Ecological linkages in a Caribbean estuary bay.

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ABSTRACT

Central America and the western Caribbean form a center of freshwater and marine biodiversity that is now receiving attention in ecological and evolutionary studies. We conducted one integrated ecological study of Amatique Bay, Guatemala, a major estuary lagoon connected to the Mesoamerican Reef System, and provide novel information for management and conservation of similar systems across the Caribbean. Important environmental drivers are the precipitation and wind regimes, which partially compensate for the weak tidal-forcing characteristic of the Caribbean Sea. Seasonal peaks in temperature and precipitation were strongly correlated to the reproduction of marine, catadromous and estuarine fish species, suggesting that the ensuing increase in primary production provides larval fish with an abundant food source. Increased abundance of marine transient species was observed during the dry season, when prey might be more abundant inshore, and environmental conditions are dominated by higher salinity and stronger onshore winds suggesting passive transport, feeding migration or both. Despite being a stopover site for many species of long-range migrating shorebirds, the Bay serves primarily as a resting place as it lacks extensive tides and tidal flats, limiting the access to invertebrate prey. Abundant freshwater, the sheltered environment, seasonally high water clarity, and low tidal amplitude likely provide good habitat for abundant seagrasses and manatees. The Lake Izabal-Amatique Bay complex demonstrates a wide range of teleconnections and connectivity among terrestrial, freshwater, and marine oceanic and reef ecosystems. This ecological and evolutionary understanding is required for the management of the multi-trophic small-scale fisheries sustained by the system.

Keywords: Fisheries, migratory shorebirds, manatee, life history, environmental drivers, tropical conservation, evolution, Central America.

INTRODUCTION

The western Caribbean is highly diverse across terrestrial, marine and freshwater realms, but a unified understanding of its coastal assemblages of fish, birds, and mammals is wanting. The paleontological and phylogenetic records suggest that the nuclear Central America was at the core of an explosive radiation of freshwater fish (Briggs 1984, Chakrabarty & Albert 2011). Part of the taxa were secondary freshwater fish originally from South America, but the invasion of freshwater ecosystems by marine species (i.e., killifishes, cichlids) came to play a major role after a sequence of saltwater intrusions and regressions (Hulsey & López-Fernández 2011). In the marine realm, the Caribbean Province has historically been the center of ecological speciation and radiation of fish and many invertebrate groups in the Atlantic producing and exporting species, but also accumulating biodiversity produced in peripheral habitats (Briggs & Bowen 2012, Bowen et al. 2013). The Caribbean province was also once an area of sirenian (manatee/sea cow) radiation. However, the closure of the Central American Seaway in the Pliocene (ca. 3 Ma) resulted in mass extinctions of sea grasses and sirenian species, and only a single species, the manatee *Trichechus manatus*, remains (Hunter et al. 2012, Velez-Juarbe et al. 2012, Benoit et al. 2013). The rise of the Isthmus of Panama prompted the migration of forest birds predominantly in the direction south to north, which presumably led to the high levels of bird diversity also observed in this region. For shorebirds (Charadriiformes), however, understanding of their original migratory behavior and home range is problematic (Weir et al. 2009, Livezey 2010, Zink 2011). Many extant Arctic Charadriiformes are long-range migrants with northern breeding grounds, and overwinter in the southern hemisphere. However, several lineages of shorebirds from the southern hemisphere are predominantly residents or short-range migrants. Thus, the present assemblages of aquatic and wetland fauna are a complex of freshwater and marine radiations and transgressions, as well as colonization by continental species. The lack of studies examining coastal species assemblages and their functions, particularly in Neotropical estuaries, hampers the understanding of ecological processes that may have driven evolution of many taxa (Sheaves & Johnston 2009, Barletta et al. 2010, Atwood et al. 2012).

Whether as a stop-over for long distance migrants like birds, a seasonal habitat for short-range migrants, or home for resident taxa, the estuarine areas of Central America and the Caribbean are important for both conservation and human utilization (Faaborg et al. 2010, Latta 2012, Somveille et al. 2013). For example, Amatique Bay in Guatemala is connected by freshwater runoff to the Mesoamerican reef, the largest barrier reef in the Western Hemisphere (Soto et al. 2009), and is a prime example of a Caribbean estuarine ecosystem. Upstream (40 km) from the bay, the low-lying Lake Izabal forms the southern boundary of the Usumacinta fish faunal province. It may have been a major route of incursion of marine species into the freshwater assemblages of Central America (Hulsey & López-Fernández 2011). To conserve this complex, natural protected areas have been implemented across the watershed, including two Ramsar wetlands sites of international importance, the Río Sarstún Multiple Reserve Zone and Punta de Manabique Wildlife Refuge (Fig.

1). Punta de Manabique alone shelters more than 450 plant species, and 810 faunal taxa (Jolón-Morales 2006). Several threatened or vulnerable migratory species, including the manatee, contribute to this biodiversity. Agriculture, herding and forestry, activities that are often preceded by slash and burning of existing vegetation, have been identified as major sources of impact on the wetland habitat in this area (Yañez-Arancibia et al. 1999). However, the presence of two harbors receiving an excess of 1200 ships annually and extensive fishing in the bay may also have a negative influence on the aquatic communities (Anon 2003). Fishing pressure is also high here and landings account for nearly 60% of the economic value generated by fishing in the Guatemalan Caribbean, supporting the livelihood of more than 1000 harvesters (Ixquiac-Cabrera et al. 2008, Andrade & Midré 2011, Heyman & Granados-Dieseldorff 2012). Thus, the range of conservation, ecological and social interests to accommodate is broad, and often conflicting.

We attempted to describe this Caribbean estuarine-marine complex with the goal of identifying ecological drivers for ecosystem functioning and evolution in Neotropical estuaries. Integrated ecological studies of Caribbean estuaries have rarely been performed. The current understanding is dispersed in data reports, fisheries statistics, and very specialized publications. Thus, we compiled environmental and ecological information from different sources, and collected new field data on vertebrates and their environment. In this work we focus on the environmental drivers, seasonal rhythms, and life cycles of fish, shorebirds and manatees in the Bay complex, and suggest how these processes may link the estuary to the riverine and marine ecosystems. Larger emphasis is placed on the growth and reproduction cycles of fish, because this group has been more intensively and regularly sampled. This case study provides an integrated view of an estuarine complex in the Caribbean and the Neotropics, which have been little studied to date.

MATERIAL AND METHODS

Study site

With an aquatic surface of 542 km^2 and additional 200 km^2 of associated wetlands, Amatique Bay (Fig. 1) is a diverse and complex shallow (average depth < 10 m) ecosystem consisting of coastal lagoons, sea-grass meadows, reefs, mangroves, and marshes that are influenced by riverine systems (Yañez-Arancibia et al. 1999, Fonseca & Arrivillaga 2003). More than half of the 12 km^2 mangrove forest in the Guatemalan Caribbean grows along the coast of the Bay as well as in the rivers draining into it (Hernández et al. 2012). The dominant species is the red mangrove *Rhizophora mangle*, but *Avicennia germinans, Laguncularia racemosa* and *Conocarpus erectus* are also common (Yañez-Arancibia et al. 1994). Seagrass beds, which are particularly abundant in La Graciosa Bay, cover approximately 38 km^2 and so far six species have been identified, with *Thalassia testudinum* as the dominant (Yañez-Arancibia et al. 1994, Arrivillaga & Baltz 1999, MacDonald-Barrios 2011). Some reef structures exist, mainly around Punta de Manabique in the form of continental carbonate banks. These reefs are dominated by sedimentation-resistant coral species, such as *Siderastrea siderea*. Live coral cover, however, is low, and non-coralline macroalgae abound (Fonseca & Arrivillaga 2003). The mud-dominated areas at the mouth of the Sarstún River give rise to the most valuable shrimp fishery in the Gulf of Honduras (Heyman & Kjerfve 2001).

Collection and analysis of meteorological and oceanographic data

Time-series of environmental data were retrieved from the Guatemalan meteorological institute (INSIVUHMEH), or extracted from NOAA or NASA open internet sources available for 1985-2010. Retrieval and treatment of these enviromental data are described in detail in Text S1 in the Supplement. These included time-series of wind speed (Wind) and direction, precipitation (Pre), air temperature (T_{air}), day length (Dayl), sea surface temperature (SST), tidal heights, and chlorophyll *a* (Chl *a*) concentration. Turbidity and nutrient concentration at the outlet of Lake Izabal were measured in 2006-2007 by Quintana-Rizzo & Machuca (2008). We separated this measurements into two periods to represent the water quality: August, October and December 2006 comprised the wet season, and February, April and June 2007 the dry season. Estimates of monthly run-off were recovered from a model using land cover scenarios for the years 2003-2004 (Burke & Sugg 2006).

Seasonal abundance of fish species in Amatique Bay

Indices and maps of fish density were derived from two sets of fishery-dependent data and one set of observations made during research surveys. The first set consists of the average monthly catch per unit effort (CPUE) of shrimp trawlers [kg (number of fishing boats x month)$^{-1}$] in the period 2006-2010, available from the national fisheries directorate (DIPESCA, Guatemala). These records of catch and by-catch are usually pooled into coarse categories that sometimes comprise several species: "Shrimp" (three Penaeid species), "Catfish" (two Ariidae species), "Corvina" (a mix of Sciaenidae and Haemulidae). The lane snapper *Lutjanus synagris* and Atlantic brief squid *Lolliguncula brevis* (hereby referred as squid) are registered as individual species (Table S1 in Supplement). Shrimp trawlers operate on soft mud bottom and are typically 10 m long vessels equipped with 120-130 hp inboard engines. The trawl gear lacks otter boards and is retrieved by hand by a small crew (González & López 2000). The legal mesh size in the codend is 64 mm (stretched), but a 51 mm cover is usually employed to improve retention of smaller sized shrimp (Ixquiac-Cabrera et al. 2008).

The second type of fishery-dependent data consisted of the estimated monthly landings from non-trawler vessels derived by Heyman & Graham (2000) and Heyman & Granados-Dieseldorff (2012). These estimates were based on information gathered by interviewing 42 experienced skippers (70% had more than 10 years of experience) of small boats (dories, skiffs) performed in 1998. The most common fishing gears were gillnets (81%), beach seines (7%), small shrimp trawl nets (locally known as "changos", 5%) and hand lines (3%). The location of their fishing villages and the species-distribution maps drawn by Heyman & Granados-Dieseldorff (2012) indicate that the catches were made mostly inside the Bay. These authors report monthly landings of many species but we limited our analyses to those that regularly comprised 90% of the total catch (Table S1 in Supplement).

The oceanographic and biological observations made by Ixquiac-Cabrera et al. (2008) during two research cruises were used to map salinity profiles and fish density across Amatique Bay. The surveys were carried out in February and August 2008 from a fishing vessel equipped with a commercial shrimp trawl (Text S2 in Supplement) and a CTD profiler. Mapping was performed after smoothing the observations from 11 fixed stations and their categorization into dry (February) and wet (August) seasons. The densities per square nautical mile ($kgNM^{-2}$) of some of the most numerous species were plotted to analyze distribution patterns. Five out of the 11 dominant species (of 79 spp. in total), accounting for 28% of the organisms sampled, were chosen to illustrate spatial occupancy during the dry and wet seasons. These species included the caitipa mojarra *Diapterus rhombeus*, lane snapper, squid, striped mojarra *Eugerres plumieri* and anchovies, a group comprised by the species *Anchoa spinifer*, *A. cayorum*, *A. colonensis* and *Anchoviella elongata* (Table S1 in Supplement).

