The temporal and spatial variability of nursery habitats for fishes in macrotidal mangrove systems of Colombia and Brazil

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Simplicity is the law of nature for men as well as for flowers

(Henry David Thoreau)

ABSTRACT

Mangrove forests are predominant features of tropical coasts. Besides providing numerous environmental and societal benefits, these ecosystems offer critical habitats for juvenile coastal fishes, many of which are targeted by commercial and artisanal fisheries. Our knowledge of how mangrove fish assemblages are organized has been particularly biased towards microtidal non-estuarine systems generally not subject to strong tidal and salinity driven changes (e.g. Caribbean Sea). The overall objective of this thesis is to determine the role of environmental filters (i.e. tides and salinity gradients) and biogeography in structuring macrotidal estuarine mangrove fish communities in the Neotropics. Here, I present a regional and local comparison of the mangrove fish assemblage structure of two major neotropical biogeographical marine regions: the Eastern Pacific (EP) and the Western Atlantic (WA). Using own field data collected in three macrotidal localities within these regions (EP: Bahía Málaga Estuary and Utría Sound, Colombian Pacific; WA: Caeté Estuary, North Brazil) and published information on mangrove fish assemblage compositions of the EP and the WA regions, I specifically aimed at answering: (1) if tides and salinity exerted the same influence on the structure of these two biogeographically isolated mangrove fish assemblages, (2) if intertidal fish assemblages in similar tidal regimes but different habitats (mangroves *vs.* rocky shores) respond similarly to tidal cycles, (3) if tide-related patterns in the structure of intertidal mangrove fish assemblages were stable over time, and (4) if historical biogeography played a role in explaining the local and regional patterns of taxonomic and functional composition in these two regions.

The studies conducted on intertidal mangrove creeks in the Colombian Pacific and North Brazil indicated the central importance of tidal and diel cycles in shaping the short-term patterns of organization and niches of intertidal mangrove fish assemblages. Tidal and diel influence on fish assemblage structure was also remarkably stable over time (> 10 years). The importance of such influences over geographical scales, however, may be regulated by the topographic characteristics of each mangrove system. Mangroves in the Colombian Pacific are located in a tectonically active area producing an erosional terrain where almost equal extents of intertidal areas are inundated during spring and neap tides. In contrast, North Brazil presents accretional mangroves where much larger intertidal areas are inundated at spring than at neap tides. These contrasting characteristics were crucial for explaining larger intertidal fish biomass during spring tides in North Brazil and the absence of consistent temporal trends in the Colombian Pacific. Similarly, salinity played a determinant role in structuring fish assemblages in both areas. Whereas low salinity creeks in Pacific Colombia were dramatically depauperated in fish richness and biomass as a consequence of a species-poor freshwater fish fauna, low salinity creeks in North Brazil were equally rich in species and biomass when compared to higher salinity creeks, reflecting the greater diversity of freshwater fish able to colonize upper reaches of estuaries in the latter area. These contrasting patterns suggest that freshwater fish biodiversity and biogeography have a significant role in explaining salinity-related gradients in estuarine fish community structure.

Intertidal migrations are a common feature of the home range of tropical coastal fishes, but the relative importance of such movements for these assemblages may be determined by the amount of intertidal habitat available for migration and the distribution of prey resources within the intertidal zone. In rocky shores, tidal migrations are undertaken by a high number of fish species most of which make opportunistic use of prey resources located in low intertidal areas. In intertidal mangroves, however, fewer fish species undertake intertidal migrations, but these movements seem to have a greater importance for a proportionally larger number of these fish species that forage in both low and high intertidal areas.

Mangrove fish assemblages of the Brazilian (WA) and the Panamic (EP) provinces are equally diverse (comprising about 25% of their respective total coastal fish faunas) and are generally dominated by the same fish families (Ariidae and Tetraodontidae, both benthic invertebrate feeders). Yet, differences in the representation of other ecologically important families between areas is likely the reflection of historical biogeographical processes and/or the product of specific seascape configurations that benefit the presence of specific fish families. An extreme rainfall regime (> 7 m year^{-1}) and the lack of a diverse freshwater fish assemblage able to colonize estuarine habitats may allow species of Centropomidae to thrive in the Colombian Pacific. In contrast, a less rainy area (2-3 m year^{-1}) and a greater number of species of freshwater origin (well established in estuarine habitats), may prevent the colonization of these habitats by Centropomidae in North Brazil. A clear example of the influence of seascape characteristics on mangrove fish assemblages was the dominance of Lutjanidae (a reef-associated family) in the Colombian Pacific and its absence in North Brazil. Despite both areas being estuarine, the presence of subtidal rocky bottoms in close proximity to mangroves in the Colombian Pacific (that are absent in North Brazil) enhanced the occurrence of such taxa. Finally, the absence of Anablepidae in the Colombian Pacific and its ecological importance in North Brazil was a clear example of the effect of the biogeographical history of Central and South America (i.e. formation of the Caribbean Sea and closure of the Isthmus of Panama) in the distribution of extant mangrove fish of these areas.

The results of this thesis highlight (1) the stability in time and across regions of tidal- and diel-related patterns of intertidal mangrove fish distribution in neotropical macrotidal areas, (2) the major effect that specific environmental conditions (e.g. rainfall regime) and seascape settings (e.g. mangrove topography and adjacent habitats) can produce in local fish community structure, (3) the varying importance that distinctive tropical intertidal habitats can have for coastal fishes, and (4) the importance that historical biogeography (of freshwater and marine fishes) can have in explaining the current patterns of distribution of mangrove fish faunas in estuarine areas of the Neotropics. Taking these four aspects into consideration will benefit our global understanding of the role of mangroves as important habitats for fishes and will aid in the development of sound comparative studies between mangrove areas of the world. Ultimately, the search for generality in patterns and processes explaining the organization of mangrove fish communities will increase our ability to better manage mangrove-associated fisheries.

Keywords: tidal and diel cycles, neotropical macrotidal mangroves, salinity gradients, fish community structure, Colombia, Brazil, Panamic province, Brazilian Province, Western Atlantic, Eastern Pacific

RESUMEN

Los bosques de manglar dominan los paisajes de muchas costas tropicales. Aparte de proveer numerosos beneficios ambientales y sociales, estos ecosistemas ofrecen hábitats críticos para peces costeros juveniles, muchos de los cuales son después objeto de pesca comercial o artesanal. Nuestro conocimiento de cómo se organizan los ensamblajes de peces de manglar esta particularmente sesgado hacia sistemas micromareales no estuarinos que generalmente no están sujetos a cambios mareales y de salinidad fuertes (e.g. Mar Caribe). El objetivo general de esta tesis es determinar el rol de los filtros ambientales (i.e. mareas y gradientes de salinidad) y la biogeografía en estructurar las comunidades de peces de manglar en zonas macromareales estuarinas del Neotrópico. Se presenta aquí una comparación regional y local de la estructura de los ensamblajes de peces de manglar de dos regiones neotropicales: El Pacífico Oriental (PO) y el Atlántico Occidental (AO). Usando datos colectados en tres localidades macromareales (PO: Estuario de Bahía Málaga y Ensenada de Utría; AO: Estuario del Caeté, norte de Brasil) e información publicada sobre la composición de los ensamblajes de manglar del PO y el AO, se pretendió responder las siguientes preguntas: (1) si los ritmos mareales y la salinidad ejercen la misma influencia en la estructura de dos ensamblajes de peces de manglar de regiones biogeográficas distintas, (2) si ensamblajes de peces intermareales en regimes de mareas similares pero hábitats distintos responden de igual manera a los ciclos mareales, (3) si los patrones en la estructura de ensamblajes de peces de manglar causados por los ciclos mareales son estables en el tiempo, y (4) si la historia biogeográfica de las regiones ha jugado un papel en explicar los patrones locales y regionales en la composición taxonómica y funcional de los ensamblajes de estas dos regiones.

Los estudios realizados en canales intermareales de manglar del Pacífico colombiano y el norte de Brasil señalaron la importancia central de los ciclos mareales y diurnos en determinar los patrones de organización y los nichos de los ensamblajes de peces intermareales de manglar. La influencia de estos ciclos también fue notablemente estable en el tiempo (> 10 años). Sin embargo, la importancia de esta influencia entre regiones podría ser regulada por las características topográficas de cada sistema de manglar. En el Pacífico colombiano, los manglares se desarrollan en una zona tectónicamente activa que ocasiona terrenos erosionados. Por ello, casi las mismas extensiones de manglar son inundadas en épocas de mareas vivas y de mareas muertas. Por el contrario, en el norte de Brasil, los manglares se desarrollan en zonas acrecionales donde áreas intermareales mucho más extensas son inundadas durante mareas vivas en comparación con las áreas inundadas durante mareas muertas. Estas características contrastantes pueden ser cruciales en explicar las mayores biomasas de peces intermareales durante mareas vivas encontradas en el norte de Brasil en comparación con la ausencia de una tendencia temporal en el Pacífico colombiano. De igual manera, la salinidad jugo un papel determinante en la estructura de los ensamblajes de peces de ambas áreas. Mientras que canales intermareales localizados en zonas de baja salinidad en el Pacífico colombiano estuvieron dramáticamente empobrecidas en riqueza y biomasa de peces debido a una baja riqueza regional de peces de agua dulce; zonas de baja salinidad en el norte de Brasil presentaron biomasa y riqueza de especies similares a las de zonas de salinidades más altas. Esto es un reflejo de la mayor diversidad de peces de agua dulce capaz de colonizar zonas altas de estuarios en el norte de Brasil. Los

patrones contrastantes encontrados sugieren que la biodiversidad de peces de agua dulce de una región juega un rol significativo en explicar como los gradientes de salinidad afectan estructura comunitaria de peces estuarinos.

Las migraciones intermareales son una característica común de los movimientos de peces de zonas costeras tropicales; sin embargo, la importancia de estos movimientos puede estar determinada por la cantidad de hábitat intermareal disponible para la migración y la distribución de las presas dentro de la zona intermareal. En costas rocosas, las migraciones mareales son realizadas por un alto número de especies de peces, la mayoría de las cuales hacen un uso oportunista de presas localizadas en zonas intermareales bajas. Sin embargo, en manglares intermareales menos especies de peces realizan migraciones intermareales, pero estos movimientos parecen ser más importantes para un mayor número de estas especies, las cuales se alimentan de presas en zonas intermareales altas y bajas.

Los ensamblajes de peces de manglar de la provincia Brasilera (AO) y la provincia Panámica (PO) son igualmente diversos (comprendiendo el 25% de sus respectivas ictiofaunas costeras) y son dominadas generalmente por las mismas familias (Ariidae y Tetraodontidae, ambas pertenecientes al gremio de los carnívoros bentónicos). Sin embargo, las diferencias observadas entre áreas en la representación de otras familias ecológicamente importantes, son probablemente el resultado de la biogeografía histórica y/o el producto de la configuracion del paisaje adyacente a los manglares. Un régimen extremo de precipitación (>7 m año^{-1}) y la falta de un ensamblaje diverso de peces dulceacuícola capaz de colonizar hábitats estuarinos, puede permitir que especies de Centropomidae abunden en el Pacífico colombiano. En contraste, una región menos lluviosa (2-3 m año^{-1}) y un mayor número de especies de origen dulceacuícola (establecido en hábitats estuarinos), podría prevenir la colonización de especies de Centropomidae en habitos estuarinos del norte de Brasil. Por otro lado, un claro ejemplo de la influencia de las características del paisaje adyacente a los manglares es la dominancia de Lutjanidae (una familia asociada a arrecifes) en el Pacífico colombiano y su ausencia en el norte de Brasil. A pesar que ambas áreas son estuarinas, la presencia de fondos rocosos (ausentes en el norte de Brasil) en proximidad de los manglares en el Pacífico colombiano incrementó la ocurrencia de este grupo. Finalmente, la ausencia de Anablepidae en el Pacífico colombiano y su importancia ecológica en el norte de Brasil es un claro ejemplo del efecto de la biogeografía histórica de Centro y Sur América (i.e. la formación del Mar Caribe y cierre del Istmo de Panamá) en la distribución de los peces de manglar de estas áreas.

Los resultados de esta tesis resaltan: (1) la estabilidad temporal y entre regiones de los patrones de organización de peces intermareales de manglar relacionados con los ciclos mareales y diurnos, (2) el gran efecto que pueden causar las condiciones ambientales (e.g. patrón de precipitación) y la configuración del paisaje (e.g. topografía del manglar y la presencia de hábitats adjacentes) en la estructura local de las comunidades de peces de manglar, (3) la importancia diferencial que ciertos hábitats intermareales pueden representar para peces costeros, y (4) la importancia que la biogeografía histórica (de peces de agua dulce y marinos) puede tener para explicar los patrones actuales de distribución de la ictiofauna de manglar en áreas estuarinas del Neotrópico. Considerar estos cuatro aspectos beneficiará nuestro entendimiento del rol de los manglares como hábitats importantes para peces y ayudará en el desarrollo de estudios comparativos adecuados entre diferentes áreas de manglar del mundo. Finalmente, la búsqueda de generalidad en patrones y procesos que expliquen la organización de comunidades de peces de manglar incrementará

nuestra habilidad para manejar de la mejor forma pesquerías que se desarrollan en cercanías a estos ecosistemas.

Palabras clave: ciclos mareales y diurnos, manglares neotropicales macromareales, gradientes de salinidad, estructura comunitaria de peces, Colombia, Brasil, Provincia Panámica, Provincia Brasilera, Atlantico Occidental, Pacífico Oriental

RESUMO

As florestas de mangue são formações predominantes de costas tropicais. Além de proporcionar inúmeros benefícios ambientais e sociais, estes ecossistemas oferecem habitats críticos para juvenis de peixes costeiros, muitos dos quais são alvo da pesca comercial e artesanal. Nosso conhecimento de como as assembleias de peixes de manguezais são organizadas tem sido particularmente voltado para sistemas não estuarinos de micro marés que geralmente não estão sujeitos a forte variação de marés e salinidade (e.g. Mar do Caribe). O objetivo geral deste trabalho foi determinar o papel de filtros ambientais (ou seja, marés e gradientes de salinidade) e biogeografia na estruturação de comunidades de peixes estuarinos de macro marés nos manguezais na região Neotropical. Aqui, é apresentada uma comparação regional e local da estrutura das assembleias de peixes de mangue de duas principais regiões biogeográficas marinhas Neotropicais: o Pacífico Oriental (PO) e o Atlântico Ocidental (AO). Usando dados de campo próprio, adquiridos em três localidades de macro marés dentro dessas regiões (EBM-US: Estuário da Bahia de Málaga e Enseada da Utría, Pacífico colombiano; ES: Estuário do Caeté, Norte do Brasil) e informações publicadas das composições de assembleias de peixes de mangue do Pacífico oriental e do Atlântico ocidental, buscou-se responder as seguintes questões: (1) se as marés e a salinidade exerceram a mesma influência sobre as estruturas dessas duas assembleias de peixes de mangue biogeograficamente isoladas, (2) se as assembleias de peixes entre marés em regimes de marés semelhantes, mas em diferentes habitats (manguezais X costões rochosos) respondem de forma semelhante aos ciclos de maré, (3) se os padrões de maré relacionados à estrutura das assembleias de peixes de mangue entre marés foram estáveis ao longo do tempo, e (4) se a biogeografia histórica desempenhou um papel para explicar os padrões locais e regionais da composição taxonômica e funcional nestas duas regiões.

Os estudos realizados em canais entre marés de mangue no Pacífico da Colômbia e Norte do Brasil indicaram a importância central dos ciclos diuturno e de marés para moldar os padrões de organização em curto prazo, e de nichos para as assembleias de peixes de mangue entre marés. A influência diuturna e das marés sobre a estrutura das assembleias de peixes também foi notavelmente estável ao longo do tempo (> 10 anos). A importância de tais influências sobre escalas geográficas, no entanto, podem ser reguladas pelas características topográficas de cada sistema de manguezal. Os manguezais do Pacífico colombiano estão localizados em uma área tectonicamente ativa, produzindo um terreno de erosão onde extensões quase iguais de áreas entre marés são inundadas durante as marés de sizígia e marés de quadratura. Entretanto, o Norte do Brasil apresenta manguezais de agregação onde maiores áreas entre marés são inundadas nas marés de sizígia do que em marés de quadratura. Estas características contrastantes foram cruciais para explicar uma maior biomassa de peixes entre marés durante as enchentes no Norte do Brasil e a ausência de tendências temporais consistentes no Pacífico colombiano. Da mesma forma, a salinidade desempenhou um papel determinante na estruturação das assembleias de peixes em ambas as áreas. Considerando que a baixa salinidade dos canais de maré no Pacifico colombiano reduzem drasticamente a riqueza e biomassa de peixes, como consequência de uma fauna pobre de peixes dulcícolas. Os canais de maré de baixa salinidade no Norte do Brasil foram igualmente ricos em espécies e biomassa, quando comparados ao aumento de salinidade dos canais de maré, refletindo uma maior diversidade de peixes de água doce capazes de colonizar o curso superior dos estuários na última área. Esses padrões contrastantes sugerem que a biodiversidade de peixes de água doce e biogeografia têm um papel significativo na explicação dos gradientes de salinidade relacionados na estrutura da comunidade de peixes estuarinos.

Migração entre marés é uma característica comum da área de vida de peixes costeiros tropicais, mas a importância relativa de tais movimentos para essas assembleias pode ser determinada pela quantidade de habitats entre marés disponíveis para migração e pela disponibilidade de presas dentro da zona entre marés. Em costões rochosos, as migrações de maré são realizadas por um grande número de espécies de peixes, onde a maioria faz uso oportunista de presas localizadas em áreas baixas entre marés. Em áreas entre marés de manguezais, no entanto, poucas espécies de peixes realizam migrações, mas esses movimentos parecem ter uma importância proporcionalmente maior para um maior número de espécies de peixes que se alimentam em ambas as áreas (altas e baixas) entre marés.

As assembleias de peixes de mangue do Brasil e das províncias Panâmicas são igualmente diversas (compreendendo cerca de 25% do total de suas respectivas faunas de peixes costeiros) e são geralmente dominadas pelas mesmas famílias de peixes (Ariidae e Tetraodontidae, ambos alimentando-se principalmente de invertebrados bentônicos). No entanto, as diferenças na representação de outras famílias ecologicamente importantes entre as zonas é provável que reflita os processos biogeográficos históricos e/ou o produto de configurações de paisagem marinha específicas que beneficiam a presença de famílias específicas de peixes. Um regime de precipitação extrema (> 7m ano^{-1}) e a falta de um diversificado conjunto de peixes de água doce capaz de colonizar habitats estuarinos pode permitir que espécies de Centropomidae prosperassem no Pacífico colombiano. Em contraste, uma área com menos chuva (2-3m ano^{-1}) e um maior número de espécies de origem de água doce (bem estabelecida em habitats estuarinos), pode impedir a colonização destes habitats por Centropomidae no Norte do Brasil. Um exemplo claro da influência das características da paisagem marinha em assembleias de peixes de mangue, foi o domínio de Lutjanidae (uma família associada a recifes de coral), no Pacífico colombiano e sua ausência no Norte do Brasil. Apesar de ambas as áreas serem estuarinas, a presença de fundos rochosos entre mares nas proximidades de manguezais no Pacífico colombiano (que estão ausentes no Norte do Brasil) aumentou a ocorrência deste taxa. Finalmente, a ausência de Anablepidae no Pacífico colombiano e sua importância ecológica no Norte do Brasil foi um exemplo claro do efeito da história biogeográfica das Américas Central e do Sul (ou seja, a formação do Mar do Caribe e o fechamento do Istmo do Panamá) na distribuição de peixes de mangue existentes nessas áreas.

Dos resultados desta tese destacam-se (1) a estabilidade no tempo e em todas as regiões dos padrões de maré e diários relacionados à distribuição dos peixes de mangue entre marés em áreas de macro marés Neotropicais, (2) o efeito principal que as condições ambientais específicas (e.g regime de chuvas) e paisagem marinha (e.g topografia do manguezal e habitats adjacentes) podem produzir na estrutura da comunidade de peixes local, (3) a variação da importância que distintos habitats tropicais entre marés podem ter para peixes costeiros, e (4) a importância que a biogeografia histórica (peixes de água doce e marinhos) pode ter para explicar os padrões atuais de distribuição da fauna de peixes de mangue em áreas estuarinas da região Neotropical. Tomando esses quatro aspectos em consideração, aumentaremos nossa compreensão global do papel dos manguezais como habitats importantes para peixes e esta informação poderá ajudar no desenvolvimento de estudos comparativos entre áreas de manguezais do mundo. Em última análise, a busca pela generalidade dos padrões e processos que explicam a organização das comunidades de peixes de mangue poderá aumentar a nossa capacidade de gerir melhor as pescarias associadas aos manguezais.

Palavras-chave: ciclos de maré e Diel, manguezais macromaré neotropicais, gradientes de salinidade, estrutura de comunidade de peixes, Colômbia, Brasil, província Panamica, Província do Brasil, Atlântico Ocidental, Pacífico Oriental

ZUSAMMENFASSUNG

Mangrovenwälder sind charakteristisch für tropische Küsten. Neben zahlreichen Vorteilen für Umwelt und Gesellschaft stellen diese Ökosystem auch entscheidende Habitate für juvenile Fische dar, von denen viele das Ziel kommerzieller und artisanaler Fischerei sind. Unser Wissen über die Organisation von Fischgemeinschaften in Mangroven beschränkte sich bisher auf mikrotidale Nicht-Ästuar-Systeme, die generell geringeren Schwankungen von Tiden oder Salinität ausgesetzt sind (z.B. Karibisches Meer). Das übergreifende Ziel dieser Arbeit ist es, die Rolle von Umweltfaktoren (z.B. Tiden und Salzgehaltsgradienten) und Biogeographie auf die Strukturierung von ästuaren makrotidalen Mangrovenfischgemeinschaften in den Neotropis zu untersuchen. Meine Arbeit vergleicht die regionalen sowie lokalen Strukturen von Mangrovenfischgemeinschaften aus zwei bedeutenden biogeographischen Regionen der Neotropis: Der Östliche Pazifik (ÖP) und der Westliche Atlantik (WA). Unter Verwendung von eigenständig gesammelten Daten aus drei Orten innerhalb dieser Regionen (ÖP: Bahía Málaga Ästuar und Utría Meerenge, Kolumbianischer Pazifik; WA: Caeté Ästuar, Nord-Brasilien), sowie bereits veröffentlichter Informationen über die Zusammensetzung von Mangrovenfischgemeinschaften im Östlichen Pazifik und Westlichen Atlantik, habe ich insbesondere versucht zu beantworten: (1) Ob Tiden und Salinität einen Einfluss auf diese zwei biogeographisch isolierten Mangrovenfischgemeinschaften ausüben, (2) ob intertidale Fischgemeinschaften in ähnlichen Gezeitensystemen, aber in unterschiedlichen Habitaten (Mangroven vs. Felsenküste), ähnlich auf Tidenkreisläufe reagieren, (3) ob von den Gezeiten beeinflusste Muster in der Struktur von intertidalen Mangrovenfischgemeinschaften über die Zeit stabil bleiben und (4) ob die historische Biogeographie für die Erklärung von lokalen und regionalen Mustern der taxonomischen und funktionellen Zusammensetzung in diesen zwei Regionen eine Rolle spielt.

Die präsentierten Studien, die in intertidalen Magrovenprielen im Kolumbianischen Pazifik und im Norden Brasiliens durchgeführten wurden, zeigen die zentrale Wichtigkeit von Tidenzyklus und Tageszeit für die Formung von kurzzeitigen Mustern in der Organisation und den Nischen von Mangrovenfischgemeinschaften in der Gezeitenzone. Es wurde gezeigt, dass der Einfluss der Faktoren Tide und Tageszeit auf die Struktur von Fischgemeinschaften über einen Zeitraum von über zehn Jahren äußerst stabil war. Die Wichtigkeit dieser Einflüsse ist jedoch, gemessen an biogeographischem Maßstab, vermutlich von den topographischen Eigenschaften eines jeden Mangrovensystems abhängig. Mangroven im Kolumbianischen Pazifik befinden sich in einem tektonisch aktiven Gebiet mit einem entsprechend erodierenden Boden in dem die Gezeitenzone bei Spring- und Nippflut zu nahezu gleich großem Ausmaße überflutet sind. Im Gegensatz hierzu sind die Mangroven im Norden Brasiliens stärker wachsend (bzw. ansteigend), so dass bei Springflut deutlich größere intertidale Gebiete überflutet werden als bei Nippflut. Unter Berücksichtigung dieser Unterschiede lässt sich die größere Fischbiomasse in der Gezeitenzone während Springtiden in Nord-Brasilien sowie das Fehlen von beständigen zeitlichen Trends im Kolumbianischen Pazifik erklären. Ebenso spielte in beiden Regionen die Salinität eine wichtige Rolle für die Strukturierung von Fischgemeinschaften. Im Pazifischen Kolumbien wiesen Priele mit niedriger Salinität eine dramatisch niedrigere

Artenvielfalt auf, was eine artenarmere Süßwasser-Fischfauna wiederspiegelt. Im Gegensatz hierzu waren im Norden Brasiliens Priele mit niedriger Salinität gleichermaßen artenreich wie solche mit hohem Salzgehalt, was die größere Diversität von Süßwasserfischen wiederspiegelt, denen es möglich ist, den oberen Teil der Ästuare zu besiedeln. Diese gegensätzlichen Beobachtungen zeigen, dass die Biodiversität von Süßwasserfischen und die Biogeographie der entsprechenden Region sehr wichtig sind, um salinitätsbedingte Gradienten in der Zusammensetzung von ästuaren Fischgemeinschaften zu erklären.

Migrationen in der Gezeitenzone gehören zu allgemeinen Verhaltensweisen tropischer Küstenfische. Die relative Bedeutung solcher Bewegungen für die entsprechenden Gemeinschaften hängt jedoch auch von der Größe des für die Migration und Verteilung von Nahrungsressourcen zur Verfügung stehenden intertidalen Habitats ab. Durch Gezeiten bedingte Wanderbewegungen werden an Felsenküsten von einer großen Anzahl von Fischarten unternommen, die opportunistischen Gebrauch von im Gezeitenbereich befindlichen Beuteressourcen machen. Im Vergleich hierzu führen in intertidalen Mangrovenwäldern weniger Fischarten solche Migrationen durch, obwohl diese Bewegungen dort eine größere Bedeutung für eine verhältnismäßig größere Anzahl an Fischarten hat, die sowohl im unteren als auch oberen Teil der Gezeitenzone nach Futter suchen.

Mangrovenfischgemeinschaften der Brasilianischen und Panameischen Domäne sind gleichermaßen vielfältig (sie enthalten jeweils etwa 25% der entsprechenden Küsten-Fischfauna) und werden generell von den gleichen Fischfamilien (Ariidae und Tetraodontidae, beide ernähren sich hauptsächlich von benthischen Invertebraten) dominiert. Dennoch gibt es zwischen beiden Regionen Unterschiede im Auftreten von anderen ökologisch wichtigen Familien. Dies wurde höchstwahrscheinlich durch historische biogeographisce Prozesse und/oder durch spezifische topographische Beschaffenheiten verursacht, die das Vorkommen bestimmter Fischfamilien begünstigen. Im Kolumbianischen Pazifik sind vermutlich das extremes Niederschlagsregime (> 7m Jahr^{-1}) und die Abwesenheit einer diversen Süßwasserfischgemeinschaft, die in der Lage wäre ästuare Habitate zu besiedeln, dafür verantwortlich, dass Arten der Familie Centropomidae erfolgreich sind. Im Gegensatz hierzu wird in Nordbrasilien die Kolonisierung dieser Habitate durch weniger Regen (2-3m Jahr^{-1}) und einer größeren Anzahl Arten mit Süßwasserursprung (die in ästuaren Habitaten gut etabliert sind) verhindert. Ein deutliches Beispiel des Einflusses von Landschaftsbeschaffenheiten auf Mangrovenfischgemeinschaften zeigte sich bei der mit Riffen assoziierten Fischfamilie Lutjanidae, die im Kolumbianischen Pazifik dominierten, während sie im Norden Brasiliens abwesend waren. Denn obgleich beide Gebiete Ästuare sind, so sind nur in Kolumbien in direkter Umgebung der Mangroven subtidale Felsenböden zu finden, welche das Vorkommen dieser Taxa unterstützen. Außerdem war die Abwesenheit der Familie Anablepidae im Kolumbianischen Pazifik und deren ökologische Wichtigkeit im Norden Brasiliens ein deutliches Beispiel für die Auswirkung von der biogeographischen Entwicklung Zentral- und Südamerikas (insb. die Entstehung des Karribischen Meeres und die Schließung der Landbrücke von Panama) auf die Verteilung von rezenten Mangrovenfischen dieser Regionen.

Die Ergebnisse dieser Arbeit zeigen deutlich (1) die Stabilität, sowohl zeitlich als auch Regionen-übergreifend, der durch Tiden oder tageszeitahängige Faktoren beeinflussten Muster von in der Verbreitung von intertidalen Mangrovenfischen in makrotidalen Regionen der Neotropis, (2) den bedeutenden Einfluss, den spezifische Umweltbedingungen (z.B. Niederschlagsregime) und Landschaftsbeschaffenheiten (z.B. Mangroventopographie oder

angrenzende Habitate) auf die Struktur lokaler Fischgemeinschaften haben können, (3) die variierende Wichtigkeit von charakteristischen tropischen Habitaten in der Gezeitenzone für Küstenfischen und (4) die Bedeutung, die die historische Biogeographie (von Süß- und Salzwasserfischen) für die Erklärung von aktuellen Verbreitungsmustern der Mangrovenfischfauna in Ästuaren der Neotropis haben kann. Unter Berücksichtigung dieser vier Aspekte wird unser globales Verständnis von der Funktion der Mangroven als wichtiges Habitat für Fische verbessert, sowie die Entwicklung aussagekräftiger vergleichender Studien zwischen verschiedenen Mangrovengebieten gefördert. Letzendlich werden Kenntnisse allgemeingültiger Muster und Prozesse, die die Organisation von Mangrovenfischgemeinschaften erklären, unsere Fähigkeit unterstützen, angemessene Management-Strategien für die von Mangroven abhängige Fischerei zu entwickeln.

Schlüsselwörter: Tidenzyklus, tageszeitabhängige Zyklen, neotropische makrotidale Mangroven, Salzgehaltgradienten, Fischgemeinschaften-Struktur, Kolumbien, Brasilien, Panamaische Domäne, Brasilianische Domäne, Westlicher Atlantik, Östlicher Pazifik

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Chapter I. General Introduction

1.1 What determines patterns of biological community structure?

The distribution of biological communities and their local diversity can be explained by the interplay of ecological, biogeographical and evolutionary processes (Ricklefts 1987). Five main factors have been proposed to explain the distribution of a clade (group of species including ancestors and descendants): (1) the ecological niche of the ancestor, (2) the geographical origin of dispersal, (3) limitations to dispersal introduced by the environment (abiotic factors) and other species (e.g. competition), (4) opportunities for niche evolution of individual species and (5) the amount of time during which niche evolution and dispersal could occur since the origin of the clade (Wiens & Donoghue 2004).

Despite this explanation being widely accepted, the fields of ecology and biogeography have been somewhat isolated for decades. This may be due to the fact that these disciplines have traditionally focused on different temporal and spatial scales. Whereas biogeography usually deals with regional and global spatial scales and temporal scales of thousands to millions of years, ecology usually treats problems at regional and local scales, and temporal scales spanning generation times to populations' cycles (Figure 1; Jenkins & Ricklefs 2011). In recent times, the unification of these two fields has become a prolific laboratory where new approaches and insightful theories have been developed (e.g. phylogenetic community ecology, Webb et al. 2002)

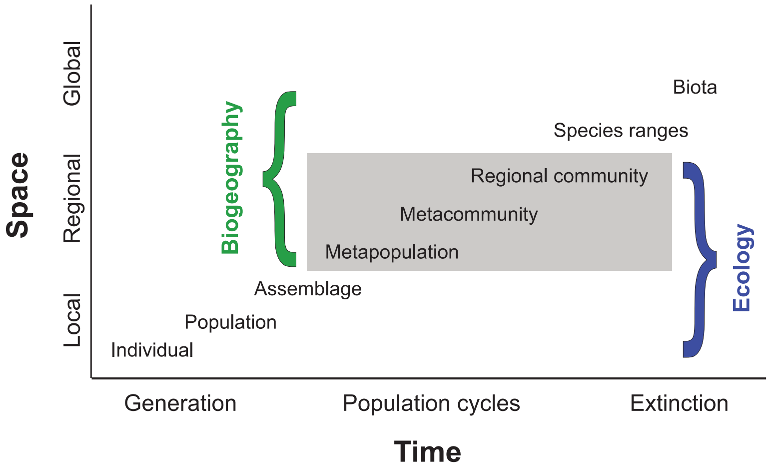


Figure 1. Spatial and temporal overlap of the fields of biogeography and ecology (adapted from Jenkins & Ricklefs 2011).

It is now recognized that the structure of biological communities can differ depending on ecological mechanisms, such as competition or constraints imposed by the abiotic setting (environmental filters), but it also depends on the evolutionary history of species determining the distribution of species characteristics in a given phylogeny (Mouquet et al. 2012). On one side, species' ecological niches or traits can be preserved along evolutionary time scales (niche conservatism) resulting in closely related species having higher ecological similarity than expected by chance. On the other hand, species' ecological niches can also be determined by environmental filters, which are thought to be contemporary processes. The strength of ecological and evolutionary mechanisms in determining community structure has proven to vary among taxa (Leibold et al. 2010).

The community structure of mangrove fish assemblages has been examined in the literature predominantly with respect to the influence of environmental filters acting on ecological (short) time scales. However, the effect that biogeographical and evolutionary processes can have on the community structure of these assemblages has been rarely acknowledged. Neotropical mangrove fishes in estuarine macrotidal areas constitute an appropriate system to investigate the relative importance of biogeography and the effect of environmental filters (e.g. salinity gradients) for the assembly rules of these communities. Disentangling the strength of these forces is fundamental to understand how these ecologically and economically important communities are structured and how they can cope with current and expected natural and anthropogenic stressors impacting these ecosystems.

1.1.1 Environmental drivers of structural changes in fish communities from macrotidal coasts

Tides

Life in the sea has evolved in the presence of numerous environmental cycles spanning short and long time periods. Over millions of years, marine organisms have synchronized many aspects of their biology to day-night, tidal, lunar and semi-lunar cycles, resulting in a variety of biological rhythms which are triggered by external stimuli (e.g. changes in light or pressure) related to the recurrent cycles of the sun or the moon (Table 1; Tessmar-Raible et al. 2011).

Circatidal rhythms and clocks are those controlled by the periodic rise and fall of water in the Ocean. Marine organisms, especially those living in coastal and estuarine habitats, modulate their behavior according to this periodic water movement, which occur in most coastlines at intervals of 12.4 hours (semi-diurnal tides). Additional to this cycle, tidal amplitudes change over the lunar cycle producing maximum (spring) and minimum (neap) tidal amplitudes approximately every 15 days. These varying environmental conditions provide stimuli to which marine organisms have adapted. Superimposed to the circatidal rhythms, circadian oscillators (day-night cycle) also affect the behavior of organisms creating a complex combination of cues to which organisms react (Wilcockson & Zhang 2008).

