Schaeffer Novelli, 1984; English et al., 1997). To examine differences in height, D_{130} and species composition between plots

Kruskal–Wallis tests and Dunn's multiple comparison procedures were implemented in Minitab.

1.3. Aerial photograph image processing and GIS analysis

Five aerial photographs used in this analysis were obtained from the Tommy Guardia National Geographic Institute of the Republic of Panama. Black and white images at a scale of 1:25,000 were obtained for 1980, 1992, 1997 and 2002 (see Fig. 1). A colour image at a scale of 1:9000 was obtained for 1990. From the image, a digital macro-photograph was taken of the area of Punta Mala Bay at 96 dpi resolution. Photographs were imported into IDRISI32 and georeferenced via nearest neighbour resampling and a linear transformation. Ground control points were obtained from a topographic map from the Tommy Guardia National Geographic Institute (scale of 1:50,000). Those GCPs that had large RMS errors were eliminated until the RMS tended towards zero. Photogrammetric rectification techniques were not required as the area is relatively flat and topographic distortions and skew were minor. All the images were resampled to the same size to allow further analysis.

As the images were mostly black and white aerial photographs it was decided that visual interpretation would provide more accurate results compared to supervised classifications, as local knowledge was available to assist the process. The delineation of mangrove areas was accomplished using a combination of grey tone differences, location and shape. Mangrove was the classification given to all mangrove areas in the bay, as preliminary field results showed that the bay was almost monospecific and the only slight differences were in vertical vegetation structure (as defined by Dahdouh-Guebas and Koedam, 2002), which could not be detected from the imagery available. The mangrove areas could be identified on intertidal areas as they appeared darker than the surrounding mud and also tended to occur in clumps in the bay. Delineation of mangrove was partly assisted by the fact that the area had undergone coastal development as the concrete bank and road surrounding the bay was much lighter and contrasted with the darker grey mangrove stands. The main problems in delineating mangrove occurred when separating mangrove from non-mangrove vegetation in the 1997 and 2002 images. This was achieved by examining the position of the vegetation in the bay (i.e. was it in a potential intertidal area, in the seaward area of the concrete bank) and using slight differences in grey tone between the mangrove and other vegetation such as grass and terrestrial trees (*sensu* Rolofoharinoro et al., 1998; Dahdouh-Guebas and koedam, 2002). Human land use was broken down into roads, residential areas, industrial and commercial areas, recreation area (baseball) and the water treatment works. Areas covered in terrestrial vegetation either fully or partially were classified as other vegetation and open ground and the internal area of the bay was classified as intertidal area. Polygons around the various land cover types were defined
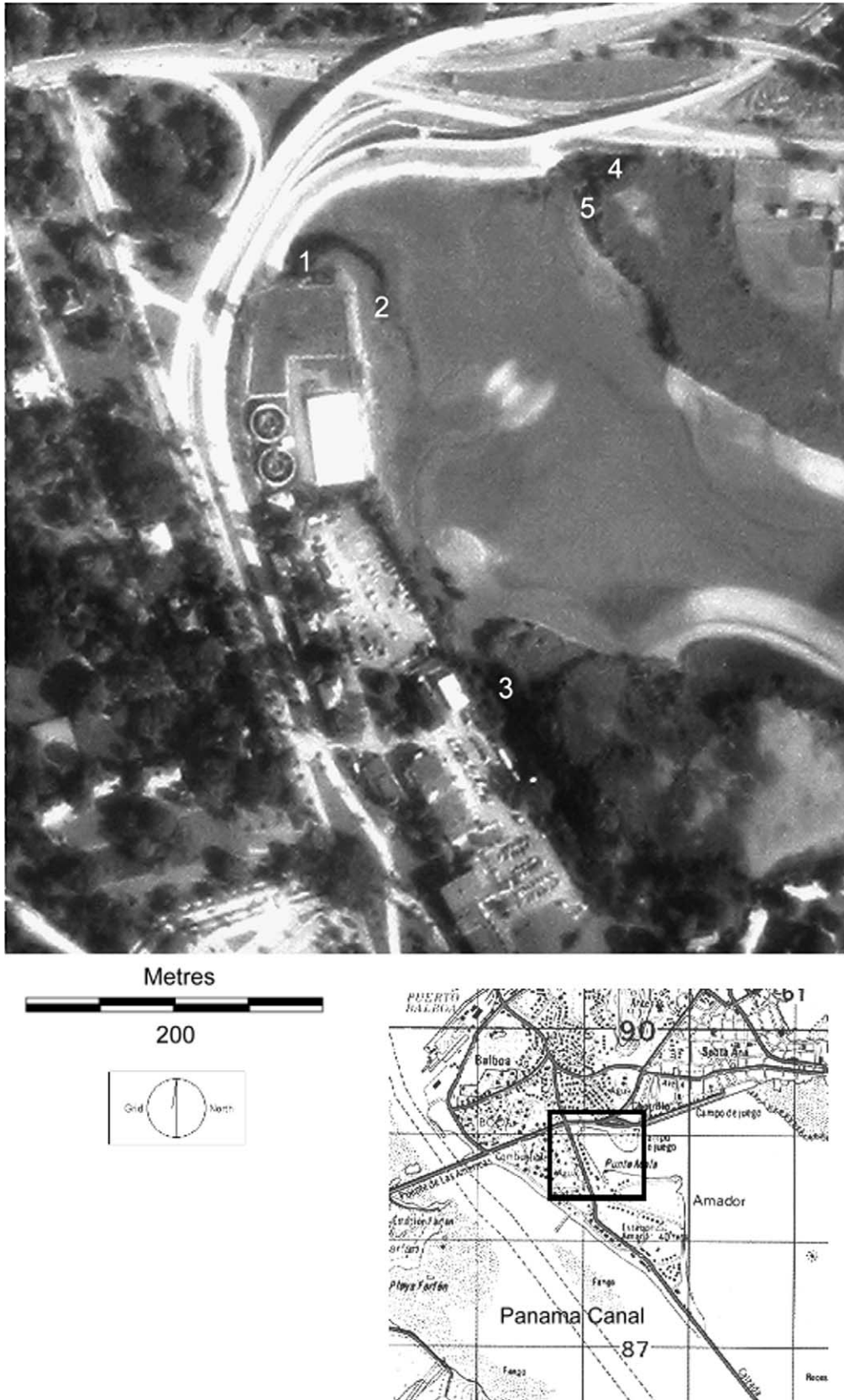
Fig. 1. An example of the aerial photographs used in this study. This image was taken in 2002 and shows the approximate location of the five survey plots used to assess forest structure. The lower image shows the location of Punta Mala Bay (within box) in Panama Bay, adjacent to the Pacific entrance of the Panama Canal.