Physiological traits of selected fish species

To investigate some of the eco-physiological traits of fish species, we performed observations of the reproduction and growth of lane snapper, grey snapper *L. griseus*, gafftopsail catfish *Bagre marinus* and snook *Centropomus undecimalis* along a year cycle. We selected these species because they were frequent in the catches and could be regularly sampled between March 2006 and April 2007 from the fresh landings in Livingston and in Puerto Barrios (Fig. 1). Snappers were usually caught with hand lines, but snook and the gafftopsail catfish were caught mainly with gillnets. The total (Wt, g) and gonad (Wg, g) weights (± 0.1g) of the fish were recorded along with their total lengths (L, cm). Monthly averages of the gonadosomatic index ($GSI = 100\ Wg / Wt$) were used as an indicator of the gonadal development and spawning seasonality (Lowerre-Barbieri et al. 2011). The condition factor ($CF = 100\ Wt\, L^{-b}$) is a body-mass index where b is the coefficient of the length-weight relationship (King 1995). Excluding the gafftopsail catfish, which is clearly sexually dimorphic, fish of both sexes were combined prior to analysis. This included an analysis of the sex-aggregated data for common snook, a commercial fish species that we have previously investigated in detail (Andrade et al. 2013).

Shorebird and manatee distribution

Observations of shorebirds in Punta de Manabique were available from August 2000 to June 2001 (Eisermann 2009). In this study, 2124 sightings were recorded along beaches, coastal lagoons and river mouths, providing an index of relative abundance. Only the most common species (n > 30 observations) as defined by the original authors were used in the analyses, and this accounted for 97% of the birds sighted and 11 out of a total of 25 species (Table S1 in Supplement). An airborne survey of manatees *Trichechus manatus* in the Izabal-Dulce-Amatique complex was performed on five occasions between July 2006 and February 2008 by Quintana-Rizzo & Machuca (2008). However, only the sightings made in October 2006 and March 2007 were utilized here to map their seasonal distribution because these two surveys had similar coverage and methodology (Text S3 in Supplement).

Statistical analysis

Relationships between monthly average abundance of selected species (fish, shorebirds) and putative explanatory variables, such as meteorological and oceanographic time-series, were analyzed by means of multivariate ordination with the software package CANOCO (ter Braak 1986, ter Braak & Šmilauer 2002, Garcia et al. 2012). Direct gradient analyses were carried out by means of Redundancy Analysis (RDA, the constrained form of Principal Component Analysis) to test whether species composition could be explained by the main environmental factors SST, precipitation and wind. This was performed on log-transformed data after examination of the gradient lengths with Detrended Correspondence Analyses (DCA) (Ejrnæs, 2000). Monte Carlo permutation tests (499 permutations) were employed to assess the statistical significance ($\alpha = 0.05$ for all statistical tests). Exploratory analyses of the shorebird species and seasonal data were also performed by means of RDA, with seasons expressed as categorical (dummy) environmental variables (Šmilauer et al. 2014). To illustrate the cyclical occurrence of selected shorebird species, their sightings were modeled using a generalized additive model (GAM) with season as predictor variable. A Poisson error structure of the sightings was assumed and a log-link was utilized, as usual for count data (McCullagh & Nelder 1989). Circular statistics (Zar 1998, Lund & Agostinelli 2014) were used to calculate means and variance of monthly wind direction. To identify linkages between pairs of time-series while accounting for auto-correlation, we used cross-correlation analyses on ln-transformed data (El-Gohary & McNames 2007, Wilkinson et al. 2009).

RESULTS

Environmental variables

The time-series of the environmental variables and Chl *a* are illustrated in Fig. 2. The air temperature varied little along the coast (yearly average 26.5 ºC, ± sd 1.9 ºC). The SST is lowest in November to May, at about 27 ºC, and reaches a maximum in September with a mean of 30 ºC (± sd 0.6 ºC). Amplitude of day duration is also small, and day length varied from 670 min of light in December to 780 min in June. Cross-correlation analyses showed that the cycles of SST, T_{air}, and day length were significantly correlated (in all cases $r > 0.5$ and $P<0.05$) and in phase (lag zero), with the SST and T_{air} series presenting the highest correlation. The average annual precipitation in the inner part of the bay exceeded 3300 mm (± sd 615 mm) in the period 1985-2010. The rainy season usually starts in June, reaching peak precipitation in July with about 430 mm, and remaining above 300 mm until November. Wind speed was highest, with an average of

10.3 km h^{-1} (± sd 2 km h^{-1}) during March and April, and lowest from September to December at 8.5 km h^{-1} (± sd 2.7 km h^{-1}). From January to September the winds are predominantly from NE, and from variable directions the rest of the year. Overall, the yearly mean wind direction was 35^{o} (circular variance 6^{o}), i.e. straight from the mouth of the bay (NNE). The salinities across the Bay vary widely depending on the season. Thus, during the dry season the increasing temperatures re-enforced by strong onshore winds give rise to a distinct marine influence. Relatively high surface (18-29 ppt, Fig. 3) and bottom (29-31 ppt) salinities are observed in February, indicating relatively good mixing (Ixquiac-Cabrera et al. 2008). During the wet season, increased precipitation, higher run-off, and lower wind stress lead to increased stratification. In August, bottom salinities range from 23 to 31 ppt and surface salinities from 8 to 20 ppt (Ixquiac-Cabrera et al. 2008), and are characteristically low close to the mouth of the Dulce River (Fig. 3). The tides follow a regime of damped mixed-cycles with average monthly tide amplitude of only 0.52 m with some yearly variation but no clear seasonal trend. Secchi-disk measurements performed by Quintana-Rizzo & Machuca (2008) in the main channel at the outlet of Lake Izabal indicate that turbidity was highest during the rainy season at 3.0 m, and lowest in dry season in February at 4.0 m. None of these values suggests outflow of water rich in suspended particulate matter. Nutrient concentrations were highly variable temporally and spatially within the lake. At the outlet of the lake, nitrate (NO^{-3}) concentrations tended to increase from baseline levels to 0.5-3.1 mg/l in August to October). This pattern was also found for ortho-phosphates (0.13 mg/l), which were normally low and variable, or un-detectable towards the end of the raining season (August-November). Inside the Amatique the Secchi depth was lower at the mouth of the rivers, particularly the Sarstún where it was about 0.8 m in July (Carrillo-Ovalle et al. 2000). The Secchi-depth increased rapidly towards the outer bay where it reached 10 m also in the rainy season, closely mirroring the horizontal salinity gradient (Fig. 3). The chlorophyll *a* and runoff cycles resembled that of precipitation: usually peaking in June-July and remaining high until October. Cross-correlation analysis showed that the precipitation cycle was significantly correlated ($P < 0.05$) and in phase (lag zero) with the chlorophyll *a* cycle ($r = 0.35$).

Fish species abundance and distribution

The bottom trawler data suggested that shrimp and by-catch were associated with the seasonal meteorological regime and the inflow of marine waters brought about by the NE winds, low precipitation, and rising SST (Fig. 4). Redundancy analysis revealed that 23% of the variation in CPUE in 2006-2010 was explained largely (96%) by the three variables selected in the analysis: SST, Pre and Wind. The forward selection analysis retained SST and precipitation as significant variables ($P < 0.05$). The RDA triplot emphasizes that SST and precipitation were not correlated, and were the main variables determining the first and second axes, respectively. As they were relatively independent they are nearly orthogonally displayed. The first (horizontal) axis contrasts warm months with higher precipitation on the left side, to colder and dry months on the right side. The second axis separates the months with species associated to high SST at the top from the species associated to increased precipitation at the bottom of the triplot. In contrast, precipitation and wind speed, which was a non-significant explanatory variable, were negatively correlated. The density of shrimp and concentration of Chl *a* presented the strongest significant associations with the environmental variables SST and precipitation. The increased SST in June-July was positively related to shrimp and squid abundances. Abundance of fish such as sciaenids, catfish and lane snapper in the bottom trawls was negatively related to the precipitation, and was higher in the dry months of March-May when onshore winds tended to be stronger.

The temperature and wind regimes drive the occurrence of the different species available to dories and skiff fishers (Fig. 5). The variables included in the RDA explained 56% of the variance in the biological data, with the first and second axis accounting for 92% of this variation. The forward selection analysis retained SST and wind as significant variables ($p < 0.05$). The first axis clearly contrasts warm months, on the right side, to colder and windy months, on the left side. The second axis separates the months and species according to the precipitation regime, with species predominant during the rainy season located at the top, and those indicative of dry season at the bottom of the triplot. The Gerridae group, lane snapper, and grouper were positively related to precipitation in November. Our own observations suggest that lane snapper caught in this net and line fishery consists mostly of late juveniles and adults (average length 23.4 cm, size range 13.3-40.4 cm). The shrimp species, the tarpon *Melagops atlanticus* and the blackbelt cichlid *Paraneetroplus maculicauda*, were positively related to SST in August-September. Snook was partially related to both wind and precipitation in October. Crevalle jack *Caranx hippos* the Spanish mackerel *Scomberomorus maculatus* and the catfish were negatively related to SST and were more common in December-March coinciding with increased onshore winds. Anchovy *Anchoa spp*, barracuda *Sphyraena picudilla*, mutton *L. analis* and "cubera" snappers were inversely related to precipitation and were, thus, more common in the period March-May. Maps of a selection of species caught in the research surveys are shown in Fig. 3. Species like the lane snapper, the squid and the anchovies are abundant during the dry season (February) but almost absent in the wet season (August). The lane snapper captured with the commercial trawl gear consisted mostly of juveniles (average length 13.4 cm, size range 3.0-28.6 cm). Species like the stripped mojarra were more abundant during the wet season. The density of species like the caitipa mojarra was apparently unaffected by the seasons.

Physiological traits of selected fish species

The species sampled for analysis of reproduction and growth included lane snapper (n=364, total length ±sd, 23.1 ± 4.2 cm), grey snapper (n=286, 28.3 ± 5.8 cm), and gafftopsail catfish (n=169 females, 46.4 ± 6.3 cm). The lane and the grey snappers displayed similar spawning and body condition cycles (Fig. 6). Their GSI showed an increasing trend from January, reaching peaks in March-June. Gonad investment was relatively low in both species compared to the snook and specially the gaftopsail catfish, with an average maximum monthly GSI of about 1.3%. In July-August, coincident with the onset of the rainy season, the GSI decreased abruptly suggesting that the main spawning event was over. From August to December, gonad investment was relatively low. This pattern matched the body condition of the fish, as both species tended to show highest CF in March-June, the dry season. Contrasting growth patterns were observed in other fish species like the common snook and, to some extent, the gafftopsail catfish. Both species recovered their body condition during the rainy season, from October to January. This seemed to trigger spawning activity earlier in the dry season, by March-April, as revealed by their GSI. The two species differ strongly, however, in their gonad investment, from 1.6% at its maximum in snook (2.5% in females; Andrade et al. 2013), to average values exceeding 10% in April for the female catfish.