Table 1. Biological rhythms and environmental cycles associated to solar or lunar influences. Adapted from Tessmar-Raible et al. (2011).

Influence	**Biological rhythm**	**Environmental cycle**	**Cycle length**
Sun	Circadian	Daily	24 hours
	Annual / seasonal	Annual	365 days
Moon	Circalunar	Lunar*	29.5 days
	Circasemilunar	Semilunar	14.8 days
	Circatidal	Tidal	12.4 hours

* Synodic lunar period

Tides can be diurnal, semi-diurnal or mixed, depending on how often per day the rise and fall of the tide occurs. Semi-diurnal tides occur when tides fall and rise twice per day. In diurnal tides, rise and fall occur only once per day and in mixed tides, the magnitude of the high and low tide contains elements of both semi-diurnal and diurnal cycles.

Tidal magnitude varies along time, usually with spring tides (increased range) occurring when the Earth, Moon and Sun are aligned (new or full Moon), whereas neap (reduced range) tides take place when the Sun and the Moon are aligned at right angles from the Earth (first and third quarter phases). There is normally a one or two days delay between the effect of the tide and the lunar phase. Due to differences in the duration of the diel cycle and the lunar day period (24 h 50 min), there is a constant delay in the occurrence of the next tidal cycle. Therefore, one may argue that each tidal cycle is unique and cannot be replicated (Krumme 2009).

The complexity inherent to tidal forces in the Ocean implies that most marine organisms adjust their biological rhythm according to this major environmental force. Therefore, marine organisms synchronize their internal molecular clocks to two interacting major forces: the tidal and the diel cycle. These two forces constitute the two main oscillators in the marine environment and organisms have adapted to these cycles for millions of years (Palmer 2000, Tessmar-Raible et al. 2011).

Remarkably, it is the intertidal area where the daily tidal oscillation (low and high tide) has the greatest influence on organisms. Intertidal migrations by crustacean, fishes and even birds have been documented in a variety of shallow water ecosystems (see review in Gibson 2003). In the specific case of fish, intertidal migrations are thought to benefit organisms by maximizing food acquisition and minimizing predation. Many intertidal areas (e.g. mangroves, rocky shores, mudflats) are rich in prey items that are easily accessible at high tide. At the same time, the relatively shallow environment in intertidal areas may restrict the access to large predators, thereby benefiting fish by reducing predation risks in intertidal areas at high tide. Intertidal migrations thus form a fundamental part of the home-range movements of a whole range of shallow water organisms (Pittman & McAlpine 2003).

Despite the combination of tidal and diel cycles being a fundamental force regulating the movement behavior of coastal fishes, surprisingly little is known about how this force regulates the organization of fish assemblages in tropical shallow ecosystems. Information regarding the influence of tides and diel cycles on fish communities can be valuable to spatial zoning within protected areas, designing representative monitoring programs and understanding the reproductive and feeding patterns of commercially important fisheries resources.

Fish migration strategies into intertidal mangroves are species-specific and the general community composition can be variable throughout the tidal cycle (Ellis & Bell 2008). Over larger temporal scales (spring vs neap tide cycles), the magnitude (fish biomass) of fish migrations can dramatically vary. At spring tides, for example, fish biomass in intertidal mangroves can be significantly higher than at neap tides (Laegdsgaard & Johnson 1995, Krumme et al. 2004). Not only the fish biomass but also the feeding activity of fish visiting intertidal mangroves is affected during spring-neap tide cycles (Brenner & Krumme 2007, Krumme et al. 2008). At spring tides, larger intertidal habitats and preys are available for fish and predation can be maximized compared to neap tide conditions where less foraging area is available.

In combination with the diel cycle, tides (meso- and macro-tides) provide different environmental conditions for fish when migrating to intertidal habitats. This is due to the different duration of the tidal and diel cycles. Fish migrating to intertidal areas at spring tides will experience different environmental conditions (e.g. light intensity, temperature) compared to fish migrating at neap tides (Krumme 2009). These different conditions translate into different fish assemblages migrating to macrotidal mangrove intertidal habitats with a specific tide-time of the day combination (e.g. in northern Brazil; Krumme et al. 2004). Despite tides and diel cycles significantly influencing the structure of fish communities, sometimes even more than seasonal changes (Krumme & Saint-Paul 2010), little is known about the effects of these factors in different tropical localities with similar tidal regimes. Testing these patterns across geographical boundaries is especially relevant considering the need to understand how mangrove nursery function varies over large spatial scales.

Salinity

The role of salinity as a major force structuring the distribution of estuarine organisms has been investigated for ca. 80 years (see Redeke 1932, Remane 1934). Initial work was carried out in temperate regions (e.g. North Sea) and further extended to tropical regions of Australia (Cyrus & Blaber 1992; Sheaves 1998). Remane (1934) illustrated with a conceptual model how species diversity changed along a salinity gradient in estuarine areas of the Baltic Sea. This conceptual model proposed that the number of freshwater and marine species decreases as transitional (estuarine) waters are approached. Brackish species then inhabit these transitional waters. This conceptual model has been used and misused sometimes extrapolating its application to other geographical areas where it may not apply (see review in Whitfield et al. 2012).

In particular, the role of salinity in shaping the organization patterns of estuarine mangrove fish assemblages has been investigated at least since the early 80's (see Blaber & Blaber 1980). Opposing conclusions have been reached, on one side, by authors that argue that salinity is not a main factor affecting the distribution of tropical estuarine and mangrove fishes (e.g. Pinto 1987, Blaber & Blaber 1980); and on the other side authors that point at salinity as a major driver of changes in community organization in these assemblages (Yañez-Arancibia et al. 1980, Lorenz & Serafy 2006). It is now clear that apart from salinity, other environmental factors that can be correlated or not to salinity, can exert an influence on the community structure of mangrove fishes. Factors such as the precipitation regime, the ENSO phenomenon, landscape configuration and biogeography (of fresh and marine fishes) can determine the patterns of organization in these communities at different temporal and spatial scales. Although the search for generality of patterns in ecology is a primary objective (Beck 1997), care should be taken when generalizing patterns found in one mangrove system to others in a different geographical area (e.g. Barletta et al. 2010). Particularly, mangrove systems from different regions may present different landscapes and biogeographical histories that together with abiotic factors, such as salinity, could lead to different fish community organization patterns.

1.2 The Neotropics

The Neotropics encompass the tropical areas of the American continent (from Mexico), including the Islands in the Caribbean, and the temperate part of southern South America (until southern Brazil). This ecoregion was part of the Gondwana paleocontinent until ca. 100 Ma, when the South American and African plates completely diverged (Schultz 2005). Currently, the Neotropics occupy three tectonic plates: the North American, South American and the Caribbean. The ecoregion has experienced a number of major tectonic events that include the emergence of the Andes and the closure of the Isthmus of Panama that have had influences on the biogeography of both marine and terrestrial biota.

1.2.1 Marine Biogeographical Provinces of the Neotropics

In a recent review of the marine biogeographical provinces of the world, Briggs & Bowen (2012) identified five warm regions (encompassing tropical and warm temperate waters): Eastern Atlantic, Western Atlantic, Western Pacific, Tropical

Indo-West Pacific and Eastern Pacific regions. Two of these regions, namely the Western Atlantic and the Eastern Pacific are located in the American continent. The Western Atlantic is further subdivided into four provinces: Carolina, Caribbean, Brazilian and Argentinian, whereas the Eastern Pacific region is subdivided into the California, Cortez, Panamian, Galapagos, Peru-Chilean and Juan Fernández. There are only two tropical provinces in the Western Atlantic: the Caribbean and the Brazilian province. In the case of the Eastern Pacific, the tropical provinces are the Cortez, Panamian and Galapagos provinces (Robertson & Cramer 2009). The Caribbean province includes Bermuda and the southern portion of Florida and extends to the Amazon River. The Brazilian province extends from the mouth of Amazon River south to 28-32° S, and the Tropical Eastern Pacific extends from Magdalena Bay on Baja California (~ 25° N), Mexico to the southern shore of the Gulf of Guayaquil (~ 4° S in northern Peru; Figure 2).

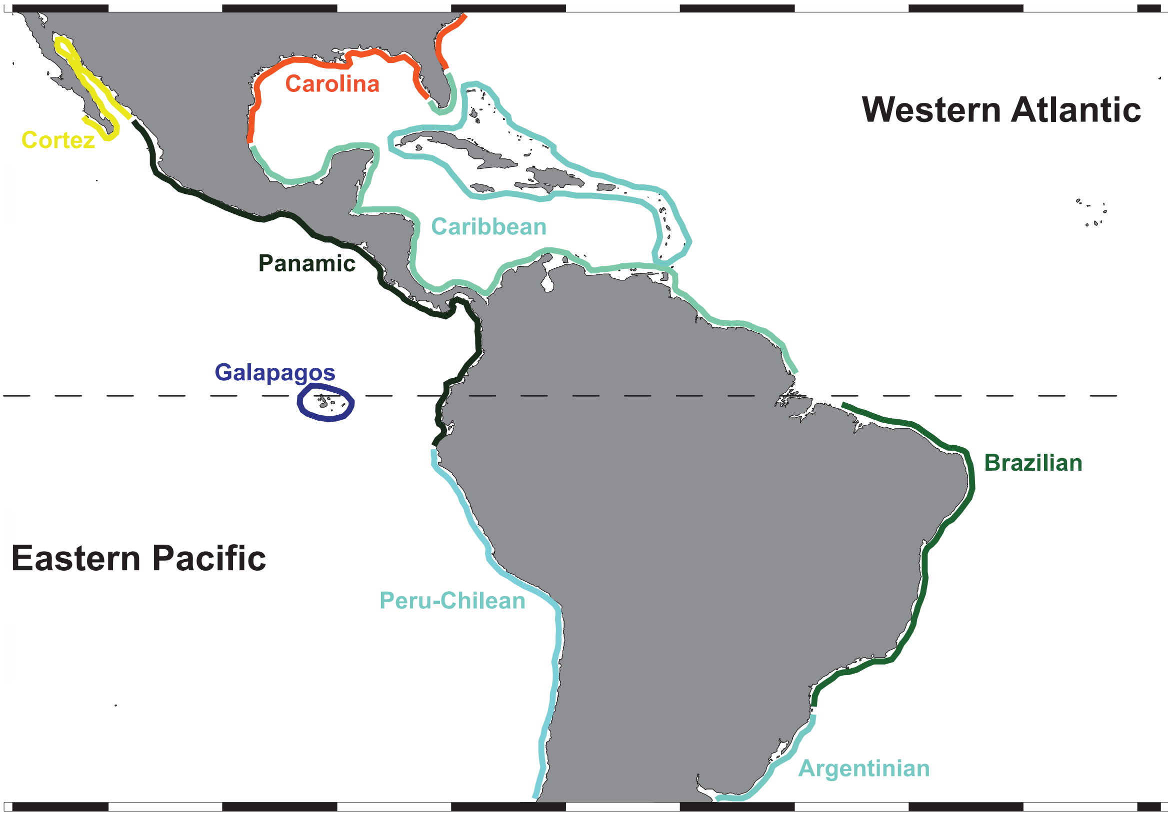


Figure 2. Map of the marine biogeographic regions in the Neotropics according to Briggs & Bowen (2012).

Processes of isolation and vicariance (emergence of a geographical barrier to dispersal and gene flow) occurring over geological timescales can largely explain the current arrangement of marine biogeographical provinces in the Neotropics. Five major barriers exist nowadays, separating the Neotropics from the principal marine center of speciation, i.e. the Indo-West Pacific region (Bowen et al. 2013). The first barrier started to form ca. 84 Ma, when South America and Africa began to separate.

At present, the distance separating both continents is > 3500 km (Mid-Atlantic Barrier) and restricts the exchange of organisms between both areas. A second barrier was formed ca. 12-18 (14) Ma, with the uplift of the Red Sea land bridge. This event closed the Tethys Seaway and separated the tropical faunas from the Indian Ocean and the Atlantic and Eastern Pacific. A third barrier, the Amazon-Orinoco plume, originating in the South American continent, divided and restricted the exchange of some marine fauna (i.e. coral reef organisms) between the Greater Caribbean and the Brazilian provinces ca. 11 Ma (Figueiredo et al. 2009). During the whole Cenozoic, the Eastern Pacific Barrier, a 5000 km deep open Ocean separating Clipperton Island (the westernmost Island of the region) from the Line Islands in the Central Pacific (Grigg & Hey 1992) has blocked dispersal of marine taxa between the Western and the Eastern Pacific (but see Robertson & Lessios 2004). Finally, the closure of the Isthmus of Panama from the late Eocene to the late Miocene times ca. 38-9 Ma (Montes et al. 2012, but see Coates et al. 2004 for a later closure date hypothesis), constitutes the most recent barrier in the Neotropics isolating the Caribbean Sea from the Eastern Pacific Ocean (Figure 3). Before the closure of the Isthmus during the Oligocene-Miocene epochs, marine biota from the eastern-most part of Brazil to Esmeraldas in Ecuador, including the Greater Antilles and the Panama's island arc, were considered so related to be defined as the Miocene Caribbean faunal province (Landau et al. 2008, Leigh et al. *in press*).

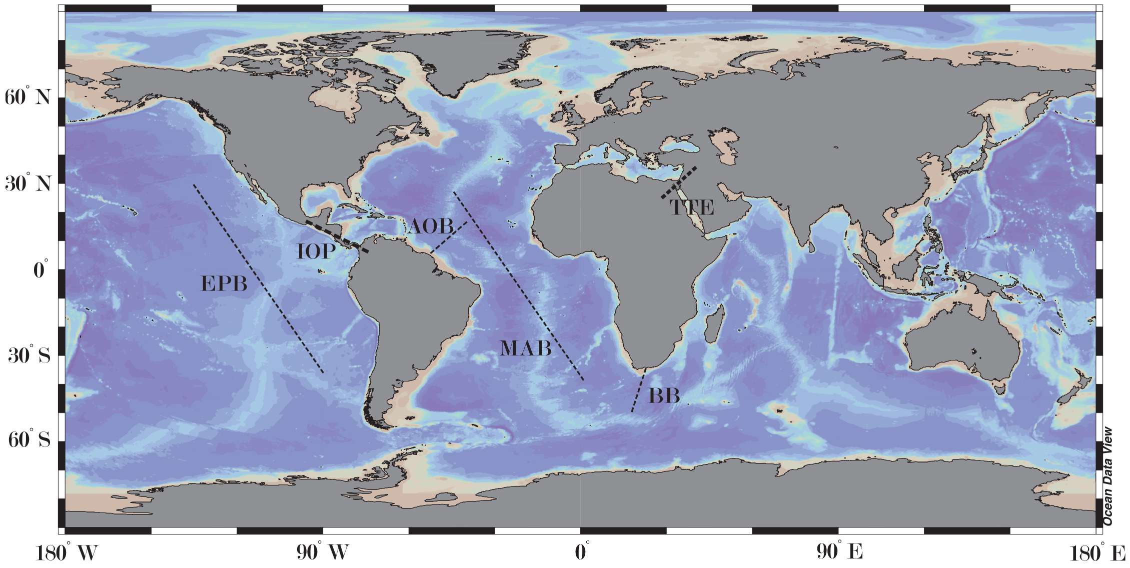


Figure 3. Major biogeographical barriers separating the marine regions of the Neotropics. EPB = Eastern Pacific Barrier, IOP = Isthmus of Panama, AOB = Amazon Orinoco Barrier, MAB = Mid Atlantic Barrier, TTE = Terminal Tethyan Event BB = Benguela Barrier (modified after to Luiz et al. 2012).

1.2.2 Coastal fish fauna in the Neotropics

The tropical portions of the Eastern Pacific and Western Atlantic contain relative species-poor assemblages of coastal fishes compared to the extremely speciose assemblages characterizing the Indo-West Pacific region, the latter being widely recognized as the center of marine biodiversity in the World (Carpenter & Springer 2005). Compared to the ca. 3000 coastal fish species that can be found there, each of the Caribbean and Brazilian provinces and the Tropical Eastern Pacific region contain no more than 1500 shore fish species (Zapata & Robertson 2007, Miloslavich et al. 2010, Miloslavich et al. 2011). Hypotheses for this longitudinal pattern include a more complex tectonic history in the Indo-West Pacific facilitating allopatric speciation and greater habitat availability in this region (Sanciangco et al. 2013).

Most of the knowledge of biogeographic structure of fishes in the Neotropics and the world comes from examples of reef fishes (e.g. Hastings 2000, Floeter et al. 2008). The biogeographic structure of coastal fish assemblages, however, can vary according to the specific habitat requirements, dispersal capabilities and traits of fish species. Whereas reef fish may have discontinuous distributions due to the inability to cross barriers that challenge their ecological requirements (e.g. the Amazon-Orinoco Plume in the Western Atlantic, Luiz et al. 2013), estuarine soft-bottom fishes may be able to cross such barriers due to their ecological characteristics not adversely affected by transitional waters. Thus, identifying concordance in the biogeographical structure between reef and estuarine soft-bottom fishes may prove valuable in identifying which mechanisms and barriers apply to a larger group of marine organisms and which apply to specific groups. To date, no comprehensive comparisons exist that allows documenting the biogeographical structure of soft-bottom estuarine or mangrove fish in the neotropical region.

1.2.3 Mangrove ecosystems in the Neotropics

Mangroves appeared between the end of the Cretaceous and the beginning of the Paleogene in the Tethys Sea ca. 66 Ma. Most genera evolved in this period and were widespread around the Tethys Sea in the late Eocene epoch. During this time until the late Miocene, when the connection between the Indo-West Pacific and the Atlantic closed, mangrove dispersal took place from east to west. After the Miocene, the distribution of extant mangrove species could be explained by vicariance events and differential extinctions due to changes in regional and local environmental conditions (Ellison et al. 1999). In the Neotropics, the most important vicariance event can be considered to be the closure of the Isthmus of Panama. This event has also influenced the present distribution of mangroves in this region (Dodd et al. 2002, Cerón-Souza et al. 2010). The predominant mangrove genus in the region is *Rhizophora*, which has dominated the vegetation of these ecosystems at least since the middle Eocene epoch (Cerón-Souza et al. 2010).

The number of mangrove tree species in the Neotropics is low compared to the Indo-West Pacific region. No more than 10 species can be observed in a single area of the Neotropics compared to places in the Indo-West Pacific where more than 30 tree species can co-exist in a given estuary. Currents largely influence the distributional limits of mangroves in the Eastern Pacific and the Western Atlantic.

Consequently, mainly the cold Humboldt Current determines the southernmost limit of mangrove distribution in the Eastern Pacific, which is located in northern Peru (Piura River, 5°30'S). Similarly, the southernmost limit of mangrove distribution in the Western Atlantic is at 28° 30'S in Santa Catarina, Brazil (Schaeffer-Novelli et al. 2000), where warm coastal waters are still present due to the southward flowing Brazilian western boundary Current (Woodroof & Grindrod 1991).

Mangroves in the Americas (Tropical Eastern Pacific and Western Atlantic) cover ca. 4.5 million ha, representing 29% of the global mangrove extension estimate (Lacerda 2002). The largest extensions of mangroves in the Neotropics are those in the Western Atlantic (ca. 2.52 million ha), followed by those in the Eastern Pacific (ca. 1.21 million ha) and the Caribbean (ca. 0.81 million ha; Lacerda 2002). Notably two regions within the Neotropics harbor extensive mangrove areas with a high degree of structural development (i.e. basal areas) and remain relatively undisturbed: the Panama Bight mangroves in the Tropical Eastern Pacific and the Guianan-Amazon Mangroves in the Western Central Atlantic (Olson & Dinerstein 2002). The Panama Bight mangroves spanning over the Pacific coasts of Panama, Colombia and Ecuador and once called by West (1956) as "the most luxuriant tidal forest of the World" contains localities where the maximum mangrove tree species richness in the Neotropics is found (ca. 10 species). Comparably representative of the Neotropical mangroves are the Guianan-Amazon Mangroves region, which covers the coasts of Brazil, French Guiana, Suriname, Trinidad and Tobago and Venezuela including the mouths of the Amazon and Orinoco rivers. Within this region the largest continuous mangrove belt of the World (7424 km^2), is found (Amazonian Macrotidal Mangrove Coast). This belt extends from the Marajó Bay east of the Amazon River mouth to the São José Bay, Maranhão (Nascimento Jr et al., 2013)

Mangroves in these two regions of the Neotropics can be considered as the predominant features of the coastal landscapes (Figure 4). Coral reefs are absent primarily due to the high river discharge occurring in these areas, linked to relatively high precipitation regimes. Furthermore, macrotides (tidal range ~ 4 m) are present in large areas of both regions. Consequently, the environmental conditions in the Panama Bight and the Guianan-Amazon mangroves are sharply in contrast to those present in the Caribbean Sea mangroves where these ecosystems develop in close connection with coral reefs and where tides are negligible (tidal range ~ 50 cm). A determinant feature that distinguishes mangroves from the Panama Bight and the Guianan-Amazon is their geological history: whereas the Panama Bight mangroves are located in a tectonically active zone (leading edge coast), the Guianan-Amazon mangroves are located in a passive not very active tectonic margin (trailing edge coast, Pilkey 2006).

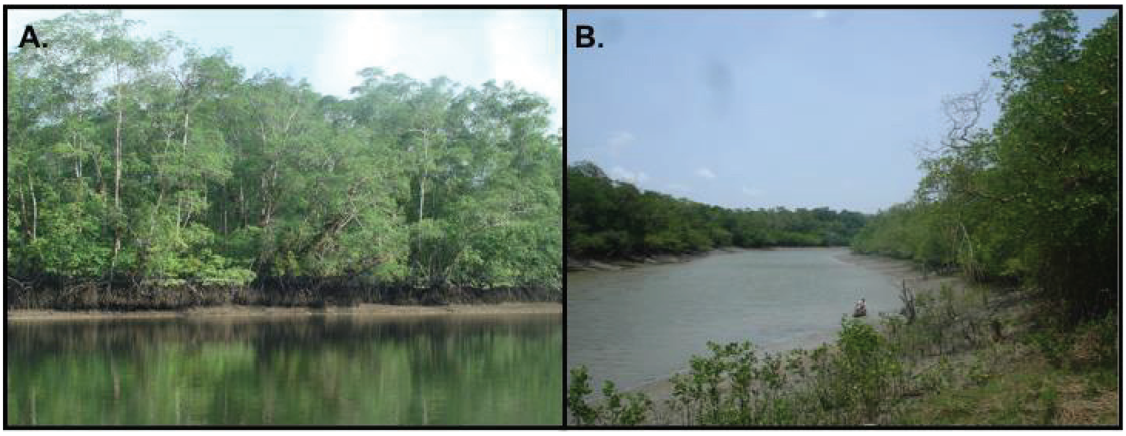


Figure 4. Representative mangrove landscapes in two macrotidal Neotropical regions at low tide: (A) Mangroves in estero Luisico creek, Bahía Málaga, Colombian Pacific (Panama Bight region); and (B) Mangroves in Furo do Meio creek, Caeté Estuary in the state of Pará, north Brazil (Guianan-Amazon region).

1.2.4 Mangroves and fishes in the Neotropics

Mangroves are a dominant seascape in the Neotropics and a primary habitat for coastal fishes in the provinces where they occur. It is especially in the Caribbean and Carolina province where most research on mangrove fish has been carried out. Disproportionate contributions from study areas like Florida (USA), and recently Curaçao in the Caribbean, contrast with a paucity of studies in areas like Pacific Panama and most of the Tropical Eastern Pacific region (see reviews in Faunce & Serafy 2006, Blaber *in press*). The consequence of such disparity is that most of the understanding of the relationship between mangroves and fish (and mangrove fisheries resources) in the Neotropics comes from a specific (microtidal) setting, which is not necessarily representative of the whole region. With the exceptions of a few systems (e.g. the Terminos Lagoon (Mexico), the Urabá Gulf and Ciénaga Grande de Santa Marta (Colombia)), mangroves in the Caribbean and Carolina provinces are non-estuarine. Additionally, these two provinces share a microtidal regime (tidal range <2 m) meaning that most mangroves in these provinces are permanently inundated. An additional feature of most mangrove systems in the Caribbean is that they occur in close proximity to seagrass beds and coral reefs forming a continuum of interconnected marine habitats where fish commute during daily home-range movements or through ontogeny.

The particularities present in neotropical mangroves of the Caribbean Sea imply the need to examine the relationships between mangroves and fish in other provinces where mangroves are: (1) intermittently inundated (meso- and macrotidal areas), (2) subject to estuarine conditions and, (3) lacking the coral reef-sea grass continuum, but alternatively presenting other seascape continuum (e.g. mudflats, sandflats or rocky shores).

1.3 Research Objectives and Outline

The overall objective of this thesis is to determine and compare the influence of environmental filters (i.e. tidal-diel cycles and salinity gradients) on mangrove fish assemblage organization in two macrotidal areas of the Neotropics (Pacific Colombia and North Brazil, Figure 5). At the same time, this thesis takes a biogeographical approach to understand how local fish assemblage organization can be influenced by the extant distribution of mangrove fish fauna of the two regions under study (the Tropical Eastern Pacific and Western Atlantic regions). This thesis also aims to determine the importance that tidal rhythms have for shallow-water fishes in space and time. By comparing the extent to which tides determine community organization in two different intertidal ecosystems (rocky shores and mangroves) and between biogeographical regions, I investigate the spatial context. The temporal context is investigated by analyzing the variation (one year) in tide-related patterns at each study area and the long-term variation (samplings in 1999 vs 2012) in North Brazil. Finally, the overall working hypothesis of this thesis is that the structure of intertidal mangrove fish assemblages in macrotidal estuarine areas of the Neotropics is equally influenced by the interaction of tidal and diel cycles, and by changes in salinity. I also hypothesize that the biogeography of the Neotropics can explain some of the patterns observed in fish assemblage structure at the local and regional level.

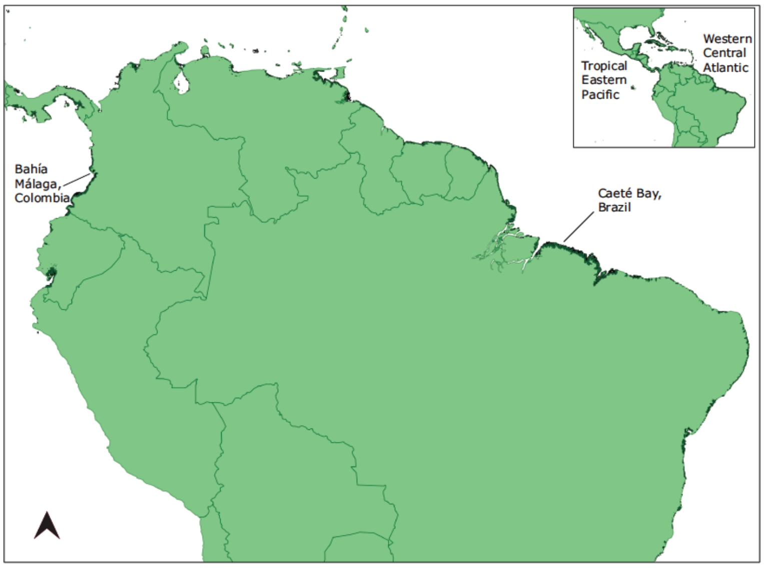


Figure 5. Map of South America showing the two regions under study (Tropical Eastern Pacific and Western Central Atlantic) and the two specific localities where sampling campaigns were carried (Bahía Málaga and Caeté Bay). Dark green color represents mangrove areas according to Giri et al. (2011).

1.3.1 Research Questions

1. What is the fish assemblage composition (species structure, functional guilds, biomass) found in intertidal mangrove areas of the Colombian Pacific (Bahía Málaga)? How do the tidal magnitude (spring-neap tide cycle) and its interaction with the diel cycle affect the structure of the intertidal mangrove fish assemblage? How does salinity affect the community structure of this fish assemblage? – *Manuscript I*

2. How does the tidal magnitude (spring-neap tide cycle) influence the distribution of shallow-water reef fish in the Colombian Pacific? Does the influence of the tidal magnitude on fish assemblages differ between rocky shores and mangrove habitats within the same region? – *Manuscript II*

3. Are there general spatial patterns in the mangrove fish assemblage composition of the Tropical Eastern Pacific biogeographical region? – *Manuscript III*

4. How similar is the composition of mangrove fish assemblages in the Tropical Eastern Pacific and those described for the Western Central Atlantic region, and how do they compare to mangrove fish assemblages in other regions of the World? – *Manuscript IV*

5. How persistent in time (wet seasons of 1999 and 2012) are tidal-related patterns in intertidal mangrove fish assemblages of the Caeté estuary (North Brazil)? - *Manuscript V*

6. How does the fish assemblage structure of two macrotidal estuarine systems in the Neotropics differ and what can we learn about the relative influence of environmental factors, biogeographical and evolutionary processes? – *Manuscript VI*

The questions one to five are more specific in scope and geographical coverage, whereas the question six is intended to synthesize what was found in some of the previous questions (one, three and four).

1.3.2 Thesis Outline

This dissertation is organized in eight chapters: an introductory and synoptic chapter and six chapters which are organized in the form of scientific publications covering different geographical areas and addressing each of the research questions indicated above (see Figure 6).

In the introductory chapter (*Chapter one*) to this dissertation, I review the main topics covered in this document from community ecology principles and biogeographical patterns to factors that determine the community organization in coastal fish assemblages at local scales. I also review what is known about mangrove ecosystems and coastal fish assemblages in the Neotropics. The following chapters (2-7) are organized in form of scientific publications that contain detailed introductions to the topics covered in each chapter.

The *second chapter* ***(manuscript I)*** of the thesis introduces a case study of the Pacific coast of Colombia (Bahía Málaga, Tropical Eastern Pacific) where I studied mangrove fish assemblages during one annual cycle. Using a standard methodology (block nets), the influence of tidal rhythms on fish community structure was assessed at two different salinity zones. The presence of an extremely high precipitation regime (> 7 m $year^{-1}$) and a species-poor freshwater fish fauna is used to explain the community organization patterns found. A general description of the trophic, spatial and estuarine use guilds of the fishes in this area is also given in this chapter.

In the *third chapter* ***(manuscript II)***, I use visual census fish data collected during six month in a coastal habitat different from mangroves (i.e. rocky shores) in the Colombian Pacific coast to investigate how reef fish assemblages use intertidal areas and how the assemblage structure in the sub- and intertidal area is influenced by tidal rhythms (flood, ebb, high and low tide). I discuss the results obtained in this study in the context of fish use of tropical intertidal habitat, including mangroves. This was done to identify whether intertidal habitats (rocky shores vs mangroves) are equally important (e.g. as shelter and/or feeding grounds) for fish assemblages living in adjacent areas.

In a *fourth chapter* ***(manuscript III)***, I review the spatial variability in mangrove fish community composition along the Western tropical coast of America (Tropical Eastern Pacific marine biogeographical region). For that purpose, I conducted a meta-analysis with own information and published studies in mangrove areas of this region (nine studies from four countries) to explore patterns in the organization of these assemblages. The study provides for the first time substantial information on mangrove fish assemblages from the Tropical Eastern Pacific and filled a gap in our knowledge that had existed for long time in the primary literature.

The *fifth chapter* ***(manuscript IV)*** of this thesis gives a general review of mangrove fish assemblages in the Neotropics (except the Caribbean Sea). Specifically, I argue that the general composition (at the family level) of estuarine mangrove fish assemblages in the Western Atlantic and the Tropical Eastern Pacific regions has significant similarities and that these assemblages are very different from the mangrove fish faunas in East Africa. This chapter contributes to clarify recent claims in the literature (Sheaves 2012) where mangrove fish assemblages from the Neotropics and East Africa were grouped into a single unit. This chapter also highlights the importance of using adequate metrics when measuring ecological equivalence in mangrove fish assemblages. This section of the thesis also serves as an introduction to the study of mangrove fish assemblages of the Western Atlantic region.

The *sixth chapter (**manuscript** V)* investigates the persistence and stability over time of tidal-related patterns in mangrove creek fish assemblages in North Brazil (Bragança Peninsula). I used field data collected by my coauthor 13 years ago during the rainy season in the Caeté Estuary and compared them with data I collected during the rainy season of 2012 using the same study site (Furo do Meio) and the same methodology (block nets) at the same mangrove creeks. The interaction of tidal and diel cycles resulted in recurrent intertidal mangrove fish assemblage compositions after 13 years, indicating how stable in time are these patterns. An atypical rainy season in 2012 (ca. 40% less precipitation) is given as the most likely explanation for a considerable decline in fish biomass and change in the dominance in the fish assemblage.

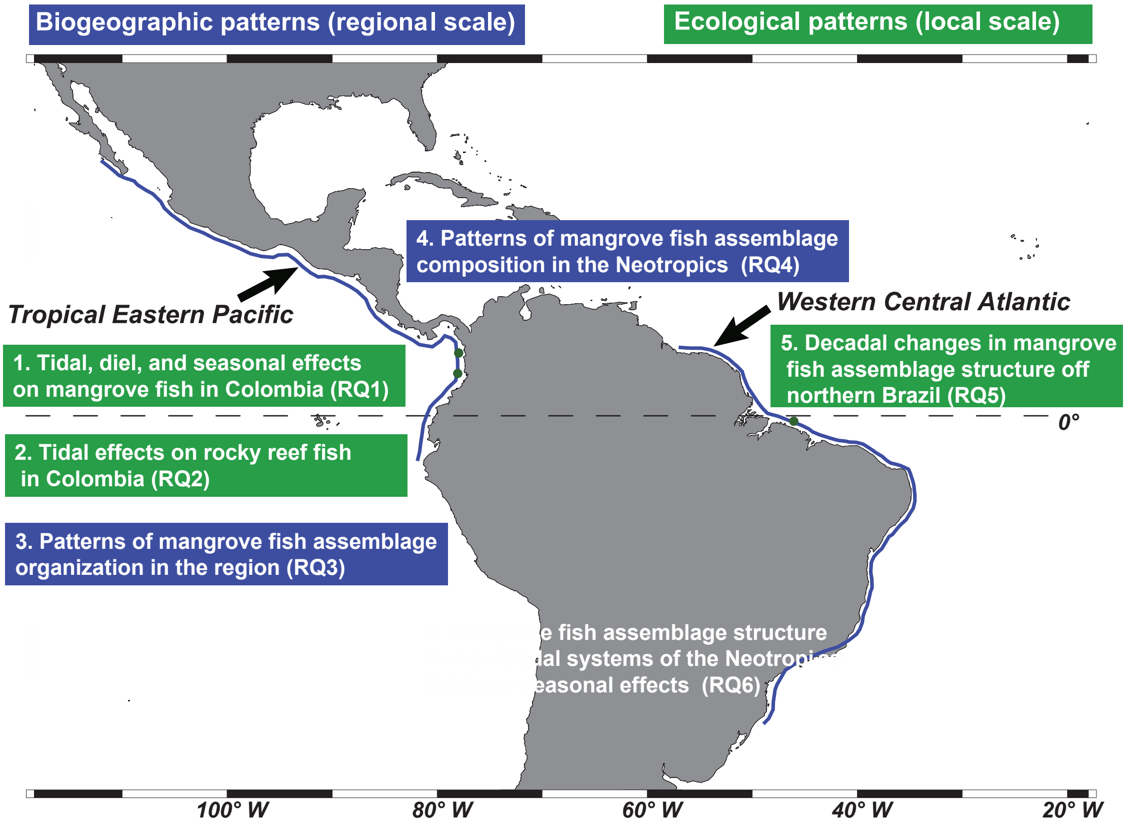


Figure 6. Topics of the manuscripts presented in this dissertation. Each topic corresponds to a research question mentioned in the text. Blue lines in the map indicate the geographic area coverage in manuscripts 3 and 4. Green dots indicate the study site locations of manuscript 1,2 and 5.