Table 1
Parameters derived from field data collected in all five plots and subplots

Plot	Position of plot in mangrove zone	No. of adult stems ($D_{130} >$ 2.5 cm, height > 1 m)	No. of saplings ($D_{130} <$ 2.5 cm, height > 1 m)	Approximate number of seedlings (per plot)	Median height		Stand basal area (m^2)	Mean stand diameter (cm)	Importance rank of species in plots	Species composition of plot (%)			Species composition of seedling subplots (%)		
					Ad	S				L	A	R	L	A	R
1	New zone 1	147	39	256	6.03	0.44	0.049	4.45	L≫A=R	98	2	0	92	0	8
2	New zone 1	48	114	264	1.63	0.12	0.018	4.86	L≫A=R	98	1	1	100	0	0
3	Zone 4	120	81	508	3.70	0.09	0.039	4.65	L≫A=R	96	4	0	97	1	2
4	Zone 2	44	63	388	2.08	0.15	0.013	3.95	L≫A=R	94	4	2	90	6	4
5	Zone 2	3	28	592	1.37	0.15	0.001	5.15	L≫A=R	97	3	0	99	1	0

The number of adults, saplings and seedlings is given per plot (10 m^2), which for seedlings was extrapolated from the twenty-five 1 m^2 subplots. Stand basal area and mean stand diameter calculated only for stems with $D_{130} >$ 2.5 cm. Note that mean stand diameter is not the average diameter for the stand but is the diameter of a stem of mean basal area. The position of the plot is with respect to the mangrove zones identified in the aerial photographs (see Figs. 1 and 2). Ad, adults and saplings (height greater than 1 m); S, seedlings in subplots; L, *Laguncularia racemosa*; A, *Avicennia germinans*; R, *Rhizophora mangle*.

by onscreen digitising in Idrisi converted to raster form upon which area calculations can be performed.

Due to the positional error of the GPS device available (30 m) and the relatively small area of the bay, it was not possible to use the GPS data to exactly position the plot locations on the images. Therefore, the plots were positioned on the 2002 map using visual clues such as the buildings, the road and the shape of the bay. An accuracy assessment of the 2002 classified image was conducted using additional sites where the presence of mangrove (seedlings, saplings or mature trees), other vegetation and human land use were known from the field visits. The ground truth points in mangrove areas were positioned on the image using references such as the coastline, buildings, roads and the proximity to other mangrove stands. The points were generated using onscreen digitising in Idrisi and were then converted to a raster file. The ERRMAT function was then used to calculate user, producer and overall accuracies and the Kappa coefficient. It was believed that due to the smaller nature of the seedlings and saplings they would be more difficult to detect and this would affect the accuracy of the final classified image and estimates of mangrove area derived from it. The accuracy assessment was only conducted for the 2002 image, as there were no ground truth data from earlier years.

The area of each land cover type through time was calculated between years (1980–1990, 1990–1992, 1992–1997 and 1997–2002). This was calculated as area in hectares and then transformed to a percentage change, whereby the percentage increase or decrease in mangrove extent was calculated on the basis of the area of mangrove in the older image, i.e. 1980 when comparing change between 1980 and 1990. CROSSTAB analysis was performed to determine the area of mangrove lost and gained between years to specific human land cover types.

2. Results

2.1. Forest structure in plots surveyed

A summary of adult and seedling parameters derived from the field data is given in Table 1. All plots contained adults, saplings and seedlings. Plot 3 had the greatest number of stems over 1 m high (adults plus saplings =201), although this was closely followed by plot 1, which had 186 stems. Additionally plot 1 also has the greatest stand basal area of 0.049 m^2 in comparison to a slightly lower value of 0.039 m^2 in plot 3. The lowest number of stems over 1 m was in plot 5, which also had the lowest stand basal area but the greatest mean stand diameter, which was biased due to the presence of only three adults. The number of seedlings was found to be greatest in plot 5 and the lowest number of seedlings was found in plot 1 (Table 1). The trees in plot 1 were tallest and those in plot 5 were shortest and the median height of trees over 1 m tall was found to be significantly