Shorebirds and manatees

The shorebirds of Amatique displayed clear seasonal patterns of occurrence (See Table S1, in Supplement). Exploratory analysis of the original sighting data by means of RDA detected four characteristic trends of seasonality in the dominant species. The most abundant group by far, with about 64% of the sightings, included some of the sandpipers (*Actitis macularius*, *Calidris minutilla*), plovers (*Pluvialis squatarola*, *Charadrius semipalmatus* and the whimbrel *Numenius phaeopus* that had relatively short stop-overs in March-May and August-November. These are the birds in group I in the RDA biplot (Fig. 7). The sighting cycle of the black-bellied plover *P. squatarola* (Pb) is shown as an example by means of a GAM (inset, Fig. 7). This cycle has the first clear top in the March-May period and the second in August-November. In the second major group (group II in Fig. 7) the black-necked stilt *Himantopus mexicanus*, the semipalmated sandpiper *Calidris pusilla* (Sse) and the sanderling *Calidris alba*, accounted for 18% of the total sightings. This group had a more pronounced presence in the late rainy season (August-November), as exemplified by the sanderling (S) in the GAM (inset). A third group composed of the collared plover *Charadrius collaris* (Pc) and the western sandpiper *C. mauri* was associated with the long rainy season from May to November. This group comprised about 13% of the overall counts, and some sporadic sightings were made in the dry season. The collared plover was the only species observed to breed in the area. The white-rumped sandpiper *C. fuscicollis* (Swr, group IV) was the only species that was observed nearly exclusively in the late dry season (March-May), and this species accounted for 2% of the sightings. The combined seasonal patterns of the most abundant groups of birds (I and II) explain why the majority of the sightings were made in the late rainy season (52%) and late dry season (25%).

According to the observations performed in aerial surveys by Quintana-Rizzo & Machuca (2008) in 2006-2007, manatees in the Lake Izabal-Amatique Bay may have a local distribution related to the seasonal precipitation regime. In these surveys, the largest densities of manatees, both adults and calves, are found in the lake Izabal and were highest during the dry season and lowest during the surveys conducted in July and October. In contrast, downstream the highest densities were found in October at the mouth of the Sarstún River, in the western Amatique Bay, where manatees were virtually absent during the dry season (Fig. 8). Manatees forming relatively large aggregations were detected in both seasons in Graciosa Bay, where abundant seagrass is available. However, the surveys covered this particular area more sporadically and it is more difficult to extract clear seasonal patterns of abundance.

DISCUSSION

Primary production in the estuary; seasonality

The main environmental drivers of the Amatique Bay ecosystem, which are most probably also important for other western Caribbean estuaries, are the precipitation, runoff and wind regimes, combined with a weak tidal forcing. Low tidal amplitudes are a characteristic of the Caribbean Sea (Kjerfve 1981), and this reduces tidal mixing. The hydrographic data presented show that the climate in Amatique Bay is dominated by a marked two-season regime. From February to May precipitation is low and river discharge is at its yearly minimum. The increase in temperature and evaporation give rise to higher salinities as marine water dominates in the bay, with reported intrusions into as far up as Lake Izabal (Brinson et al. 1974). Despite weak tidal currents resulting from low tidal amplitudes, a steady onshore (NE) breeze provides good vertical mixing inside the bay. From July to December, the rainy season dominates and the run-off into the bay combined with weaker and variable sea breezes results in a distinct halocline in the water column. The precipitation cycle in Amatique preceded or was in phase with the chlorophyll *a* cycle suggesting that primary production responds quickly to fresh water input and/or enhanced stratification (Fig. 9). The rapid linkage between runoff and nutrient loadings has been shown for other tropical and subtropical semi-enclosed bays, including Kaneohe Bay, Hawaii and the microtidal Patos Lagoon estuary, Brazil (Hoover et al. 2006, Abreu et al. 2010, Drupp et al. 2011). The validity of the remote chlorophyll *a* data could be challenged (Dierssen 2010), but additional measurements indicate that the water flowing from the lake has peak concentrations of nutrients and low volumes of suspended particles at the onset of the rainy season (Carrillo-Ovalle et al. 2000, Quintana-Rizzo & Machuca 2008). This confirms that peak primary production remotely measured can be probably associated with the seasonal flooding. Further studies should, however, attempt to describe this cycle in more detail and investigate the trophic linkage to zooplankton and zooplanktivorous larvae of fish and shrimp. The primary and secondary production cycles are thought to be more tightly coupled in the tropics than in temperate areas, responding quickly (days to weeks) to the hydrological regime (Hoover et al. 2006, Chew & Chong 2011, Atwood et al. 2012).

Fish spawning and aggregations

In Amatique Bay, spawning of fish like the grey snapper, lane snapper, the snook and probably the gafftopsail catfish occur just prior to or during the rainy (and warmer) season, in the months of March-November (Fig. 9). From July to November primary production is high and may favor larval survival and growth. These observations are similar to those reported for east Africa where fish spawning is associated with the monsoon and rainfall events (Blaber 2000). Increased abundance of larvae of lane and grey snappers has been shown to overlap with periods of high chlorophyll concentrations in other localities in the Caribbean (Yáñez-Arancibia et al. 1993, Falfan Vazquez et al. 2008). Similarly, growth rates and survival of snook recruits (age < 100 days) are known to be higher for juveniles spawned during the rainy season (Aliaume et al. 2000). While we observed three potential spawning events for snook, low GSI values during the dry season suggest the importance of the rainy season for spawning in this species. Overall, the two snappers and snook invest relatively little in gonadal mass, or have a protracted spawning period given their average low GSI, as it has been suggested for other species spawning in the tropics (Longhurst & Pauly 1987, Houde 1989). Part of the variation in gonadal investment can also be explained by a geographic gradient, as suggested earlier for snook (Andrade et al. 2013). Thus, this species achieves greater gonado-somatic indices during a shorter spawning season in cooler winter waters (e.g. Florida). Analogous reproductive strategies have been reported in important Lutjanids and Centropomids in the tropical belt of the Indo-Pacific. For example, in northern Australia, the red snappers *L. erythropterus* and *L. malabaricus* had more defined spawning peaks in the spring-summer months than their conspecifics from eastern Indonesia (Fry et al. 2009). Contrastingly, in the more tropical environment of Indonesia, spawning cycles were longer, less synchronized across sampling sites and apparently more influenced by the precipitation cycle than the temperature cycle. In an important centropomid of Asia and Australia, the barramundi *Lates calcarifer,* reproduction is also under strong influence of the monsoon regime (Blaber et al. 2008). Towards the end of the dry season the barramundi migrate to spawning sites where reproductive activity is secondarily modulated by the monthly tidal-cycle. During the wet season, post-larvae of barramundi enter coastal swamps under the influence of spring tides (Blaber et al. 2008). High rainfall and warmer temperatures have been related to the increased survival and growth of young barramundi and other coastal species in Queensland, Australia, giving rise to increased fishing yields (Balston 2009, Meynecke & Lee 2011).

The timing of spawning of the gafftopsail catfish has been associated with the increased temperatures and the onset of the rainy season in other tropical localities (Mendoza-Carranza & Hernández-Franyutti 2005, Pinheiro et al. 2006). Our observations suggest, however, that spawning may start prior to the rainy season as reflected by the increased GSI in March 2007 and further decrease in April. Extensive investment in gonadal products, large egg size (up to 19 mm in our observations), and parental mouth breeding in the gafftopsail catfish may ensure the survival of the larvae, even if spawning occurs markedly earlier than the onset of the rains and the planktonic production cycle (Rimmer & Merrick 1982). Biogeographic studies may help resolving discrepancies in the timing of spawning and physiological adaptations across latitudinal gradients.

The fishery landings combined with reproductive observations of lane and grey snappers, gafftopsail catfish and snook suggest that pre-spawning migrations or spawning migrations in March-November either increase the catchability of these species or that fishers simply target them during this time period (Fig. 9). Similarly, the formation of spawning aggregations has been used to explain the increased catchability of tarpon, goliath grouper and Gerridae in other estuaries and coastal waters of the Caribbean (Sadovy & Eklund 1999, Rueda & Defeo 2001, Hammerschlag et al. 2012). Although fishing spawning aggregations is not always detrimental, trade-offs between fish size and fishing effort must analyzed to derive a simple and adequate fishing regime in the different seasons (van Overzee & Rijnsdorp 2015).

Seasonal abundance of fish

Climate variables affected differently the landings of trawlers and those of dories and skiffs. Trawlers operate mostly where shrimp are abundant, especially on soft bottoms near river mouths. The multivariate analyses showed that these fish assemblages were clearly affected by precipitation and river runoff. Increases in rainfall and temperature are thought to trigger offshore migration of juvenile penaeids (Nagelkerken et al. 2008, Nemeth 2009). In Amatique Bay, landings of shrimp were related to increasing seawater temperatures in the months of June and September, at the height of the rainy season (Fig. 9). Hidalgo et al. (2004) describe penaeid catches in Amatique as consisting mainly of subadults spawned in the previous November-December period. Thus, the increased landings of shrimp appear to occur during dispersal from the nursery grounds. This has also been noted in the nearby Celestun lagoon, Mexico (Pérez-Castañeda & Defeo 2001, Pérez-Castañeda & Defeo 2004).

In contrast to the trawlers, skiffs and dories employing hooks and lines operate in rocky bottoms or along the Punta de Manabique coast (Heyman & Granados-Dieseldorff 2012) and their major catches occurred during the cooler dry season. Occurrence and landings of engraulids, sciaenids, catfishes, barracuda, jacks, mackerels and, to a lesser extent, of mutton snapper, were greatest, from December to April, and were associated with the onshore wind regime and intrusion of marine waters (Fig. 9). These species are often categorized as marine stragglers (*sensu* Potter et al. 2013). The engraulid fishery, locally known as "manjua,", which may comprise up to 15 species, accounts for 20% of the total landing volume in the whole Gulf of Honduras, and has peak catches in April (Boix-Morán 2008, Heyman & Granados-Dieseldorff 2011). This happens simultaneously with increased abundances of juveniles of other fish species in Amatique and other estuaries of the Caribbean (Ixquiac-Cabrera et al. 2008, Burgos-Leon et al. 2009, Poot-Salazar et al. 2009). Thus, it is likely that catches of barracudas, jacks and mackerels are more directly related to active feeding migrations than to passive advection. Active feeding migrations have also been suggested elsewhere in the Caribbean (Manjarrés-Martínez et al. 2010), an indication that these oceanic species are not merely 'stragglers' into the estuaries. On the other hand, these predators and the cubera and grey snappers form spawning concentrations from March to September in marine waters nearby, including the atoll of Gladden Spit (Boomhower et al. 2010, Manjarrés-Martínez et al. 2010, Granados-Dieseldorff et al. 2013). Trophodynamic studies supplemented by investigations of reproduction are needed to resolve the proximate causes of their migration, but attention must also be paid to ontogenetic factors. For instance, we observed that the peak trawler by-catch of small lane snapper occurs during the dry season when juveniles are abundant. Contrastingly, the peak catches of larger lane snappers were performed in reef areas during the rainy season, coinciding with the main spawning event. This is in agreement with the observations of Whaley et al. (2007) who in Charlotte Harbor, Florida, found juveniles normally associated with seagrass and soft bottoms, and adults predominantly associated with coral reefs or rock offshore. Hence, the lane snapper uses the Bay both as a nursery and spawning area (Fig. 9) and should be classified as a marine estuarine-opportunist, following the scheme of Potter et al. (2013).

Species at the extreme of physiological adaptation to estuarine life are the brief squid which probably represents the only hypo-saline adaptation of cephalopods (Bartol et al. 2002), and the blackbelt cichlid *Paraneetroplus maculicauda*. These are examples of the type of transgression processes that may have occurred many times in the evolutionary history of the region as also suggested for zooplankton species (Pérez et al. 2013). Abundance of the brief squid in Amatique Bay, just as in the Chesapeake Bay (Bartol et al. 2002), was related to increased seawater temperature and salinity. However, the close relationship between landings of squid and shrimp found in Amatique also suggests a targeted feeding migration by this squid, as crustaceans are the most important prey item in their diet (Coelho et al. 2010, Jereb & Roper 2010). The abundance of the blackbelt cichlid was related to rising SST in August, after a period of intense runoff (Fig. 2). This species is very common in Lake Izabal and Dulce River under freshwater conditions (Dickinson 1974, Salaverría and Jolón-Morales 2002). As other Central American cichlids this species is known to be tolerant of brackish waters and capable of crossing narrow sea barriers (Miller 1966, Hulsey & López-Fernández 2011).