In the *seventh chapter (**manuscript** VI)*, I examine the spatial and temporal patterns of mangrove creek fish assemblages in the Caeté estuary, North Brazil and compare the results obtained with the study performed in the Tropical Eastern Pacific (Colombia, Chapter 2) and previous studies from the area. In the Caeté estuary, I collected mangrove fish data with the same methodology as used in Colombia (block nets) during 11 months (2011-2012) at three intertidal sites following a salinity gradient. I discuss the implications of these results for the general understanding of the relationship between fish and mangroves in macrotidal areas of the Neotropics.

The synoptic chapter at the end (*chapter eight*) discusses the main findings of this dissertation in the context of their contribution to the general understanding of mangrove fish community organization in macrotidal areas of the Neotropics. I highlight the importance that tidal rhythms play in structuring coastal fish communities in estuarine macrotidal areas, but also emphasize the importance of local seacapes (geomorphologic settings) and biogeography in explaining the present-day organization patterns in mangrove fish assemblages.

Finally, an outlook of future research questions in the field of mangrove fish community ecology is given.

1.3.3 List of manuscripts

Manuscript 1.
Tidal, diel and seasonal effects on intertidal mangrove fish in a megahumid area of the Tropical Eastern Pacific. Manuscript in press in *Marine Ecology Progress Series.*

Manuscript 2.
Tidal influences on fish distributions on tropical eastern Pacific rocky shores (Colombia). Manuscript published in *Marine Ecology Progress Series* (2010) 416:241-254.

Manuscript 3.
Spatial variability of mangrove fish assemblage composition in the tropical eastern Pacific Ocean. Manuscript published in *Reviews in Fish Biology and Fisheries* (2013) 23:69-86.

Manuscript 4.
Mangrove fish assemblages from under-represented regions and the measurement of ecological equivalence: Comment on Sheaves (2012). Manuscript published in *Marine Ecology Progress Series* (2013).

Manuscript 5.
Long-term stability of tidal-related patterns in mangrove creek fish assemblages in North Brazil. Submitted to *Estuarine and Coastal Shelf Science*

Manuscript 6.
Fish habitat use in macrotidal mangroves of the Neotropics: tidal, salinity and biogeography effects on assemblage structure and function. Target journal: *Journal of Biogeography* (submission November 2013).

1.3.4 Contribution of Authors

Manuscript 1.

Castellanos-Galindo G.A., Krumme U., Willis T.J. (2010) Tidal influences on fish distributions on tropical eastern Pacific rocky shores (Colombia). *Marine Ecology Progress Series* 416:241-254.

Uwe Krumme and I developed the concept and experimental design. I performed the fieldwork and produced a preliminary manuscript draft. Trevor Willis provided input into new multivariate analysis approaches. The three authors participated in the writing of the manuscript.

Manuscript 2.

Castellanos-Galindo G.A., Krumme U., Rubio E.A., Saint-Paul U. (2013) Spatial variability of mangrove fish assemblage composition in the tropical eastern Pacific Ocean. *Reviews in Fish Biology and Fisheries* 23:69-86.

Uwe Krumme and I developed the concept and experimental design. I compiled the data, performed the analyses and elaborated the first draft. Uwe Krumme improved on this first draft. Efrain Rubio provided data and feedback on a first manuscript draft. Ulrich Saint-Paul provided feedback on various versions of the manuscript.

Manuscript 3.

Castellanos-Galindo G.A., Krumme U. Tidal, diel and seasonal effects of intertidal mangrove fish in a megahumid area of the Tropical Eastern Pacific. Manuscript in press in *Marine Ecology Progress Series.*

Uwe Krumme and I developed the concept and experimental design. I performed the fieldwork, compiled the data, performed the analyses and elaborated the first draft. Uwe Krumme improved subsequent manuscript drafts.

Manuscript 4.

Castellanos-Galindo G.A., Krumme U. (2013) Mangrove fish assemblages from data-sparse regions and the measurement of ecological equivalence: Comment on Sheaves (2012). *Marine Ecology Progress Series* 474:299-302.

I developed the concept. Uwe Krumme provided raw data from mangrove fish assemblages in the Western Central Atlantic and other references. Uwe Krumme and I wrote the manuscript.

Manuscript 5.

Castellanos-Galindo G.A., Krumme U. Long-term persistence of tidal-related patterns in mangrove creek fish assemblages in northern Brazil. Submitted to *Estuarine Coastal and Shelf Science.*

Uwe Krumme developed the concept. I performed the field campaign in 2012. Uwe Krumme provided raw data from sampling campaigns in 1999. I analyzed the data and wrote the first manuscript draft. Uwe Krumme improved on the subsequent manuscript drafts.

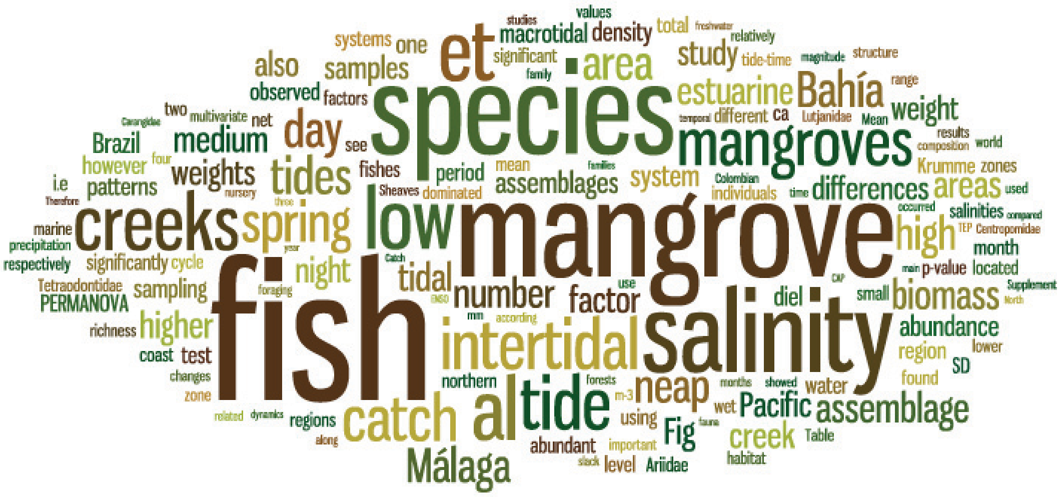
Manuscript 6.

Castellanos-Galindo G.A., Krumme U. Fish habitat use in macrotidal mangroves of the Neotropics: tidal, salinity and biogeography effects on assemblage structure and function. Target journal: Journal of Biogeography (planned submission: November 2013).

Uwe Krumme and I developed the concept and experimental design. I conducted the fieldwork, compiled the data, analyzed the data and elaborated on the first draft. Uwe Krumme improved on the subsequent manuscript drafts.

Chapter II. Tidal, diel and seasonal effects on intertidal mangrove fish in a megahumid area of the Tropical Eastern Pacific

Gustavo A. Castellanos-Galindo and Uwe Krumme



Cite as: Castellanos-Galindo GA, Krumme U (in press) Tidal, diel and seasonal effects on intertidal mangrove fish in a megahumid area of the Tropical Eastern Pacific. *Marine Ecology Progress Series*. doi: 10.3354/meps10512

ABSTRACT

Mangroves are recognized as nursery areas for a large number of marine organisms. Yet many properties of this nursery function and its equivalence between geographical areas remain poorly understood, especially in macrotidal estuarine systems. The influence of tides, diel and seasonal variation on intertidal mangrove fish assemblages in a megahumid area of the Tropical Eastern Pacific region is investigated. Block net samplings were carried on the annual cycle of spring-neap tides during day-night while considering the salinity gradient. Clupeidae dominated catch abundances of a 50 species-rich assemblage. Catch weights, however, were dominated by Lutjanidae, Tetraodontidae and Ariidae. Fish biomass was low, likely as a result of a poor benthic in- and epi-faunal biomass in a mangrove system of low nutrient status, due to extremely humid conditions. Higher salinity creeks yielded significantly greater catches and higher number of species than low salinity creeks. A depauperate freshwater fish fauna in this beogeographical region, unable to compensate for the lack of marine-estuarine species in a low salinity environment, may explain this pattern. A notable increase in rainfall at the end of the year correlated to a decrease in mangrove fish biomass. Partially in agreement with studies from other macrotidal areas, specific combinations of tidal magnitude and diel cycle explained recurring changes in fish assemblage structures, clearly observed at the species level, but not in the number of species or biomass. These results indicate not only how important tidal and diel cycles can be for fish habitat use in macrotidal mangroves, but also highlight how regional (biogeography) and local (geomorphology, precipitation) factors should be incorporated into further investigations of mangrove ecosystem equivalence over large geographical scales.

Keywords: intertidal mangrove creeks, fish community, block nets, macrotides, Tropical Eastern Pacific, Panama Bight mangroves, Colombia, Bahía Málaga

INTRODUCTION

Mangroves are among the most threatened ecosystems in the world with a loss rate of 1–2% per year (Valiela et al. 2001, Polidoro et al. 2010). Carbon storage, sediment trapping, protection against storm surge and increased fisheries yields in adjacent waters are some of the ecosystem and economic benefits provided by mangroves (Alongi 2002, Donato et al. 2011). 30% of the world's commercial fish species are considered mangrove-dependent (Naylor et al. 2000). Nevertheless, the role of mangroves as a fish habitat and nursery continues to be little understood (Beck et al. 2001) and has proven to be very variable across geographic areas (Sheaves 2005).

Many of the studies highlighting the nursery function of mangroves thus far have been carried out in the Caribbean biogeographical realm where mangrove forests are comparatively small and microtidal systems (Krumme 2009, Nagelkerken 2009; but see Blaber (2000) for a review of studies in the Indo-Pacific and African regions). However, mangroves elsewhere may be subject to medium or large tidal amplitudes and present a different habitat configuration from the mangrove-seagrass-coral reef continuum most often described in the literature. In meso- and macro-tidal regimes (range 2 to > 6 m), fish accessibility to mangroves is limited to periods of intertidal inundation. Therefore, the dynamics of fish assemblages and value of the mangrove as a nursery habitat in these regions may be distinctly different compared to those in microtidal systems.

Fish assemblages on macrotidal coasts exploit temporarily accessible habitats via tidal movements that are an important part of their home-ranges (Gibson 2003). The importance of tidal movements for fish, however, varies according to habitat. On the rocky shores of the Colombian Pacific these movements are not related to spring-neap tide cycles (Castellanos-Galindo et al. 2010) whereas in the mangroves, complex interactions in the organization of intertidal fish assemblages have been found following changes in spring/neap, diel and lunar cycles (Davies 1988, Krumme et al. 2004, Krumme 2009). These short to medium temporal scales are seldom considered in the study of fish community structure dynamics (Wilson & Sheaves 2001), although crucial to understanding the dynamics of these assemblages.

The influence of abiotic factors in shaping fish communities (salinity, turbidity) has been relatively well studied in different ecosystems throughout the world (Blaber 1997). Although most estuarine fish species can be considered euryhaline, in estuarine mangrove systems a strong relationship between salinity and fish community composition has been found (Sheaves 1998). Changes in salinity are ultimately a consequence of the precipitation regime, seasonality of the rainfall and size of the drainage system at each study site. Most investigations examining the relationship between salinity and fish assemblage structures have been carried out by sampling in the main channels of estuaries (Barletta et al. 2005, Simier et al. 2006). Only few studies have examined how intertidal mangrove creek fish assemblages (and fish tidal migrations) are affected by salinity change and/or precipitation (but see Lorenz & Serafy 2006; Giarrizzo & Krumme 2007 and Rehage & Loftus 2007).

Mangrove forests on the Pacific coast of the Americas cover ca. 1.21 million ha (Lacerda et al. 2002). Important artisanal fisheries throughout the region depend either directly or indirectly on mangroves as they are considered essential habitats for the juveniles of commercial species (Aburto-Oropeza et al. 2008). The majority of these mangroves are located in the Panama Bight ecoregion (covering the Pacific coasts of Panama and Colombia and the coast of Ecuador), one of eight major mangrove areas identified as a global conservation priority (Olson & Dinerstein 2002). Despite being relatively undisturbed, these mangroves are subject to environmental (i.e. ENSO events) and human-driven (deforestation and pollution) stressors that pose serious threats to local human populations and could drive major changes in coastal food webs (Valiela et al. 2012, Restrepo 2012).

This study examines, for the first time, the small and mid-term spatial and temporal patterns of mangrove creek fish assemblage structure in a macrotidal mangrove area of the Tropical Eastern Pacific Ocean (Colombian Pacific coast), filling a gap in the understanding of mangrove fish assemblage dynamics in this area (Faunce & Serafy 2006, Sheaves 2012, Blaber in press). For this purpose, three questions were raised: (1) What is the taxonomic and functional composition of the intertidal mangrove fish assemblage in a megahumid area of this region? (2) How does the variability introduced by changes in the tidal magnitude (spring-neap tide cycle) and its interaction with the diel cycle affect the structure of the intertidal mangrove fish assemblage? and (3) How does an extremely high precipitation-low salinity period affect the structure of this mangrove fish assemblage?

MATERIALS AND METHODS

Study area

Bahía Málaga is located in the central region of the Colombian Pacific coast (3º 56’ - 4º 05’N and 77º 19’ - 77º 21’W) in the Tropical Eastern Pacific (TEP) region (Figure 7) and is an estuarine embayment (*sensu* Pritchard 1967) formed during a tectonic event which occurred in the Miocene-Holocene Epoch. It is believed that the bay was a narrow channel of an old (Pleistocene) tributary system of the San Juan River (one of the largest deltas along the west coast of South America) that was flooded after a tectonic uplift of the northwestern region of Bahía de Buenaventura (Martínez & López-Ramos 2011, Figure 7).

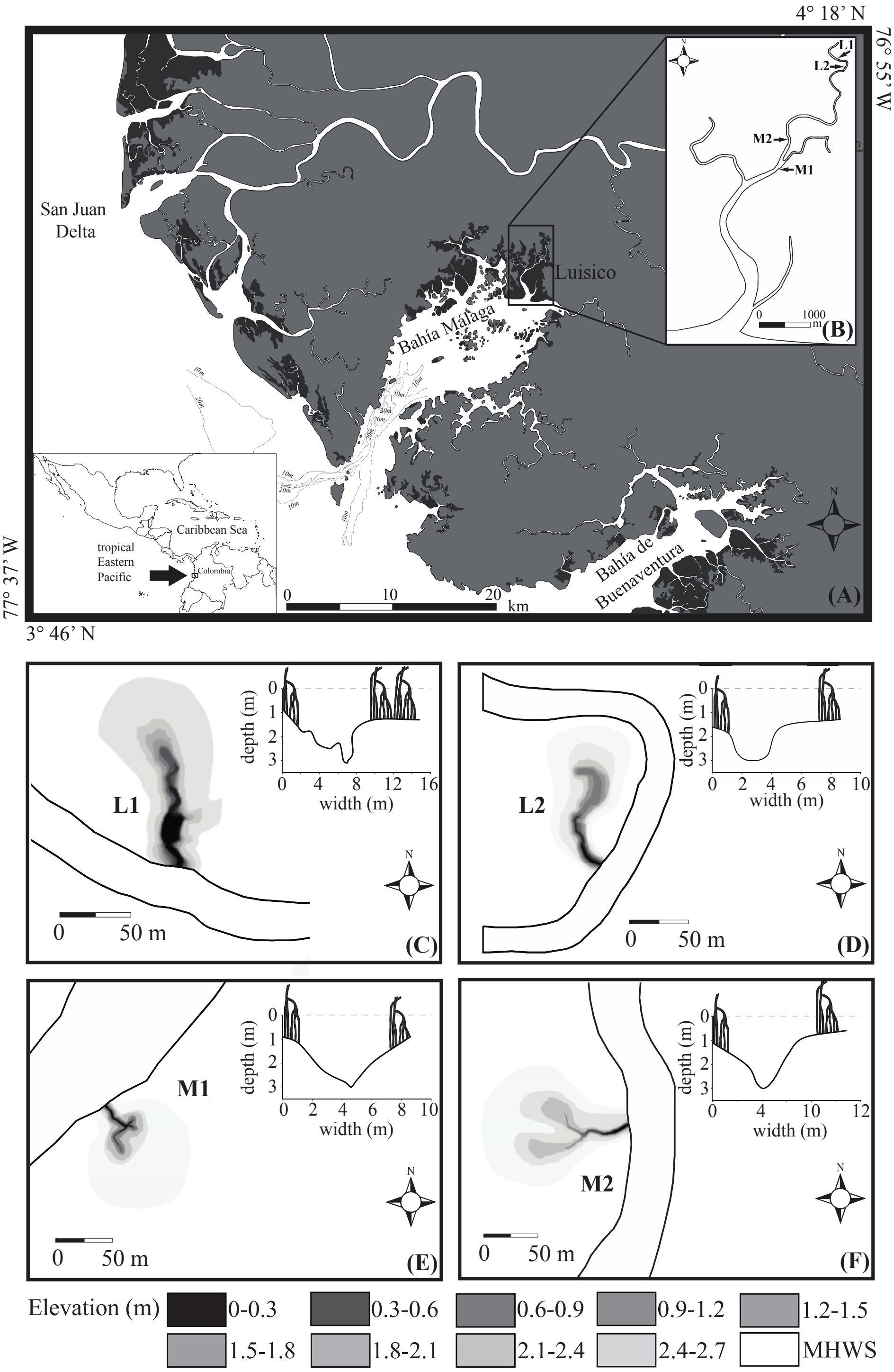


Figure 7. (A) Coast of the Tropical Eastern Pacific region and location of Bahía Málaga. (B) Location of the four intertidal mangrove creeks (C–F) in the Luisico tributary inside Bahía Málaga sampled during December 2009 – November 2010. Bathymetric maps of the two low-salinity creeks (C:L1, D:L2) and the two medium-salinity creeks (E:M1, F:M2). MHWS = Mean high water at spring tides. Subfigures C-F with cross-sectional profile from the creek entrance.

The study area is located in one of the wettest regions of the American continent (Poveda & Mesa 2000). The average annual rainfall (1969-2010) in Bahía Málaga is 7399 mm year^{-1} (SD±1623), with a wet period from January to April ($\bar{x}$ =422 mm month^{-1}) and a very wet period from May to December ($\bar{x}$ =746 mm month^{-1}, IDEAM meteorological station No. 5407003 – Malaguita, ca. 10 km North of Luisico sampling points 4° 11'N, 77° 12'W).

The bay has a surface area of ca. 130 km^2 and a mean water depth of 15 m. The coast is bordered by rocky cliffs composed of tertiary sediments, such as sandstones and mudstones, strongly modified by erosion and covered by well-developed riverine and fringe-type mangroves (ca. 4400 ha) and mudflats in depositional zones (Correa & Morton 2010). Several small rocky islands (as close as ca. 4 km to mangroves) are scattered within the bay. Some of these rocks can be completely submerged at high tide. Mangroves in Bahía Málaga are predominantly concentrated in the inner areas and are dominated by two species of *Rhizophora* (*R. racemosa* and *R. mangle*) with trees up to 40 m high (Cantera et al. 1999). Other less abundant mangrove species are *Avicennia germinans*, *Pelliciera rhizophorae* and *Mora oleifera*. The mangrove forests are drained by large dendritic subtidal channels ("esteros"). These are mostly composed of a soft bottom (mud, sand), but rocks and gravel banks can also be intermittently found in the range of 100 m apart from mangroves. The catchment areas upstream of the mangroves are small, with no larger rivers draining into the bay. These mangroves are probably exposed to some of the wettest conditions on earth, in an erosional rather than accretional environment. This is indicated by the low sediment accumulation around the base of the mangroves, resulting in a low elevation of the forest in relation to mean sea level. For this reason, the floor of most mangrove areas is already largely inundated at neap tides (see Annex I, Supplemental Figure A1). Tides on the Pacific coast of Colombia are semidiurnal. In the inner part of Bahía Málaga, the mean tidal amplitude is 3->4.5 m at spring tides and 2-3 m at neap tides. Mean air temperature is 25º C, sea surface temperatures range between 26-29 °C throughout the year. Human population density on the Pacific coast of Colombia has been historically very low, currently it is between 5-17 persons km^{-2} (Etter et al. 2006). Approximately 4000 people, distributed in small villages, live in Bahía Málaga.

Sampling design

From December 2009 to November 2010, an equal number of sampling campaigns was completed at spring and neap tide periods (six times each; see Annex I, Supplemental Figure A2). On a monthly basis, four intertidal mangrove creeks with similar topographic characteristics and dominated by *Rhizophora* spp. trees, de-watering directly into the Estero Luisico were blocked at the mouth at slack high tides using block nets (20 m x 4 m, 12 mm mesh size; Figure 7). Creeks occurred over a ca. 5 km gradient that captured the salinity variability observed in the bay (0-23). Block nets are a common method for artisanal fishers in several parts of the world including the Colombian Pacific. The method is regarded as highly efficient in capturing fish that enter intertidal vegetated creeks, and thereby accurately represent the composition of fishes using intertidal mangrove resources (Bozeman & Dean 1980, Thayer et al. 1987, Vance et al. 1996). At each creek a block net was deployed at the creek mouth at low tide. The lead line of the net was pushed into the mud with hands and feet from one side to the other, the entire net enrolled and fixed with small wooden sticks at intervals on top of the mud to prevent lifting of the net during flood tide. A wooden pole (ca. 5 m above ground) was put vertically in the middle of the creek. The net was lifted the following high slack water with the headline moored to the top of the wooden pole (i.e. above the water level), thus completely blocking the creek mouth. The pole also retains the block net during strong ebb tide periods. At late ebb tide all fish entangled in and concentrated in the already drained intertidal creek upstream of the net were intensively searched and collected by hand. Due to the time delay of the tidal cycle with respect to the diel cycle, slack low waters (LW) during spring and neap tides occur at different times. Slack low water at spring tides occurred approximately at midday and midnight (00:00 and 12:00h), whereas slack low tide at neap tides usually occurred around sunrise and sunset (6:00 and 18:00h). Therefore, a factor tide-time of day with four levels was established corresponding to the samples when fishes could enter the intertidal mangrove creeks: 1. until the early morning (approximately 06:00), spring tide – day (SD); 2. after dusk (approx. 18:00 – 19:00), spring tide – night (SN); 3. until midday, neap tide – day (ND); 4. until midnight, neap tide – night (NN). Two of the selected intertidal creeks were located in a low salinity zone (salinity at: high tide: $\bar{x}$ ± SD= 12.3 ± 5.7, low tide: $\bar{x}$ ± SD = 1.9±1.8) and two were located in a medium salinity zone (salinity at high tide: $\bar{x}$ ± SD = 16.5±4.2, low tide: $\bar{x}$ ± SD = 7.8±4.3; Figure 8). Creeks were on average 10 m wide and 3 m high at the mouth and 80-100 m long. Samples were taken during both day and night LWs. For each sampling trip, the maximum water level at slack high water in the entrance of each creek and the surface salinity were measured. Salinities at low water were also measured in the main channel approximately at the creek mouths. Sampling of the four creeks was completed in two consecutive days of the corresponding spring or neap tide period (i.e. day one: lower salinity creeks; and day two: medium salinity creeks).

The topography of each creek was surveyed using GPS, a compass and a tape measure. Maps of the creeks were produced and a relationship between flooding height and inundated area (m^2) and volume (m^3) was established using a 3D model in GIS (see Annex I, Supplemental Table A2). This information was used to standardize the catch abundance and weights to density (number of fishes m^{-2} or m^{-3}) and biomass (g m^{-2} or m^{-3}), respectively.

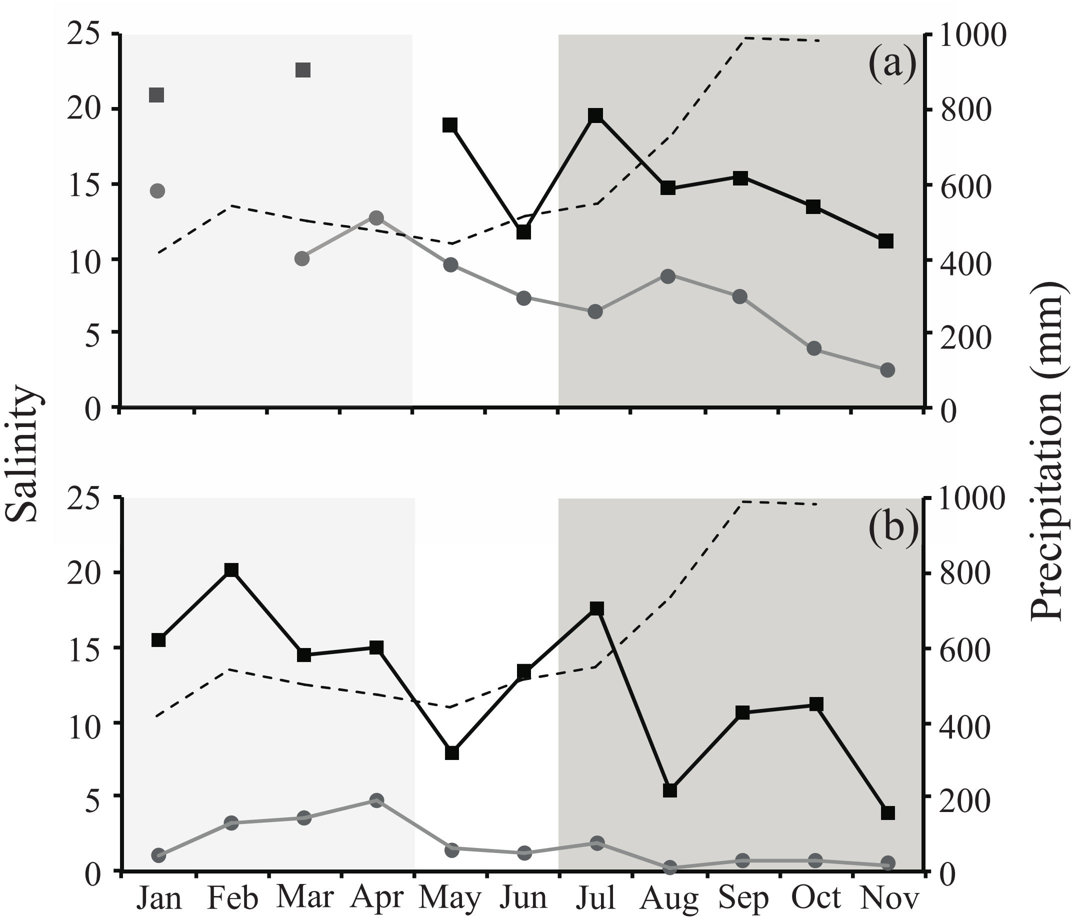


Figure 8. Salinity variation at high (black lines and dots) and low tide (grey lines and dots) during the sampling period (January-November 2010) at (a) the medium salinity zone and (b) the low salinity zone. No data for December 2009 was recorded. Total monthly rainfall from the nearest meteorological station is shown by the dashed lines. El Niño conditions: light grey box, La Niña conditions: dark grey box (according to the monthly Oceanic El Niño Index (ONI) http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears .shtml).

All sampled fishes were preserved in 10% formalin and later transferred to 70% ethanol in the laboratory. They were subsequently identified using taxonomic keys for the area (Fischer et al. 1995, Robertson & Allen 2008), measured (total length-TL) and wet weighed (g±0.1). Each fish species was then assigned to one spatial and trophic guild group according to own stomach content analyses or to information derived from Elliot et al. (2007) and Froese & Pauly (2012).

Data analyses

Individual-based rarefaction curves were constructed for each creek to evaluate the representativeness of the number of samples taken using EstimateS software (Colwell 2009). The non-parametric Chao1 species richness estimator was used to estimate the asymptotic species richness for each creek. Species abundance distribution models (SADs) were used to obtain a general description of the mangrove fish assemblages (log-numerical abundance vs rank-plots; McGill et al. 2007).

An initial assessment of the effect of consecutive sampling in the same creeks revealed no significant correlations between the catch mass and the consecutive sampling events in any of the four creeks (see Annex I, Supplemental Figure A2). In contrast to other studies that have found reduced catches when consecutive sampling in the same area were completed (Vance et al. 1996, Rönnbäck et al. 1999, Huxham et al 2004), in our study an interval of ca. one month between sampling intervals was sufficient for the fish assemblage to recover from any disturbance.

Species richness, abundance and catch mass differences between the factors salinity zone, tide-time of day and month (repeated measure) were analyzed with one way parametric ANOVAs and/or non-parametric Kruskal-Wallis tests (for each factor), depending on the violation of any of the assumptions of parametric statistics. When significant differences were observed pairwise comparisons were carried out (Tukey's HSD and Nemenyi-Damico-Wolfe-Dunn tests). Moreover, differences in fish density (individuals m^{-3}) and biomass (g m^{-3}) between salinity zones were tested using the non-parametric two-sample Wilcoxon test (equivalent to a Mann-Whitney test).

Additionally, multivariate statistic techniques were employed to analyze data related to fish assemblage organization. A PERMANOVA test (permutational multivariate analysis of variance, Anderson 2001) was used to evaluate differences in fish assemblages between salinity zones (fixed factor with two levels: low and medium) and tide-time of day combination (fixed factor with four levels: SD, SN, ND, NN). Since there is no repeated measures module in PERMANOVA, we accounted for repeated measures by including factor month as fixed in the model. The routine PERMDISP was used to identify if differences obtained with the PERMANOVA test were an artifact of differences in dispersions among groups (Anderson 2006, Anderson et al. 2008). To visualize multivariate patterns revealed by PERMANOVA, unconstrained (principal coor dinates analysis – PCO, a parametric analogue of multidimensional scaling) and constrained (canonical analysis of principal coordinates – CAP) ordination techniques were used (Anderson & Willis 2003). Based on the strength of the correlation (>0.4) of individual species with the canonical discriminant axes (CAP1 or CAP2), fish species with a frequency of occurrence of more than 0.2 were identified as responsible for differences in the observed patterns. All multivariate analyses were based on Bray-Curtis distances calculated from square-root transformed data and conducted using the Vegan package of the R statistical environment (Oksanen 2010) and PERMANOVA+ for PRIMER software (Anderson et al. 2008).

RESULTS

Taxonomic, trophic and estuarine use composition

A total of 2993 fish from 50 species and 26 families were recorded during the entire sampling period. The most speciose families were Lutjanidae (six species), Carangidae (five species) and Gobiidae, Engraulidae, Centropomidae, Gerreidae and Eleotridae (each family with three species). *Lile stolifera* (Clupeidae) was the most abundant species representing one third of all individuals collected. *Centropomus armatus* (Centropomidae), *Lutjanus argentiventris* (Lutjanidae) *Diapterus peruvianus* (Gerreidae) and *Ariopsis seemanni* (Ariidae) accounted for 12, 8, 7 and 5% of the total abundance, respectively. In terms of catch weight, three species accounted for ca. 60% of the total catch weight (*L. argentiventris*, *Sphoeroides rosenblatti* – Tetraodontidae and *A. seemanni*). The family Lutjanidae (snappers) represented 28% of the total catch weight in this mangrove fish assemblage, followed by Tetraodontidae (20%) and Ariidae (19%) (Table 2). The fish assemblage was dominated by zoobenthivores and to a minor extent by zooplanktivores. The former trophic guild accounted for 66% of the total number of species and represented 47% and 84% of the total abundance and catch weight, respectively (e.g. Lutjanidae, Centropomidae, Tetraodontidae, Ariidae). Zooplanktivores were very abundant (36% of the total number of individuals) but were only represented by four species that contributed 6% of the total catch weight (Clupeidae, Atherinopsidae). Piscivores were almost as important as zooplanktivores in catch weight percentages (5%), and were mainly composed of jacks (Carangidae) and needlefishes (Belonidae). Most fish species in Bahía Málaga were marine estuarine opportunistic (42%), whereas estuarine species accounted for only 28% (14 species). Marine estuarine opportunistic species were also dominant in number of individuals (49%), followed by estuarine residents (27%) and marine estuarine dependent species (19%). Catch weights, however, were dominated by estuarine resident species (49%) with marine estuarine dependent and marine estuarine opportunistic species representing almost all the remaining catch weights (30% and 18%, respectively) (Table 2).

Table 2. Fish species composition in four mangrove creeks of Bahía Málaga collected from December 2009 – November 2010. Common fish names are given in Annex I, Supplemental Table A3. Total number of individuals (*n*), total and spring-day (SD), spring-night (SN), neap-day (ND), neap-night (NN) catch weights and mean and range of total length (TL) for each species. Max-TL: Maximum TLs reported in the literature (Robertson & Allen 2008). Spatial guilds (SG): pelagic (P), benthopelagic (BP), demersal (D), reef associated (RA) and freshwater (F) according to Froese & Pauly (2012); and trophic guilds (TG): zooplanktivore (ZP), detritivore (DV), herbivore-phytoplankton (HVP), piscivore (PV), zoobenthivore (ZB), omnivore (OV) and estuarine use functional groups (in superscript) according to own stomach inspections and Elliot et al. (2007). Numbers in bold show the two highest catch weights in any of the tide-time of day combination levels (SD, SN, ND, NN) for the top 15 species.