Table 2
Error matrix for 2002 classified image

Image classification	Reference data									Total	User's accuracy (%)
	Mangrove	Intertidal	Other vegetation and open ground	Road	Car park	Industrial/commercial	Residential	Water treatment works	Recreation area		
Mangrove	61		7							68	89.7
Intertidal	24	46	1							71	64.8
Other vegetation and open ground	1		36							37	97.3
Road				10						10	100
Car park					4					4	100
Industrial/commercial						4				4	100
Residential							3			3	100
Water treatment works								5		5	100
Recreation area									2	2	100
Total	86	46	44	10	4	4	3	5	2	204	
Producer's accuracy (%)	70.9	100	81.2	100	100	100	100	100	100		
Overall accuracy (%)	(61+46+36+10+4+4+3+5+2)/204=83.8%										
Overall Kappa	0.7807=78.1%										

The overall accuracy of the classified image was 83.8% and the user's accuracy for mangrove were high, whilst the producer's accuracy was lower than other land use categories. Intertidal areas were not classified as well in comparison to mangrove, other vegetation and open ground and human land use categories.

different between all the plots (H (adjusted for ties)= 297.18, df=4, $p < 0.001$) except for plots 2 and 4. The median D_{130} was also found to be significantly different amongst plots (H (adjusted for ties)=22.71, df=4, $p < 0.001$). The median D_{130} was greatest in plot 5, although it was based only on three trees with D_{130} greater than 2.5 cm. The smallest median D_{130} was located in plot 3. Median seedling heights varied significantly amongst plots (H (adjusted for ties) =143.31, df=4, $p < 0.001$) except between plots 2 and 4 and plots 2 and 5. As reported for the adults, the height of seedlings was also higher (median of 0.44 m) in plot 1, which differed significantly from the other four plots and smallest seedlings were observed in plot 3 (median of 0.09 m).

Table 1 also shows the importance and dominance of *Laguncularia racemosa* in all plots compared to the other two species found in very low numbers which were *Avicennia germinans* and *Rhizophora mangle*. *L. racemosa* was also the most frequent species found in seedling subplots and again *R. mangle* and *A. germinans* seedlings were in very low numbers. No significant difference in adult species composition was found between the plots ($H=4.59$, df=4, $p=0.332$). However, the species composition of seedlings amongst the plots was significantly different (H (adjusted for ties)=22.05, df=4, $p < 0.001$). Plot 4 significantly differed from plots 2, 3 and 5, which could be accounted for by this plot having the highest percentage of *A. germinans* as well as a relatively high percentage of *R. mangle*. Plot 1 was found to differ from plot 5 and this is perhaps due to plot 1 having only *R. mangle* in addition to *L. racemosa* and plot 5 having only *A. germinans*.

2.2. Accuracy assessment

The Kappa coefficient used here as an accuracy assessment was 0.78, indicating that the classification avoided 78% of errors compared to a random classification (Table 2). The user's accuracy for mangrove was high (89.7%), indicating that the map produced represents the mangrove distribution in situ adequately enough so that further calculations of mangrove area can be relied on. Classification of other vegetation and open ground also had a high user's accuracy (93%), as did all the human land use areas (100%). However, intertidal areas had a poorer user's accuracy of 64.8% due to confusion with mangrove areas, which subsequently lead to mangrove having a low producer's accuracy (70.9%) compared to the other land cover types due to the omission of some mangrove areas. The overall map accuracy was high at 83.8%.

2.3. Mangrove and land use distribution (1980–2002)

The mangrove areas that grew over the period examined were numbered zones 1, 2, 3, 4, new zone 1 and new zone 3 to allow for easier discussion of the results and their position is highlighted on Fig. 2. However, this 'zone' annotation
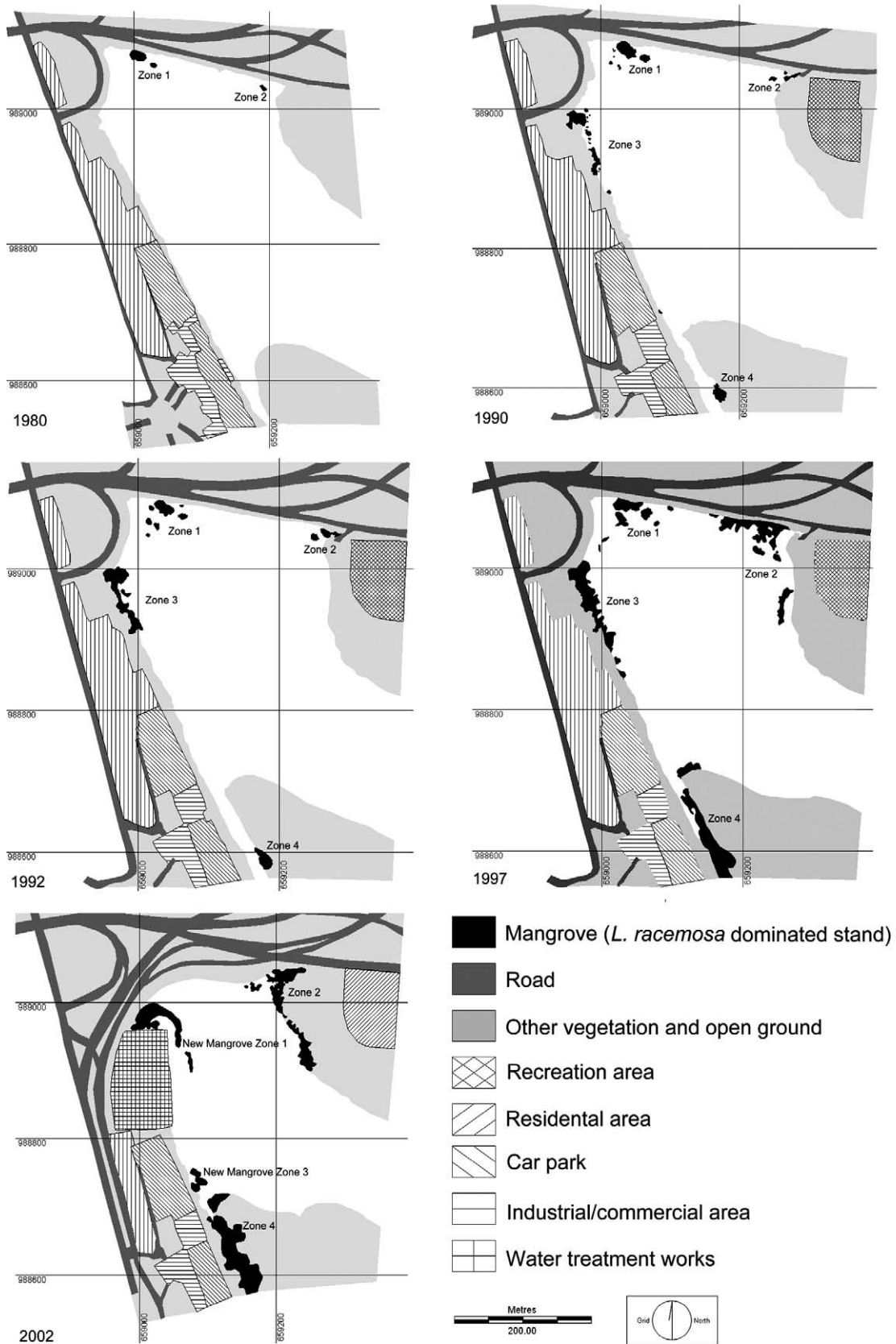
Fig. 2. The five land cover maps generated from classification of the aerial photographs. Four mangrove zones were identified to assist in discussions of the results, and the 'zone' annotation in no way relates to the biology or field surveys conducted in the plots. The mangrove zones were almost completely dominated by *Laguncularia racemosa* (see Section 2.1). Plots 1 and 2 were taken in new mangrove zone 1, plot 3 is located in Zone 4 and plots 4 and 5 are located in Zone 2.