Zoogeographic patterns of fish

The present observations of the occurrence of the fish fauna in the commercial catches are consistent with some of the general zoogeographic patterns of tropical estuaries. Thus, the fish communities are dominated by marine species and both their diversity and abundance are higher during the dry season (Ixquiac et al. 2008). This pattern is also observed in permanently open microtidal estuaries in temperate Australia (Valesini et al. 2014) and upper estuaries in tropical West Africa and Australia (Castellanos-Galindo & Krumme 2013a). Nevertheless, there are distinct patterns in Amatique, as well as in other Neotropical estuaries. In common with the microtidal Términos Lagoon in the Caribbean and estuaries of the western central Atlantic the families Ariidae, Engraulidae, Gerreidae and Tetraodontidae are prevalent, and Clupeidae and Claroteidae are less important or absent (Table 1) (Blaber 2000, Barletta & Blaber 2007, Ixquiac et al. 2008, Castellano-Galindo & Krumme 2013b, Castellanos-Galindo et al. 2013). In this respect, Amatique Bay has stronger affinity with the western tropical Atlantic and the tropical eastern Pacific, than with the tropical eastern Atlantic. This is also evident from the dominance of Ariidae and Tetraodontidae in terms of biomass and of Gerridae in terms of numbers (especially in mesotidal systems). In addition, the families Lutjanidae and Centropomidae that support important fisheries in Amatique are less common in the Tropical Eastern Atlantic (Castellano-Galindo & Krumme 2013b). In contrast, the Sciaenidae are less abundant than in West Africa, despite similar species richness. The similarity between Amatique and the eastern Pacific region must reflect somewhat similar ecological conditions and, in particular, the short isolation history (3 Ma). This similarity with the Pacific contrasts with the observations performed in the other vertebrates.

Shorebirds and manatees

The great majority of the shorebirds sighted in Punta de Manabique are visitors (Eisermann 2009). The largest group of shorebirds, comprising many sandpipers and plovers (group I), consisted of long-distance migrants that have summer breeding areas in the tundra of North America (Poole 2005). Their clear bi-modal pattern of occurrence suggests that these are transient birds with wintering areas in South America. These shorebirds probably use Amatique Bay for short stop-overs only. Less important, but still common, visitors (groups II and III) with breeding areas in temperate to high Arctic areas of America, seem to utilize the area for somewhat longer wintering periods, normally late in the rainy season. Among the more common species, only the collared plover *Charadrius collaris* has a regional distribution limited to the Caribbean. It breeds in Amatique and stays for a longer period, from June to November, and probably makes some limited seasonal migration thereafter. This may represent, therefore, a less common, and probably more recent, adaptation to match the fledging and early growth period to the productive rainy season in the Bay (Fig. 9.). Eisermann (2009) characterized the Punta de Manabique Wildlife Refuge as a shorebird migration site of secondary importance. This is in agreement with the observed decline in the abundance of overwintering or migrating shorebirds in the Gulf Coast south of the Tropic of Cancer (23^o 27’ N) (Withers 2002). Further, Barrantes & Chaves-Campos (2009) demonstrated a lower abundance of migrating shorebirds on the east coast of Costa Rica as compared to its Pacific coast. A likely reason for this longitudinal contrast may be the lack of extensive tides and tidal flats in the western Caribbean in contrast to the Pacific coast. This may limit the access of many shorebirds to aquatic invertebrates, which are their main prey. Thus, the Amatique region most likely has greatest value as a transient resting area, rather than an important feeding or breeding ground for most shorebird species.

Interestingly, the physical processes that may be responsible for the low abundance of shorebirds may also have played a role in the adaptation and persistence of sirenian populations in the Caribbean. The abundance of freshwater, the sheltered environment, water clarity, and very low tidal amplitude lead to abundant seagrass and suitable habitat for manatees in the Caribbean. This may help explain why these taxa are either absent (sirenians) or scarce (sea grasses; Green & Short, 2003; Samper-Villarreal et al. 2014) along the Pacific coast of Central America. The aerial surveys performed by Quintana-Rizzo & Machuca (2008) suggest that seasonal movements related to the hydrological cycle and to the life-cycle of manatees occur within the Lake Izabal-Amatique Bay complex (Fig.9). A larger number of sightings in the Bay proper were achieved during the wet season. Three possible reasons for the larger coastal affinity during the wet season are a wider access to areas with drinkable freshwater, strong river currents, and increased turbidity and subsequent loss of submerged vegetation upstream (Auil 2004). Although the density of manatees in some of the Caribbean populations may be relatively stable, there is still much needed research with regard to the environmental, behavioral and physiological basis of manatee migration as essential information for the implementation of a regional management plan (Harborne et al. 2006, UNEP 2010, Castelblanco-Martínez et al. 2013).

Conclusion

Ecological connectivity can be defined as the strength of the interactions among ecosystem components by movement of organisms, often at different stages of their life-cycles, as well as by the exchange of nutrients and organic matter (Nagelkerken 2009, Sheaves 2009). Migration to and from estuaries can range from large scale seasonal movements related to reproduction, feeding and ontogeny, to short incursions during the twilight (Krumme 2009). The most conspicuous linkage between the freshwater system and the estuary in Amatique are the movements of snook, the blackbelt cichlid and, in part, the manatees. These movements are related to both spawning cycles and the precipitation cycle. For example, the common snook moves in and out from freshwater environments to forage and spawn at sea thus interconnecting freshwater and marine environments (Taylor et al. 1998, Barbour & Adams 2012). The migrations of these fish species towards the sea may reflect the general trend for catadromy observed in relict marine taxa in the tropics. The more recent affinity for freshwater may reflect an adaptation to the relatively higher food availability in freshwater than in the sea (Gross 1988, Lucas et al. 2001). Manatees also play an important role in the re-cycling of nutrients in the western Caribbean, and they are probably responsible for a net export of nutrients to adjacent ecosystems downriver (Castelblanco-Martínez et al. 2012). The reverse (oceanic) input to the estuary is triggered by the massive migration of several species of penaeid shrimp, which are thought to use the mangroves, and by engraulids, which probably use the Bay for spawning. These aggregations attract a great number of transient coastal and oceanic predators comprising, among others, the families Carangidae, Loliginidae, Lutjanidae, Scombridae and Sphyraenidae, especially during the dry season. At this time of the year Bullshark, *Carcharinus lecuas*, and large-tooth sawfish *Pristis perotteli* have also been reported to enter Lake Izabal (Dickinson 1974). Predators like the Lutjanidae have, however, a marked reef-ecosystem, rather than oceanic, affinity. Thus, our observations strongly suggest an ontogenetic change in the utilization of different habitats in the Bay from soft bottom to reefs, by different life-stages of the lane snapper.

A contrasting use of Amatique is made by most shorebirds, which mostly depend on the bay and estuaries as a perennial refuge and contribute less to nutrient cycling. They represent, however, a teleconnection with the high-latitude systems of North and South America of conservation interest. At different levels of the food chain there is a multitude of exploitation strategies by fishers from different fleets, social and ethnic groups, indirectly involved in competing small-scale fisheries. Previous observations suggest that in an apparently complex system, these fishers achieve reasonable levels of agreement and co-existence (Andrade & Midré 2011). It may be that the large focus on the shrimp and engraulids at the lower trophic levels corresponds to an example of a balanced fishery with output reasonably proportional to productivity (Garcia et al. 2012). Future studies should investigate the match of size distributions in the harvest and in the sea, as well as the consequences of fishing at the lower trophic levels. Another issue of interest for population management is the timing of the rotational fishery closures and their suitability for protection of spawning aggregations. These closures were agreed by the fisher groups in a participatory manner with the primary purpose of avoiding conflicts related to gear saturation (Andrade & Midré 2011).

The range of ecological linkages observed has had major roles in the evolutionary processes in the western Caribbean, and it is motivating to integrate them in fishery and conservation plans.

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Table 1. Comparison of different metrics from mangrove and estuarine fish assemblages from Amatique Bay (Caribbean), the tropical Eastern Pacific, Western Central Atlantic and tropical Eastern Atlantic. Contribution in number of species, abundance (no. of individuals) and biomass (B) at the family level. Adapted and expanded from Castellanos-Galindo & Krumme (2013b).

Family	Amatique Bay (Caribbean)[a]			Tropical Eastern Pacific [b]			Western Central Atlantic [b]			Tropical Eastern Atlantic [b]		
	No. of Species (%)	No. ind. (%)	B %	No. of Species (%)	No. ind. (%)	B %	No. of Species (%)	No. ind. (%)	B %	No. of Species (%)	No. ind. (%)	B %
Ariidae	3.3	14.3	31.7	6.7	4.0	19.1	7.4	31.5	32.4	4.3	1.3	3.4
Cichlidae	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	4.3	0.0	0.1
Claroteidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.3	0.5	1.5
Clupeidae	4.9	2.0	1.2	2.5	15.4	6.9	2.4	2.4	0.4	5.7	46.5	27.2
Eleotridae	0.0	0.0	0.0	2.5	0.8	0.6	0.8	0.1	0.1	1.4	0.0	0.0
Elopidae	0.0	0.0	0.0	0.3	0.1	0.0	0.9	0.0	0.0	1.4	0.3	0.4
Engraulidaee	8.2	5.9	3.4	5.4	9.5	0.0	10.0	18.2	7.4	0.0	0.0	0.0
Gerreidaee	4.9	37.4	12.5	4.1	20.4	1.6	2.9	1.6	0.8	2.9	0.1	0.1
Mugilidae	0.0	0.0	0.0	1.3	8.7	1.3	4.6	8.5	8.7	7.1	2.2	2.7
Polynemidae	3.3	0.2	0.2	0.6	0.7	0.0	0.7	0.0	0.0	4.3	1.7	3.4
Pristigasteridae	1.6	0.5	0.1	1.0	0.2	0.0	0.8	0.0	0.0	0.0	0.0	0.0
Sciaenidae	16.4	9.8	8.8	12.4	3.1	0.3	16.6	10.4	9.1	8.6	39.7	50.4
Tetraodontidaee	6.6	1.2	1.0	2.9	3.0	19.5	3.9	9.2	21.9	1.4	0.1	0.1

[a] Data from research surveys performed with shrimp bottom trawler (Ixquiac et al. 2008) (see Supplementary material Text S2);
[b] Data from Castellanos-Galindo (2013a) citing different sources.