Species	*n*	SG	TG	Catch weight (g)					TL (cm)	Max TL (cm)
				Total	SD	SN	ND	NN	X (range)	
Lile stolifera (Clupeidae)^{1}	1015	P	ZP	5765.3	**2491**	**2814.9**	410.5	48.9	9.2 (6.8-11.2)	15.0
Centropomus armatus (Centropomidae)^{3}	356	D	ZB	5650.2	704.3	**2043.7**	497.2	**2405**	10.7 (5.6-23.6)	37.0
Lutjanus argentiventris (Lutjanidae)^{2}	237	RA	ZB	21472.6	3207.4	**9699.5**	2302.2	**6263.6**	15.4 (38.8-5.6)	71.0
Diapterus peruvianus (Gerreidae)^{2}	206	D	ZB, DV	1359.4	**412.7**	**460.8**	222	263.9	7.8 (3.0-15.6)	38.0
Ariopsis seemanni (Ariidae)*^{3}	143	D	ZB	19980.1	2971.6	**5134.2**	2984.7	**8889.6**	24.4 (15.6-34.0)	35.0
Sphoeroides rosenblatti (Tetraodontidae)^{3}	109	D	ZB	20665.1	**9871.2**	1877.1	**6796.9**	2356.5	19.5 (14.0-35.0)	30.0
Centropomus medius (Centropomidae)^{3}	89	D	ZB	3133.8	425.8	**1582.4**	119	**1006.6**	13.9 (8.0-34.5)	65.0
Poeciliopsis turrubarensis (Poecilidae)^{4}	62	BP	DV	82.9	11.6	**28.5**	0.6	**42.2**	5.0 (3.4-6.0)	9.0
Caranx caninus (Carangidae)^{1}	55	P	PV	1254.8	**643.3**	136.3	**472.3**	2.9	12.2 (6.4-20.0)	101.0
Oligoplites altus (Carangidae)^{1}	54	BP	ZB	997.4	**429.2**	88	**461.9**	18.3	12.7 (6.2-27.1)	56.0
Caranx sexfasciatus (Carangidae)^{1}	53	RA	PV	1729.2	**1171.4**	18.4	**539.4**	-	13.4 (7.2-23.0)	120.0
Gobiomorus maculatus (Eleotridae)^{4}	51	D	ZB	578.7	**94.9**	46.4	**419.7**	17.7	11.1 (7.4-18.3)	35.0
Lutjanus jordani (Lutjanidae)^{2}	51	RA	ZB	4531.3	580.1	**1472.7**	523.8	**1954.7**	14.9 (5.6-29.4)	61.0
Strongylura scapularis (Belonidae)^{2}	51	P	PV	2169.2	461.2	**693.6**	218.1	**796.2**	31.3 (7.8-41.0)	40.0
Lutjanus guttatus (Lutjanidae)^{1}	48	RA	ZB	844.9	**297.4**	**463.5**	73.4	10.6	10.0 (6.1-18.7)	80.0

Table 2. (continued)

Species	*n*	SG	TG	Catch weight (g)					TL (cm)	Max TL (cm)
				Total	SD	SN	ND	NN	X (range)	
Bathygobius andrei (Gobiidae)[3]	47	RA	ZB	759.8	12.1	193.4	187.3	367	11.2 (3.6-21.7)	15.0
Citharichthys gilberti (Paralichthyidae)[1]	45	D	ZB	377.9	135.2	47.7	135.8	59.2	9.9 (6.1-16.6)	30.0
Atherinella serrivomer (Atherinopsidae)[1]	42	P	ZP	243.1	141.5	63.9	21.4	16.3	10.0 (9.4-12.4)	17.0
Brycon meeki (Characidae)[4]	34	BP,F	OV	983.5	259.8	58.5	574.1	91.1	14.5 (7.6-28.0)	
Opisthonema medirastre (Clupeidae)[1]	30	P	HVP	1564.1	-	-	1564.1	-	19.6 (17.7-21.3)	30.0
Daector dowi (Batrachoididae)[3]	29	D	ZB	203.8	47.2	87.2	21.9	47.5	8.7 (6.4-13.8)	16.0
Bairdiella ensifera (Sciaenidae)[1]	26	BP	ZB	265.8	11.3	-	183.3	71.2	10.2 (8.4-15.9)	35.0
Eucinostomus currani (Gerreidae)[1]	22	D	ZB	324.3	70.7	231.9	-	21.7	10.8 (6.1-13.8)	21.0
Mugil cephalus (Mugilidae)[2]	22	BP	DV	1387.6	246.3	448.8	15.5	677	16.7 (8.6-32.0)	135.0
Pomadasys macracanthus (Haemulidae)[1]	20	BP	ZB	3864.2	474.3	1124.1	1396.6	869.2	19.2 (5.5-33.1)	37.0
Lutjanus colorado (Lutjanidae)[5]	12	RA	ZB	1257.6	473.7	268.9	319.3	195.7	17.4 (8.1-34.9)	107.0
Centropomus unionensis (Centropomidae)[1]	10	D	ZB	124.6	-	94	20.1	10.5	9.3 (6.9-21.1)	46.0
Chloroscombrus orqueta (Carangidae)[1]	9	BP	ZP	168.1	-	12.2	155.9	-	13.6 (12.2-15.1)	31.0
Halichoeres aestuaricola (Labridae)[3]	7	D	ZB	297.5	209.5	-	77.4	10.6	13.7 (9.4-19.1)	30.0
Lutjanus novemfasciatus (Lutjanidae)[1]	6	RA	ZB	1024.1	302.5	-	721.6	-	21.5 (7.2-30.0)	170.0
Rypticus nigripinnis (Serranidae)[1]	6	RA	PV	275.3	21.4	182.4	-	71.5	14.3 (11.8-16.9)	35.0
Cathorops steindachneri (Ariidae)[3]	5	D	ZB	271.0	-	-	271.0	-	21.0 (15.2-25.0)	36.0
Eleotris picta (Eleotridae)[4]	5	D	ZB	45.3	-	3.5	5.4	36.4	10.7 (8.2-13.5)	53.0
Hyporhamphus snyderi (Hemiramphidae)[1]	5	P	ZP	72.1	25.4	29.5	17.2	-	19.5 (19.0-19.9)	19.0

Table 2. (continued)

Species	*n*	SG	TG	Catch weight (g)					TL (cm)	Max TL (cm)
				Total	SD	SN	ND	NN	X (range)	
Eugerres brevimanus (Gerreidae)[1]	4	BP	ZB	16.7	11.6	-	3.2	1.9	7.1 (5.8-9.6)	32.0
Selene brevoortii (Carangidae)[1]	4	BP	ZB	52.6	-	2.1	50.5	-	14.0 (5.4-17.2)	42.0
Achirus mazatlanus (Achiridae)[1]	3	D	ZB	9.4	-	-	2.3	7.1	6.2 (5.5-6.8)	20.0
Epinephelus quinquefasciatus (Serranidae)[2]	3	RA	ZB	1252.4	-	-	354.2	898.2	28.6 (21.4-39.3)	250.0
Synodus scituliceps (Synodontidae)[1]	3	D	ZB	53.1	-	28.7	24.4	-	-	55.0
Cynoscion phoxocephalus (Sciaenidae)[2]	2	D	ZB	9.3	-	-	5.7	3.6	8.3 (7.7-8.9)	66.0
Lophogobius sp. (Gobiidae)[3]	2	D	ZB	7.1	1.7	5.4	-	-	6.5 (5.2-7.8)	11.0
Ophidion fulvum (Ophidiidae)[3]	2	D	ZB	31.4	21.1	-	-	10.3	14.7 (13.6-15.8)	18.0
Anchoa exigua (Engraulidae)[5]	1	P	ZP, HVP	0.7	-	-	-	0.7	5.9	7.5
Anchoa sp. (Engraulidae)[5]	1	P	ZP, HVP	1.6	-	1.6	-	-	6.8	-
Anchoa spinifer (Engraulidae)[5]	1	P	ZP, HVP	5.6	5.6	-	-	-	10.2	26.0
Batrachoides pacifici (Batrachoididae)[3]	1	D	ZB	402.9	-	-	-	402.9	30.2	43.0
Ctenogobius sagittula (Gobiidae)[3]	1	D	DV	0.5	-	-	0.5	-	5.2	20.0
Guavina micropus (Eleotridae)[3]	1	D	ZB	22.7	-	-	-	22.7	12.6	11.5
Lutjanus aratus (Lutjanidae)[1]	1	RA	ZB	238.8	-	238.8	-	-	24.7	100.0
Pisodonophis daspilotus (Ophichthidae)[3]	1	D	ZB	87.8	87.8	-	-	-	47.0	68.0
Total	**2993**			**106153.7**	**26331.8**	**29682.6**	**22170.4**	**27968.9**		

* considered as *Sciades seemanni* by Marceniuk et al. (2012).

[1] Marine estuarine-opportunist

[2] Marine estuarine-dependent

[3] Estuarine residents

[4] Freshwater migrants

[5] Marine stragglers

The individual-based rarefaction curves indicated that the observed number of species (S_{obs}) for the creeks with low salinity (26 and 27 for L1 and L2, respectively) was lower than the observed number of species in the creeks with medium salinity (35 and 37 for M1 and M2, respectively; Figure 9). The Chao1 species richness estimator (S_{Chao1}) stabilized for three of the four creeks (M1 at 39 spp., L1 and L2 at 27 spp.) well before all the individuals were collected in these creeks. Only creek M2 did not show an asymptote as the S_{Chao1} continued to increase until the final number of individuals was collected, resulting in a final mean number of 53 species and the largest number of singleton species (11 spp. represented by a single individual). The overlapping number of species for all creeks at the lower number of individuals collected at creek L1 (277 individuals) indicates a considerable density effect with creeks in the low salinity zone having less individuals than creeks in the medium salinity zone. Therefore, mangrove creeks with low salinities have lower species density, but not necessarily less species richness than mangrove creeks with medium salinities (see Gotelli & Colwell 2001, for explanation of this species density artifact). A relatively even fish assemblage was found in the intertidal mangrove creeks of Bahía Málaga. The shape of the SAD using individual abundance as a currency resembled that of a log-normal distribution (Figure 10).

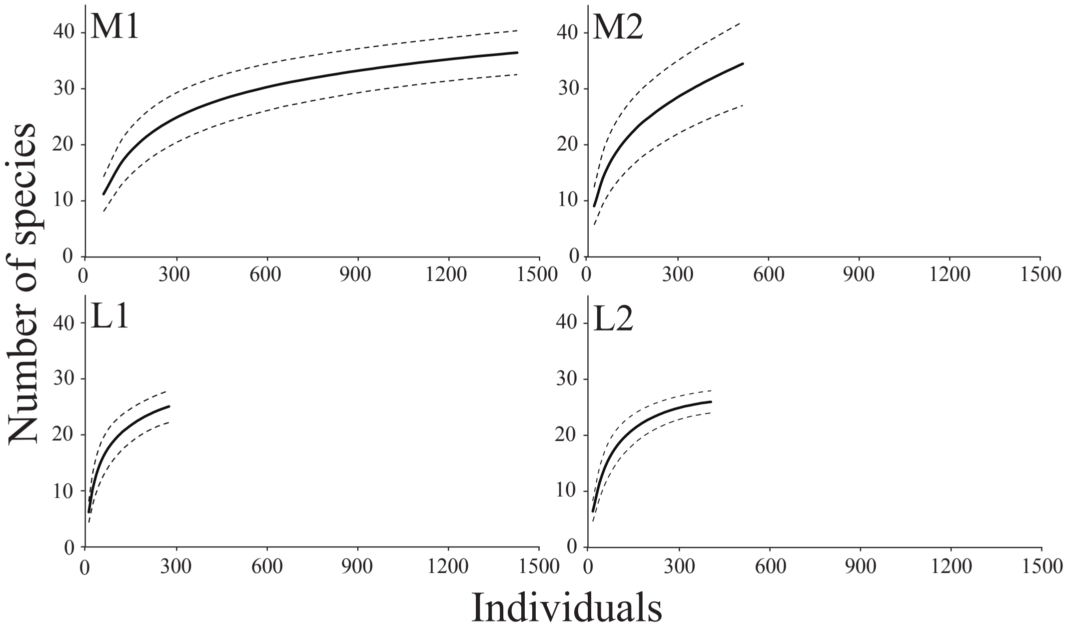


Figure 9. Individual-based rarefaction curves of mangrove creek fish species from medium-salinity creeks (M1 and M2), and low-salinity creeks (L1 and L2) sampled from December 2009 – November 2010 in Bahía Málaga, Colombia, Tropical Eastern Pacific. Dashed lines indicate 95% confidence intervals.

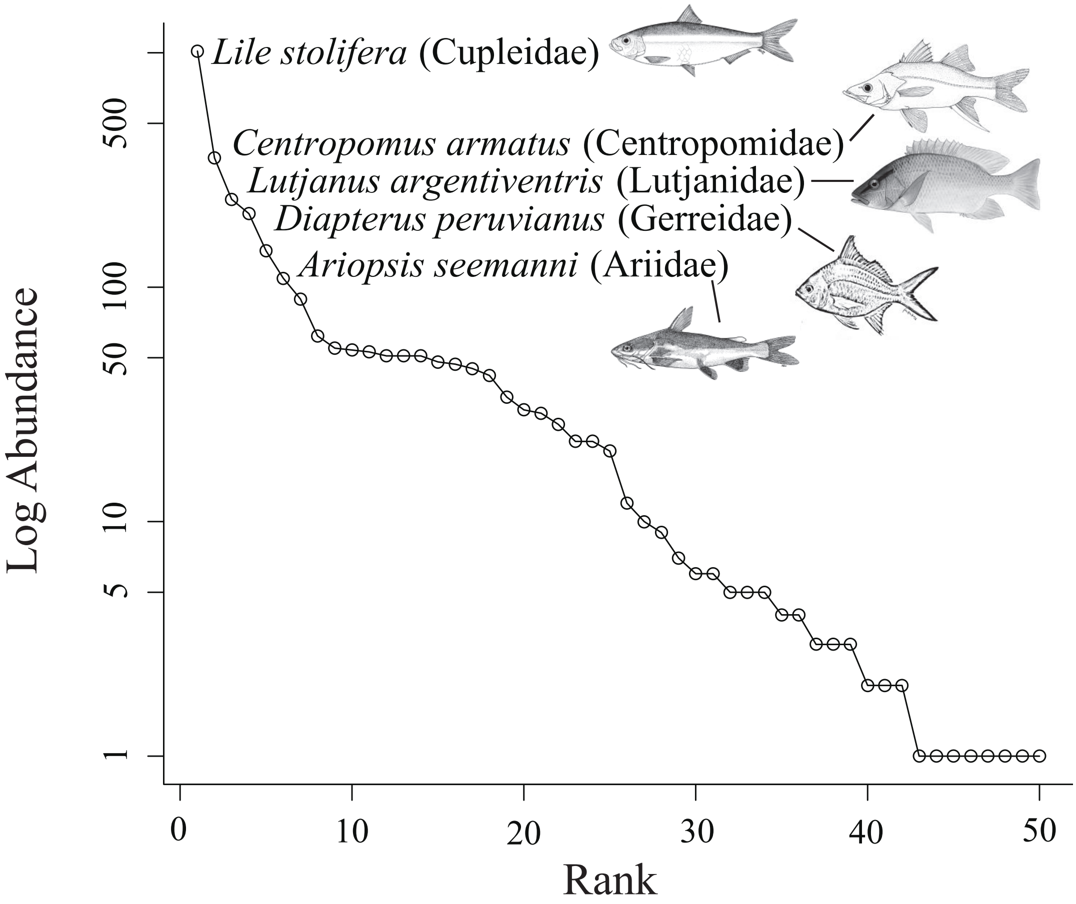


Figure 10. Rank-abundance plot of intertidal mangrove fishes captured in Bahía Málaga, Tropical Eastern Pacific during one year (2009-2010).

Tide-, diel- and salinity-related patterns

The temporal niche axis of the mangrove fish assemblage in Bahía Málaga was divided by a combination of the tidal magnitude and the diel cycle. Most zoobenthivores species had higher catch weights during the neap and spring tides occurring at nights (i.e. *C. armatus*, *L. argentiventris*, *A. seemanni*). Catch weights of the most abundant species in the intertidal mangrove creeks of Bahía Málaga, the zooplanktivore clupeid *L. stolifera*, was highest only during spring tides, at both day and night. The zoobenthivore pufferfish *S. rosemblatti* had higher catch weights during days at spring and neap tides. The catch weights of the piscivore species of the family Carangidae (*C. caninus*, *C. sexfasciatus*, and *O. altus*) were especially high during days at both spring and neap tides (Table 2).

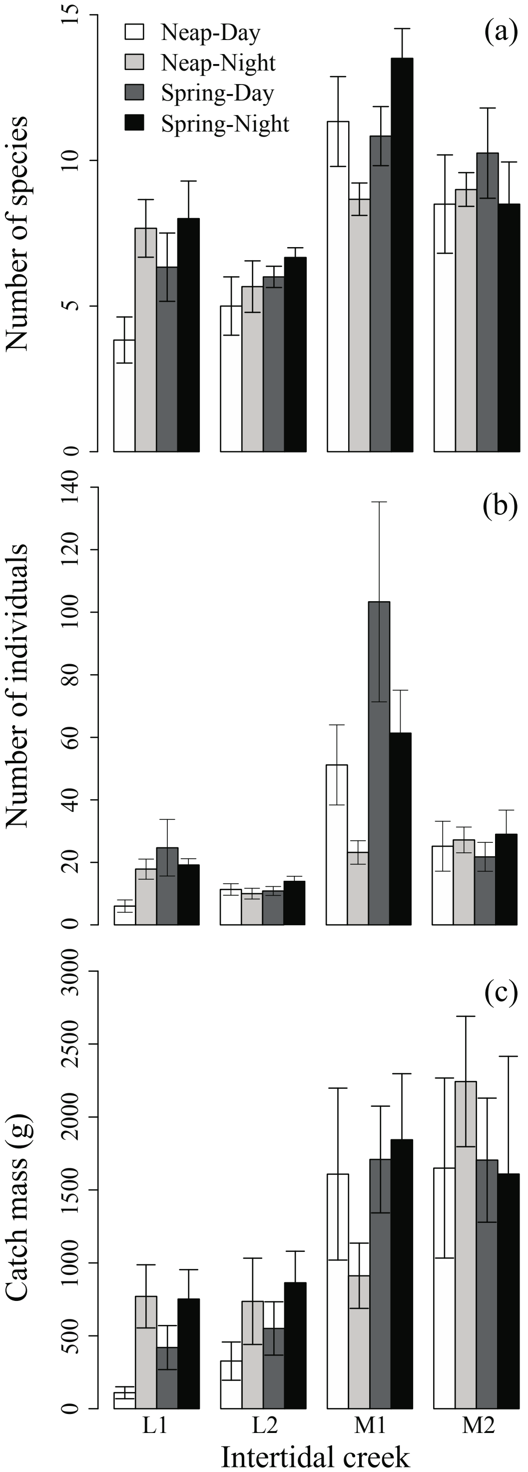


Figure 11. (a) Mean number of species, (b) abundance (number of individuals) and (c) catch mass (±SE) per block net sample in four intertidal mangrove creeks (M1, M2 and L1, L2) during Spring tide – Day (SD), Spring tide – Night (SN), Neap tide – Day (ND) and Neap tide – Night (NN) in Bahía Málaga, Tropical Eastern Pacific (2009-2010).

Species richness differed significantly between salinity zones (t = -6.8697, p-value < 0.0001), with medium salinity creeks (M1 and M2) having consistently more species than low salinity creeks (L1 and L2). Mean species richness did not differ significantly between tide-time of day ($F_{3,88}$ = 1.5018, p-value = 0.2197; Figure 11a) or between months (repeated measures ANOVA, $F_{11,68}$ = 0.926, p-value = 0.521). Mean fish abundance was significantly different between creeks (K = 40.6265, p-value < 0.0001, Figure 11b), with the highest abundance values in medium salinity creeks and the lowest values in the two creeks with the lowest salinity. Mean catch weight also varied significantly between salinity zones, with higher values in medium salinity than in low salinity creeks (salinity factor, W = 390, p-value < 0.0001; Figure 11c). Abundance and catch weight, however, were not significantly different between levels of the tide-time of day factor (K = 4.6392, p-values = 0.2002, for abundance; and K = 5.112, p-value = 0.1638 for catch weight; Figure 11b, c) or between months (K = 12.4499, for abundance, and K = 15.8155, p-value = 0.1481, for catch weight).

Mean overall fish density (± SD) was 0.013 ±0.016 ind. m^{-2} (range: 0.0666-0.0007) or 0.021±0.026 ind. m^{-3} (range: 0.106-0.001). Mean overall fish biomass (± SD) was 0.515±0.657 g m^{-2} (range: 2.852-0.008) or 0.851±1.194 g m^{-3} (range: 5.925-0.001). Both fish density (W = 1894, p-value < 0.0001) and biomass (W = 1823, p-value < 0.001) were significantly higher in medium salinity than in low salinity zones (Figure 12). Catch weights for each creek were always higher during the wet than during the very wet season. These differences, however, were not statistically significant (Figure 13).

The PERMANOVA test showed significant effects for the factors salinity zone, tide – time of day and month; and for the interaction between salinity zone x time of day and salinity zone x month (Table 3). The PERMDISP routine, however, indicated that these results should be taken with caution due to artefacts introduced by multivariate dispersion in the case of the factor tide – time of day ($F_{3,88}$ = 8.62; p=0.0002) and salinity ($F_{1,90}$ = 4.63; p = 0.0437). Individual pairwise tests and visual inspection of unconstrained ordinations (nMDS) showed that for the factor tide – time of day, only samples from the neap-day combination were particularly overdispersed (average Bray-Curtis distance-to-centroid = 57%). Unconstrained ordinations also indicated clear differences between samples from low salinities and medium salinities, despite distinctly different multivariate variances (according to the PERMDISP test). The PERMDISP routine for the factor month was non-significant ($F_{11,80}$ = 2.15; p = 0.0787, respectively), indicating that the differences shown in the PERMANOVA test were real. Most pairwise comparisons in the PERMANOVA test for the factor month, however, were non-significant, indicating that overall significant effects were only due to differences from a few samples from specific months (June and October).

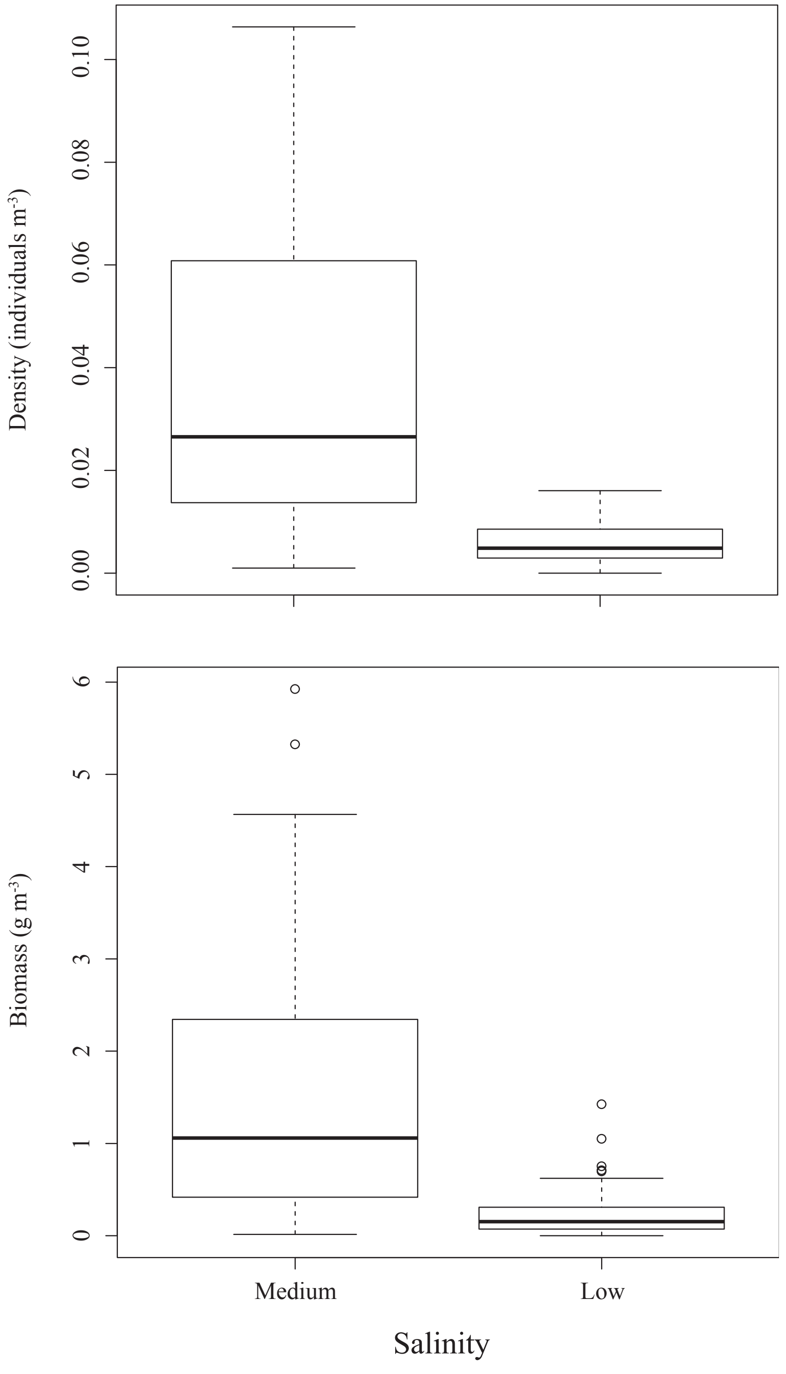


Figure 12. Boxplots showing differences in (a) density and (b) catch weight of intertidal mangrove creek fishes collected from a low and medium salinity zone in Bahía Málaga, Tropical Eastern Pacific. Bold lines indicate medians, hinges indicate the 25th and 75th percentiles, whiskers indicate the largest and smallest observation within a distance of 1.5 the box size and circle represent outliers.

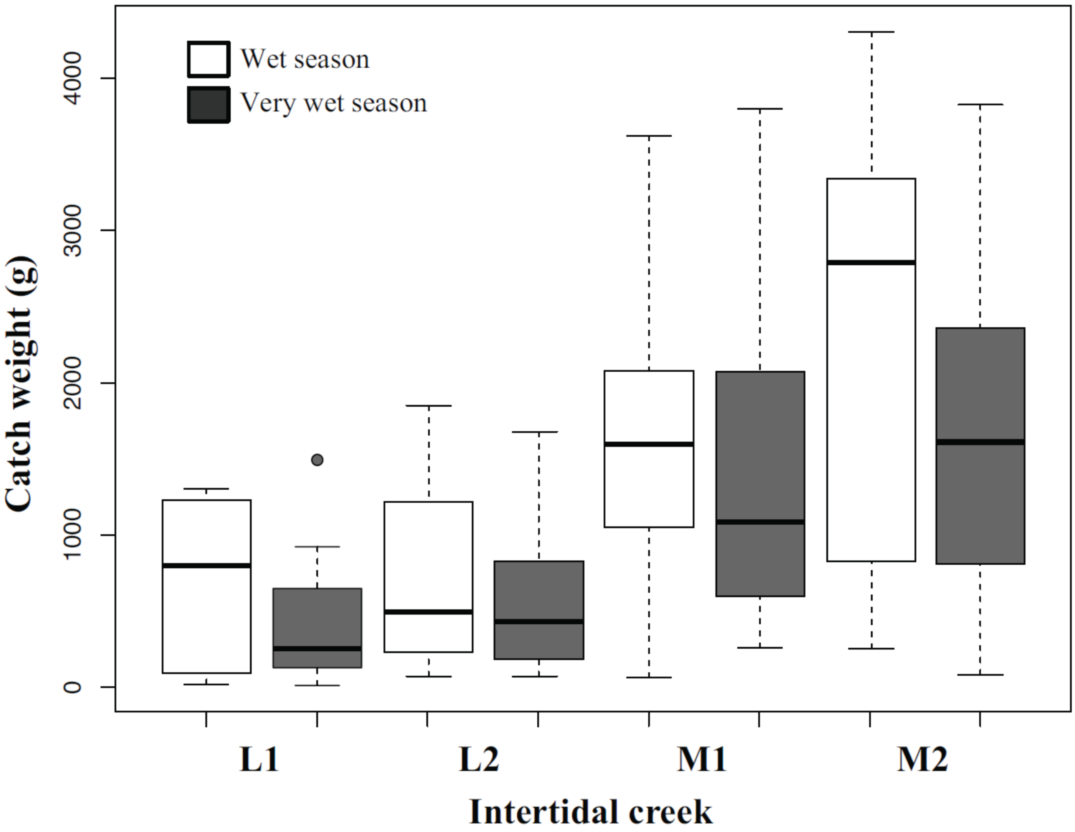


Figure 13. Boxplots of catch weight of mangrove fish assemblages per block net sample from four intertidal creeks (L1, L2, M1, M2) in Bahía Málaga, Tropical Eastern Pacific during wet (January-April) and very wet period (May-December) in 2009-2010. Bold lines indicate medians, hinges indicate the 25th and 75th percentiles, whiskers indicate the largest and smallest observation within a distance of 1.5 the box size and circle represent outliers.

Table 3. Results of a three-way model PERMANOVA testing the effects of salinity zone (medium vs low), tidal amplitude and time of day combination (spring day – SD, spring night – SN, neap day – ND, neap night – NN) and month (12 levels, repeated measures component) on mangrove creek fish assemblages in Bahía Málaga, Colombia, Tropical Eastern Pacific.

Source	**df**	**SS**	**MS**	**F**	**p**
Salinity zone	1	27149	27149	13.046	0.0001
Tide – time of day	2	16213	8106.4	3.8956	0.0001
Month	10	34805	3480.5	1.6726	0.0002
(Salinity zone) x (tide – time of day)	2	9206.1	4603.1	2.212	0.0012
(Salinity zone) x (month)	10	26581	2658.1	1.2774	0.0286
(Tide – time of day) x (month)	10	25858	2585.8	1.2426	0.0519
(Salinity zone) x (tide – time of day) x (month)	10	15157	1515.7	0.72836	0.9837
Residual	44	91561	2080.9		
Total	91	272100			

A deeper examination of the factors in the PERMANOVA test, with the CAP and PCO routines, showed that the factors salinity and tide-time of day could be discriminated (Figure 14, 15), but not the factor month. Overall leave-one-out allocation success was 72.8% for the factor tide-time of day (Table 4). Spring (day and night) were clearly separated from neap (day and night) tides along the CAP2 axis, whereas night samples were divided from day samples along the CAP1 axis, irrespective of the tidal magnitude (i.e. spring or neap; Figure 14). Three species (*A. seemanni*, *C. armatus* and *S. scapularis*) were strongly correlated with neap-night samples and one species (*L. stolifera*) was correlated with spring tide samples (both at day and night; Figure 15a).

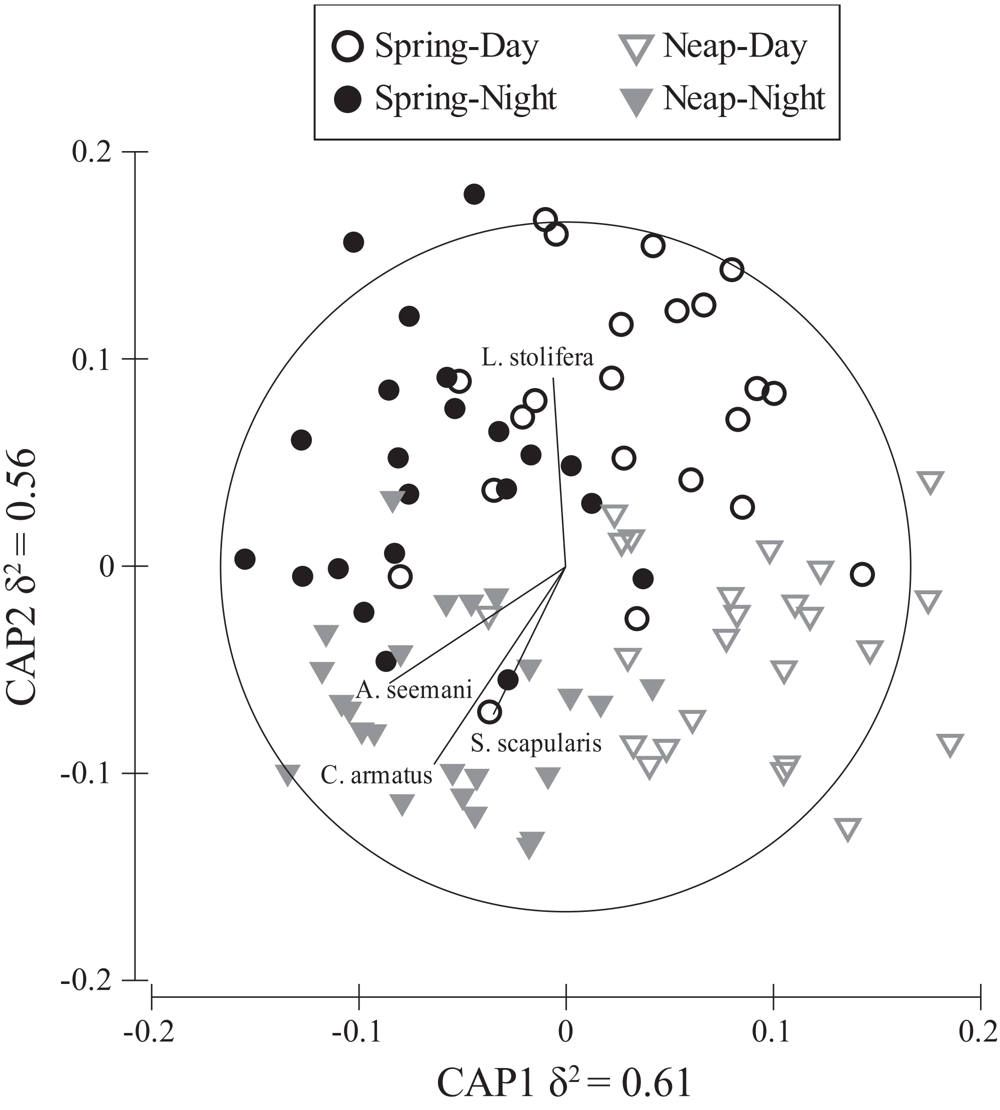


Figure 14. Canonical analyses of principal coordinates (CAP) of intertidal mangrove creek fish assemblages taken at different Tide-Time of Day combinations in Bahía Málaga, Tropical Eastern Pacific. Symbols represent individual block net catches and vectors represent correlation of individual species with CAP1 or CAP 2 axes.

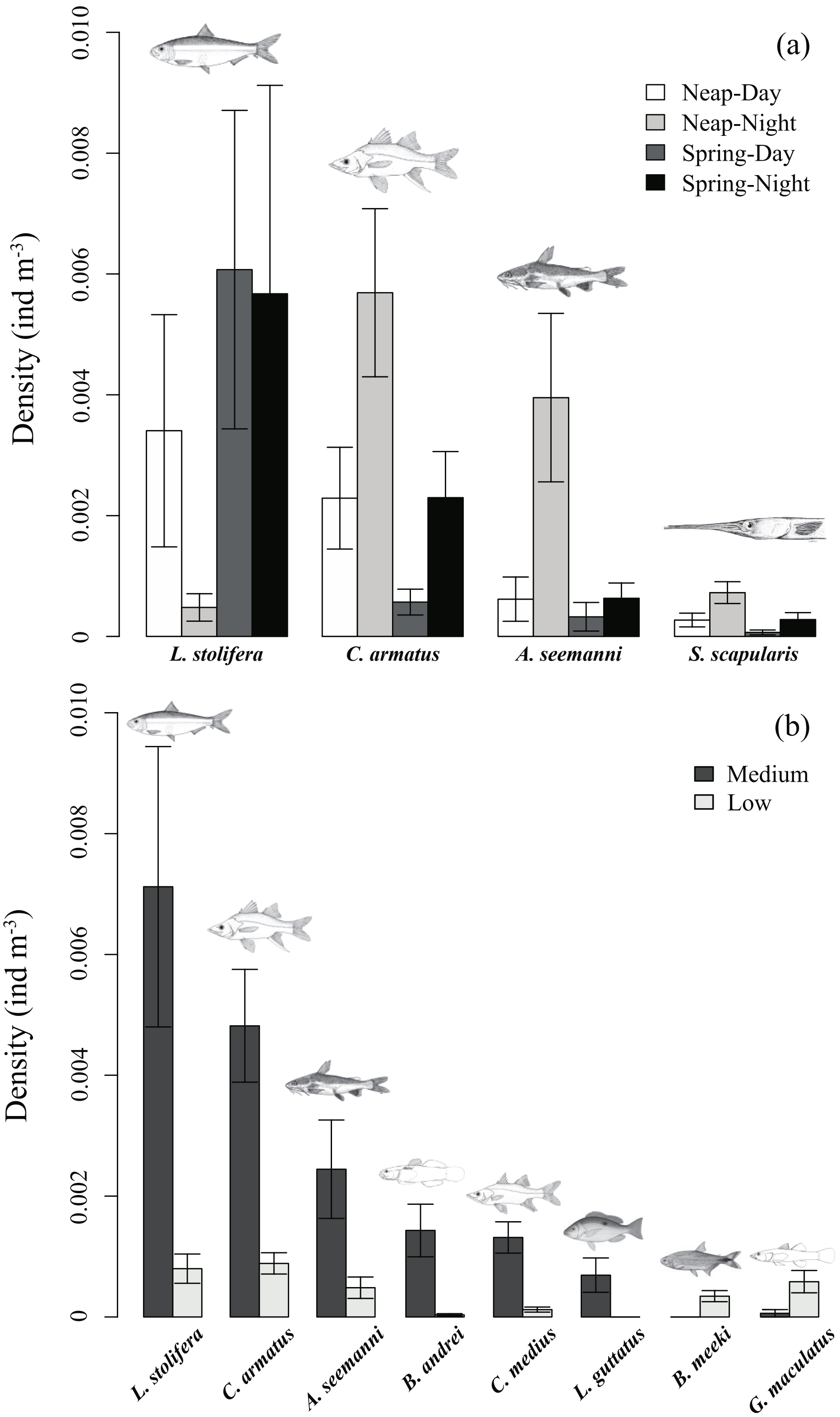


Figure 15. Mean density (±SE) of fish species responsible for differences in (a) Tide-Time of Day factor combinations, and (b) salinity zones in Bahía Málaga, Tropical Eastern Pacific.