Table 3
Gain/loss of mangrove for each of the four mangrove zones, in m^2 for each of the time periods considered and percentage gain/loss per year (− indicates loss)

	1980–1990		1990–1992		1992–1997		1997–2002	
	Area (m^2)	%yr^{-1}	Area (m^2)	%yr^{-1}	Area (m^2)	%yr^{-1}	Area (m^2)	%yr^{-1}
Mangrove zone 1/new mangrove zone 1	198.1	6.1	34.7	7.4	536.1	17.8	− 1140.6	− 20.0
Mangrove zone 2	98.5	31.7	108.6	37.2	2318.0	215.0	− 508.15	− 3.7
Mangrove zone 3/ new mangrove zone 3	827.2	10.0	729.1	36.0	1037.6	12.3	− 2299.01	− 20.0
Mangrove zone 4	283.2	10.0	115.3	20.4	1901.7	115.5	1402.46	12.2
Road	13.0	0.1	6152.0	35.9	− 1479.0	− 6.4	16300	74.8
Other vegetation and open ground	5530.0	9.0	3757.0	5.8	7394.0	9.9	13452	38.0
Human land use	8471.0	25.3	1565.0	3.7	− 1789.0	− 4.1	− 5365	− 36.5

The percentage gain/loss per year is calculated as a percentage of the area of mangrove in the earlier year (i.e. 1980 for 1980–1990). Rates are calculated assuming equal growth rates per year.

does not correspond to the numbered field plots surveyed or to differences in their vegetation structure. These maps show that between 1980 and 1997 the mangrove in the bay was spatially dynamic in nature (as defined by Dahdouh-Guebas and Koedam, 2002). In 1980 there were two relatively small areas of mangrove (zones 1 and 2) located in the northerly area of the bay, which grew in area by 61 and 317%, respectively, by 1990 (Table 3). Two new mangrove areas also appeared during this period, one to the eastern side of the bay (zone 3) and the other in the south of the bay (zone 4) (Fig. 2). By 1992, zones 1, 2 and 3 were becoming well established and all were increasing in area (Fig. 2). In 1997, mangrove growth was most apparent in zones 2 and 4, and mangrove in zone 2 had begun to move towards the northeast and project itself into the bay, in discontinuous clumps. The growth in zone 4 originated from the small clump that appeared in 1990 and has grown northwards and outwards to cover the channel (Fig. 2; 1990 and 1997).

The most obvious changes in the location and expansion of mangrove and other land were observed in 2002 (Fig. 2). Mangrove in zones 1 and 3 were lost and two new distinct clumps colonised (Fig. 2; 2002). The new mangrove zone 1 in the north-western area of the bay actually occupies part of the area previously covered by mangrove, whilst the new mangrove zone 3 in the westerly part of the image is in an area not previously occupied by mangrove vegetation. Mangrove in zone 2 experienced a loss of nearly 19% of its previous area, which was focused at its westerly end. However, its southerly area did not appear to be affected and in 2002, there was a more continuous area of forest extending towards the south and into the bay. The only area of mangrove whose location and extent was not affected in 2002 was zone 4. This zone grew by 61% to occupy more area in the channel and began to extend into the southerly edge of the bay (Fig. 2, Table 3). The changes in mangrove location in zones 1, 2 and 3 areas were associated with shifts in human land use. A new road and water treatment works were constructed along the northerly edge of the bay between 1997 and 2002 (Fig. 2).