FIGURES

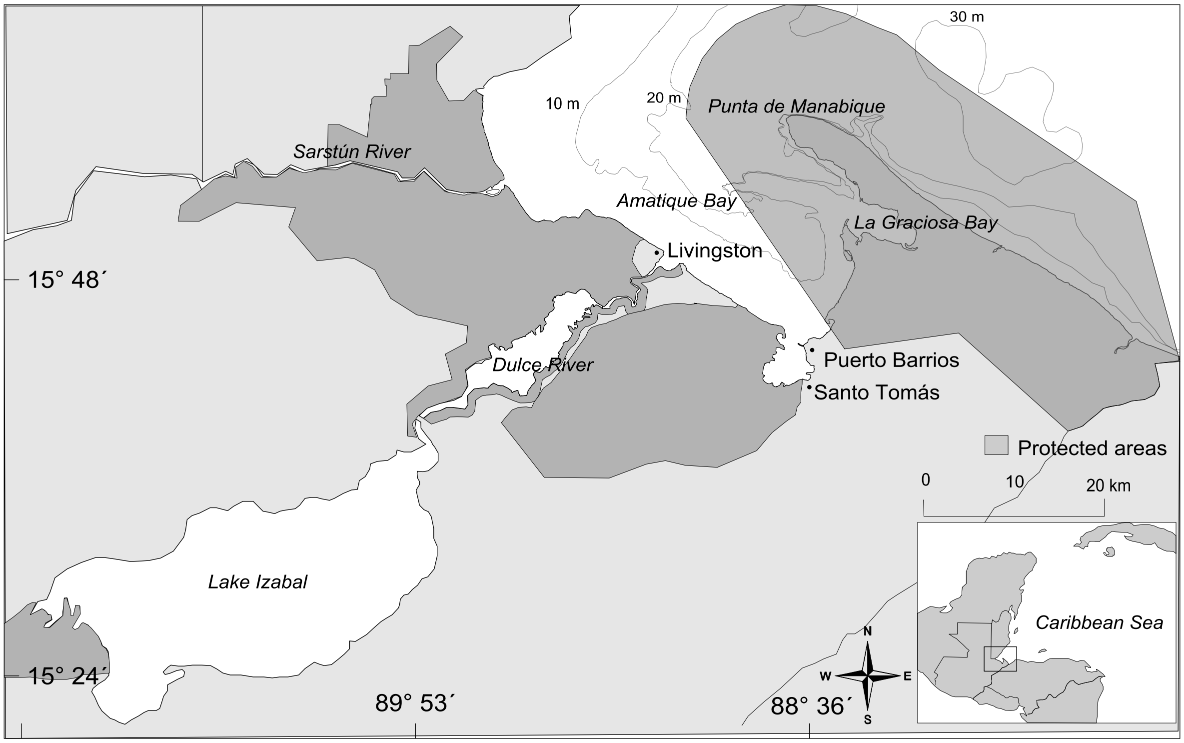
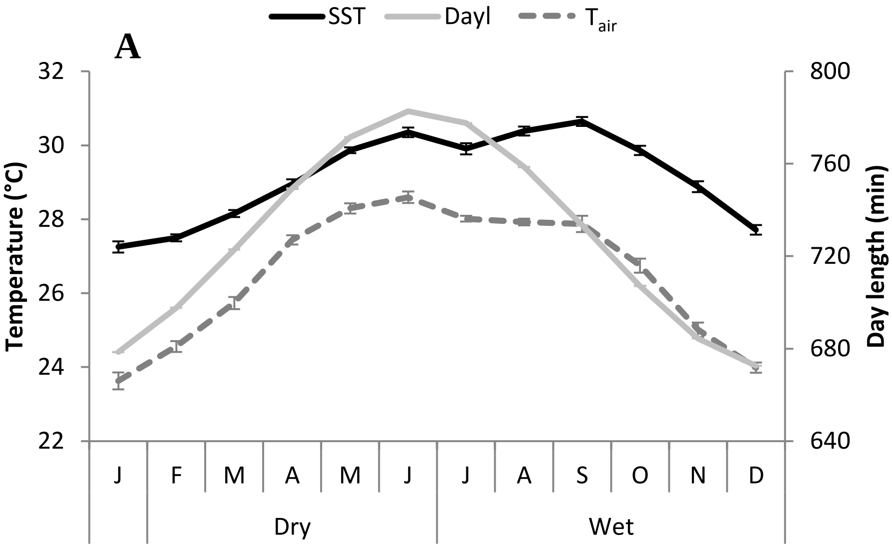
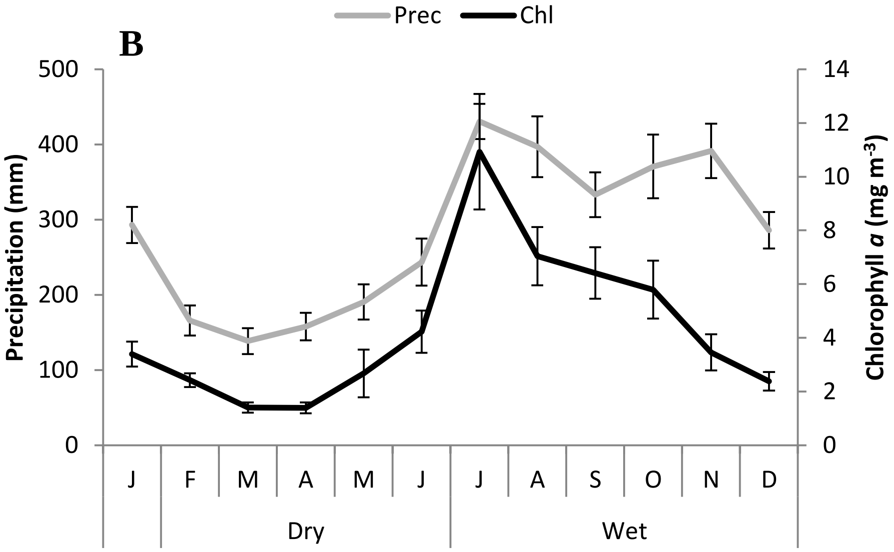


Fig. 1. Map of Amatique Bay and current protected areas (gray). Punta de Manabique includes a protected marine zone (shaded).


SST
Dayl
T_{air}
A
Temperature (°C)
Day length (min)
32
30
28
26
24
22
800
760
720
680
640
J
F
M
A
M
J
J
A
S
O
N
D
Dry
Wet

931


Prec
Chl
B
Precipitation (mm)
Chlorophyll *a* (mg m^{-3})
500
400
300
200
100
0
14
12
10
8
6
4
2
0
J
F
M
A
M
J
J
A
S
O
N
D
Dry
Wet

932

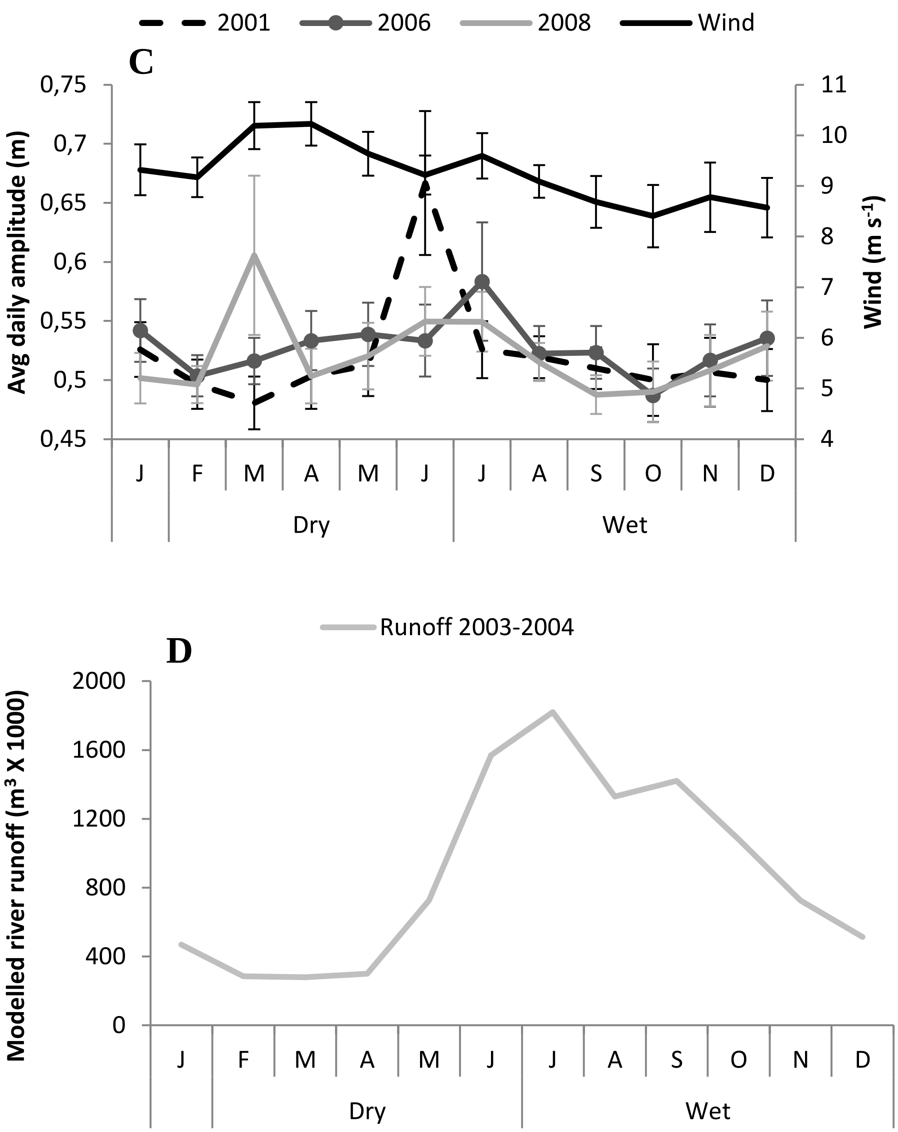


Fig. 2. (A) Sea surface temperature (SST, ºC; 1985-2009), air temperature (T_{air}, ºC; 1990-2010) and day length (Dayl, min; 1985-2010); (B) Annual cycles of precipitation (Prec, mm; 1985-2010) and chlorophyll *a* (Chl, mg m^{-3}; 2002-2010); (C) wind (m s^{-1}; 1990-2010) and tide amplitude (predicted for 2001, 2006 and 2008); and (D) modelled river runoff (m^3 X 1000; 2003-2004 in Burke & Sugg (2006)) in Amatique Bay, Guatemala. Bars denote the standard error of the mean of the observations made in the years indicated. Sources: INSIVUMEH and NASA.