Table 4. Results of canonical analysis of principal coordinates (CAP) testing the effect of tidal amplitude and time of day combination (spring day – SD, spring night – SN, neap day – ND, neap night – NN) on mangrove creek fish assemblages in Bahía Málaga, Colombia, Tropical Eastern Pacific.

Data	**m**	**%Var**	**Allocation success (%)**				**Total**	**δ^2**	**P**
			SD	SN	ND	NN			
Tide – time of day	7	63.63	63.6	63.6	83.3	79.2	72.8	0.605	0.0001

%Var = percentage of the total variation explained by the first *m* principal coordinate axes;
Allocation success = percentage of points correctly allocated into each group;
δ^2 = square canonical correlation

Overall leave-one-out allocation success for the factor salinity was high (93.48%) with few misallocations between medium and low salinity samples (Table 5). An unconstrained ordination (PCO, Figure 16) showed that samples from low and medium salinities could be differentiated and that two species were especially correlated with low salinities (*B. meeki* and *G. maculatus*) and at least 11 species were correlated with medium salinities (Figure 15b, 16).

Table 5. Results of canonical analysis of principal coordinates (CAP) testing the effect of salinity zone (medium vs low) on mangrove creek fish assemblages in Bahía Málaga, Colombia, Tropical Eastern Pacific.

Data	**m**	**%Var**	**Allocation success (%)**		**Total**	**δ^2**	**P**
			Medium	Low			
Salinity	17	98.24	88.64	97.92	93.48	0.755	0.0001

%Var = percentage of the total variation explained by the first *m* principal coordinate axes;
Allocation success = percentage of points correctly allocated into each group;
δ^2 = square canonical correlation

Finally, the CAP analysis was not able to reliably allocate samples according to the factor month. Overall leave-one-out allocation success was 18.5% with most of the months having an allocation success of < 30% (Table 6). This indicates that despite having a significant difference in the PERMANOVA test for the factor month, samples were not easily distinguishable from each other.

Combined results from the PERMANOVA and CAP routines showed that the factors salinity and tide-time of day drive changes in the structure of the intertidal mangrove fish assemblage in Bahía Málaga. Examination of unconstrained plots for these two factors shows a clear separation between the samples, despite differences in multivariate dispersions between groups. Month, despite being significant for the overall PERMANOVA test, was not identified as a reliable factor that could separate samples based on *a posteriori* pairwise comparisons and the CAP ordination.

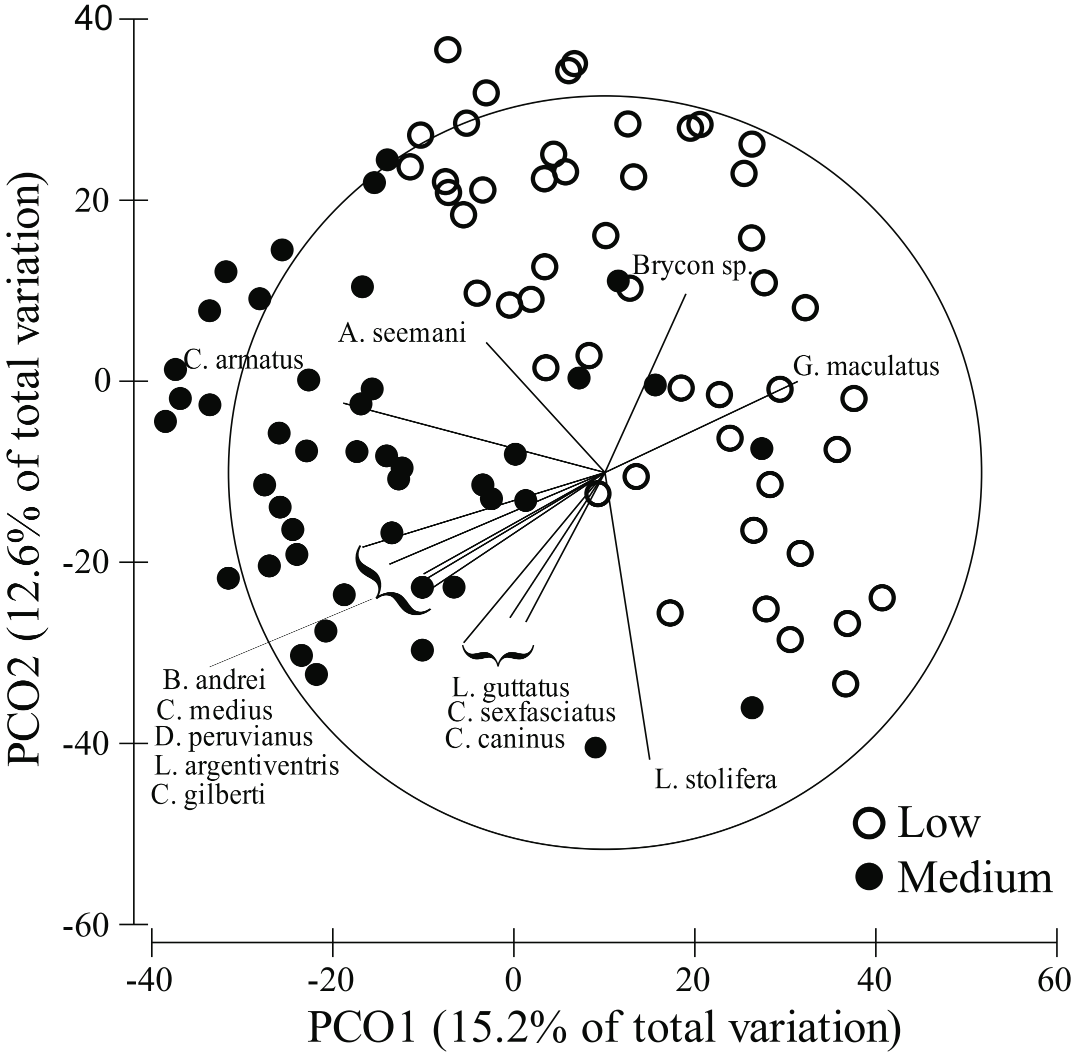


Figure 16. Principal coordinate analysis ordination (PCO) of intertidal mangrove creek fish assemblages in Bahía Málaga, showing variation between low and medium salinity zone. Species in vectors have high correlation (> 0.4) with axes. Symbols represent individual block net catches and vectors represent correlation of individual species with CAP1 or CAP2 axes.

Table 6. Results of canonical analysis of principal coordinates (CAP) testing the effect of month (Dec 2009 – Nov 2010) on mangrove creek fish assemblages in Bahía Málaga, Colombia, Tropical Eastern Pacific.

Data	m	% Var	Allocation success (%)												Total	δ^2	P
			Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov			
Month	16	95.9	17	13	0	25	25	0	13	38	13	13	38	25	18.5	0.77	0.0001

%*Var* = percentage of the total variation explained by the first *m* principal coordinate axes;
Allocation success = percentage of points correctly allocated into each group;
δ^2 = square canonical correlation

DISCUSSION

The study provides strong evidence that fish inhabiting intertidal mangrove forests in macrotidal areas establish their niches along temporal scales subject to the interaction of tidal and diel cycles. The endogenous circadian rhythm of the fish (diel cycle) interacts with the spring – neap tide cycle, enabling coexistence of a set of species using the intertidal mangroves. The study also provides the first evidence of the influential role of salinity on fish assemblage structure in the wettest mangrove area of the Neotropics. Additionally, we suggest that the trend in fish biomass reduction in mangroves of Bahía Málaga during the rainiest months (August-November), although weak, could be related to the notable freshening of the system at the end of the year.

The composition of the fish faunas observed in this study, in comparison to other studies in the TEP and similar macrotidal areas of the western central Atlantic (i.e. northern Brazil), is similar at the family level. Mangrove fish assemblages in the TEP are dominated by Gerreidae, Clupeidae, Engraulidae, Mugilidae and Centropomidae (Castellanos-Galindo et al. 2013). All these families were also abundant in the present study with the exception of Engraulidae and Mugilidae. Similarly, mangrove creek fish assemblages in the macrotidal areas of northern Brazil are dominated in catch weight by Ariidae and Tetraodontidae (Barletta et al. 2003, Krumme et al. 2004, Giarrizzo & Krumme 2008, Castellanos-Galindo & Krumme 2013). In our study area, both Ariidae and Tetraodontidae ranked among the first three families in terms of catch weight. Lutjanidae is the most important family in the intertidal mangroves of Bahía Málaga, an indication of the unique environmental configuration of this coastal area. From the earliest life stages of the Lutjanidae, the fish move between the mangroves and the rocky subtidal habitats in Bahía Málaga. The yellow snapper *L. argentiventris* is a particularly well-known example in the TEP which shifts its ontogenetic habitat between mangroves and rocky reefs (Aburto-Oropeza et al. 2009).

Effects of salinity on fish assemblage composition

Our results indicate that the fish biomass in intertidal mangroves can be substantially affected by salinity. Salinity has been demonstrated to be one of the major determinants of the dynamics of estuarine mangrove fish assemblages (Cyrus & Blaber 1992). Extremely high precipitation producing high runoff through the subtidal channels is the main driver of salinity changes in Bahía Málaga. Creeks located in low salinity zones had significantly lower number of species, fish densities and biomasses than creeks in medium salinity zones. This is partly explained by the lack of tolerance of most coastal-marine fish species to long-term low salinities in the upper reaches of the estuary (Sheaves 1998), but is also explained by the lack of a regionally diverse and abundant freshwater fish fauna in a very small drainage system that could compensate for the absence of estuarine and marine fishes in the upper estuary (North Andean Pacific slopes; Abell et al. 2008). In contrast, Barletta et al. (2005) found in the main channel of the Caeté River (North Brazil) the highest number of species and greatest biomasses in the upper estuary (lower salinities). This pattern was explained by higher biomasses of a single estuarine species (Sciaenidae), but also by a significant contribution of freshwater-related catfishes (i.e. Aspredinidae, Auchenipteridae, Pimelodidae) in a region where the freshwater fish fauna is rich and abundant. Therefore, it seems likely that low numbers and biomass of fish species in the upper estuaries in different parts of the world (tropical Australia, West Africa; Sheaves 1998, Simier et al. 2006) can be explained by the lack in tolerance of most estuarine and marine fish species to long-term low salinity values, but also to the depauperate freshwater fish fauna of these regions.

Tide-related patterns

Fish species-specific tide- and diel-related patterns were clearly observed and closely resemble those observed in other macrotidal mangrove systems in the Neotropical area (i.e. North Brazil; Krumme et al. 2004). Similar patterns in intertidal use that were also consistent across taxonomic groups involve the families Ariidae and Tetraodontidae. Catch weights of Ariidae in Bahía Málaga and North Brazil were consistently higher at night. In northern Brazil, however, catch weights for this family were higher at spring tide. In Bahía Málaga, catch weights of Ariidae were higher at neap tide night compared to spring tide night. For Tetraodontidae, important species both in Brazil and Colombia (*Colomesus psittacus* and *S. rosenblatti*, respectively) were more abundant during the day at both spring and neap tide. Regardless of taxonomic affinity, the zoobenthivorous trophic guild had higher catch weights at night in the Colombian and Brazilian mangroves. This may be the result of a higher level of activity of their potential prey (predominantly shrimp) at night (e.g. Vance 1992). Very abundant Centropomidae in Bahía Málaga had higher catch weights at night both during the spring and neap tides. Similarly, in estuarine systems of north-eastern Australia, *Lates calcalifer* (Latidae, closely related to Centropomidae) was found to be extremely abundant during night in the mangroves (Ley & Halliday 2007). Finally, piscivores belonging to Carangidae presented their highest catch weights in Bahía Málaga during the day at both spring and neap tides, very similar to Carangidae as shown in Ley & Halliday (2007). Similarities in the diel and tidal patterns in taxonomically related species across mangroves in different areas indicate the existence of a phylogenetic signal related to foraging strategies. This phylogenetic signal, however, seems to be influenced by the ecological and environmental features specific to a particular mangrove system.

The total catch weight and species richness in our study area was not significantly influenced by tidal magnitude or the diel pulse interaction (SD, SN, ND, NN). These results do not agree with results obtained in a macrotidal mangrove system in northern Brazil (Krumme et al. 2004). In that system, Krumme et al. (2004) found that the number of species and catch weight of fish entering intertidal mangrove creeks was highest during spring tides (particularly at night), whereas at neap tide these numbers decreased considerably. In northern Brazil, mangrove progradation has occurred for the last 2000 years (Cohen et al. 2005) causing mangrove forests to grow in even higher elevation zones in relation to mean sea level. Consequently in northern Brazil mangrove forests are only flooded during spring tides, providing fish with greater accessibility to intertidal habitats and food sources. During neap tides the tidal creeks become flooded but the mangrove areas remain relatively dry at high tide; the reduced inundation of intertidal habitats means less foraging area for the fish.

At our study site in the TEP, *Rhizophora* trees feature impressive above-ground stilt root systems (often >5m high) on a mangrove floor that is usually located below the mean high water level and which is extensively inundated each tide (see Annex I, Supplemental Figure A1). As a consequence, mangroves are inundated at high tide during both spring and neap tides and fish have almost equal accessibility to food sources at high tide, irrespective of tidal magnitude. This difference in the interplay between geomorphological settings and the tidal pulse can possibly explain why tide-related patterns in the structure of intertidal mangrove fish assemblages can vary in strength. In regions where the mangrove floor is located above mean high water level, most of the mangrove area will be only available for foraging fish at spring tides (i.e. northern Brazil and other accretional mangroves). Therefore, foraging during spring tides would maximize prey availability for these fishes. In contrast, in regions where the mangrove floor is located below mean high water level, an almost equal extent of mangrove area will be available for fish at spring and neap tides (i.e. Colombian Pacific and other erosional mangrove regions). In this case, foraging during spring tides will not represent a significant increase of foraging grounds, thus resulting in a weak signal in tidal-related patterns in fish distribution. This geomorphological influence on fish habitat use has been acknowledged before for intertidal marshes (Kneib 1997), but has never been thoroughly considered when analyzing intertidal mangrove habitat use by fishes (but see Lugendo et al. 2007).

Mangrove fish productivity

Mean fish biomass and density estimates at our study site were strikingly low in comparison to the estimates from other mangrove creek systems in the world (Table 7). For example, mean biomass (g m^{-3}) was threefold higher in the intertidal mangrove creeks of northern Brazil compared to the values obtained from the TEP region. Studies from the relatively undisturbed areas in Australia also showed considerably higher densities. Huxham et al. (2004) estimated lower fish density values in Gazi Bay (Kenya) than those obtained from our study. Low values were attributed to: problems with the efficiency and location of the sampling method, overexploitation, intrinsic characteristics of the mangrove fish fauna of the region and differences in the predation refuge function of the mangrove system in Gazi Bay.

For Bahía Málaga, overfishing as a cause for low biomasses in mangrove fishes is unlikely because of the low human population density and minimal fishing activity compared to other areas of the world. The sampling method used in the present study is regarded as highly efficient to estimate fish biomass in vegetated intertidal creeks (Bozeman & Dean 1980). Some degree of underestimation of fish abundance and catch masses might have occurred especially at slack high water, when small fishes could have escaped to the main channel by swimming away from the net. Further experiments to estimate this potential bias will be needed.

Table 7. Comparison of the number of species, mean fish density and biomass estimates from different intertidal mangrove creek studies where block nets and stake nets have been used; studies sorted according to marine biogeographical regions and descending by density.

Study	**Number of species**	$\overline{X}$ **Density**	$\overline{X}$ **Biomass**	
		Ind m^{-2}	**g m^{-2}**	**g m^{-3}**
Tropical Indo-West Pacific region				
Indo-Polynesian province				
Luzon, Philippines (Roennbaeck et al. 1999)	37	5.1	10.4	-
Queensland, Australia (Robertson & Duke 1990)	92	3.5	-	10.9
Embley River, Australia (Vance et al. 1996)	55	0.83	3.9	-
Trang province, Thailand (Grinvalds & Krumme, unpubl. data)	117	0.02	0.2	-
Western Indian Ocean Province				
Gazi Bay, Kenya (Huxham et al.2004)	30	0.004	-	-
Western Atlantic region				
Caribbean province				
Rockery Bay-Florida, USA (Ellis & Bell 2013)	69	4.56	6.61	25.22
Brazilian province				
Curuça estuary, Brazil (Giarrizzo & Krumme 2007)	65	0.3	6.0	-
Caeté estuary, Brazil (Barletta et al. 2003)	49	0.11	2.06	-
Caeté estuary, Brazil (Krumme et al. 2004)	40	0.1	1.4	2.6
Eastern Pacific region				
Panamic province				
Bahía Málaga, Colombia (this study)	50	0.013	0.515	0.851

However, we assumed these losses to be minor and unlikely in explaining the low catch weight values obtained in this area. It can be that the low intertidal fish biomass and density can be attributed to differences in the productivity of the mangrove systems between biogeographical regions. This explanation was also proposed by Huxham et al. (2004) but ruled out, due to the similarity of the fish diversity in Gazi Bay compared to other mangrove systems. Nevertheless, diversity does not necessarily translate into a productive system. The intertidal mangrove creeks of northern Brazil with a similarly diverse fish assemblage to that in Bahía Málaga (ca. 50-60 species) sustain a higher biomass of second and third order consumers that can rely on a rich epifaunal biomass and nutrients that are recycled in the system (Saint-Paul & Schneider 2010). In contrast, in the megahumid Bahía Málaga epifaunal biomass and diversity is relatively low (Cantera et al. 1999), probably reflecting low nutrient supply from relatively short rivers draining a small pristine catchment area. This is likely to result in a system with very low productivity where fish biomass is naturally low.

Effects of an extreme precipitation regime

Our sampling campaign took place during an ENSO event of 2009-2011 and included a first period of a warm phase (El Niño; December 2009-April 2010) and a second period of a cold phase (La Niña; July – November 2010). Our results, however, cannot confirm any causal effects from ENSO on potential changes in mangrove fish assemblage structures because data is lacking on non-ENSO periods. Furthermore, the intra-annual variability in precipitation in this particular area is not significantly affected during ENSO years. In 2010, a wet period between January-July (400-550 mm month^{-1}), followed by a very wet period from August –November (700-1000 mm month^{-1}) was observed. This pattern, despite occurring during an ENSO period, lies within the normal historical inter-annual rainfall variability occurring in this area (see Annex I, Supplemental Figure A6 and Figure 8). Fish catch weights in intertidal mangroves during the very wet period were always lower (but non-significant) than those during the wet season. The extreme freshening of this mangrove system during the last five months of the year may have had adverse consequences on marine organisms (including fish) of this region as was observed on the Pacific coast of Panama (Valiela et al. 2012).

Conclusions

This study illustrates the complexity that can be encountered in the organization of mangrove fish assemblages in (neotropical) macrotidal areas. Despite similarities, which can be found in the way mangrove fish assemblages segregate along the temporal axis (tide- and diel-related patterns) between macrotidal regions, it is clear that specific patterns can change according to local environmental characteristics. When referring to the megahumid area of the Tropical Eastern Pacific, the geomorphological setting seems to play an important role influencing how fish use the mangroves according to the tidal cycles. Comparably important are the local precipitation regimes and the diversity and abundance of regional freshwater fish faunas. These two factors can explain the distribution of fishes along salinity gradients in mangroves and also help to understand differences in the productivity between geographical areas. The understanding of how fish use mangrove ecosystems, including how the mangrove nursery function varies across geographical areas, has increased over the last years (Sheaves 2012, Blaber in press); such knowledge, however, needs to be carefully interpreted in the light of local characteristics when extrapolation and equivalence from one system to another is attempted.

Supplementary data is given in Annex I

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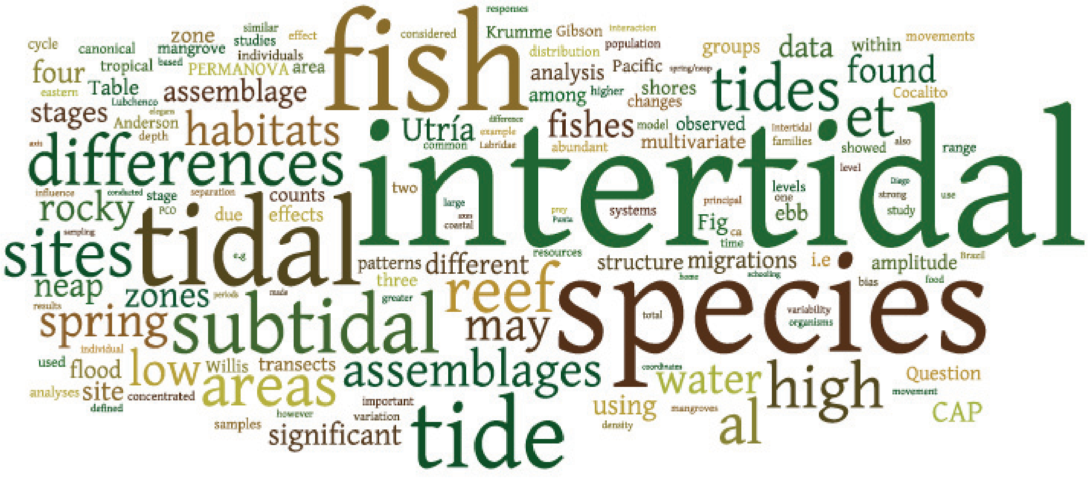
Chapter III. Tidal influences on fish distributions on tropical eastern Pacific rocky shores (Colombia)

Gustavo A. Castellanos-Galindo, Uwe Krumme and Trevor J. Willis



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ABSTRACT

On coasts with high tidal ranges fishes regularly establish linkages between subtidal and intertidal habitats via tidal movements, such that the home range incorporates habitat that is only intermittently available. To examine the responses of shallow-water reef fish assemblages to tidal water level changes in a macrotidal area of the tropical eastern Pacific, daytime underwater visual fish surveys were carried out in intertidal and subtidal zones at different tidal stages in the Utría National Park, Colombia. Labridae and Pomacentridae were the most abundant families, but species within these families changed between intertidal and subtidal zones. Of 106 species, >70% used the rocky intertidal zone. Benthic opportunistic reef species comprised ca. 85% of the intertidal migrants species, whereas the remaining 15% corresponded to ubiquitous reef and pelagic species. Little variation in subtidal and intertidal fish assemblages was observed between spring and neap tides, but there were large changes detected over the tidal cycle that were attributed to species-specific use of the intertidal zone at high tide. Intertidal fish assemblages comprised a defined sub-set of species that differed significantly from those of subtidal areas. Our data suggest that rocky intertidal habitats are alternative habitats for most reef fishes in Utría, but a few common species shifted more than 90% of their population into intertidal habitats during high tide, indicating that for those taxa, intertidal habitats provide important foraging opportunities. This may introduce a significant source of local-scale bias to density estimates of subtidal reef fishes, and reef fish monitoring programmes should specifically factor tidal state as a controlling influence in macrotidal areas.

Keywords: tidal migrations, rocky intertidal, reef fishes, tropical eastern Pacific, Utría

INTRODUCTION

Coastal shallow-water organisms show multiple movement patterns varying in space and time throughout their life cycles. Home range movements, defined as those undertaken by organisms routinely to feed, rest or defend a territory, constitute a significant part of these patterns. Two short-term cycles may influence coastal organisms' home range movements: tides and light intensity changes (Gibson 1992; Palmer 2000, Pittman & McAlpine 2003, Tolimieri et al. 2009). Although widely recognized as a force affecting coastal organisms, tides are often neglected in studies aimed at identifying processes responsible for spatial changes in coastal shallow-water community distribution (Gibson 1999).

Intertidal migrations by many fish species have been directly and indirectly demonstrated in different systems such as temperate sandy beaches (e.g. Ansell & Gibson 1990, Burrows et al. 1994), rocky shores (Rangeley & Kramer 1995, Faria & Almada 2006), salt marshes (Kneib 1997, Laffaille et al. 2000), tropical seagrasses (Robertson 1980, Dorenbosch et al. 2004) and mangroves (Krumme et al. 2004). Apart from intertidal migrations, fishes may use tides to move within and between habitats (Gibson 2003). Their tidal movements can either be considered migrations (*sensu* Dingle 1996) or opportunistic movements within a home range (Pittmann & McAlpine 2003). Unsworth et al. (2007) found no clear patterns in reef fish responses to tidal variability in an area of Sulawesi (Indonesia) with maximum tidal amplitude of 2.3 m. On the other hand, on reefs of Tulear (Madagascar), an area with semidiurnal tides and tidal ranges between 2-4 m, Vivien (1973) found that the fish response to daily tidal variability was species-specific, with groups of species that apparently did not show any response to tides and some other groups moving from deeper reef to inner reef zones at high tide. The varying results suggest the need for a more comprehensive understanding of the influence of tides on reef fish distribution in meso- and macrotidal areas of the world.

The ecological functions of fish intertidal migrations are commonly linked with benefits associated with increased food availability and a reduction in predation risk (Norton & Cook 1999, Gibson 2003). These benefits, however, may vary among different intertidal systems (i.e. mangroves, seagrasses and rocky shores). For example, on sandy beaches and rocky shores resources are concentrated around lower intertidal levels (Ansell & Gibson 1990, Lubchenco et al. 1984), whereas in mangrove forests, resources are concentrated around the above-ground root system at higher intertidal levels (Koch 1999). Sheaves (2005) suggests that due to the presence of abundant benthic prey and structural complexity, mangrove intertidal areas are unique habitats, where juvenile fish abundance and species richness are greater than in other shallow-water habitats.

The tropical eastern Pacific (TEP) is predominantly a meso and macro-tidal (range 2 - > 6 m) region where fish responses to tidal fluctuations have been poorly investigated. Most reef fish monitoring methodologies in the area (e.g. Garzón-

Ferreira et al. 2002) do not acknowledge the potential bias on density estimates that may arise from sampling at different tidal stages. This may confound comparisons between sites and considerably reduce the statistical power of between-treatment comparisons (Willis et al. 2006). Estimating the short-term temporal variability induced by tides in reef fish assemblages will help to better account for this potential systematic bias in experimental and monitoring studies.

Tidal influences on fish assemblages may arise from two sources of variability: the instantaneous effect of tidal state that controls the accessibility of intertidal habitats (flood, high, ebb, and low tide), and the amplitude of the tidal range (i.e. springs versus neaps) that controls the accessibility of higher shore habitats.

This study aims to identify the importance of tidal water level changes in reef fish distribution, and at the same time characterize the role that rocky intertidal areas might have as temporarily accessible habitats. Five specific questions were posed: (1) what is the fish species composition in rocky intertidal and subtidal habitats at four sites on the Colombian Pacific coast? (2) Are there differences in the structure of the fish assemblages in intertidal or subtidal zones over spring/neap cycles (tidal amplitude)? (3) Are there variations in the structure of subtidal fish assemblages over tidal stages (low, flood, high and ebb tide)? (4) At high tide, are there differences in the structure of fish assemblages between the rocky subtidal and the intertidal zones? (5) If significant variation with tidal state and/or amplitude is found, which species utilise intertidal habitats, and how important are these habitats to the local assemblage?

MATERIALS AND METHODS

Study area

The tropical eastern Pacific (TEP) extending from ca. 25° N to ca. 4° S (Robertson & Cramer 2009) is considered the most isolated marine biogeographical province of the world (Robertson et al. 2004). This isolation is due to the emergence of the Isthmus of Panama 3.1 Ma ago (Coates & Obando 1996) and a 5000 – 7000 km uninterrupted deep-water gap that has separated the province from the western and central Pacific for the past 65 million yr (Grigg & Hey 1992). The continental shelf along the province‘s coastline is very narrow with a mosaic of estuaries, mangrove forests, sandy beaches and rocky shores with few coral reef areas (Glynn & Ault 2000).

Utría is a national protected area in the Colombian Pacific (5°53‘ – 6°11‘N, 77°9‘ – 77°24‘W) that includes 15000 ha of seabed. The most conspicuous geological feature within the park is the Utría Sound, which is four km long and 800 m wide at low tide with a south-north orientation and average depth of 30 m (Figure 17). Rocky intertidal and subtidal shorelines constitute the predominant seascape of the park. Rains occur throughout the year with a small decrease during December -

April (annual precipitation: *ca.* 7 m). Tides are semi-diurnal with tidal ranges of ca. 2 – 3 m at neap and 3 to >4 m at spring tides, with flood and ebb tides being symmetrical.

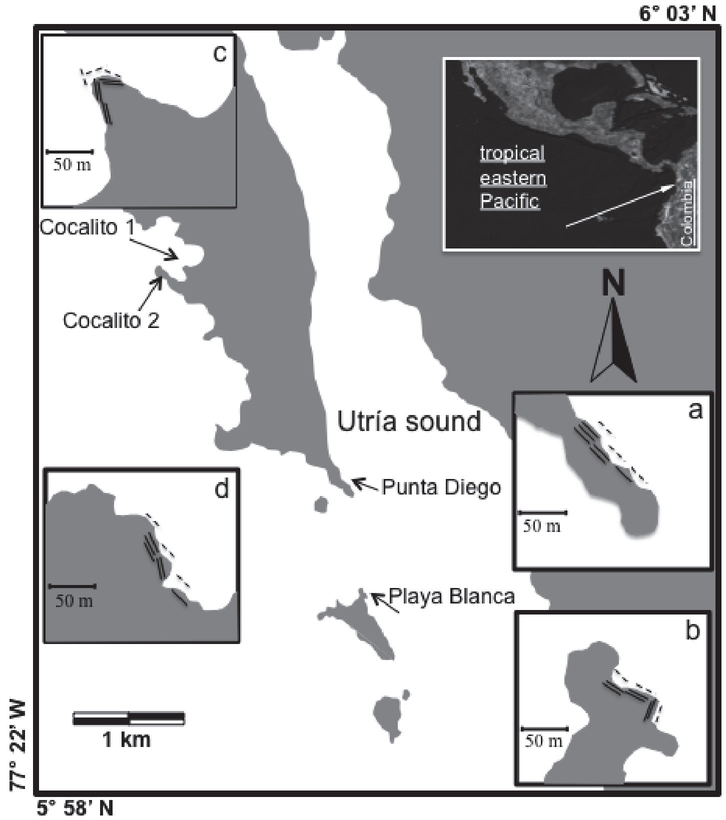

Figure 17. Map of the Utría Sound with its position within the tropical eastern Pacific. Location of intertidal (continuous lines) and subtidal transects (dashed lines) is indicated for each site: (a) Punta Diego; (b) Playa Blanca; (c) Cocalito 1; (d) Cocalito 2.

Sampling design

During a preliminary field trip to the Utría National Park in September 2007, several sites in the inner and outer part of the Sound were visited. Four sites were selected according to a qualitative assessment of similarities in intertidal and subtidal areas (depths, slopes, inundated intertidal areas, substratum cover; Figure 17). In a subsequent field trip in November, nine permanent 25 x 2 m transects at each of the four selected sites were established at neap tide and marked with painted stones (36 transects in total). Three transects were located at medium intertidal, low intertidal and subtidal zones using mean emersion time as a proxy of transect‘s intertidal height. Slack high and low water corresponded accurately to the tide tables from the nearest point (Bahía Solano; IDEAM 2006, 2007). Low intertidal transects were established in zones that could be surveyed three hours after slack low tide; medium intertidal transects were submerged one hour before slack high water (> 1 m water depth). Subtidal transects were established at water depths < 3 m at low tide. Replicate transects at the four sites were chosen attempting to be as similar as possible in substratum cover to avoid confounding effects of this factor.

From November to December 2007 and from the end of January to the beginning of March 2008, weekly UVCs were made at the four sites (one site per day) in the previously defined strip transects using snorkelling gear. Fish observations were made during most of the day-light tidal cycle covering low water, flood, ebb and high water periods. Sampling time during the week was selected according to the days with the greatest or lowest tidal amplitude during spring or neap tide periods, respectively (one or two days after each lunar phase). Due to the time delay of the tidal cycle with respect to the diel cycle, slack high water occurred between 9:00-11:00 at neap and between 15:00-17:00 at spring tides. Slack low water occurred between 15:00-17:00 at neap and between 9:00-11:00 at spring tides. Counts were restricted to when water transparency was >3 m. Reduced visibility was, however, infrequent and occurred when heavy rains preceded censuses or when material was suspended at some spring tidal stages.

Data treatment

We used PERMANOVA (permutational multivariate analysis of variance, Anderson 2001) to test hypotheses about differences in fish assemblages between sites, depth zones (intertidal vs subtidal, tidal stage (low water, flood, high water and ebb) and tidal amplitude (spring vs neaps). This “semi-metric MANOVA” constructs an analogue Fisher’s *F* test-statistic based on any measure of dissimilarity and obtains P-values using permutations. PERMANOVA, like ANOSIM and other similar multivariate tests may be sensitive to differences in the dispersion of points (analogous to heterogeneity of variance in univariate tests). Hence, the routine PERMDISP (a test of homogeneity of multivariate dispersion analogue to the univariate Levene’s test) was used to check that statistically significant differences between groups detected with PEMANOVA were not an artifact of differences in dispersion among groups (Anderson 2006, Anderson et al. 2008).