Other vegetation and open ground is the dominant land coverage in all years, but only substantially increased

between 1997 and 2002 with a 38% gain in area (Table 3). The road area increased between 1990 and 1992 with the construction of an additional strip of road in the northerly area of the map. However, the largest increase in road area occurred between 1997 and 2002, which resulted in a 74.8% increase in road area (Table 3). The area covered by human land use did not change considerably between 1990 and 1997 until the construction phase began in 1998. Between 1997 and 2002 human land use for residential and industrial/commercial purposes was reduced due to the construction of the wastewater treatment plant and the road.

2.4. Causes of mangrove loss and gain

Yearly rate changes for mangrove growth and loss (Table 3) were calculated upon the assumption that growth or loss was continuous over the time period (*sensu* Ramírez-Garcia et al., 1998). In all four zones between 1980 and 1997 it was found that net growth occurred ranging from 6% per year (zone 1 between 1980 and 1990) to 215% per year (zone 2, between 1992 and 1997) and the growth rate was generally greater in zone 2 (Table 3). The largest gain in area was 2318.0 m^2 in zone 2 between 1992 and 1997 and the lowest growth in area was in zone 1 between 1990 and 1992 (34.7 m^2). This growth was mainly attributed to the reclamation of the intertidal area by mangrove (Fig. 3). Growth can also be attributed to replacement of other vegetation and surrounding open ground (Fig. 3). The peak growth rate for zones 1, 2 and 4 was between 1992 and 1997, 17.8, 215 and 115.5% per year, respectively. However, in zone 3 the peak growth occurred between 1990 and 1992 (Table 3), when growth was associated with mangrove replacing other vegetation and open ground (Fig. 3).

From 1997 to 2002, new mangrove colonised zones 2 and 4 by reclaiming areas of the intertidal zone, and during this period the new zones 1 and 3 were also formed by this reclamation process (Figs. 3 and 4). There appears to be more mangrove gain via reclamation of the intertidal zone in the northern part of the bay. Despite these gains, zones 1, 2 and 3 all exhibited net area loss between 1997 and 2002 (Table 3). Zones 1 and 3 lost 100% of their area due to
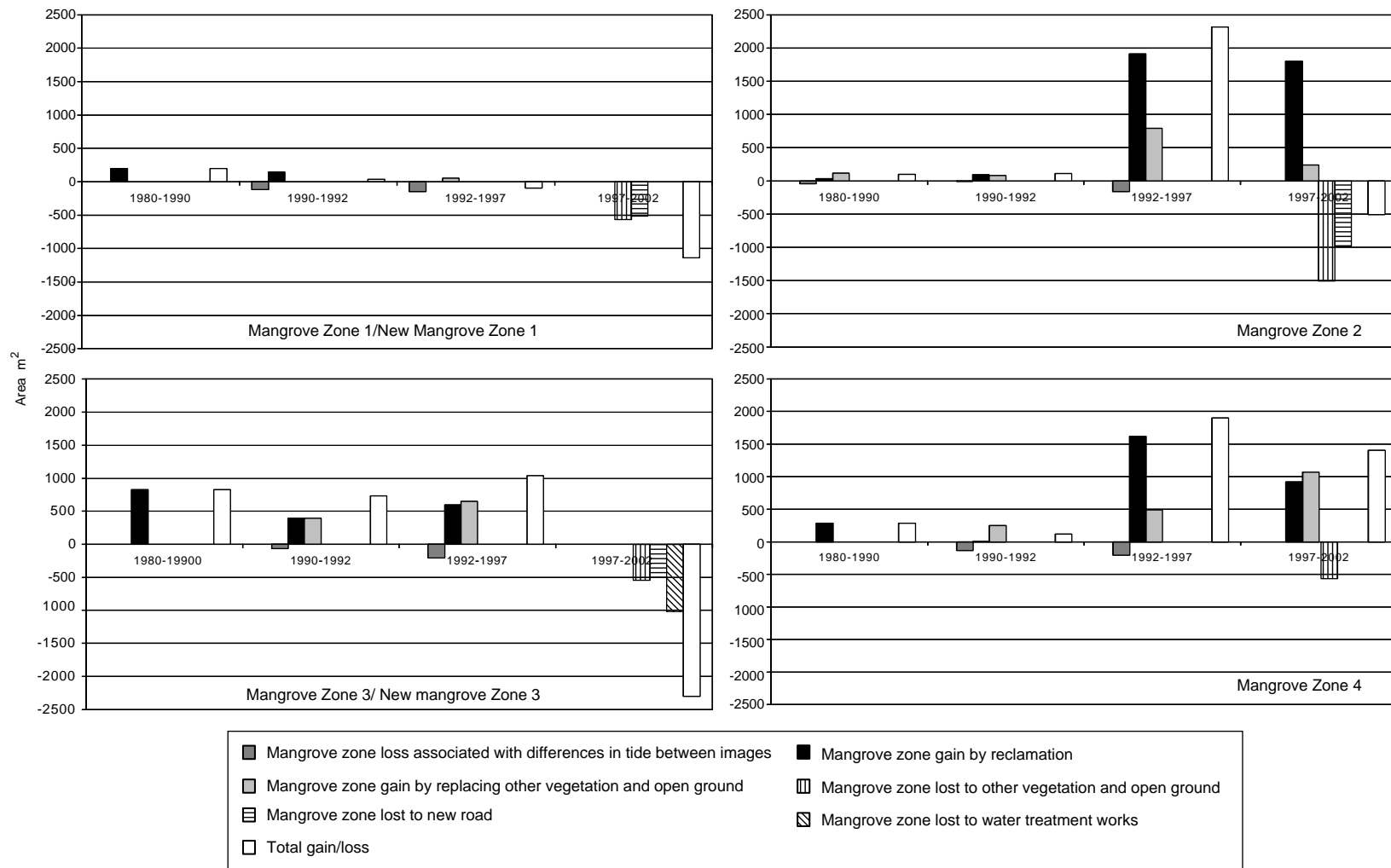
Fig. 3. Factors influencing mangrove zone growth and decline between 1980 and 2002 in the four mangrove zones of Punta Mala Bay.
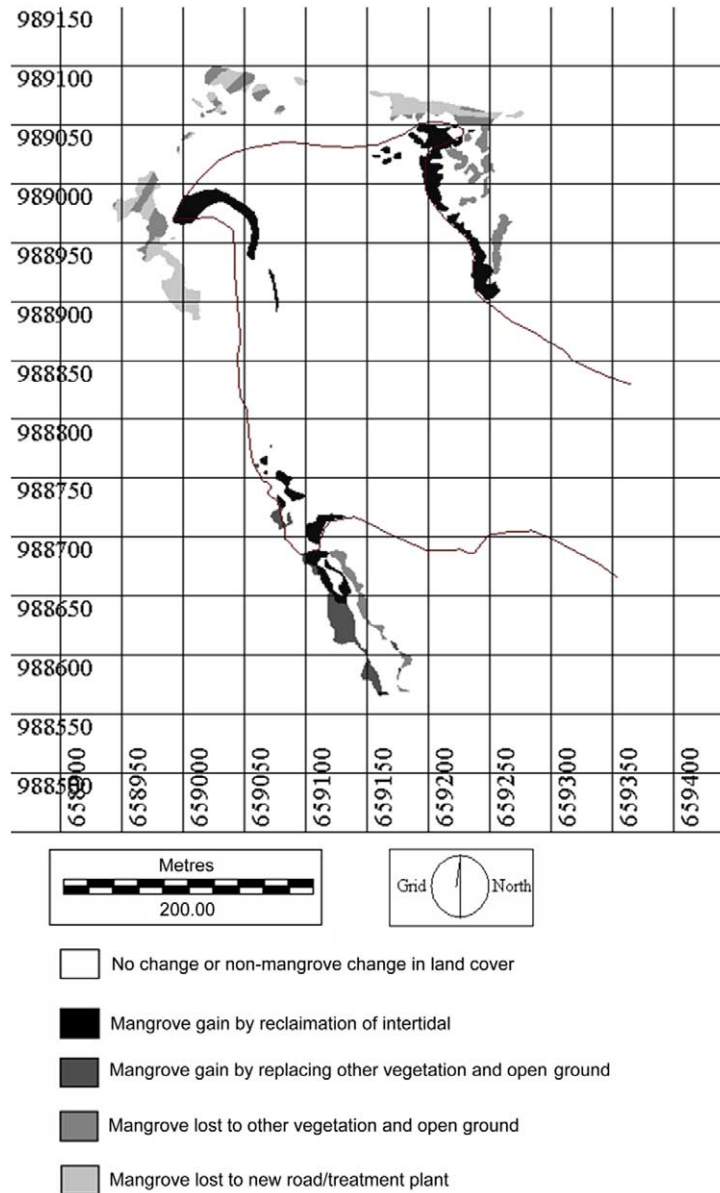
Fig. 4. Map produced from the result of CROSSTAB analysis in GIS, showing the location of mangrove zone gain and loss, and the influencing factors between 1997 and 2002.