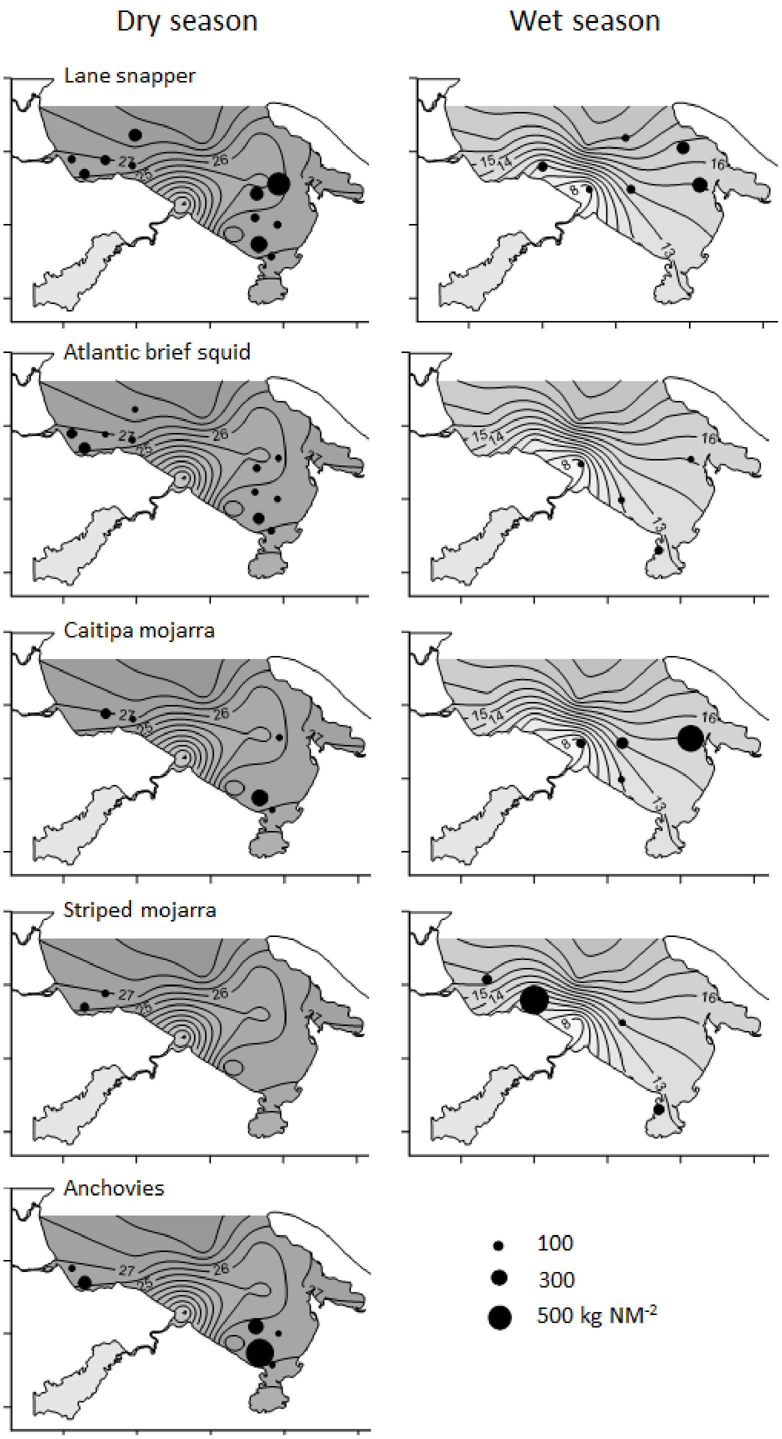


Fig. 3. Surface salinity (ppt) and distribution of selected species in research trawls (calculated density per square nautical mile (kg NM^{-2}): Lane snapper *Lutjanus synagris*, Atlantic brief squid *Lolliguncula brevis*, Caitipa mojarra *Diapterus rhombeus*, Striped mojarra *Eugerres plumieri* and Anchovies group (*Anchoa spinifer*, *A. cayorum*, *A. colonensis* and *Anchoviella elongata*) in the dry (February) and wet (August) seasons in Amatique Bay, 2008. No anchovies were registered in the wet season. Isolines denote salinity gradients (ppt). Source: Ixquiac-Cabrera et al. (2008).

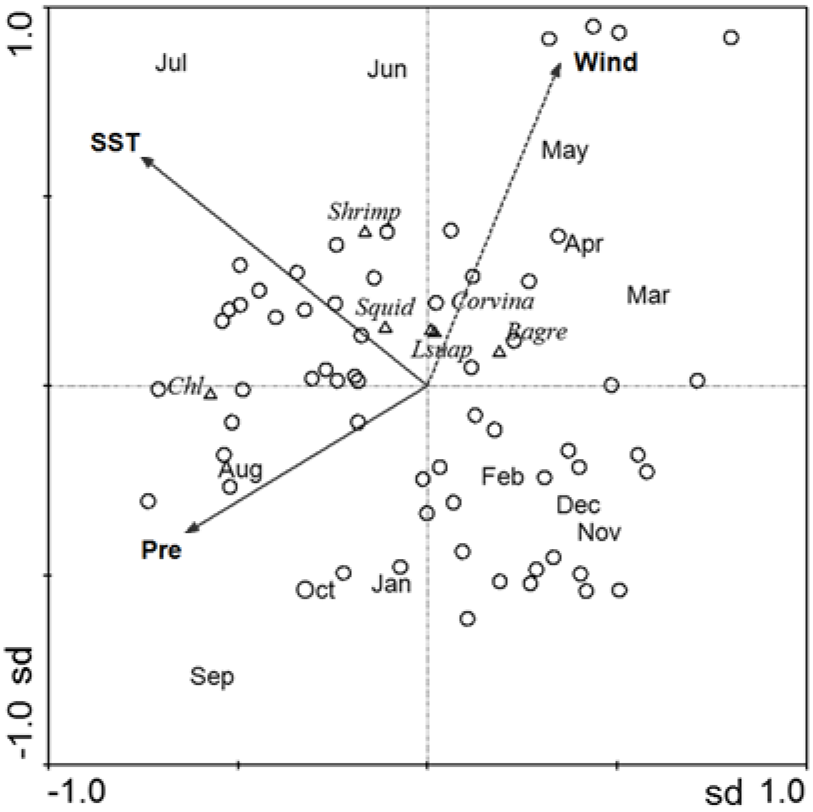


Fig. 4. Redundancy analysis (RDA) of monthly catch rates –CPUE- [kg (boat X fishing days)$^{-1}$] of shrimp trawlers (circles), in the period 2006-2010 in Amatique Bay. The vectors indicate the influence of the two significant environmental variables precipitation (Pre) and sea surface temperature (SST), as well as of wind speed (stippled line), during the same period. Names in italics indicate the individual or group of species analyzed and are represented by triangles: lane snapper *Lutjanus synagirs* (Lsnap); Penaeid species (Shrimp) including *Litopenaeus schmitti*, *Farfantepenaeus notialis* and *Xiphopenaeus kroyer*; the Atlantic brief squid *Lolliguncula brevis* (Squid); Catfish group (Bagre), composed by *Bagre marinus* and *Ariopsis assimilis*; a mix of Sciaenidae and Haemulidae, (Corvina), probably *Protosciaena bathytatos* and *Pomadasys corvinaeformis;* and Lane snapper *Lutjanus synagris*. Chlorophyll *a* (Chl) was also treated as a biological group. Source: official shrimp trawler landings; DIPESCA.

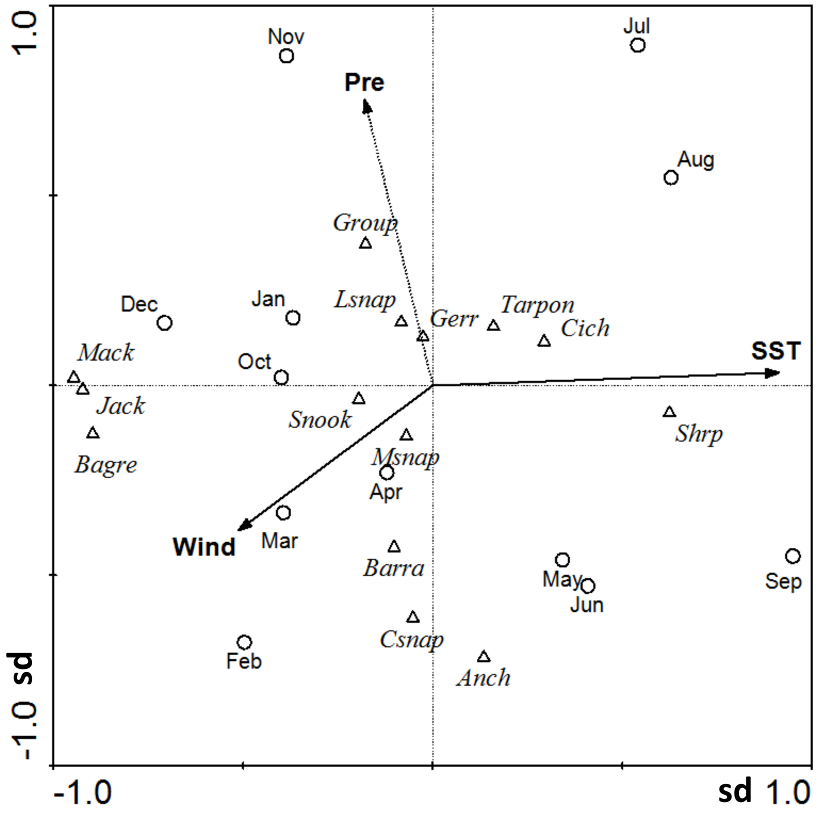
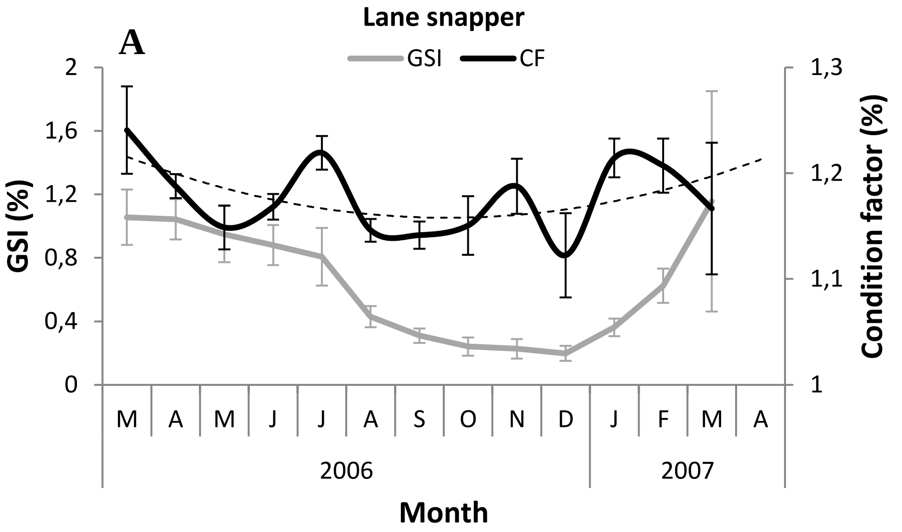
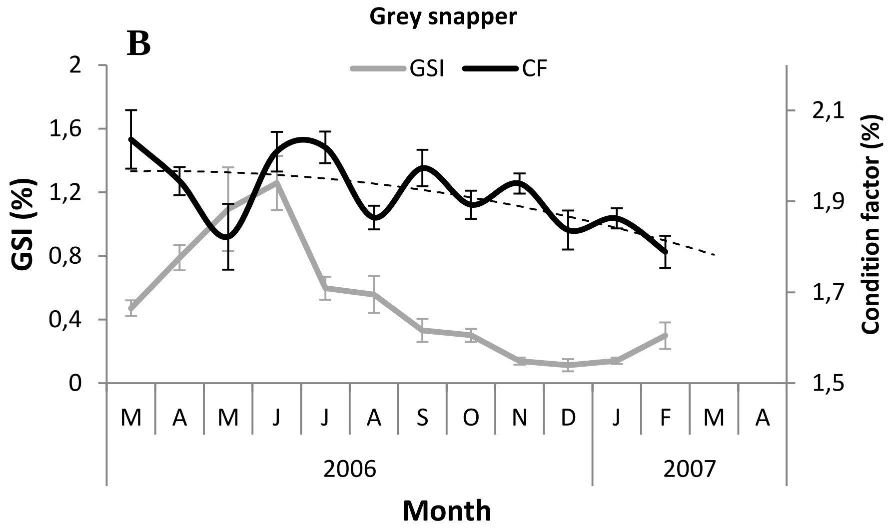


Fig. 5. Redundancy analysis (RDA) of commercial species landed by dories and skiffs, using nets and hook gear, in Amatique Bay during 1998. The vectors indicate the influence of the two significant environmental variables wind speed (Wind) and sea surface temperature (SST), as well as of precipitation (Pre) (stippled line) in the same period. Names in italics indicate the individual or group of species analyzed: Crevalle jack *Caranx hippos* (Jack); Spanish mackerel *Scomberomorus maculatus* (Mack); Gafftopsail catfish *Bagre marinus* (Bagre); "Mojarras" mixed group of Gerridae including *Diapterus rhombeus* and *Eugerres plumieri* (Gerr), Barracuda *Sphyraena picudilla* (Barra); Mutton snapper *Lutjanus analis* (Msnap); "Cubera" snapper group (Csnap) including the Cubera snapper *Lutjanus cyanopterus* and grey snapper *Lutjanus griseus*; Anchovies *Anchoa* spp (Anch); Blackbelt cichlid *Paraneetroplus maculicauda* (Cich); Penaeid species (Shrimp) including *Litopenaeus schmitti*, *Farfantepenaeus notialis* and *Xiphopenaeus kroyer*; Common snook *Centropomus undecimalis* (Snook); Tarpon *Melagops atlanticus* (Tarpon); lane snapper *Lutjanus synagris* (Lsnap); and the Goliath grouper *Epinephelus itajara* (Group), which are represented by triangles. The initials of the months are given, as well as their exact positions (circles). Source: estimates derived by Heyman & Graham (2000) and Heyman and Granados-Dieseldorff (2012) upon interviews to 42 experienced fishers.