To visualize multivariate patterns revealed by PERMANOVA we used a combination of unconstrained and constrained ordination techniques: principal coordinates analysis (PCO, a parametric analogue of multidimensional scaling. The well-known Principle Components Analysis is a form of PCO that uses Euclidean distance as the distance measure) and canonical analysis of principal coordinates (CAP, Anderson & Willis 2003). CAP is a form of canonical discriminant analysis, based on any distance measure, that uses PCO axes to search for the vectors in multivariate space that maximize the differences among *a priori* defined groups. The species responsible for any differences were then identified based on the strength of their correlation with the canonical discriminant axes. All multivariate analyses were done using the PERMANOVA+ for PRIMER software (Anderson et al. 2008). The identities of species responsible for patterns were determined using correlations of the individual species variables with the PCO or CAP axes of the ordinations

(Anderson & Willis 2003). All multivariate analyses were based on Bray-Curtis distances calculated from square-root transformed data.

The five questions posed in the introduction were addressed as follows:

*Question 1: S*ite and depth zone differences were determined using a combination of descriptive statistics and CAP.

Question 2: The effects of tidal amplitude (neap vs spring tides) on fish assemblages in subtidal and intertidal habitats could not be tested using data collected over all four tidal stages, since intertidal data cannot be collected at low tide. Therefore, the effect of tidal amplitude was tested using data collected during flood tide, high tide, and ebb tide. Separate tests were done for intertidal and subtidal zones, because of large compositional differences in fish assemblages between the two zones (see Results). PERMANOVA analyses were conducted on square-root transformed data, treating the factor Site as a random effect. A canonical analysis of principal coordinates – CAP (Anderson & Willis 2003) was also used to examine differences in spring and neap tide data.

Question 3: Variation in the structure of fish assemblages with tidal stage was examined using a Site (four levels; random) × Stage (four levels: low water, flood, high water and ebb tide; fixed) model on subtidal transect data with the spring and neap tide data pooled. Since sites varied considerably in their composition, individual CAPs for tidal stage were performed for each site to observe in more detail the differences between tidal stages.

Question 4: Subtidal fish assemblages were compared to intertidal assemblages using a combination of PERMANOVA and CAP conducted on high tide data. The PERMANOVA was a two-way mixed model testing the effects of site (random effect) and zone (fixed effect). CAP was used to visualize differences between 8 groups (4 sites × 2 zones). Species responsible for differences along the CAP axes were determined as above, with those species having a frequency of occurrence > 0.2 and correlations > 0.4 considered to have made a significant contribution to the separation of groups (Anderson & Willis 2003).

Question 5: To determine the effects of tidal stage on counts of key fish species (identified from the CAP analysis of sites × zones), we used a generalized linear model to estimate differences in density of subtidal counts at high and low tide. Since count data are generally overdispersed and have heterogeneous variances (i.e., the standard deviation tends to increase with the mean), the data were modelled using a log-linear model structure assuming a Poisson distribution. These models express the counts, Y, as

$$Y \sim Poisson(\lambda)$$

where *Poisson*(λ) denotes a (possibly overdispersed) Poisson distribution with expected value of λ, and log(λ) is modelled as a linear function of the effects. For example, the count of a species in replicate *j* at site *i* and depth *k* is modelled by

$$\log(\lambda_{ijk}) = \alpha_i + \beta_k$$

where α and β denote effects due to site and depth, respectively. The right-hand side of this equation can be modified to include any interactions of interest. Log-linear model analyses were conducted using SAS.

RESULTS

Fish assemblage composition (Question 1)

We counted a total of 66846 fish from 106 species and 41 families in 661 transect observations (intertidal and subtidal). Nine families accounted for 52% of the total number of species: Carangidae, Haemulidae, Labridae, Lutjanidae, Muraenidae, Pomacentridae, Scaridae, Serranidae and Tetraodontidae. The most abundant species were *Thalassoma lucasanum*, *Stegastes acapulcoensis* and *Chromis atrilobata*, representing 48% of all the fish counted.

In 299 transects completed in intertidal areas, a total of 17836 fish were counted. 73 species grouped in 30 families were observed. Pomacentridae and Labridae were the most important families in number of species and individuals. *Thalassoma lucasanum*, *S. acapulcoensis* and *Halichoeres notospilus* accounted for most of the individuals (19%, 18% and 16%, respectively). Another three pomacentrids (*Abudefduf concolor*, *A. troschelii* and *Microspathodon bairdii*) were also abundant (Table 8).

Benthic reef species were found to be the most important component of the intertidal fish assemblage accounting for ca. 85% of the total abundance. The remaining 15% contained reef ubiquitous and pelagic species from the Kyphosidae (*Kyphosus elegans* and *K. analogus*), Mugilidae (*Chaenomugil proboscideus* and *Mugil curema*), Carangidae (*Caranx caninus* and *C. sexfasciatus*), Belonidae (*Tylosurus pacificus* and *T. crocodilus fodiator*) and Lutjanidae (*Lutjanus* spp.). Although individual size was not recorded during censuses, intertidal reef ubiquitous and pelagic species were generally larger than intertidal benthic reef species.

Table 8. Relative abundance (RA %), mean densities (individuals 50 m^{-2}) and frequency of occurrence (F) at intertidal and subtidal areas of the most representative fish species. Species sorted by their RA % in the intertidal area. The ten most abundant species in the whole assemblage (intertidal and subtidal) in bold.

Species	Subtidal			Intertidal		
	RA %	**Density (± SE)**	**F (%)**	**RA %**	**Density (± SE)**	**F (%)**
Thalassoma lucasanum[1]	21.32	26.14 ± 1.30	94.99	18.50	9.79 ± 1.09	41.78
Stegastes acapulcoensis[3]	15.94	20.43 ± 0.54	99.25	17.54	9.52 ± 0.47	92.06
Halichoeres notospilus[3]	2.23	3.12 ± 0.23	74.46	16.42	8.95 ± 0.33	95.94
Abudefduf troschelii[3]	2.07	3.02 ± 0.26	55.99	8.77	5.12 ± 0.64	58.46
Abudefduf concolor[3]	0.65	0.92 ± 0.11	35.78	6.98	3.89 ± 0.17	92.46
Microspathodon bairdii[3]	0.29	0.48 ± 0.08	19.27	4.66	2.94 ± 0.15	80.84
Chaenomugil proboscideus[2]	0.04	0.09 ± 0.06	1.37	4.60	3.22 ± 0.59	17.60
Kyphosus elegans[2]	2.98	4.19 ± 1.25	23.60	4.42	3.17 ± 0.65	45.19
Ophioblennius steindachneri[1]	1.28	1.80 ± 0.12	68.68	3.54	1.95 ± 0.20	42.11
Mugil curema[2]	0.19	0.37 ± 0.10	6.94	2.47	1.73 ± 0.30	17.92
Caranx sexfasciatus[2]	1.85	3.29 ± 0.70	11.80	1.70	1.64 ± 0.51	10.69
Caranx caninus[2]	0.49	0.89 ± 0.29	5.20	1.32	0.80 ± 0.31	8.05
Microspathodon dorsalis[1]	3.64	4.63 ± 0.38	60.69	1.13	0.73 ± 0.11	23.68
Holacanthus passer[1]	0.96	1.37 ± 0.08	61.65	0.91	0.59 ± 0.05	31.73
Chromis atrilobata[5]	18.81	25.05 ± 2.03	48.84	0.84	0.57 ± 0.27	2.42
Lutjanus argentiventris[2]	0.59	0.90 ± 0.08	42.62	0.55	0.40 ± 0.05	28.07
Johnrandallia nigrirostris[1]	0.77	1.19 ± 0.08	53.55	0.53	0.37 ± 0.04	26.93
Plagiotremus azaleus[1]	0.47	0.70 ± 0.06	35.35	0.38	0.27 ± 0.04	16.37
Arothron meleagris[1]	0.34	0.58 ± 0.04	39.10	0.37	0.27 ± 0.03	19.94
Stegastes flavilatus[1]	2.69	3.68 ± 0.21	72.69	0.36	0.29 ± 0.05	18.60
Canthigaster punctatissima[1]	5.01	6.19 ± 0.33	85.95	0.35	0.31 ± 0.04	21.24
Sargocentron suborbitalis[1]	1.22	1.60 ± 0.17	40.40	0.35	0.28 ± 0.05	16.62
Epinephelus labriformis[1]	0.86	1.24 ± 0.07	59.09	0.23	0.21 ± 0.03	16.67
Cephalopholis panamensis[1]	1.27	1.75 ± 0.09	72.82	0.17	0.15 ± 0.02	13.30
Haemulon sexfasciatum[1]	0.84	1.18 ± 0.50	10.60	0.12	0.10 ± 0.03	5.96
Halichoeres chierchiae[5]	1.12	1.66 ± 0.11	67.54	0.06	0.06 ± 0.02	4.21
Halichoeres nicholsi[5]	1.31	1.97 ± 0.10	73.03	0.05	0.05 ± 0.01	3.89
Cirrhitichthys oxycephalus[5]	0.84	1.23 ± 0.09	49.01	0.02	0.02 ± 0.01	1.30
Haemulon maculicauda[5]	1.53	2.32 ± 0.37	17.55	0.01	0.01 ± 0.01	0.59

Categories described in text: [1]Opportunistic reef species; [2]Mid-water species; [3]Permanent reef species; [5]No response to tides

Other less abundant taxa in decreasing abundance: *Malacoctenus* sp., *Tylosurus pacificus, Cirrhitus rivulatus, Scarus ghobban, Tylosurus crocodilus fodiator*, *Sufflamen verres, Caranx caballus, Lutjanus novemfasciatus, Chaetodon humeralis, Acanthurus xanthopterus, Bodianus diplotaenia, Mulloidichthys dentatus, Kyphosus analogus, Prionurus laticlavius, Scarus rubroviolaceus, Lutjanus aratus, Diodon hystrix, Scarus perrico, Scarus compressus, Gymnomuraena zebra, Halichoeres dispilus, Myripristis leiognathus, Ostracion meleagris meleagris, Pseudobalistes naufragium, Arothron hispidus, Axoclinus lucillae, Fistularia commersonii, Rypticus bicolor, Zanclus cornutus, Echidna nebulosa, Hypsoblennius brevipinnis, Muraena lentiginosa, Pomacanthus zonipectus, Acanthemblemaria hancocki, Aetobatus narinari*, *Scorpaena mystes*, *Seriola rivoliana, Anisotremus caesius, Canthigaster* cf. *janthinoptera, Coralliozetus springeri, Diodon holocanthus, Echidna nocturna*, *Gerres simillimus*, *Mycteroperca xenarcha*.

Twenty-seven species were found at all the four intertidal sites sampled, indicating their status as regular visitors. In contrast, 30 species were seldom found in these intertidal sites (<10 individuals) having low frequency of occurrence, and can be considered as accidental visitors (Table 8). Other species were abundant in the intertidal areas at single sites (i.e. *Caranx sexfasciatus* and *Tylosurus pacificus*) suggesting site preferences of these species.

Fish assemblage variation over spring/neap tides (Question 2)

Analysis of the effect of tidal amplitude was based on three (high tide, ebb tide, and flood tide) of the four tidal stages, since data cannot be collected at low tide in the intertidal zone. In subtidal zones, the PERMANOVA analysis showed significant differences in fish assemblages among sites, but not between spring and neap tides (Table 9). This was further confirmed by the canonical analysis of principal coordinates, which showed little differences between spring and neap tide multivariate data (Table 10).

Table 9. Results of two-way mixed model PERMANOVAs testing the effects of tidal amplitude (Springs vs Neaps) on Utría subtidal and intertidal reef fish assemblages at 4 sites (Site is treated as a random effect and Amplitude as a fixed effect). Subtidal samples were pooled omitting low tide observations. Data from surveys carried out from November 2007 – March 2008.

Subtidal					
Source	*df*	SS	MS	*F*	P
Site	3	96445	32148	29.26	0.0002
Amplitude	1	1694	1694	1.24	0.2676
Site × Amplitude	3	4134	1378	1.25	0.1214
Residual	279	306510	1098		
Total	286	410470			

Intertidal					
Source	*df*	SS	MS	*F*	P
Site	3	99150	33050	30.18	0.0002
Amplitude	1	4346	4346	1.76	0.0089
Site × Amplitude	3	7568	2523	2.30	0.0002
Residual	241	263920	1095		
Total	248	377230			

Table 10. Results of canonical analysis of principal coordinates (CAP) testing the effect of tidal amplitude (Springs vs Neaps) on Utría subtidal reef fish assemblages.

Data	**m**	**%Var**	**Allocation success (%)**			**δ^2**	**P**
			Neap	Spring	Total		
Subtidal	20	95.34	62.09	56.18	59.17	0.1252	0.0004
Intertidal	15	97.38	56.74	67.59	61.45	0.173	0.0002

%Var = percentage of the total variation explained by the first *m* principal coordinate axes;
Allocation success = percentage of points correctly allocated into each group;
δ^2 = square canonical correlation

The overall leave-one-out allocation success in the discriminant analysis was 59.2%, which is very near a value suggesting a random distribution of samples (50% allocation success) when considering only two groups (spring and neap). Hence, fish assemblages of subtidal transects did not differ consistently between spring and neap tides. In the intertidal zone, the effects of Site and Amplitude were both statistically significant, as was the interaction between them (Table 9). Variation in multivariate dispersion was not the cause (PERMDISP, p>0.15 at all four sites), so sites were subjected to PCO ordination separately, which showed that there were differences between spring and neap tides at Cocalito 1, some differences at Cocalito 2, but no difference at the remaining two sites (Figure 18), which explains the significant interaction term. The Amplitude difference at both Cocalito sites was primarily due to higher densities of *Mugil curema* found in intertidal habitats during neap tides (see biplots overlaying, Figure 18). These differences were reflected in the CAP analysis which returned a somewhat higher allocation success to spring tides (Table 10). Hence, differences between spring and neap tide intertidal assemblages were only observed at two sites on which the presence of a single species accounted for most of the variation at neap tides.

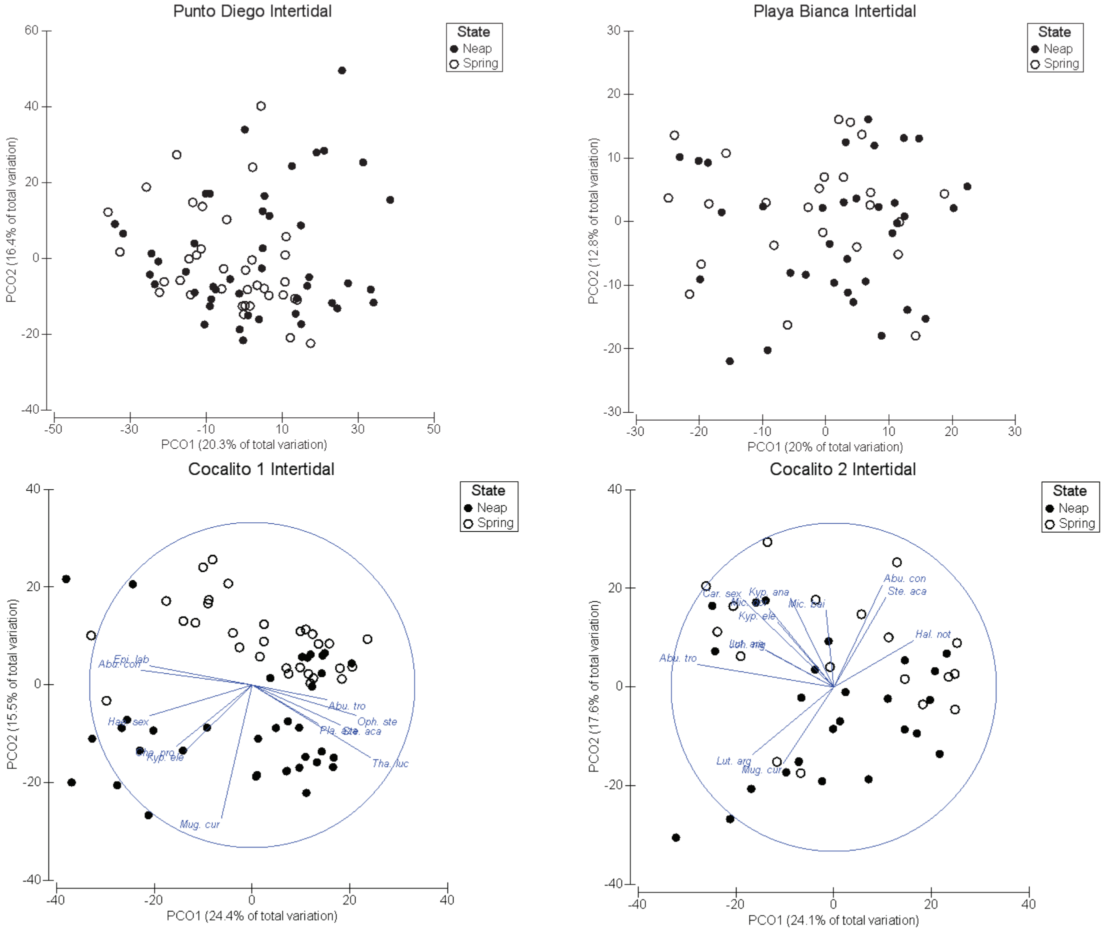

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Figure 18. Principal coordinates analysis (PCO) ordinations of intertidal fish assemblages at four sites during high tide showing variation between neap and spring tides.

Subtidal fish assemblage variation with tidal stage (Question 3)

A 2-way mixed-model PERMANOVA using subtidal data (4 sites × 4 tidal stages; tidal amplitude was omitted on the basis of the result above) showed significant differences in fish assemblages at different tidal stages and different sites (with no interaction between these two main effects, Table 11). This was indicative of consistent differences in fish assemblages between tidal stages regardless of site. Pairwise comparisons indicated that the main differences were observed between high-flood and low-ebb combinations of tidal stages. These results were confirmed by the individual CAPs for each site (Figure 19). At two sites (Punta Diego and Playa Blanca) low water and ebb tide samples were distributed to the left, whereas high water and flood tide samples aligned to the right of the CAP axis 1 (Figure 19). At Cocalito 2, low water samples were also distributed to the left, but ebb tides samples tended to be more separated by CAP2. At Cocalito 1 there was little separation between groups. The principal species for which significant correlations with one of the canonical discriminant axis were found were *Thalassoma lucasanum, Kyphosus elegans* and *Halichoeres chierchiae* (associated with low water and ebb tides), and *Cephalopholis panamensis*, *Bodianus diplotaenia* and *Sufflamen verres* (associated with high water and flood tides; Table 12, Figure 20).

Table 11. Results of 2-way mixed model PERMANOVA testing the effects of tidal stage (low water, flood tide, high water, ebb tide) on Utría subtidal reef fish assemblages at 4 sites.

Source	***df***	**SS**	**MS**	***F***	**P**
Site	3	111670	37224	33.095	0.0002
Tidal stage	3	8019	2673	2.1646	0.0008
Site × Tidal stage	9	11168	1240.9	1.1033	0.2166
Residual	344	386920	1124.8		
Total	359	524070			

Table 12. Fish species with significant correlations with CAP1 or CAP2 in Figure 19. Species with negative correlations with CAP 1 are associated with samples on the left of the CAP plot and species with positive correlations with samples to the right.

Species	**Punta Diego**		**Playa Blanca**		**Cocalito 1**		**Cocalito 2**	
	CAP1	**CAP2**	**CAP1**	**CAP2**	**CAP1**	**CAP2**	**CAP1**	**CAP2**
Thalassoma lucasanum	-0.4742	0.3012	-0.3084		-0.375		-0.2034	0.5871
Abudefduf troschelii	-0.4153							
Kyphosus elegans	-0.3749	0.3043	0.2081	-0.3497	-0.5356	-0.2326	-0.23	0.4934
Halichoeres chierchiae	-0.3369	0.43	-0.3065				0.3343	0.2978
Halichoeres notospilus	-0.2625	-0.2003						
Haemulon maculicauda	-0.2252	0.2697	0.2948					
Bodianus diplotaenia	-0.2059		0.2454		0.3115	-0.259		
Cephalopholis panamensis	0.2181				0.2163	-0.306	0.4815	
Halichoeres dispilus	0.2436	0.2437						
Mulloidichthys dentatus	0.3056	0.3623						
Ophioblennius steindachneri			-0.4936	-0.306	0.2656			
Microspathodon bairdii			-0.4489				-0.6913	-0.2111
Axoclinus lucillae			-0.385				0.2091	
Chaetodon humeralis			-0.3342					
Plagiotremus azaleus			-0.2907					
Sargocentron suborbitalis			-0.274					
Mugil curema			-0.2437	-0.2266				
Acanthemblemaria exilispinus			-0.2197					
Abudefduf concolor			-0.2061		-0.3236	0.3325	-0.6129	
Sufflamen verres			0.276		0.2289	-0.2648	0.3298	
Scarus rubroviolaceus			0.2763					
Canthigaster punctatissima					-0.3072		0.2066	

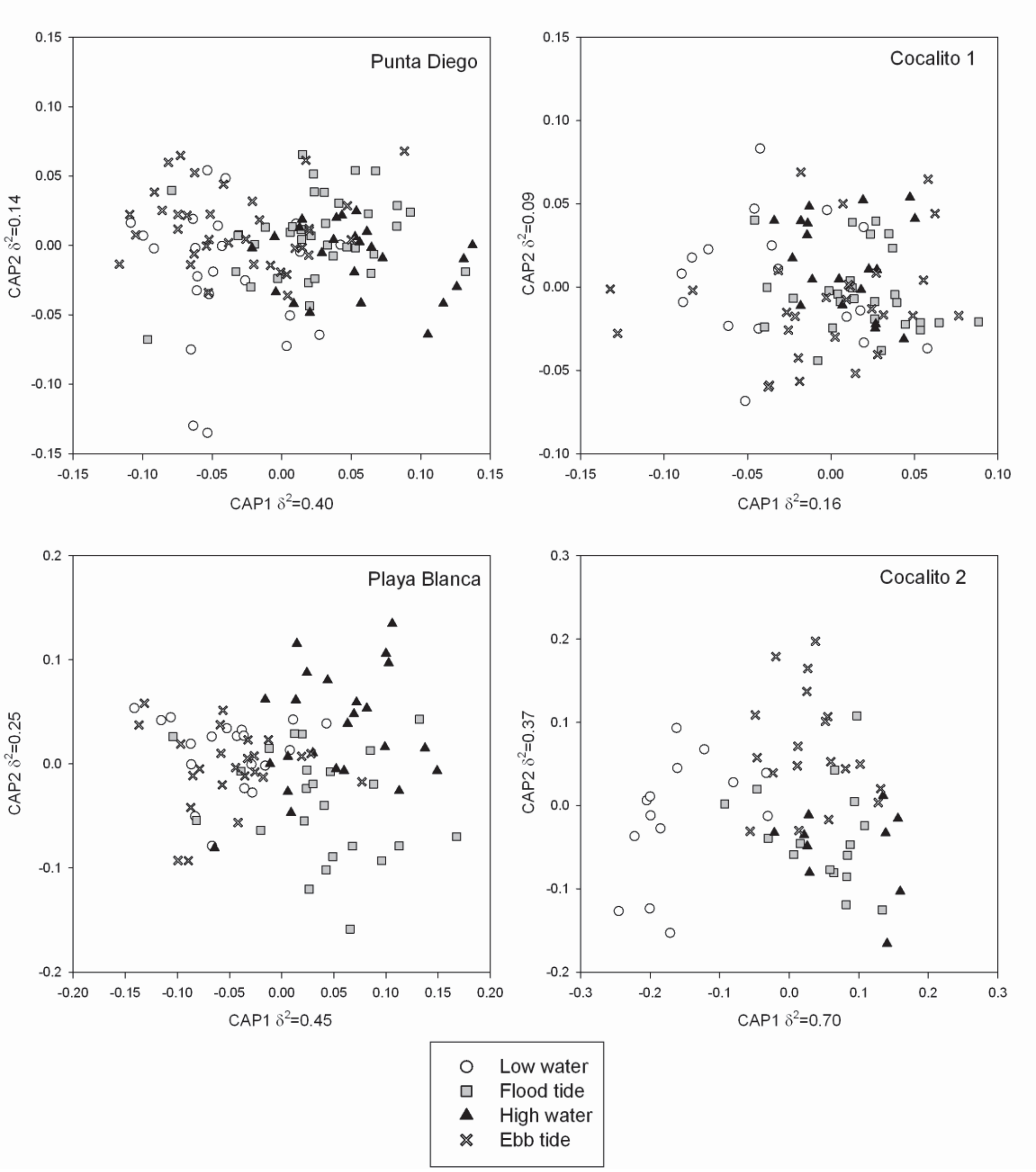

Figure 19. Canonical analysis of principal coordinates (CAP) of Utría reef fish transect counts taken at different tidal stages in the subtidal zone at four sites.

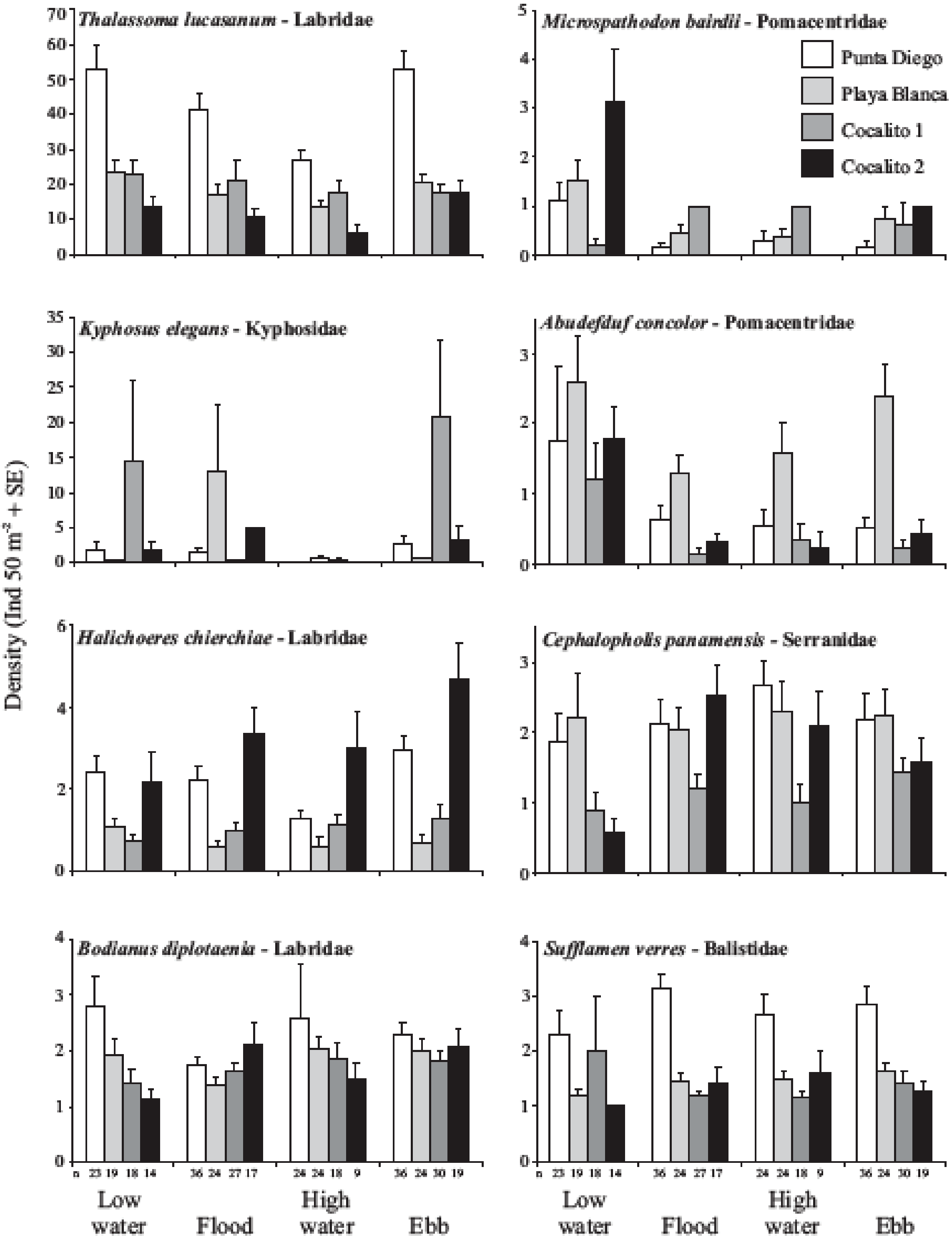

Figure 20. Mean density of the principal fish species responsible for differences between tidal stages at the four sites.

Intertidal vs subtidal fish assemblage variation at high tide (Question 4)

A 2-way PERMANOVA testing site and zone returned significant main effects as well as a significant interaction between them (Table 13). The significant site × zone interaction is explained by the CAP ordination: although sites are discriminated along CAP 2, and CAP axis 1 generally separates subtidal samples from intertidal samples at all sites, the degree of intertidal/subtidal separation at Punta Diego and Cocalito 2 is much greater than seen at Playa Blanca and Cocalito 1 (Figure 21a). Overall leave-one-out allocation success for the CAP analysis was 89.6%, with the few misallocations occurring between sites, and none between tidal zones. This indicates that while both site and tidal zone were strong and predictable determinants of fish high tide assemblage structure, between-zone differences within sites were stronger than those between sites.

Table 13. Comparison of subtidal and intertidal fish assemblages at high water at 4 sites using mixed effects PERMANOVA. Type III (partial) sums of squares was used, and P-values generated using 5000 permutations of residuals under the reduced model.

Source	**df**	**SS**	**MS**	**Pseudo-F**	**P**
Site	3	37046	12349	10.47	0.0002
Zone	1	64583	64583	6.89	0.0006
Site × Zone	3	31020	10340	8.77	0.0002
Residual	136	160380	1179		
Total	143	299780			

Differences between both Cocalito sites and Punta Diego and Playa Blanca were attributed to differences in densities of *Ophioblennius steindachneri* and *Microspathodon dorsalis*. Most of the dissimilarities between Punta Diego and the rest of the subtidal sites were accounted for by *Canthigaster punctatissima* (Figure 21b).

Intertidal key fish species and effects of tidal stage on their counts (Question 5)

There were strong species correlations with the first canonical axis, corresponding to the separation of subtidal and intertidal assemblages (Figure 21b). The four species that were strongly correlated with intertidal assemblages at high tide (i.e. positively correlated with CAP1 of Figure 21a) tended to be also those that were associated with low water subtidal assemblages in earlier analyses (Table 12). This indicates that these species (*Kyphosus elegans*, *Abudefduf concolor*, *Halichoeres notospilus* and *Microspathodon bairdii*) make regular excursions to intertidal zones on the rising tide, returning to subtidal habitats as the tide ebbs.

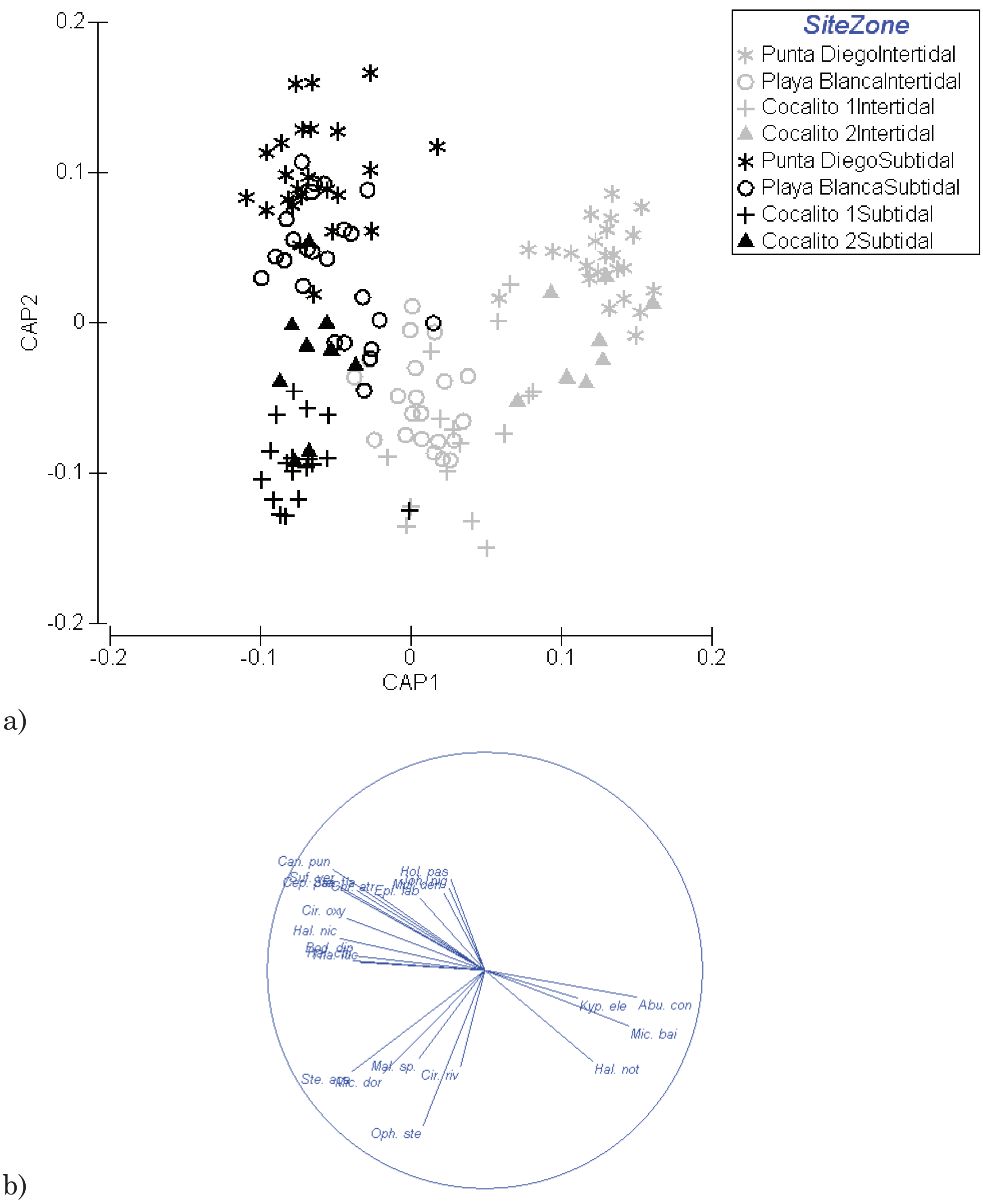

Figure 21. Canonical analysis of principal coordinates (CAP) of Utría reef fish transect counts taken at intertidal and subtidal areas at high tide. a) Constrained ordination: proportion of variance explained = 0.95, δ^2_{CAP1}=0.91, δ^2_{CAP2}=0.78. b) Biplot showing individual species correlations with the two CAP axes where $|r|$>0.4.