the construction of the new road and the subsequent replacement of mangrove by other vegetation and open ground (Figs. 3 and 4). However, the new mangrove zone 1 developed covering an area of 1254 m², a similar size to the original zone 1, despite being in a different location (Fig. 2). However, the loss of area in zone 3 was greater than in the other zones and the new mangrove zone 3 (498 m²) did not replace the original area lost (2299 m²). Hence, the two new areas of mangrove that grew after construction do not yet replace the original area of mangrove lost. In addition to zone 3 losing area to the road, it also lost area during the erection of a new water treatment plant, which the other three zones were not subject to (Fig. 4). Although, mangrove zone 2 also lost some area (508 m², Table 3) this was not as great as either zones 1 or 3 but it was also due

to the road construction and mangrove replacement by other vegetation (Fig. 4). Losses were counteracted in zone 2 by seedlings established in some areas (Fig. 3). Zone 4 also showed the greatest losses in area (583 m²) over this period than at any other time period studied (Fig. 3), but unlike the other three mangrove areas these losses were not directly due to the construction of the road but were due to replacement of mangrove by other vegetation and open ground (Fig. 3). Despite these losses net growth continued in zone 4 during the period 1997–2002, unlike the other mangrove areas. However, the area gained and the rate of gain was not as great as the previous period, 1992–1997 when it grew by 578% (Table 3). The increases in area are mainly due to reclamation again, but mangrove replaces other vegetation and open ground also (Fig. 4).