Lane snapper
A
GSI
CF
GSI (%)
Condition factor (%)
2
1,6
1,2
0,8
0,4
0
1,3
1,2
1,1
1
M
A
M
J
J
A
S
O
N
D
J
F
M
A
2006
2007
Month


Grey snapper
B
GSI
CF
GSI (%)
Condition factor (%)
2
1,6
1,2
0,8
0,4
0
2,1
1,9
1,7
1,5
M
A
M
J
J
A
S
O
N
D
J
F
M
A
2006
2007
Month

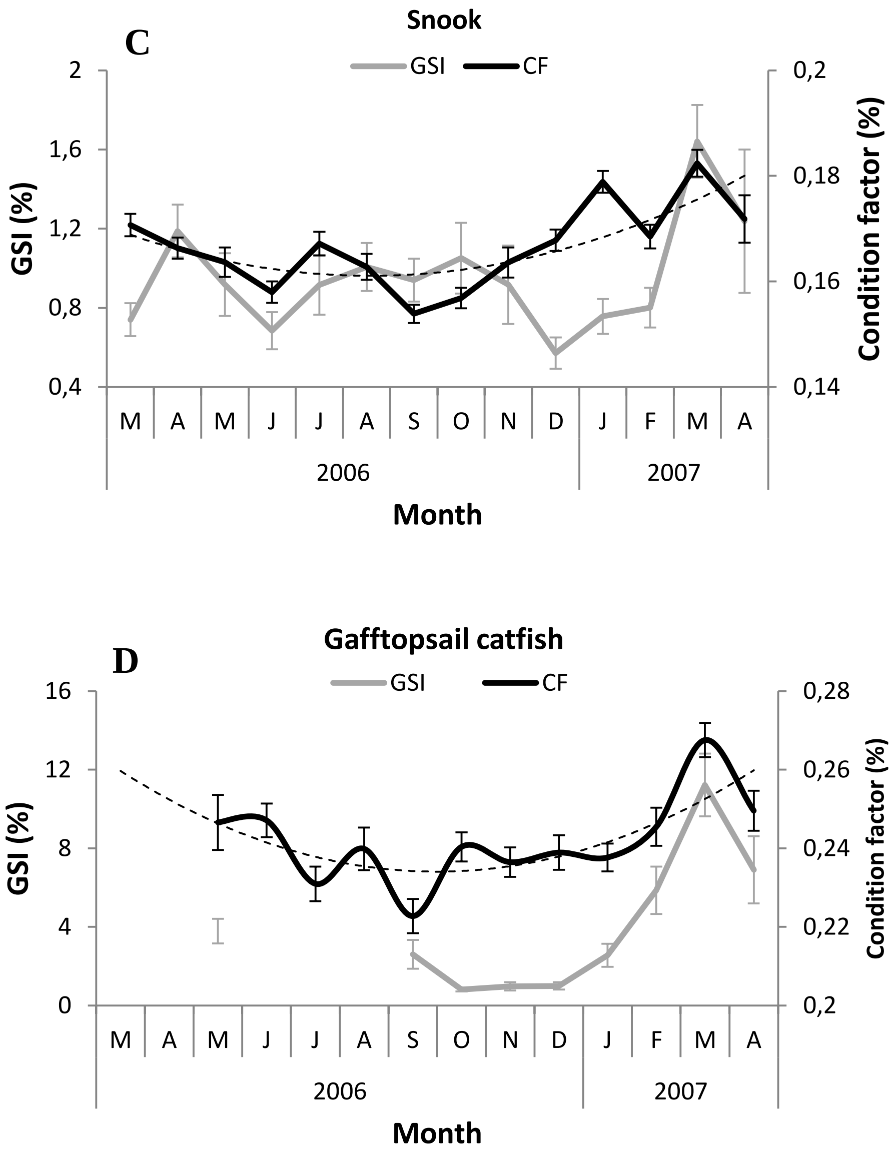


Fig. 6. Annual cycles of the gonadosomatic index (GSI, dark lines) and condition factor (CF, grey lines) of (A) lane snapper *Lutjanus synagris*, (B) grey snapper *L. griseus*, (C) common snook *Centropomus undecimalis* and (D) females of gafftopsail catfish *Bagre marinus*, sampled from March 2006 to April 2007 in Livingston and Puerto Barrios, Guatemala. Vertical bars denote standard errors of the means of sex-pooled observations and the stippled line a second degree polynomial fit to the mean CF.

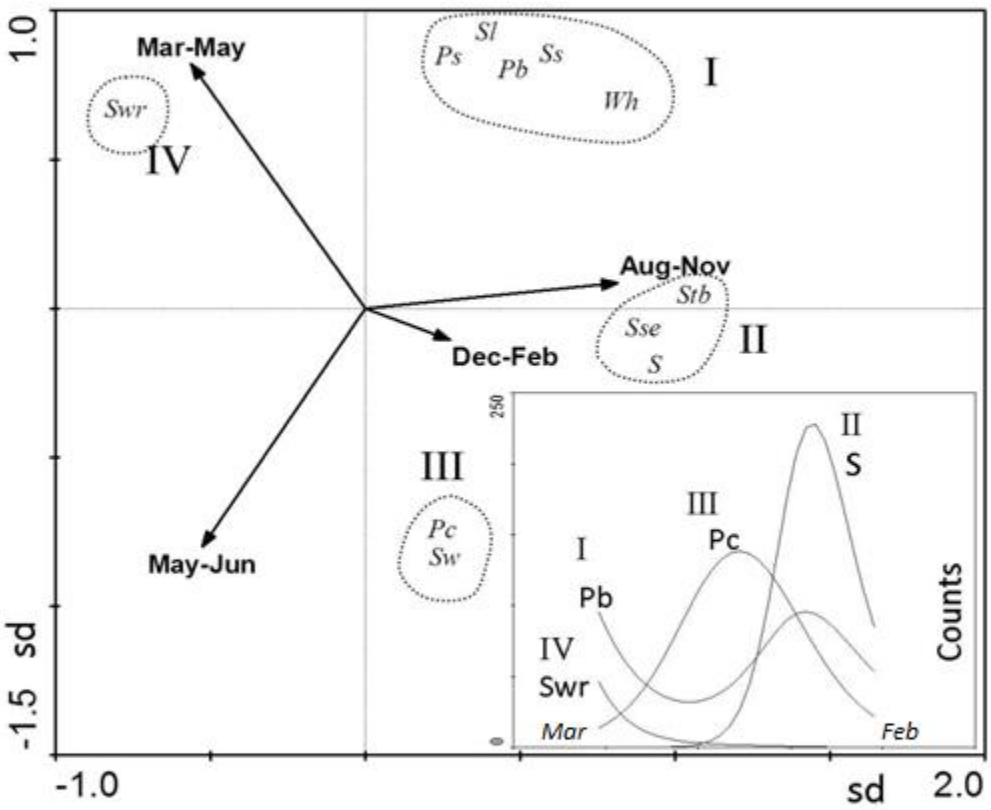


Fig. 7. Bi-plot of a redundancy analysis illustrating the seasonal occurrence of the 11 most common species of shorebirds reported by Eisermann (2009): Black-bellied Plover *Pluvialis squatarola* (Pb), Semipalmated Plover *Charadrius semipalmatus* (Ps), Spotted Sandpiper *Actitis macularius* (Ss), Whimbrel *Numenius phaeopus* (Wh), Least Sandpiper *Calidris minutilla* (Sl), Black-necked Stilt *Himantopus mexicanus* (Stb), Sanderling *Calidris alba* (S), Semipalmated Sandpiper *Calidris pusilla* (Sse), Collared Plover *Charadrius collaris* (Pc), Western Sandpiper *Calidris mauri* (Sw), White-rumped Sandpiper *Calidris fuscicollis* (Swr). These species were divided into four main groups (I-IV) based on the seasonal patterns of sightings, and are indicated by the stippled lines. GAM regressions were fitted to the seasonal sightings of four species representative of each group (inset).

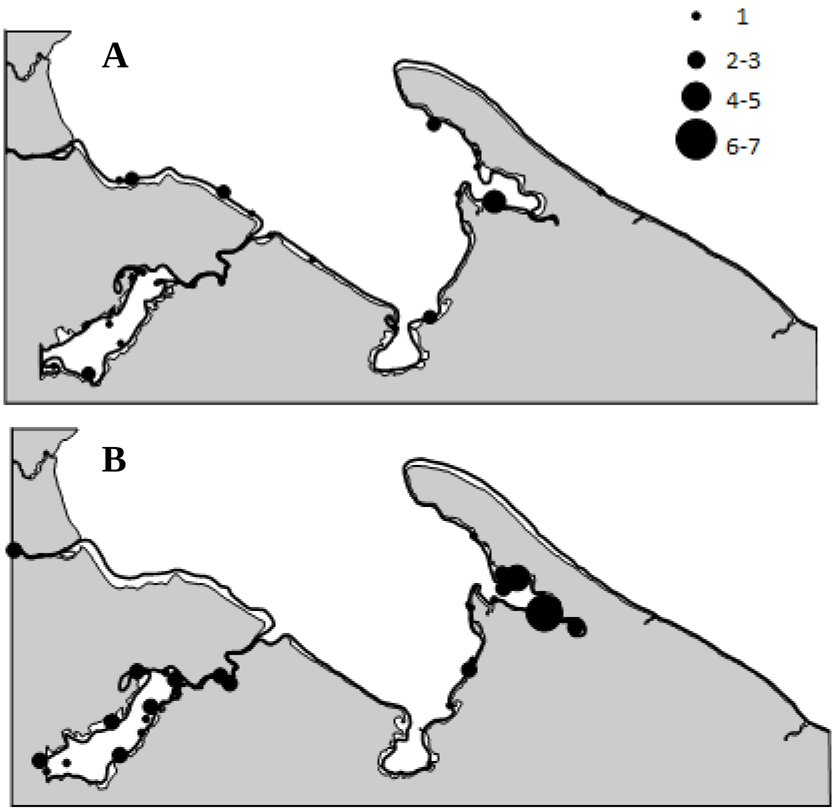


Fig. 8. Distribution of manatee *Trichechus manatus* from aerial counts performed in (A) October 2006 (wet season) and (B) March 2007 (dry season) in Amatique Bay, 2007. Adapted from Quintana Rizo & Machuca (2008).The black line denotes the survey tracks.