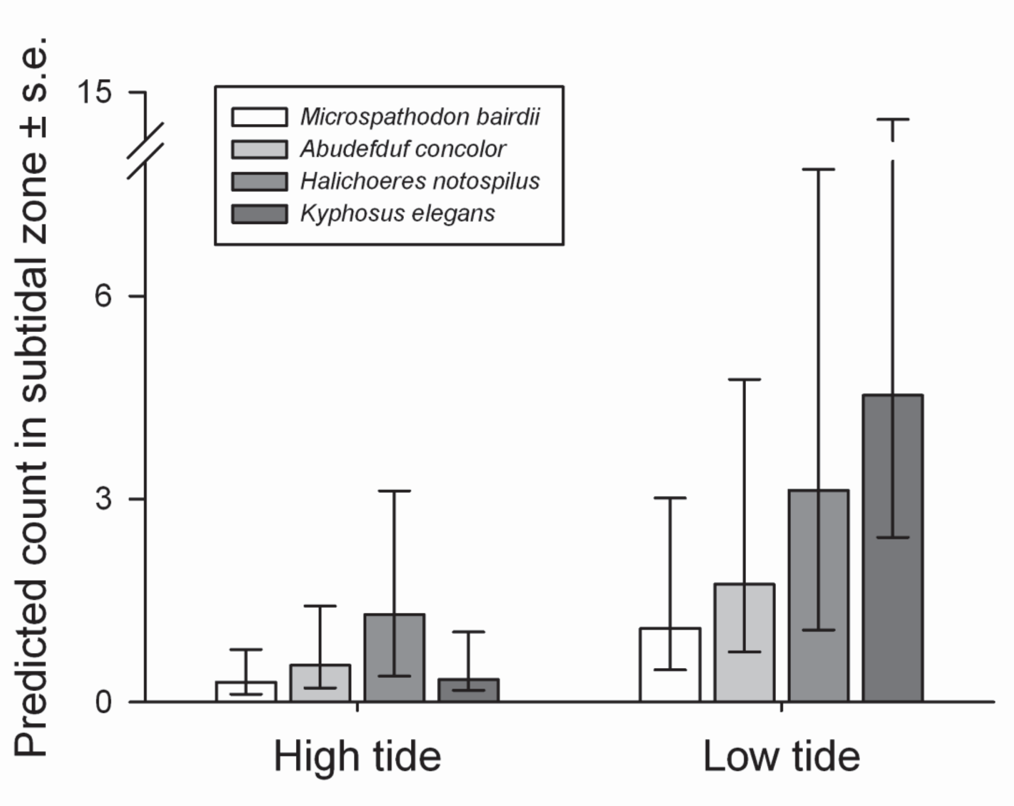

Figure 22. Predicted subtidal counts of four key fish species during high tide and low tide. Note that error bars are of unequal length around the point estimate because the SE are calculated on the log scale, and hence are multiplicative on the arithmetic scale.

Log-linear model estimates of the difference between low tide and high tide counts of these four species (Figure 22), showed that subtidal counts made during high tide may underestimate actual abundance by anything from 140% (for *Halichoeres notospilus*) to 1260% (for *Kyphosus elegans*) (Table 14).

Table 14. Log-linear model estimates of differences in density between subtidal counts of key fish species at high tide and low tide expressed as ratios (low tide:high tide) with their 95% confidence limits and likelihood ratio statistics.

Species	**Ratio (low tide:high tide)**	**Lower 95% CL for ratio**	**Upper 95% CL for ratio**	χ^2	***P***
Microspathodon bairdii	3.7	1.2	11.5	5.3	0.022
Abudefduf concolor	3.2	1.1	9.5	4.4	0.036
Halichoeres notospilus	2.4	1.1	5.5	4.5	0.033
Kyphosus elegans	13.6	3.0	61.5	11.5	<0.001

DISCUSSION

This study shows that a high proportion of the fish species inhabiting shallow subtidal areas (> 70%) may use the adjacent rocky intertidal areas during inundation periods, but that certain species – especially highly mobile schooling species – may desert the subtidal reefs almost entirely at high tide and forage in the intertidal zone. This is similar to findings from mangrove creek systems of Brazil, where most of the species inhabiting adjacent subtidal habitats at low tide were later found in the intertidal creeks (Krumme et al. 2004). This strategy, classified by Gibson (2003) as intertidal migrations, is found in both temperate and tropical intertidal areas (e.g. Kneib 1987; Burrows et al. 1994; Rangeley & Kramer 1995; Faria & Almada 2006). It remains largely unknown, however, how consistent these migrations are at different levels: among species within an assemblage, among individuals within populations and individuals themselves (Pittman & McAlpine 2003). The scarce evidence suggests the existence of at least three patterns at the population level: (1) the movement of the whole population into a higher tidal level, (2) an up-shore spreading of the population due to individuals' differential movement and (3) an ontogenetic separation of the population into migrant and non-migrant individuals each tide (Gibson 2003), e.g. where only juvenile fish from a particular species migrate into the intertidal zone and sub-adult and adult fish stay in subtidal areas.

This study found three times more fish species entering rocky intertidal areas compared to similar studies carried out within the tropical eastern Pacific region (Lubchenco et al. 1984, Vinueza et al. 2006), most probably due to a greater sampling intensity. However, similarities between the fish assemblage compositions of these studies were evident. Lubchenco et al. (1984) in Taboguilla Island (Panama), found 22 species in rocky intertidal shores, which are common to the present study, except for three species (*Balistes polylepis*, *Prionurus punctatus*, *Nicholsina denticulata*). For the Galápagos Islands, Vinueza et al. (2006) reported 19 species at high tide in intertidal rocky shores with a predominance of species from Pomacentridae and Labridae. Fourteen of these species are shared with Utría. Among the five species that are not shared, *Stegastes arcifrons*, very abundant in the Galapagos, is likely replaced by its sister species, *S. acapulcoensis*, in Utría. This suggests that tidal migrations in rocky shores of the region are consistent in space and constitute an important and overlooked part of the home-range movements of a relatively high number of reef fish species.

Six different migratory categories for reef fishes in Utría were observed: (1) opportunistic benthic reef fish species of a broad size class spectrum who entered intertidal areas. (2) Ubiquitous schooling species that moved to intertidal areas coming from outside reefs from the Families Kyphosidae, Carangidae, and Mugilidae. (3) Small size classes of reef fish species that entered intertidal areas (i.e. Scaridae). (4) Reef fish that moved up-shore from deeper reefs with the tides, but did not enter intertidal areas (i.e. *Paranthias colonus*). (5) Reef fish that moved in the water column, not necessarily to intertidal areas, with tidal stage changes; and (6) Intertidal resident species (i.e. *Malacoctenus* sp.). Similar divisions were drawn by Vivien (1973) for reef fishes off Madagascar where tidal responses were very variable among species. The assemblage was split into a "permanent" portion that appeared unaltered by the tidal change, and a "temporary" portion that moves to feed in shallow reef areas with the tides.

The spring/neap tide cycle has been shown to influence coastal fish assemblages at different levels (Krumme et al. 2004). In mangroves of north Brazil, clear relationships between spring tides and an increase in species richness, abundance and catch weight of fishes entering intertidal creeks were found. The results obtained in Utría – where the tidal regime is similar to north Brazil – indicate that reef fish assemblages in intertidal and subtidal areas at daylight were little affected by the spring/neap tide alternation. In Utría, a larger intertidal area available during spring tides did not attract more fishes. This may be reasonable in rocky shores of the tropical eastern Pacific, where prey or food resources for fishes are usually more abundant and concentrated at low intertidal areas (Lubchenco et al. 1984). Therefore, foraging in the upper intertidal zones, only available at spring tides and during limited time, may not represent an advantage compared to low intertidal zones (Rilov & Schiel 2006). This highlights a major habitat-specific difference in the intertidal habitat use by fishes. For example, temporal patterns in intertidal mangrove use by fishes were explained by the greater inundated area and food accessibility in mangroves at spring tides in Brazil (Krumme et al. 2004, Krumme & Liang 2004). If it is considered that a large biomass of organisms (especially crabs) are concentrated in upper intertidal levels of mangroves (Koch 1999), spring tides may provide fishes a very rich food source when accessing high intertidal areas. Consequently, we suggest that the vertical distribution of food resources in different intertidal habitats may influence the magnitude of spring-neap tide fish migrations to these habitats. We propose that the overall ecological significance of fish intertidal migrations in different system habitats (but subject to similar tidal regimes) may be dictated by the specific characteristics of each intertidal habitat. In rocky shores or sandy beaches, greater colonization at spring tides may be a lower pay-off strategy for fishes due to relatively small inundated areas and intertidal prey resources concentrated in the lower eulittoral. In contrast, fishes on coasts with intertidal mangrove or salt marsh systems habitats may greatly benefit from stronger colonization at spring tides due to relatively large inundated areas with dendritic creek systems and intertidal prey resources concentrated in the higher eulittoral (e.g. Brenner & Krumme 2007, Krumme et al. 2008).

The results obtained for reef fishes in Utría indicate that these migrations are species-specific. This has also been found in mangrove fishes of Brazil (Brenner & Krumme 2007, Krumme et al. 2008). The small changes observed in the subtidal reef fish assemblage over the tidal cycle indicate that intertidal migrations were restricted to just a few species of the entire reef fish assemblage; and even more, to only one part of a population within these specific species. Similar results where obtained in mangrove systems of Florida by Ellis & Bell (2008), where only one group of species showed clear tide-related movements (*Eucinostomus* spp.). Tolimieri et al. (2009), using acoustic telemetry at Puget Sound (USA), found different patterns in the movement behaviour and home range size of three fish species. The movement behaviour, however, was related to the diel and tidal cycles in the three species, with some of them moving at daylight on the flood tide, while others moving at night on the flood tide. Movements of entire populations from subtidal to intertidal areas, as found by Rangeley & Kramer (1995) in pollock (*Pollachius virens* – Gadidae) populations were rare in Utría, though groups of the bumphead damselfish *M. bairdii* were found to regularly commute between distinct subtidal and intertidal sites.

Despite resource accessibility being restricted to immersion periods, the few common fish species entering intertidal areas may exert strong top-down control on rocky shore communities of the area as suggested by Lubchenco et al. (1984). In Utría species from herbivorous (i.e. Kyphosidae, Mugilidae, Scaridae) and carnivorous guilds (i.e. Labridae, Lutjanidae) were among the most common in intertidal areas and were observed feeding intensively there (G Castellanos-Galindo, pers. obs). Further manipulative studies on these rocky shores are needed to determine the importance of fish predation in regulating macroalgae and invertebrate intertidal communities.

Although differences between the four sampling sites in Utría were detected, they were less strong than the subtidal/intertidal differences consistently observed among the four sampling sites. This indicates that the intertidal fish assemblage was comprised of a defined sub-set of subtidal species. The observed site differences in both subtidal and intertidal fish assemblages in Utría may be a consequence of the degree of wave exposure of the sites, as well as a function of small-scale differences in habitat (Santin & Willis 2007). Wave exposure has been suggested to be a major factor shaping the structure of fish communities (Fulton et al. 2005) and although it was not measured in this study, is likely to affect the fish community structure of rocky and coral reef areas of the region.

The variability in reef fish responses over tidal stages raises the question on whether tidal stages should be considered in reef fish monitoring in macrotidal areas. Surprisingly few studies have acknowledged the potential bias that fish census carried out at different times of the day or tidal stages may have (but see Kingsford & MacDiarmid 1988, Thompson & Mapstone 2002, Willis et al. 2006, McClanahan et al. 2007). Small differences in overall fish assemblage structure, as determined by multivariate analyses, can mask large and predictable changes in the densities of individual species, especially where the dataset consists of many species and there are compositional differences among sites (Willis et al. 2006). In New Zealand and

Italy, Willis et al. (2006) found no significant differences in the reef fish assemblage structure at three differing times during daylight hours. They did not, however, sample over a complete tidal cycle. Nevertheless, they point out that if common species exhibit strong differences in activity patterns during the day due to tidal redistribution, for example, comparing counts taken at different tidal stages may result in significant bias. In this study, univariate analyses showed clearly that at Utría, counts of some common species that habitually utilize intertidal habitats may vary in relative density by more than 100% (much more for schooling species) between high and low tide. Thus, subtidal fish counts conducted at high tide may significantly underestimate the density of important species at local scales, and introduce bias at the site level that increases the variance of counts across larger scales. Importantly, studies of the trophic structure of coastal systems could underestimate the extent of herbivory, for example, if schooling fishes forage extensively in intertidal zones.

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Chapter IV. Spatial variability of mangrove fish assemblage composition in the tropical eastern Pacific Ocean

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ABSTRACT

Mangroves in the tropical eastern Pacific (TEP) constitute a dominant coastal ecosystem that harbours diverse and economically important fish assemblages. We describe here regional scale patterns in the composition of this poorly documented mangrove ichthyofauna. A review of available studies (including own data) from five countries covering the entire region was performed. Species abundance distribution curves were constructed and compared among studies. Relative abundance data of fish species and families were analysed with classification and ordination techniques. Common species and families responsible for differences among localities were identified. Overall, 315 fish species associated to mangroves of the TEP were identified. Fifteen fish families accounted for 80% or more of the relative abundance of all studies. Despite the use of different sampling techniques, common features arose for most of the mangrove fish assemblages. Clupeidae were numerically dominant throughout the region, while Gerreidae were particularly dominant in the northern mangroves. The catch mass contributions of families from studies where these data were available indicated a dominance of Ariidae, Centropomidae, Lutjanidae and Tetraodontidae. A relatively uniform composition at the family (and sometimes species) level supports recent claims to merge the Panamic with the Mexican province in the TEP according to the distribution of the shore fish fauna. Similarities found with other estuarine-mangrove ichthyofaunas in the Neotropics may be related to the connectedness of these regions in past geological times. Quantitative assessments of mangrove fish communities in four areas of the TEP would improve further zoogeographic analyses and facilitate the development of conservation strategies.

Keywords: biogeographical patterns, community composition, estuarine systems, mangrove ichthyofauna, Neotropics, tropical eastern Pacific

INTRODUCTION

Mangrove ecosystems dominate many of the coastal landscapes across tropical and subtropical regions. The existence of these ecosystems is, however, threatened by a number of human activities such as conversion into aquaculture ponds or coastal development (e.g. Valiela et al. 2001) and has resulted in a ca. 35% decline in mangroves over the past two decades (Alongi 2002). This decline is reflected by a loss in the ecological functions that this ecosystem provides. Mangroves provide habitat for a wide spectrum of marine and terrestrial organisms, which spend part of their life cycles in these areas. The paradigm of mangroves as nurseries has been argued in several academic and conservation forums for a long time. At the same time, a number of direct and indirect evidences support the idea that mangroves increase the biomass of fishes and fisheries yields in adjacent habitats (Manson et al. 2005a; Aburto-Oropeza et al. 2008).

Mangroves in the tropical eastern Pacific (TEP) region are extensive in area and represent a highly threatened ecosystem (Polidoro et al. 2010). The second largest mangrove area in the Neotropics is located in the TEP totalling 1.21 million ha and representing 26.6% of the New World mangroves (Lacerda et al. 2002). Moreover, several small-scale artisanal fisheries operate within these mangroves increasing fisheries yields in adjacent coastal areas and producing important revenues for local economies (see Aburto-Oropeza et al. 2008, for an example in the Gulf of California).

Quantitative comparisons of fish assemblage compositions from tropical mangrove-dominated estuaries over large geographical areas are rare. Exceptions are comparisons made in tropical Australia (Robertson and Duke 1992; Ley 2005; Sheaves and Johnston 2009) and northern Brazil (Giarrizzo and Krumme 2008). Robertson and Duke (1992), compared mangrove fish assemblages in different habitats of four relatively arid estuarine systems in northern Australia and concluded that the number of microhabitats present at each area had a major influence on fish community structure and that species richness was a function of tidal amplitude, water clarity and salinity fluctuations. Along 1400 km adjacent to the Great Barrier Reef in Australia, Ley (2005) employed gillnets of different mesh sizes to compare the fish fauna of 11 mangrove estuaries. She concluded that tide and wave dominated systems were clearly discriminated by the presence of specific fish families and that the variation in fish assemblages was explained mainly by a combination of physical attributes of the estuaries (e.g. catchment hydrology, substrate, mangrove area). Finally, Sheaves and Johnston (2009) compared small mesh cast nets' fish catches compositions of 21 estuaries over 650 km at the north eastern coast of Australia, finding that differences in faunal composition were better explained by estuary-level ecological variables (e.g. intertidal, subtidal or mangrove areas, sediment index) than by differences in climatic zones or the estuaries' position relative to other estuaries. In northern Brazil, where ca. 650 km of macrotidal coastline comprise the largest contiguous mangrove area of the world, Giarrizzo and Krumme (2008) found similarities at the family and species level in the intertidal mangrove fish composition using block nets. Nevertheless, the species and family contributions (catch mass) differed among sites as a function of their relative distance to the Amazon River mouth.

There are about 1300 near-shore fish species in the TEP region, which is low compared to other tropical regions (Zapata and Robertson 2006). A great proportion of these species is considered to be endemic to the region (ca. 72%). Shore fish diversity gradients for the entire endemic species in the TEP show two peaks: between 8° - 10° N (Panama-Costa Rica) and 23° - 29° N (lower Gulf of California; Mora and Robertson 2005a). Robertson and Cramer (2009), based on the overall near-shore fish species distribution, redefined the biogeographical subdivisions within the area in three main provinces: The Cortez (Gulf of California and lower Pacific Baja), the Panamic (southward) and the Ocean Island province (comprising five sets of islands including the Galapagos islands), merging the previously defined Mexican province with the Panamian province (Figure 23). Previous studies of the shallow-water fish fauna in the TEP have used the category "soft bottom fishes", which includes species associated to mangrove, estuarine and mud/sandy bottoms up to 100 m depth (ca. 375-487 species) (Mora and Robertson 2005b; Zapata and Robertson 2006). However, a further distinction of this category into more habitat-specific fish assemblages, explicitly referring to mangrove-associates, does not yet exist in the literature.

This study fills a gap, acknowledged in the literature (Faunce and Serafy 2006), in documenting the mangrove fish composition of this region. Although a number of studies dating back to the late 1970's on mangrove-associated fish assemblages in the region are available in the published and grey literature, no attempts have been made to synthetize this knowledge. We combine previous studies with our own information to examine if general patterns on this specific portion of the shore fish fauna can be derived. The present study aims to identify general patterns in mangrove fish assemblage composition for the TEP region using a compilation of ecological studies that cover most of the geographic range where mangroves occur.

MATERIALS AND METHODS

Study area

The tropical eastern Pacific extends from ~25°N to ~5°S along the western coast of the Americas (Robertson and Cramer 2009) (Figure 23). The coastline is ca. 12000 km long, dominated by a mosaic of rocky shores, sand/mud bottoms and mangrove habitats and a very marginal representation of corals and seagrasses (Glynn and

Ault 2000; Santamaría-Gallegos et al. 2006). The coasts in the TEP are dominated by mountain ranges and an alternation of narrow coastal plains and steep sectors.

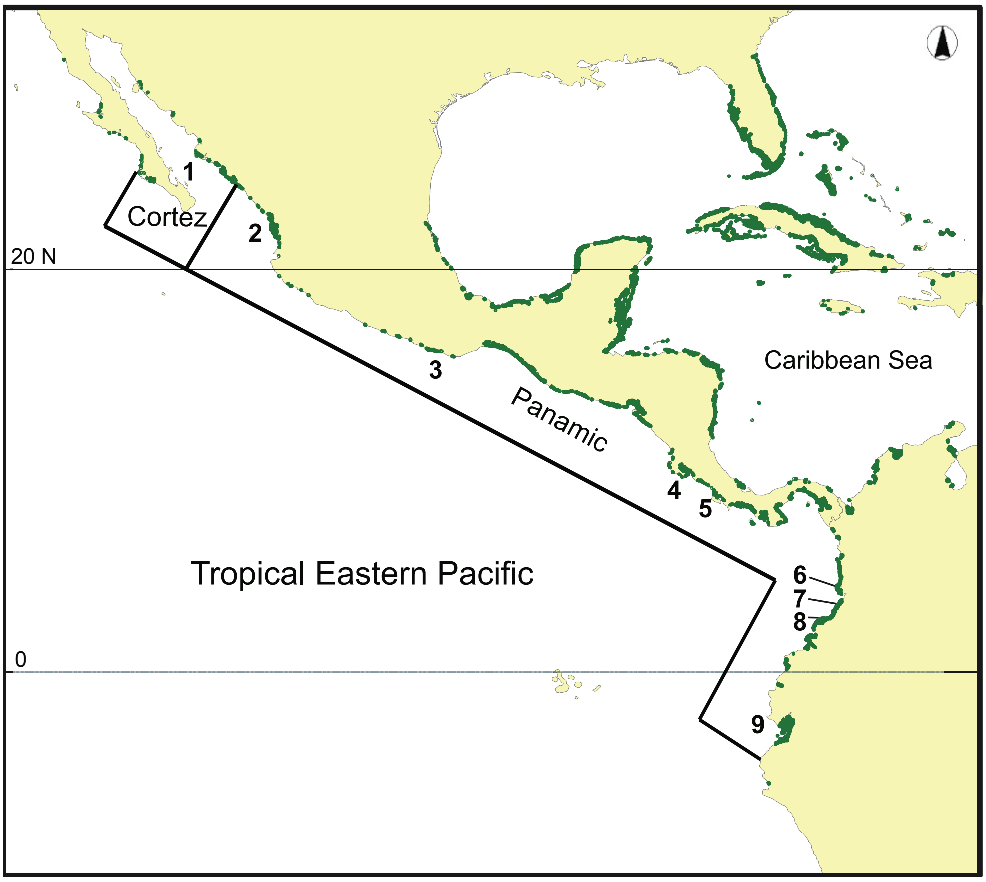

Figure 23. Map of the tropical eastern Pacific region showing mangrove distribution (source: UNEP-WCMC; http://data.unep-wcmc.org/datasets/6) and the localities where the mangrove fish fauna studies used in the present analysis were carried out. 1. El Conchalito, La Paz Bay, Baja California Sur, Mexico – (MEX LP), 2. Teacapán-Agua Brava Lagoon, Mexico – (MEX-TL), 3. Chacahua Lagoon, Oaxaca State, Mexico - (MEX-CL), 4. Golfo de Nicoya, Costa Rica – (COS-GN), 5. Golfo Dulce, Costa Rica – (COS-GD), 6. Bahía Málaga, Colombia – (COL-BM), 7. Bahía de Buenaventura, Colombia – (COL-BB) 8. Sanquianga, Colombia – (COL-SA) and 9. Palmar, Ecuador – (ECU-PA). Tropical eastern Pacific subdivisions according to shore fish fauna distribution are shown (Robertson and Cramer 2009).

The climatic conditions in the region range from arid areas at the limits of the region (Baja California and southern Ecuador) with precipitations of 200 mm y^{-1}, to extremely rainy areas at the central and northern Colombian coast where mean rainfall can reach 8000 mm y^{-1} (Table 15). In the southern part of the TEP, rivers drain the steep slopes of coastal ranges carrying large amounts of sediments (i.e. Colombia), whereas coastal lagoons, with sometimes hyper-saline conditions and virtually no freshwater input during dry seasons are common in northern areas of the region (i.e. Mexico). Macrotides are common in Colombia, Panama and the Gulf of California, whereas mesotides occur on the other coasts of the TEP.

Table 15. Characteristics of mangrove forests of countries with coasts in the Eastern Pacific region. Tidal types: * mixed semi-diurnal, **semi-diurnal.

Country	Mangrove area (ha)	Mean annual rainfall (mm)	Tidal range (m)[1]	Reference
Mexico	261864	200 - 2000	0.2-2.5*	CONABIO (2009)
Guatemala	16086	1000-2000	1.5-2.0**	Jimenez (1992)
Salvador	35235	1000-2000	2.0-3.0**	Jimenez (1992)
Honduras	46869	1000-2000	4.0**	Jimenez (1990)
Nicaragua	39310	1000-3000	2.0-3.0**	Jimenez (1990)
Costa Rica	41292	1000-5500	2.5-3.0**	Jimenez (1994)
Panama	164968	~1000-3000	4.5-6.0**	D'Croz (1993)
Colombia	283000	~2000-8000	3.5-4.5**	Sánchez-Páez et al. (1997)
Ecuador	149688	400-2000	2-3.6**	Sanchez & Moran (1999)
Peru	4550	>200	~1.0**	FAO (2007)

1. Tidal ranges taken from Bird (2010)

Mangrove forest structure and physiognomy in the region are specially regulated by climatic conditions, with less structurally developed (basal areas = 4 –30 m^2 ha^{-1}) and smaller mangroves (< than 20 m in height) in dry environments and well developed (basal areas = 20 - 30 m^2 ha^{-1}) fringe or riverine mangroves reaching heights of 30 m, partially > 40 m and belt widths of up to 24 km inland at extremely humid coastal areas (West 1956; Jiménez 1990). Colombia and Mexico rank first and second in terms of their mangrove extension. The Mexican coastline (ca. 6500 km) harbours extensive mangrove areas, especially in the northern portion (Nayarit and Sinaloa) where coastal lagoons are common features (CONABIO 2009). In Colombia, the central and southern alluvial coast give rise to large mangrove forests that grow behind sand/mud barrier islands and along deltas. The smallest mangrove area is located in north Peru at the southern limit of mangrove distribution in the Eastern Pacific (see Table 15).

Mangrove fish studies carried out in the region were compiled from scientific publications available in local and international journals from 1984 to 2010 and our own unpublished data from Colombia were also used. The selected studies employed different fishing gears (trawls, gillnets, blocknets, flownets, beach seines) (Table 16). These gears were mainly employed along the main channels of estuarine systems containing mangroves (subtidal) or in close proximity to intertidal mangroves. All these studies sampled at least two locations during wet and dry seasons. Studies that contained only species lists or collected at single locations with no temporal replicates were not considered. Nine studies from Mexico, Costa Rica, Colombia and Ecuador were compiled (Table 16).

A matrix of the species found in all the studies was constructed and the validity of scientific names was checked using the web resource Catalog of Fishes (http://www.calacademy.org/research/ichthyology/catalog). For all but one study (Rojas et al. 1994; Costa Rica) a measure of relative abundance for each species was available (i.e. percentage of individuals) in order to account for possible differences in sampling intensities among studies. Species abundance distribution models (SADs; log-abundance vs. Rank plots) were constructed to obtain a general description of each of the assemblages avoiding the loss of information that occurs when employing other univariate descriptors of community structure (i.e. Shannon, Simpson; McGill et al. 2007). Classification analyses (hierarchical agglomerative clustering) from a similarity matrix that used untransformed relative abundance data at the fish species and family level were carried out. For this purpose, Bray-Curtis similarity metric was used, as it does not treat absences to derive similarity between groups (Clarke 1993). Non-metric mutidimensional scaling (nMDS) ordination was used to inspect data in two dimensions. A permutation procedure, the similarity profile routine (SIMPROF), was used to test the null hypothesis of no multivariate structure in the data being analysed (Clarke et al. 2008). Pearson correlations with MDS1 and MDS2 in nMDS plots were carried out to identify species and families related to the different studies analysed. All analyses were carried out with the VEGAN and BiodiversityR packages of the R programme (Oksanen 2010) and with the PRIMER 6 software (Clarke and Gorley 2006).

Table 16. Mangrove fish fauna studies carried out in the tropical eastern Pacific region where quantitative data was available (1984-2011).

Country	System	Sampling intensity	Sampled habitats	Sampling gear	Number of species	Dominant species	Rainfall (mm year^{-1})	Reference
Mexico	El Conchalito, Baja California 24° 08'- 24° 07' N; 110° 21'- 110° 20'	One year (1996-1997; four seasons)	Mouth of a tidal channel	Flow net (30 x 2 m, 6 mm mesh size)	34	*Eucinostomus currani, Anchoa ischana, Diapterus peruvianus, E. entomelas, E. gracilis*	219	González-Acosta et al. (2005)
Mexico	Teacapán-Agua Brava (22°04'-22°35'N; 105° 50'W)	One year (1979-1980; four samplings)	Main channel along 20 stations	Trawling and monofilament nets, beach seine	75	*Lile stolifera, Cathorops liropus, Mugil curema, Hyporhamphus* sp., *Eucinostomus dowii*	1000-1500	Alvarez-Rubio et al. (1986)
Mexico	Chacagua Lagoon (15°58'–16°00'N, 97°42'–97°39'W)	One year (1992-1993; Five every two months)	Lagoon surrounded by mangroves	Trawl net (5 m length, 2.5 m mouth opening, 20 mm mesh size)	33	*Diapterus peruvianus, Centropomus robalito, Anchovia macrolepidota, Lile stolifera, Lutjanus novemfasciatus*	700-2500	Mendoza et al. (2009)
Costa Rica	Golfo de Nicoya (9°52'-10°15'N; 84° 42'-85°15'W)	15 months (1992-93; Three sites)	Sandy and mud bottoms adjacent to mangroves	Beach seine (25x1.80 2.5cm mesh size, 50x5 net (mesh size (8.75cm)	75	*Ariopsis seemani, Notarius osculus, Sciades dowii, Lutjanus colorado, Centropomus robalito (catch weight)*	~ 1600	Rojas et al. (1994)
Costa Rica	Gofo Dulce (8°22'-8°45'N, 83° 05'-83°30')	2005 rainy and 2007 dry season (10 sites)	Sandy and mud bottoms in adjacent to mangroves	Gillnets, beach seine, cast net	82	*Anchoa mundeola, Mugil curema, Diapterus peruvianus, Sphoeroides* sp., *Centropomus armatus*	4500-5500	Feutry et al. (2010)

Table 16. (continued)

Country	System	Sampling intensity	Sampled habitats	Sampling gear	Number of species	Dominant species	Rainfall (mm year^{-1})	Reference
Colombia	Bahía Málaga (3º 56' - 4º 05'N and 77º 19 - 77º 21'W)	One year (2009-2010; four sites, monthly)	Intertidal mangrove creeks	Block nets (20 x 4 m, 12 mm mesh size)	50	*Lile stolifera, Centropomus armatus Lutjanus argentiventris*, *Diapterus peruvianus*, *Ariopsis seemani*	7435	Castellanos-Galindo and Krumme (unpublished data)
Colombia	Bahía de Buenaventura (3° 54' N and 79° 5' W)	Three stations between 1978-1980	Intertidal mangrove & adjacent soft bottoms	Block nets, beach seines, gill nets, cast nets	178	*Lile stolifera, Sphoeroides annulatus, Anchoa panamensis, Mugil cephalus, Anchoa nasus*	~6000	Rubio (1984)
Colombia	Sanquianga National Park (2° 40' N and 78° 28' W)	1980 (three sampling sites)		Block nets, gill nets, beach seines	150	*Lile stolifera, Mugil cephalus, Ophistonema libertate, Lutjanus guttatus, Sphoeroides annulatus*	4000	Rubio and Estupiñan (1990)
Ecuador	Palmar (2° 01' S and 80° 44' W)	2003 Dry and 2004 wet seasons	Main channel, 2 creeks and adjacent river	Bag seine (7x2 m, 3mm mesh size)	36	*Mugil curema*, *Atherinella serrivomer*, *Ctenogobius sagittula*, *Evorthodus minutus*, *Lile stolifera*	250-300	Shervette et al. (2007)

RESULTS

A total of 315 fish species from 69 families and 162 genera inhabiting mangroves in the TEP were identified. Twelve families and 23 species were cartilaginous fishes (Chondrichthyes) and the remaining species and families corresponded to bony fishes (Osteichthyes). The most speciose families were Sciaenidae (39 species). Carangidae and Ariidae ranked second (each with 21 species). Other important families were Engraulidae, Gobiidae (both with 17 species), Haemulidae (16) and Gerreidae (13) (Table 17).

Studies with the greatest species richness (150-178 species) were located in the central and southern Colombian coasts (Table 16, Figure 24), where large areas of mangrove forests are present. In contrast, studies with < 40 species and the lowest species richness were identified for two areas in Mexico (MEX- LP, MEX-CL) and Ecuador (ECU-PA) which generally presented very low mangrove area coverage (Table 18, Figure 24). All SADs for the eight studies showed a log-normal distribution shape, reflecting the dominance of very few abundant species and a predominance of rare species. This was especially evident for two studies in Mexico (MEX-LP, MEX-CL) and Ecuador (ECU-PA) where evenness was lower. In contrast, studies with the higher evenness were found in Colombia (COL-BB, COL-SA) and in Costa Rica (COS-GD). In these studies the slopes of the plots were less pronounced indicating more diverse fish assemblages (Figure 24).

The most common mangrove fish species in terms of relative abundance was the Pacific piquitinga *Lile stolifera* (Clupeidae), which was the most abundant species in 50% of the studies (Figure 24). Catfishes (*Ariopsis* spp.), snooks (*Centropomus* spp.), mojarras (*D. peruvianus*) and pufferfishes (*Sphoeroides* spp.) were present in most of the studies in significant proportions (Table 16, Figure 24). In all the studies, 15 common families accounted for 80% or more of the total fish abundance (Table 17). Gerreidae, Clupeidae, Engraulidae, Mugilidae and Centropomidae were the most abundant components of the fish assemblages in almost all the studies. Based on the mean relative abundance expressed in percentages, Gerreidae was the most important family in the area ($\bar{x}$ = 20.4 %), mainly driven by their numerical dominance in two Mexican studies (i.e. MEX-LP, MEX-CL; Table 17). Clupeidae and Engraulidae ranked second and third with a mean relative abundance of 15.4% and 9.5%, respectively. The contribution of Clupeidae was especially high for a study in Mexico (MEX-TL) and one in Bahía Malaga, Colombia (COL-BM). The relative abundance of Engraulidae was high (>15%) for the studies in the Gulf of California (MEX-LP), Colombia (COL-BB) and Costa Rica (COS-GD).