3. Discussion

One of the most notable factors to emerge from this study is the dominance in Punta Mala Bay of *L. racemosa* with *A. germinans* and *R. mangle* present in small numbers. This is contrary to Jiménez (1994) who stated that this species was not commonly found on the Pacific coast of Panama. Results presented here and observations in Coiba Island located in western Pacific Panama (H. Guzman 2002, pers. obs) show that *L. racemosa* can colonise this area when conditions are suitable. This dominance is not usual in such a low intertidal position, where one would normally expect to find *R. mangle* and *A. germinans* (Rabinowitz, 1978b,c; Ellison and Farnsworth, 1993) but the variety of factors operating in mangrove environments may cause the positions of species to change (Tomlinson, 1999). One explanation for this dominance may lie in the wide tolerance limits of this species to soil pore salinity and substrate type. Additionally the propagules of *L. racemosa* sink more rapidly and have a reduced stranding time compared to *A. germinans* and *R. mangle*, allowing them to take root easier in areas of frequent tidal inundation (Delgado et al., 2001; Rabinowitz, 1978b). The distribution of *L. racemosa* in this study counters the conclusions of Elster (2000) who felt that it was unable to establish in open sites due to the size of its propagules and the effects of direct sun. An additional reason for the dominance of *L. racemosa* may be due to its ability to thrive in disturbed environments (Bacon, 1975; Thom, 1967), which is particularly relevant in this case. Elster (2000) found that in open coastal sites in Colombia disturbed by deforestation that *L. racemosa* seedlings had high survival rates, suggesting higher light intensities at such sites was a causal factor.

L. racemosa continued to grow in areas of zones 2 and 4 despite the disturbance of construction and two new areas developed during 1997–2002. The ability of *L. racemosa* to colonise bare sites without conspecifics may be one explanation for its dominance over *A. germinans*, as colonisation studies have found that certain species have difficulty colonising bare areas without conspecifics, probably due to the more favourable conditions for propagule and seedling survival created by established mangrove (Bosire et al., 2003). Low numbers of parental *A. germinans* and *R. mangle* in the bay may be preventing these species from regenerating and becoming more important in the bay, as this has been found to be crucial in the natural regeneration of other species (Kairo et al., 2001). Toledo et al. (2001) found that the natural regeneration of *A. germinans* and *R. mangle* was slow in a clear-cut mangrove zone in Baja California and this may explain the low numbers of these species in this study site after disturbance. Previous studies have reported negative correlations between the predation of propagules and the dominance of mangrove species in the canopy and variations in predation depending on availability of preferred food (Smith, 1987a; McGuiness, 1997).

Preference for *A. germinans* and *R. mangle* over *L. racemosa* and the lower abundance of these in the canopy may be additional factors resulting in the dominance of *L. racemosa*. The improved survival of *L. racemosa* seedlings in disturbed areas of Punta Mala Bay would explain its dominance in the adult population, which looks set to continue until other mangrove species become more established.

The primary growth mechanism in the bay has been via reclamation of the intertidal mud banks and forest has developed even where conspecifics have not been present and disturbance has occurred. The older aerial images can be used as evidence that historically the mangrove in the bay was spatially dynamic (Dahdouh-Guebas and Koedam, 2002) and growth was particularly high before construction began, especially in zones 2, 3 and 4. The growth of mangrove in four distinct zones throughout the bay and their development has presumably been controlled in the past by the time when they established themselves and environmental and biotic variables. Important environmental factors potentially controlling distribution and growth are tidal inundation, soil pore water salinity, sediment stability and type and fresh water input as discussed by several authors (Rabinowitz, 1978a,b,c; Jiménez et al., 1985; Smith, 1987a,b; Cardona and Botero, 1998; Jiménez and Sauter, 1991; Clough, 1992; Smith, 1992; Ellison and Farnsworth, 1993; Duke et al., 1998; Elster, 2000). Additionally the importance of predation on propagules and seedlings has been found to be important in establishment of mangrove. There are many grapsid crabs in the intertidal area around new zone 1/plot 1 and the leaves in all zones/plots were being attacked by herbivores (S. Benfield 2001, pers. obs), a problem previously reported for Panama (Smith, 1992). It has been noted that grapsid crabs increase in abundance when larger canopies develop (Smith, 1992; Ellison and Farnsworth, 1993; Elster, 2000) and this may be the cause of the low number of seedlings in plot 1 in relation to the number of adults. Grapsid crab predation has been identified as a threat to regeneration of mangrove by Dahdouh-Guebas et al. (1998) and hence predation may be a limiting factor for future propagules and seedlings establishing.

Differences in growth were seen between new mangrove zones 1 and 3 despite having established at the same time (after construction). The greater growth in new zone 1 is supported by field data collected in plot 1, which was found to have the greatest mean stand diameter and the tallest adults and seedlings, indicating that it had developed quickly over the 5 years compared to other sites. The sheltered corner location of zone 1, the increased light and lower pore salinity (due to freshwater input from storm drains) on the mudflats may have boosted propagule and seedling survival and hence growth. Increases in nutrients from decomposing deforested mangrove and the deposition terrestrial sediment during construction work could have increased the nutrients available to developing seedlings. The growth may have also been assisted by the presence of

a propagule or seedling bank left from the original zone 1 (Rabinowitz, 1978c; Duke and Pinzón, 1993), although this may not have been sufficient for regeneration on its own (*sensu* Farnsworth and Ellison, 1997). The smaller size of new mangrove zone 3 may be due to its more exposed location across from the bay's entrance, which would affect propagule and seedling abilities to establish (Field, 1998; Elster, 2000). The sediment in the area was unstable when the tide was out and such conditions are known to be detrimental to the growth of *L. racemosa* and *A. germinans* (Elster, 2000).