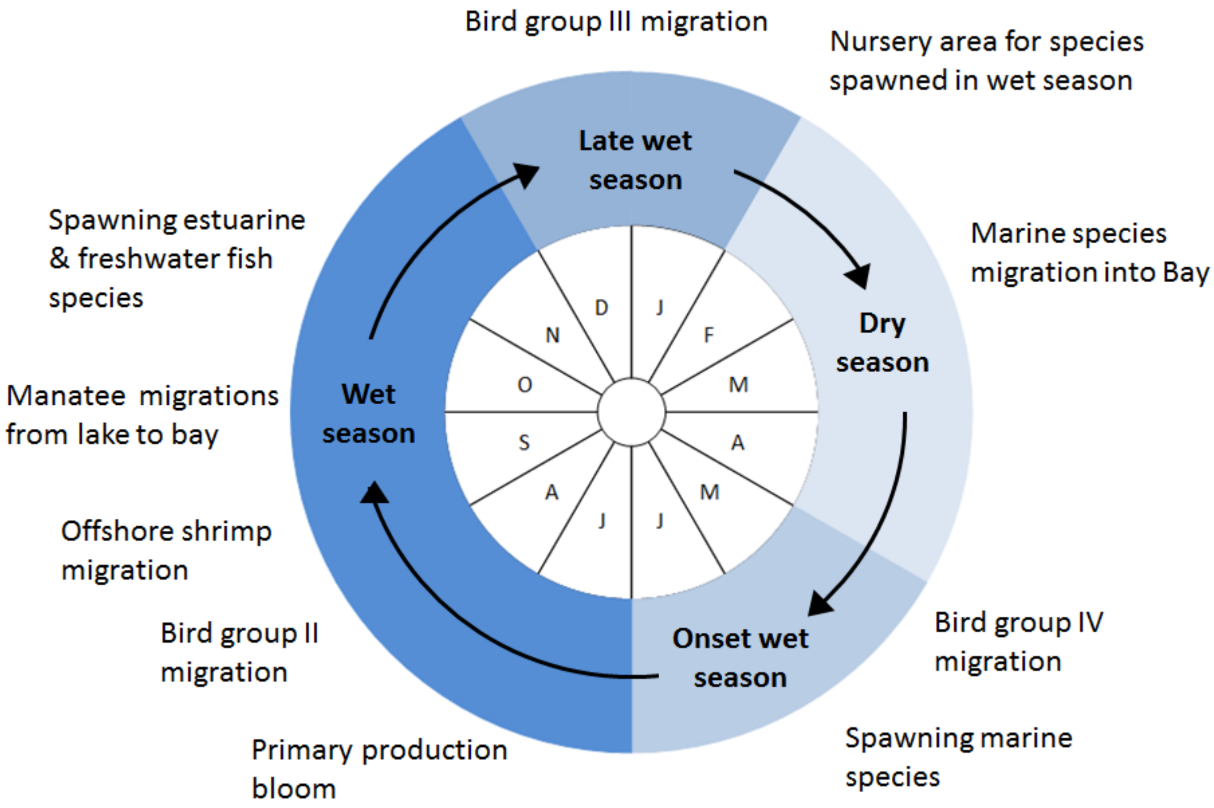


Fig. 9. A conceptual model of the precipitation-driven seasonal cycle in Amatique Bay, with focus on fish, seabirds and manatees. Color depth denotes precipitation intensity, from low (light blue) to strong (dark blue). Composition of bird groups is given in Table S1 (Supplementary material).

Supplement. Ecological linkages in a Caribbean estuary bay

The supplement contains the following items:

- **Text S1.** Retrieval and treatment of enviromental data
- **Text S2.** Biological observations during research cruises
- **Text S3.** Collection of manatee data
- **Table S1.** Composition of landed species in Amatique Bay analyzed in this study
- **Literature cited in the supplement**

Supplement

Text S1. Collection and analysis of meteorological data

To study environmental variability we extracted time-series of precipitation, air temperature, sea surface temperature, chlorophyll *a* concentration and run-off from open internet sources as either historical records measured in the area or as satellite-derived data. Monthly precipitation (Pre, mm) from 1985 to 2010, monthly average air temperature (T_{air}, °C) from 1990 to 2010, wind direction from 2006-2010 and wind speed (Wind, km/h) from 1990-2010 and forecast tide data for the random years 2001, 2006 and 2008 were obtained from the national meteorological institute (INSIVUMEH 2012), using data from the Puerto Barrios, Izabal meteorological station, located near the Bay. Months of low wind stress, classified as "calm" or "variable" at the source, were not considered in calculation because the mean direction was not available. Average and dispersion of wind direction was calculated using Lund & Agostinelli (2014). Forecasted tide data were available as day maxima and minima (m). The tidal amplitude was calculated as the difference between daily maximum and minimum, and averaged on a monthly basis. Average monthly sea-surface temperature (SST, °C) from July 1985 to December 2009 and from 2003-2010 was derived from satellite imagery processed by NOAA/NASA's AVHRR Oceans Pathfinder global and MODIS/Aqua mission (Halpern et al. 2001). The former series was employed to study meteorological correlations as historical records span over a longer time period but limited to 2009. The later series was related to fish landing data in the period 2006-2010. Day length (sunlight duration, min) was calculated using NOAA's solar calculation algorithm for the Puerto Barrios geographical coordinates at 15º 44' N and 89º 33' (NOAA 2012).

Estimates of monthly run-off were derived by Burke & Sugg (2006) using a model for the Sarstún and Dulce rivers that accounts for the physical environment (elevation, slope, soils, precipitation, and land cover) in the drainage basin for the years 2003-2004.

Chlorophyll *a* concentration (Chl, mg m^{-3}) from July 2002 to 2010 was obtained through NASA's Giovanni Ocean Color Radiometry data product visualization using SeaWIFS and MODIS databases. The temporal and spatial resolutions were 8 days and 4 Km respectively calculating averages for the polygon at latitudes (15.618, 15.984) and longitudes (-88.936, -88.437) inside the Bay. There is a lack of field data to ground truth satellite measurements in Amatique and this is of concern as remote chlorophyll *a* measurements can be biased (Dierssen 2010). Therefore, we attempted to compare and relate remote measurements of chlorophyll *a* in the bay with the turbidity measurements performed with a Secchi-disk and the concentrations of nutrients measured at the outlet of Lake Izabal by Quintana-Rizzo & Machuca (2008).

Text S2. Biological observations during research cruises

In 2008, four research cruises were performed by Ixquiac-Cabrera et al. (2008) in Amatique Bay to record prevailing oceanographic conditions and fish abundance. A 12 m fiberglass boat with a 150 Hp engine and a commercial trawl was employed. The trawl was 18 m long with a 14 m headline and mesh size of 1¾”. The trawl was recovered by hand. Eleven stations were covered across the bay, with depths ranging between 5-25 m. The gear was towed for 30 min at a speed of 3 knots. All organisms were frozen for posterior identification in the lab. The swept area method was employed to estimate species abundances (Sparre & Venema 1998, Ixquiac-Cabrera et al. 2008). We employed data gathered in February and August to represent environmental conditions and species distributions during the dry and wet seasons respectively**.**

Text S3. Collection of manatee data

To estimate manatee abundance, aerial surveys were performed by Quintana-Rizzo & Machuca (2008) using the aerial survey replicate count methodology developed by Lefebvre & Kochman (1991). This method requires that after manatees have been spotted, the plane must be maneuvered back to the site of sighting, at a lower altitude and speed to confirm observations and perform recounts. An experienced primary observer (>100 hours) sat beside the pilot and a secondary observer (26 hours) sat behind allowing for continuous search on both sides of the plane. The aerial surveys were performed between 9 AM and 10 AM to maximize visibility and on a Beaufort wind force scale of 0-2. Average altitude ranged between 152-213 m and average speed was 160 km/h. The survey track was set about 500 m from the shoreline from Lake Izabal, to Punta de Manabique (Fig. 8).

Table S1. List of fished species and birds analyzed in this study (and abbreviations). Sources: A. Estimates from dories and skiffs landings based on fishers anecdotal information in 1998 (Heyman & Graham 2000, Heyman & Granados-Dieseldorff 2012); B. Official shrimp trawler landings (DIPESCA, Guatemala); C. bottom-trawl research cruises (Ixquiac-Cabrera et al. 2008); D. Own data, E. Shorebird sightings (Eisermann 2009); F. manatee counts (Quintana-Rizzo & Machuca 2008).The last column suggest a preliminary classification of these species into functional groups based on results from Amatique.

Class	**Common name or group of species analysed**	**Scientific name**	**Sources**	**Presumed functional group in Amatique**
Malacostraca	"Shrimp" group (Shrp, main species)	*Litopenaeus schmitti,* *Farfantepenaeus notialis* *Xiphopenaeus kroyeri*	A, B, C	Estuarine dependent
Cephalopoda	Atlantic brief squid (Squid)	*Lolliguncula brevis*	B,C	Marine transient
Actinopterygii	Crevalle jack (Jack)	*Caranx hippos*	A	Marine transient
	Spanish mackerel (Mack)	*Scomberomorus maculatus*	A	Marine transient
	Common snook (Snook)	*Centropomus undecimalis*	A, D	Diadromous
	Tarpon (Tarpon)	*Melagops atlanticus*	A	Marine & fresh water
	Barracuda (Barra)	*Sphyraena picudilla*	A	Marine transient
	Goliath grouper (Group)	*Epinephelus itajara*	A	Marine transient
	Mutton snapper (Msnap)	*Lutjanus analis*	A	Marine transient
	Lane snapper (Lsnap)	*Lutjanus synagris*	A, B,C, D	Marine & estuarine
	Anchovies (Anch)	*Anchoa* spp	A	
		A.spinifer, A. cayorum, A. colonensis and *Anchoviella elongata*	C	Marine
	"Catfishes" (Bagre)			
	Gafftopsail catfish	*Bagre marinus*	A, B, D	Marine & estuarine
	Mayan catfish	*Ariopsis assimilis*	B, C	Marine

	"Mojarras" mixed group of Gerridae (Gerr)	Mainly *Diapterus rhombeus* and *Eugerres plumieri*	A	Estuarine & freshwater
	Caitipa mojarra	*Diapterus rhombeus*	C	Estuarine
	Striped mojarra	*Eugerres plumieri*	C	Freshwater-estuarine
	Blackbelt cichlid (Cich)	*Paraneetroplus maculicauda*	A	Freshwater transient
	"Cubera" snappers (Csnap)	Common misidentification		
	Cubera snapper	*Lutjanus cyanopterus*	A	Marine transient
	Grey snapper	*Lutjanus griseus*	A, D	Marine & estuarine
	"Corvina": Mixed group of Scianidae and Haemulidae	probably *Protosciaena bathytatos* and *Pomadasys corvinaeformis*	B,C	Probably marine
Aves	Black-bellied Plover (Pb)	*Pluvialis squatarola*	E	Group 1: Long migratory - short stopovers in Amatique during dry season
	Semipalmated Plover (Ps)	*Charadrius semipalmatus*	E	
	Spotted Sandpiper (Ss)	*Actitis macularius*	E	
	Whimbrel (Wh)	*Numenius phaeopus*	E	
	Least Sandpiper (Sl)	*Calidris minutilla*	E	
	Black-necked Stilt (Stb)	*Himantopus mexicanus*	E	Group 2: Long migratory with longer stopovers at late rainy season.
	Sanderling (S)	*Calidris alba*	E	
	Semipalmated Sandpiper (Sse)	*Calidris pusilla*	E	
	Collared Plover (Pc)	*Charadrius collaris*	E	Group 3: Migratory with longer stopovers at late rainy season. Pc breeds in Amatique
	Western Sandpiper (Sw)	*Calidris mauri*	E	
	White-rumped Sandpiper (Swr)	*Calidris fuscicollis*	E	Migartory. Only observed in dry season
Mammalia	Manatee	*Trichechus manatus*	F	Freshwater migrations

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