Recently in the bay's history, the distribution of mangrove and its growth have been altered by human activities that have resulted in the total loss of mangrove in some areas. Additionally, growth rates were seen to slow in zone 4 during the period of construction, which was not directly affected by deforestation. This reduction in growth may have been due to indirect effects of development such as changes in sedimentation, hydrology or clear cutting of trees by locals. Assuming that the rate of change in mangrove area was constant between years, the rates of loss during 1997–2002 were high, up to 20% per year in zones 1 and 3, although actual rates for 1998–1999 when the construction took place would no doubt be much higher. Ramírez-Garcia et al. (1998) concluded the rate of loss seen in Mexico of 1.4% annually was high and Adeel and Pomeroy (2002) notes that declines of 2–8% per year were fast.

Dahdouh-Guebas and Koedam (2002) explain that it is possible to incorporate previous maps of past mangrove extent with current field data on vegetation structure to gain insight into current and future mangrove dynamics. Using this principle, the historical aerial photographs indicate that the mangrove has been spatially dynamic and current field data show that all the mangrove plots examined have a complete vertical vegetation structure and contain unequal numbers of adults, saplings, and seedlings. This implies that the majority of mangroves within Punta Mala Bay have J-type dynamics, and can be defined as a normal rejuvenating forest (Dahdouh-Guebas and Koedam, 2002). However, plot 4 (zone 2) has a slightly more static forest nature due to it having more equal numbers of adults and saplings (Dahdouh-Guebas et al., 2000; Dahdouh-Guebas and Koedam, 2002). This would indicate that the mangrove is recovering from the disturbance caused and will continue to rejuvenate into the future. The pioneering nature of *L. racemosa* and the preservation of some mangrove during this coastal development work no doubt aided the survival and continued growth of mangrove forest in the bay (Bacon, 1975; Lee et al., 1996; Tomlinson, 1999). The mangrove in the bay regenerated through natural processes and was not assisted by reforestation and this disputes Farnsworth and Ellison (1997) who stated that mangrove recovery is universally slow after disturbance unless assistance is given. Despite this apparent regeneration, it is suggested that sites disturbed by logging are less likely to regenerate and function like the pre-disturbed site as the mix of species,

tree density and location and animal numbers will have changed (Field, 1998; Kairo et al., 2001). The only way to assess this for Punta Mala Bay is to compare its recovery in terms of vegetation structure and fauna with other mangrove areas along the coast as no historic field data are available. However, naturally regenerating mangroves tend to be more similar to the original mangrove vegetation (Field, 1998) and thus the current composition may be similar to that present before the disturbance. However, in other regions artificial regeneration and restoration techniques have been required (Lewis et al., 1998; Toledo et al., 2001) and these may be needed if one wanted to assist the regeneration of *A. germinans* and *R. mangle* in the bay as these species have slower natural rejuvenation (Toledo et al., 2001). If growth rates seen in previous years are repeated in the bay in the future, the mangroves could recover to an area equivalent to that in 1997 in approximately 5 years, allowing them to continue to support firewood and food collection by local people. However, changes in hydrology and sedimentation may occur if plans to develop a housing complex near zone 4 and a new marine development in neighbouring Amador go ahead and this may have a negative impact on mangrove recovery. If losses in mangroves occur in this area it may also be detrimental to local people that utilise associated mangrove produce, who may experience a loss of income due to the reduction in products they can harvest from the bay and sell to others.

This study has highlighted the value of aerial photography for assessing historic mangrove dynamics, monitoring and mapping mangroves. The lower user's accuracy of the intertidal classification is most likely due to the omission error associated with missing clumps of small seedlings and saplings which cannot be detected on the image due to their lower leaf mass and small size. Whilst the missing seedling areas did not affect the user's accuracy of mangrove classification the actual area covered by mangrove will have been underestimated. However, the overall accuracy of the final map (83.8%) was adequate for examining mangrove extent and similar to the 92, 88.5 and 85.2% achieved with Landsat, although different classification categories were used (Green et al., 1998; Ramírez-Garcia, 1998; Gao, 1999, respectively). Higher accuracies have been achieved with CASI (96% Green et al., 1998) and colour aerial photography (94% Chavaud et al., 1998) due to improved spectral resolution allowing easier discrimination between mangrove, non-mangrove and intertidal areas. Whilst new satellites such as Ikonos and Quickbird and alternative aerial sensors such as CASI can be used effectively for mapping and monitoring smaller, fringing areas of mangrove and may allow identification of mangroves to a species level (Green et al., 1998; Dahdouh-Guebas and Koedam, 2002) these satellites as yet do not have extensive historic archives. Hence, the potential availability of aerial photography archives for providing historic and current information on mangrove extent should not be overlooked.

It is recommended for future monitoring of mangrove in this bay and in other areas that colour photographs of high spatial resolution (1:10,000) be obtained where possible as these are easier for visual delineation and supervised classification techniques can be readily applied to them. Alternatively for current and future mapping and monitoring users may prefer to utilise high resolution satellite imagery where finances allow and potentially compare these to older aerial photographs as the two are of similar resolution. Field surveys should be conducted at the approximate time the aerial photographs are taken to reduce inaccuracies. We would also recommend that other users obtain field data on salinity, sediment type, herbivory, predation and metals analysis to assist in understanding variations in mangrove development, recovery and distribution identified via remote sensing.

4. Conclusions

This study showed the dominance of *L. racemosa* at all intertidal levels of Pacific Panama, in contradiction to some previous studies on the distribution of this species. The value of aerial photography as a means to evaluate coverage by mangrove and spatial vegetation dynamics over time was demonstrated. The use of historic aerial photography in conjunction with forest structure data indicated that mangrove was undergoing normal rejuvenation and is recovering naturally from the intense coastal development. The recovery was probably assisted by the pioneering nature of *L. racemosa* and the retention of some mangrove during the construction, which highlights the importance of conserving some mangrove during coastal developments.

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