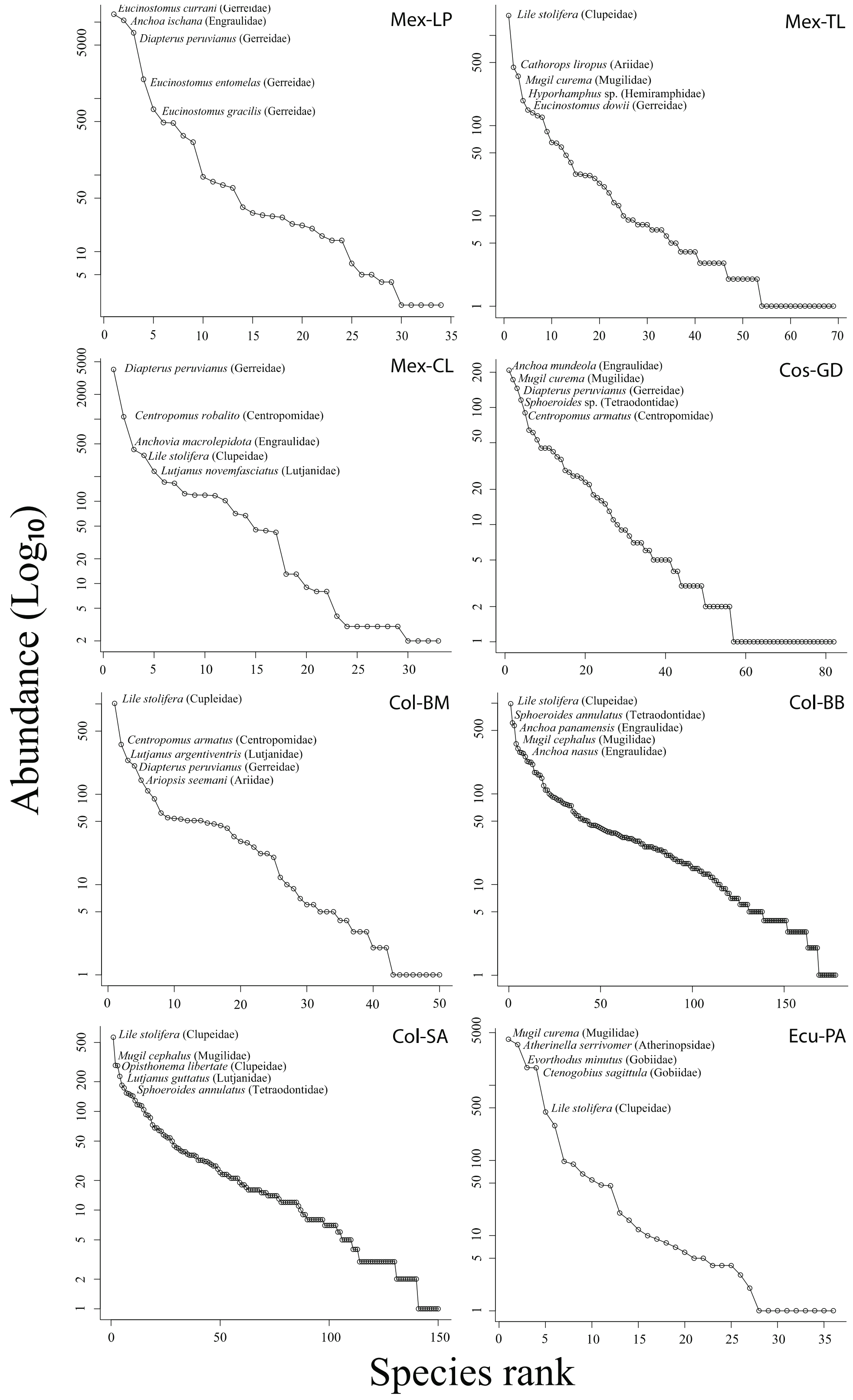

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Figure 24. Rank-abundance ($\log_{10}$ transformed) plots for eight mangrove fish studies carried out along the tropical eastern Pacific Ocean. 1. El Conchalito, La Paz Bay, Baja California Sur, Mexico – (MEX LP), 2. Teacapán-Agua Brava Lagoon, Mexico – (MEX-TL), 3. Chacahua Lagoon, Oaxaca State, Mexico - (MEX-CL), 4. Golfo Dulce, Costa Rica – (COS-GD), 5. Bahía Málaga, Colombia – (COL-BM), 6. Bahía de Buenaventura, Colombia – (COL-BB) 7. Sanquianga, Colombia – (COL-SA) and 8. Palmar, Ecuador – (ECU-PA). The five most abundant species are given.

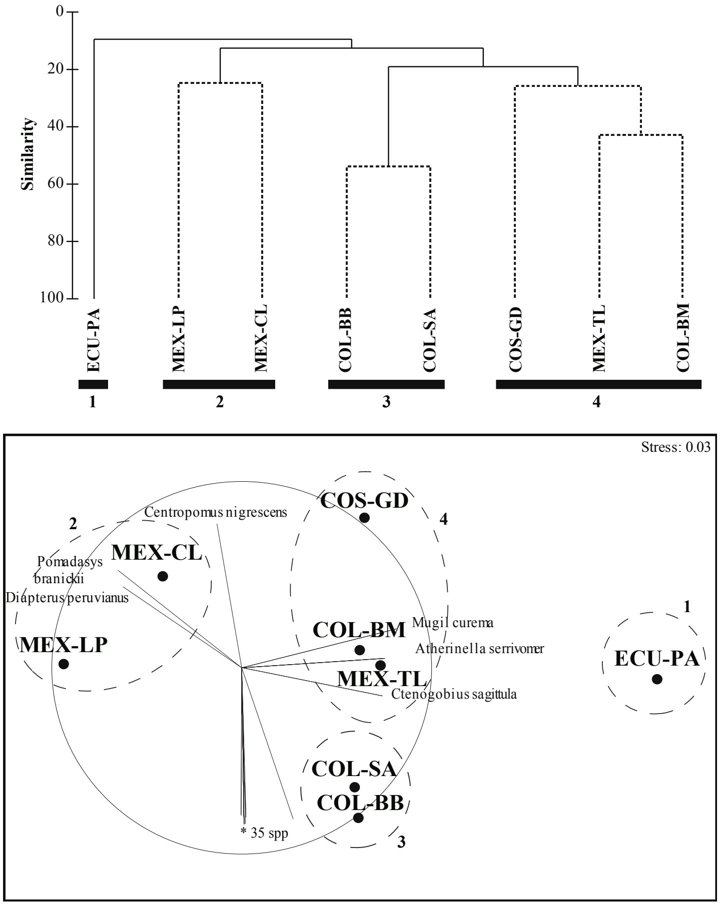

Figure 25. Cluster dendrogram and nMDS ordination plot of data (% abundance of species; Bray-Curtis metrics and average linkage algorithm) from eight mangrove fish studies in the tropical eastern Pacific. Dotted lines in dendrogram represent groups where no further internal structure can be found according to the SIMPROF test. Species with correlation with MDS1 and MDS2 axes (Pearson) > 0.75 are shown. **Aetobatus narinari*, *Anchoa nasus*, *Bathygobius ramosus*, *Batrachoides pacifici*, *Cerdale ionthas*, *Chaenomugil proboscideus*, *Chaetodipterus zonatus*, *Cynoponticus coniceps*, *Diplectrum rostrum*, *Dormitator latifrons*, *Epinephelus analogus*, *Haemulon sexfasciatum*, *Hemicaranx leucurus*, *Hemieleotris latifasciata*, *Hyporhamphus gilli*, *Ilisha fuerthii*, *Menticirrhus nasus*, *Mugil cephalus*, *Myrophis vafer*, *Narcine entemedor*, *Nebris occidentalis*, *Notarius troschelii*, *Opisthopterus equatorialis*, *Ophichthus remiger*, *O. zophochir*, *Paralonchurus dumerilii*, *Parapsettus panamensis*, *Polydactilus opercularis*, *Prionotus horrens*, *Rhinobatos planiceps*, *Sphoeroides annulatus*, *Sphyrna tiburo*, *Syngnathus* sp., *Trinectes fonsecensis*, *Urotrygon aspidura.*

Table 17. Contribution of the 15 most abundant families (% number of individuals) across eight mangrove fish fauna studies carried out in the tropical eastern Pacific region; the five most important families of each study in bold. 1. El Conchalito, La Paz Bay, Baja California Sur, Mexico – (MEX LP), 2. Teacapán-Agua Brava Lagoon, Mexico – (MEX-TL), 3. Chacahua Lagoon, Oaxaca State, Mexico - (MEX-CL), 4. Golfo Dulce, Costa Rica – (COS-GD), 5. Bahía Málaga, Colombia – (COL-BM), 6. Bahía de Buenaventura, Colombia – (COL-BB) 7. Sanquianga, Colombia – (COL-SA) and 8. Palmar, Ecuador – (ECU-PA). Studies are sorted by latitude (from north to south). *Sum of all species occurring across the eight studies.

Family	**Species***	**MEX-LP**	**MEX-TL**	**MEX-CL**	**COS-GD**	**COL-BM**	**COL-BB**	**COL-SA**	**ECU-PA**
Gerreidae	13	**64.83**	**12.96**	**56.90**	**10.37**	**7.73**	2.81	**7.24**	0.46
Clupeidae	8	**1.36**	**42.48**	**6.51**	3.32	**34.91**	**14.32**	**16.76**	**3.60**
Engraulidae	17	**30.24**	0.87	**5.78**	**15.71**	0.03	**17.40**	4.24	1.53
Mugilidae	4	**1.39**	**9.07**	0.18	**10.94**	0.74	**5.80**	**7.81**	**33.46**
Centropomidae	6	-	2.19	**16.68**	**10.37**	**15.20**	2.49	4.97	0.42
Gobiidae	17	**0.97**	0.18	1.61	0.25	1.67	4.22	3.46	**28.08**
Atherinopsidae	5	-	-	0.00	2.39	1.40	3.75	0.30	**28.37**
Lutjanidae	7	0.03	1.88	**5.44**	6.66	**11.85**	1.19	**8.02**	-
Ariidae	21	-	**12.07**	1.68	7.73	5.00	2.66	2.70	-
Carangidae	21	0.08	**4.48**	1.68	**7.80**	**5.80**	5.14	4.82	0.56
Sciaenidae	39	0.05	1.38	0.00	6.72	0.97	**5.47**	**9.98**	0.00
Tetraodontidae	9	0.07	0.10	0.11	7.29	3.60	**6.51**	4.02	**2.42**
Haemulidae	16	0.61	1.32	0.95	5.08	0.70	1.33	6.51	-
Paralichthyidae	7	-	0.87	1.56	1.07	1.50	3.38	1.51	0.09
Hemiramphidae	5	0.06	4.81	0.04	-	0.17	3.08	0.45	-
Total	195	99.69	94.66	99.12	95.70	91.27	79.55	82.79	98.99

For all the classification and ordination analyses at the family and species level, the studies with the greatest similarities were those carried out in the central and southern Colombian coast (COL-BB and COL-SA). These two studies shared several species, which were only found at these sites (Figure 24, 25).

Using the species relative abundance of each study, four clusters were formed according to the SIMPROF test: (1) an isolated study from Ecuador (ECU-PA), (2) two studies from Mexico (MEX-LP and MEX-CL), (3) the two closely related studies from Colombia (COL-BB, COL-SA), and (4) the remaining studies from Costa Rica (COS-GD), Mexico (MEX-TL) and Colombia (COL-BM). These same groups were also observed and supported in the nMDS representation (Figure 25). Cluster (1) was characterized by *Mugil curema* (Mugilidae), *Atherinella serrivomer* (Athesinopsidae), and *Ctenogobius sagittula* (Gobiidae) (Figure 24). These species were exceptionally abundant and represented ca. 75% of the relative abundance in this study. Cluster (2) was characterized by *D. peruvianus*, which occurred in similar relative abundances at both sites. Both studies of cluster (3) shared three of their five most abundant species in similar proportions (*L. stolifera*, *Sphoeroides annulatus*/Tetraodontidae and *Mugil cephalus*/Mugilidae) (Figure 24). The arrangement of this group was supported by the large amount of common and unique species shared by these studies (Figure 25). Cluster (4) was characterized by the great dominance of *L. stolifera* at MEX-TL and COL-BM and the large contribution of *D. peruvianus* and *Lutjanus argentiventris* (Lutjanidae).

Table 18. Mangrove fish fauna studies carried out in the tropical Eastern Pacific Ocean with environmental characteristics of the specific study sites.

Study	Mangrove area (ha)	Tidal amplitude (m)	Rainfall (mm y^{-1})
Conchalito, La Paz, Baja California, Mexico – MEX-LP	18.5	1.0-1.3	219
Teacapán Agua Brava Lagoon, Mexico –MEX-LT	80000	0.9-1.3	1000-1500
Chacahua Lagoon, Oaxaca State, Mexico – MEX-CL	2550	0.9-1.3	1300
Golfo de Nicoya, Costa Rica – COS-GN	15176	3.0	1800
Golfo Dulce, Costa Rica – COS-GD	2000	1.76	4500-5500
Bahía Málaga, Colombia – COL-BM	4400	4.0	7345
Bahía de Buenaventura – COL-BB	9709.2	3.7	4700
Sanquianga, Colombia – COL-SA	70000	3.5	3000-3500
Palmar, Ecuador – ECU-PA	30	2.5-3.0	250-300

At the fish family level three significant groups were formed in the cluster dendrogram according to the SIMPROF test (Figure 26): (1) The study from Ecuador (ECU-PA), (2) two studies from Mexico (MEX-CL and MEX-LP) and (3) the remaining fives studies (MEX-TL, COS-GD, COL-BB, COL-BM and COL-SA; Figure 26). The study in Ecuador was clearly separated from the rest by the dominance of species from Mugilidae, Atherinopsidae and Gobiidae, with the last two families being extremely dominant only in this study. The separation of the two studies from Mexico (second cluster) from the rest of studies is attributed to the disproportionately high contribution of Gerridae to relative abundance (> 55% in each study). Finally, the third cluster was comprised by five of the eight studies (Figure 26). Fifteen families accounted for > 80% of the total abundance in these studies (Table 17). Carangidae characterised these five studies with a correlation > 0.75 with the MDS2 axis (Figure 26) and contributed a relatively high proportion to the total abundances. Carangidae were almost absent from the studies of Ecuador and Mexico (ECU-PA, MEX-CL and MEX-LP). Similarly, Ariidae and Tetraodontidae were abundant families in terms of individuals in at least four of these five studies (Table 17). Finally, these five studies were also the ones having relatively high number of families represented in their assemblages (> 25). This feature clearly differentiated this cluster from the other two clusters which were poorer in the number of families (< 20 families).

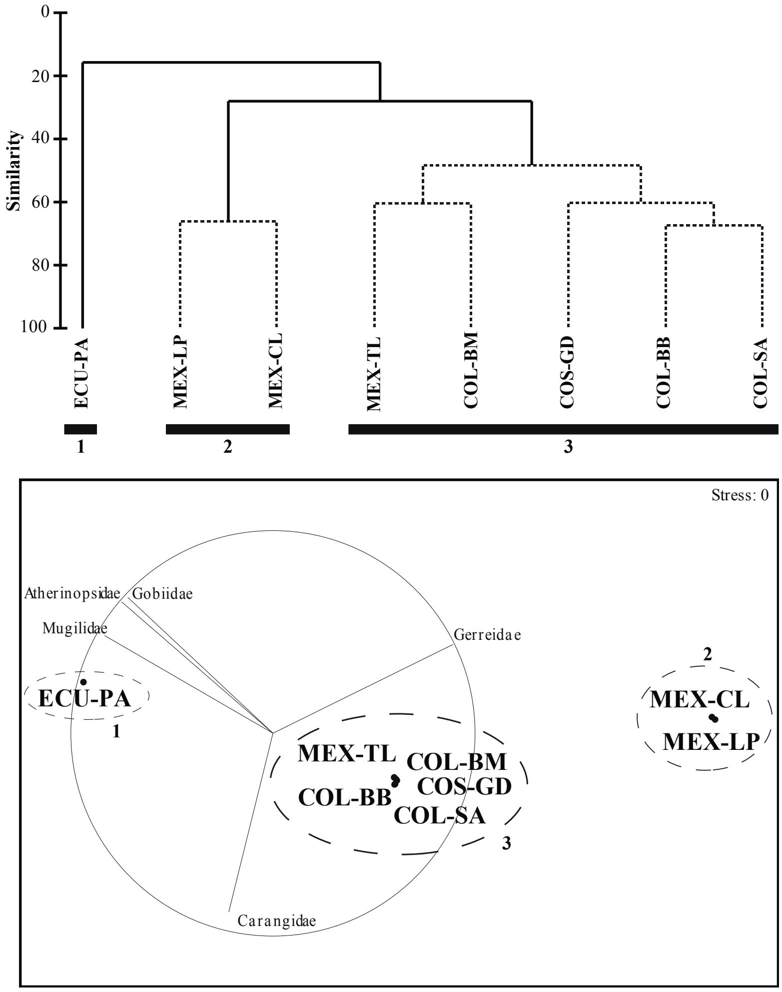

Figure 26. Cluster dendrogram and nMDS ordination plot of data (% abundance of families; Bray-Curtis metrics and average linkage algorithm) from eight mangrove fish studies in the tropical eastern Pacific. Dotted lines in dendrogram represent groups where no further

internal structure can be found according to the SIMPROF test. Families with correlation with MDS1 and MDS2 axes (Pearson) > 0.75 are shown.

DISCUSSION

The shore fish fauna in the TEP region has been relatively well documented in terms of its overall composition (but see Zapata and Robertson (2006), for an account of the shore fish species yet to be described). However, detailed studies documenting patterns in the structure and composition of mangrove fish assemblages along the entire region do not exist. This information can prove valuable when identifying ecological functions of mangrove ecosystems in the TEP (e.g. nursery function). The present analysis constitutes a first attempt to understand how mangrove ichthyofaunas may be structured in this marine biogeographical region.

Our analysis showed that the greatest mangrove fish species richness occurred at the central and southern coast of Colombia, coinciding with the most extensive mangrove areas in the whole TEP region. This pattern requires an examination of the mangrove ichthyofauna in Pacific Panama where a great diversity in environmental conditions (Robertson and Cramer 2009) might favour the presence of species-rich assemblages similar to those of Pacific Colombia.

Low similarity values among studies at the species level (except for the two most speciose assemblages in Colombia) indicate that considerable variability exists among mangrove fish assemblages in the region. This may be influenced by the specific seascape characteristics of each system as identified in other biogeographical regions (Giarrizzo and Krumme 2008; Sheaves and Johnston 2009). It would have been expected that studies carried out in proximate areas along the Pacific coast of Colombia were more related to each other in their fish composition. However, a study carried out in Bahía Málaga (COL-BM) showed little association at the species level with the remaining studies carried out in Colombia (COL-BB and COL-SA, ca. 30 and 180 km south of Bahia Malaga, respectively). Bahía Málaga is located in a previous valley of the San Juan River which was flooded after a tectonic uplift of the northwest part of Bahía de Buenaventura (COL-BB) and further tectonic events associated to active faults. These events took place from the late Miocene to the Holocene Epochs (Martínez and López-Ramos 2011) giving rise to a mosaic of rocky, sandy and muddy habitats including well-developed mangrove areas. The presence of this diversity of habitats favours species from families such as Lutjanidae that undertake ontogenetic migrations between mangroves and rocky habitats (Aburto-Oropeza et al. 2009). This contrasts with the geological setting in Bahía de Buenventura (COL-BB) and Sanquianga (COL-SA) where there is an almost complete absence of rocky substrates and small rivers have extremely high water discharge and sediment load. These seascape differences among nearby locations are likely to explain the differences in the mangrove fish faunas in the Pacific Colombia.

Nevertheless, the fact that the species composition of a study in Mexico (MEX-TL) was very similar to one in Colombia (COL-BM) indicates that despite the considerable differences in mangrove configuration and environmental conditions among the two areas (e.g. in terms of tidal regime and rainfall) (Table 15), a common fish species composition might be encountered at distinct mangrove areas of the TEP. Further explanations for the spatial variability in mangrove fish composition along the region could be rooted in the different energy flows and food web structures among estuarine/mangrove systems.

It is unclear if the dominance of Gerreidae in the northern portion of the TEP constitutes a consistent element in the composition of the mangrove fish fauna of this area, or if this is just an artefact of the sampling methodology employed in these studies (flow and trawl nets).

Despite Sciaenidae being the most speciose fish family in mangrove fish studies in the TEP (39 species), their average contribution to the number of individuals in all studies was only 3%. Only the studies carried out in Costa Rica (COS-GD) and Bahía de Buenaventura and Sanquianga in Colombia (Rubio 1984; Rubio and Estupiñan 1990) had slightly higher proportions of individuals within this family (5-10%). In these studies, species from the genera *Cynoscion*, *Bairdiella*, *Larimus* and *Ophioscion* contributed ca. 1-2% each to the total number of individuals, with the remaining species within the family representing very marginal numbers. Giarrizzo and Krumme (2008) argued that the contribution of Sciaenidae in intertidal mangrove creek fish assemblages of northern Brazil might be influenced by the presence of stronger marine conditions at the specific sampling sites. Increased marine influence in Sanquianga National Park suggests that this may also be the case in the TEP where the highest contribution of Sciaenidae to the overall mangrove ichthyofauna of the region was found. Sanquianga National Park is a deltaic system with relatively close contact to fully marine conditions in spite of a recent human-made river diversion that is increasing the freshwater influence of this system (Restrepo and Cantera 2011). Apparently, Sciaenidae are not common inhabitants of semi-enclosed and intermittently hypersaline lagoon systems of Pacific Mexico as their contribution to these assemblages was negligible. Mangroves may be a rather marginal habitat for Sciaenidae being more abundant and occurring in higher biomasses in adjacent soft bottom assemblages in the area (e.g. Bianchi 1991).

Correspondence to the previously defined TEP subdivisions

In the present analysis 64-84% of the soft-bottom ichthyofauna of the TEP defined by previous macroecological studies were recorded (Mora and Robertson 2005b; Zapata and Robertson 2006). Our results support the recent re-definition of the TEP subdivisions where the Panamic province is proposed as a large unit extending from Mexico to Ecuador (Robertson and Cramer 2009) (Figure 23). Similarities in mangrove fish species assemblage composition - 17 common species, some of them in very similar proportions - between Colombia (i.e. COL-BM) and Mexico (i.e. MEX-TL) support this claim. Moreover, the only study carried out in mangroves of the Cortez province (MEX-LP) did not show any indication, in terms of endemic fish species, for a further separation of the mangrove fish fauna from that of the Panamic province. Of 34 fish species found in MEX-LP, only three were found to be endemic to the Cortez province. The remaining species are well distributed along most of the TEP region. MEX-LP showed the closest association with another study in Mexico (MEX-CL), which is part of the Panamic province (Figure 25). This association was largely driven by the dominance of *D. peruvianus*, a widely distributed mojarra in the TEP. Consequently, our comparison suggests that no dispersal barriers affect the distribution and exchange of mangrove fish species along this province, in contrast to what occurs with certain TEP reef fish families (e.g. Chaenopsidae; Hastings 2000).

Number of individuals vs. catch mass

It is worth noting that the results of the present study can only be considered preliminary due to the systematic bias caused by the reliance on abundance data in most of the studies. Results based on catch mass are likely to significantly change dominance relationships on all taxonomic levels. For example, in one of the few quantitative studies that generated standardized catch mass estimates, Castellanos-Galindo and Krumme (unpublished data) sampled in intertidal mangrove creeks of central Colombia (COL-BM). They found that Clupeidae, Centropomidae and Lutjanidae dominated the assemblage in terms of relative abundance whereas catch mass was dominated by Lutjanidae, Tetraodontidae, and Ariidae. Similarly, the studies carried out in Costa Rica (COS-GN) and Mexico (MEX-TL; MEX-LP) consistently highlighted the greater contribution in catch mass of Ariidae, Centropomidae, Tetraodontidae, Gerreidae and Mugilidae to their fish assemblages, so that abundance and catch mass-based rankings result in very different dominance structures. Studies in Colombia (COL-BM) and Mexico (MEX-LP), the only ones providing both abundance and catch mass contribution estimates, clearly highlight the importance of Tetraodontidae when catch mass estimates are used. Both studies also show that Gerreidae and schooling species (i.e. Engraulidae, Clupeidae) reduce their contribution to the respective assemblage when catch mass is used instead of abundance (Figure **27**). Even if the relative abundances of Lutjanidae, Tetraodontidae, Ariidae or Centropomidae reach values between 1-5%, it is very likely that these families will dominate the catch mass percentages, downplaying the contribution of schooling species like Clupeidae or Engraulidae. Quantitative studies using relative catch mass from different mangrove areas along the TEP region are needed before a full picture of the spatial patterns in mangrove fish assemblage composition can be drawn. Yet, we consider that the overall patterns (i.e. species and family compositions) and the possible explanations for spatial variability described here will not change severely.

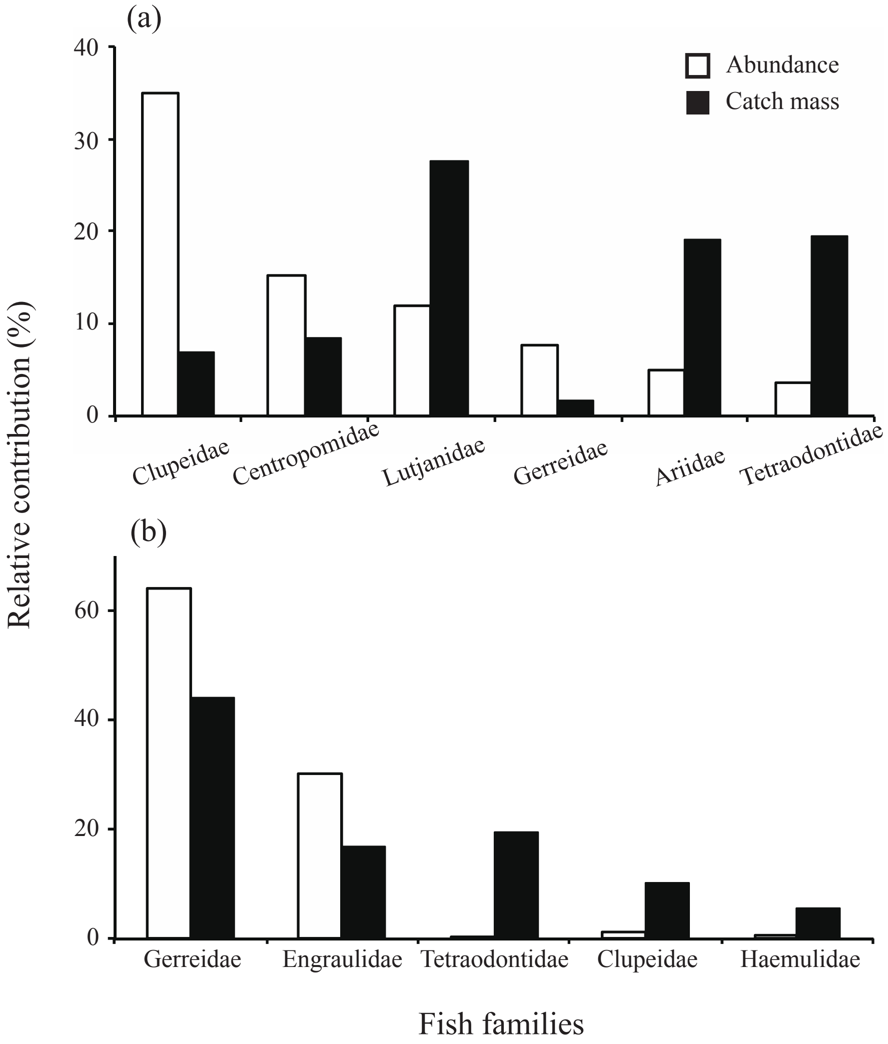

Figure 27. Examples of asymmetry between the relative total abundance and catch mass of the principal fish families of two mangrove fish studies from the tropical Eastern Pacific. (a) Bahía Málaga, Colombia – (COL-BM) and (b) El Conchalito, La Paz Bay, Baja California Sur, Mexico – (MEX LP).

The mangrove fish fauna of the TEP in comparison to other tropical areas

The overall biogeographical structure of the TEP shore fish fauna seems to be less complex than those of other tropical regions (i.e. Australia, Indo Pacific region) (Allen 2008; Last et al. 2011). This could be explained due to the relatively uniform geographic configuration of the continental shelf that despite eustatic changes in sea level has not originated in large barriers. This might have thus influenced the distribution and exchange of demersal soft-bottom fishes, including the mangrove ichthyofauna in the TEP (Robertson and Cramer 2009; Mora and Robertson 2005a).

A few zoogeographical considerations, especially those referring to neotropical mangrove areas, can be drawn from our analysis. As expected, mangrove ichthyofauna from an isolated marine biographical region like the TEP contains almost 50% less species than the very rich mangrove fish fauna of the tropical Indo-West Pacific where more than 600 species have been recorded (Blaber 2007). Most studies in the Indo-West Pacific (IWP) have identified Ambassidae, Leiognathidae, Clupeidae and Engraulidae families as the most numerically dominant components of the mangrove fish fauna in that region (i.e. Australia, Malaysia, Philippines; Chong et al. 1990; Pinto 1990; Blaber and Duke 1990; Sheaves and Johnston 2009). This dominance, however, is likely to change if species were ranked according to catch weight. In Malaysia, for example, family dominance changed to Ariidae, Ambassidae and Mugilidae when catch weights were considered (Chong et al. 1990). Likewise, Blaber and Duke (1990), in mangroves of Alligator Creek (Australia), found Latidae (*Lates calcarifer*) and Sparidae (*Acanthopagrus berda*) to be important components of the fish community using catch weight. The most common families in the IWP such as Leiognathidae and Ambassidae are absent from the Neotropics, however, Gerreidae in the TEP may be an ecological counterpart of the former family. Similarly, the importance of Latidae in some mangrove areas of the IWP may be replaced by the important representation that Centropomidae have in the TEP. Latidae and Centropomidae have been identified as phylogenetically related and may occupy similar ecological niches in estuarine mangrove environments of their respective regions (Li et al. 2011). On the other hand, Ariidae are of minor importance in Australia whereas catfishes are abundant and diverse in the TEP and the Tropical Western Atlantic (TWA). Similarities between the TEP and the IWP can be found when looking at the numerical dominance of the schooling families Clupeidae and Engraulidae in both regions. Blaber (2000; 2002) highlighted the minor importance of Sciaenidae in most mangrove fish assemblages in the IWP region. Although very diverse in the TEP (39 species), Sciaenidae also showed a minor representation in numerical abundance in most of the studies analyzed in this region.

The estuarine/mangrove fish community of the Tropical East Atlantic Ocean (TEA) was documented by Albaret et al. (2004), in a relatively undisturbed system, the Gambia Estuary. The authors argued that this fish community had the main fish families likely to be found in the TEA (but see, Vidy (2000) for an atypical example of mangrove fish composition in this region). The system was dominated by five families: Sciaenidae, Clupeidae, Mochokidae, Polynemidae and Ariidae, representing more than 90% and ca. 95% of the total fish catch weight and abundance, respectively. Among these families, the relative catch weight and abundance of Sciaenidae and Clupeidae was remarkable (totalling 78 and 86%, respectively). None of the studies analysed in the TEP region showed the dominance of two single fish families. Clupeidae, however, was in both regions (TEP and TEA) a dominant group of mangrove estuarine ichthyofauna. Nevertheless, the dominance of Sciaenidae in the Eastern Atlantic contrasts with the marginal representation of this family in the TEP. Albaret et al. (2004), found that the dominance of Sciaenidae was due to the disproportionate contribution of *Pseudotolithus elongatus*, a permanent inhabitant of the estuary, occurring in all seasons and all sites. This species was also numerically abundant in mangrove creeks in the same area (Vidy et al. 2004). The TEA mangrove ichthyofauna clearly had an underrepresentation of very important families in the TEP such as Tetraodontidae, Ariidae, Centropomidae and Gerreidae.

The mangrove fish composition of the TEP compared to the IWP and the TEA regions can be considered similar at the family level in terms of the dominance of schooling species of Clupeidae and Engraulidae. However, each mangrove fish fauna has components that are not present in the other regions (Ambassidae and Leiognathidae in the IWP; Mochokidae in the TEA, and Centropomidae in the TEP), which are the result of the particular biogeographic history of each region. Most of these endemic fish fauna components may ocuppy a similar ecological niche as their counterparts in other biogeographical regions.

The mangrove ichthyofauna in non-estuarine areas of the Caribbean is dominated by the families Haemulidae, Scaridae, Lutjanidae and Gerreidae (Acosta 1997). These families, especially Haemulidae, Scaridae and Lutjanidae are found in these systems largely due to the dependence that some species have with the mangrove-seagrass-coral reef continuum present in islands of the Caribbean (Nagelkerken 2007). In contrast, when estuarine mangrove habitats in the Caribbean are analysed, the fish composition shows a dominance of Centropomidae, Ariidae, Gerreidae, Tetraodontidae and Engraulidae (Golfo de Urabá and Ciénaga Grande de Santa Marta, Colombia and Terminos Lagoon in Mexico) (Rueda and Defeo 2003; Correa-Rendón and Palacio-Baena 2008; Sosa-López et al. 2010). All these families are also well represented in the mangrove fish fauna of the TEP. Tetraodontidae, Ariidae and Gerreidae have been rarely referred to in most mangrove fish studies from the Caribbean, albeit these families are abundant in catch weights in the estuarine mangrove systems of this region.

The mangrove fish faunas in the TEP and north Brazil in the TWA share the numerical dominance of Engraulidae or Clupeidae at most of the sampling locations. The mean contribution of these two families to the total fish abundance in the TEP was 25% whereas at some localities in north Brazil this contribution was 16% (Krumme et al. 2004). In north Brazil, Tetraodontidae (notably *Colomesus psittacus*) is a dominant component (both in number of individuals and catch mass) of mangrove habitats. This is concordant with the dominance (at least in catch weight) of Tetraodontidae in some of the mangrove fish studies of the TEP (e.g. COL-BM, MEX-LP). A clear difference in the mangrove fish assemblages of these two regions is the low contribution of Centropomidae and Gerreidae in the TWA compared to their substantial importance in most of the TEP localities (number of individuals and catch mass). A further difference between these two regions is the greater importance of Ariidae to the total assemblage in the equatorial Western Atlantic compared to the TEP. Whereas catfish abundances in north Brazil can reach ca. 35%

(Krumme et al. 2004), in the TEP it rarely exceeded 10% (Table 17). This is also true when catch masses for this family are compared among regions (33% vs. 19%; Giarrizzo and Krumme 2008, Castellanos-Galindo and Krumme, unpublished data). These differences may be explained by the biotic and ecological characteristics of the mangrove systems present at each biogeographical region. In northern Brazil, mangrove systems have high epifaunal biomass (Wolff et al. 2000; Koch and Wolff 2002), thus, favouring benthophage fish species (i.e. Ariidae). Humid mangrove systems of the TEP influenced by low fluvial sediment input, extremely high precipitation and high amplitude tidal regimes that regularly inundate large intertidal areas and that lack a mangrove plateau, might export most of their primary production to adjacent waters, thereby, sustaining relatively low mangrove epifaunal biomass. In the absence of this important food resource, fish with different feeding strategies (e.g. carnivorous-piscivorous) could thrive (i.e. Centropomidae, Lutjanidae).

Although, the three marine biogeographical regions in the Neotropics (TEP, Caribbean and TWA) share components of their mangrove ichthyofaunas that can be explained by their previous connectedness in geological times, the present composition of these assemblages could be further explained by: (1) the different trajectories (isolation, extinction episodes, environmental changes) characterizing each region once major gaps were formed (i.e. Panama Isthmus closure) and by (2) the local characteristics of mangrove systems within each region, including the interplay of tidal regime, coastal topography, and the productivity of each system.

Caveats of the approach

Although some of the studies analysed hereattempted to draw general spatial and temporal patterns within their own locations, it is evident that accurate generalizations about patterns in the whole region are still difficult to draw. This is partly due to the different sampling methodologies employed at each locality and the specific habitats and seascape configurations of the mangroves (Table 15). For example, the fish composition of the mangrove system in Ecuador (ECU-PA) was consistently different from the other studies examined. This study shared common families with the rest in the TEP (e.g. Mugilidae, Clupeidae), but the disproportionate contribution of Atherinopsidae and Gobiidae may be an artefact of the sampling methodology (small bag seine). Thus, a clearer picture of the variability in fish assemblage composition among mangrove areas in the TEP will be obtained once data from mangrove sites with different seascape settings collected with similar quantitative methodologies are available.

Priority areas pending sampling

At least four areas in the TEP need quantitative examination of their mangrove fish faunas: (1) The Gulf of Fonseca, shared by El Salvador, Honduras and Nicaragua, is one of the largest mangrove areas on the Central American Pacific coast (ca. 60000 ha) providing important revenues from artisanal fisheries in estuarine areas (Dewalt et al. 1996); (2) mangrove areas in the Gulfs of Panama, Chiriquí, and San Miguel in Panama constitute >70% of the total country mangrove areas. A few published studies and technical reports (e.g. http://www.cathalac.org/manglaresvspesqueria; D´Croz and Kwiecinski 1980) exist on the contribution of mangrove fishes to fisheries, but no quantitative measures of mangrove fish community structure are available; (3) mangroves of the Esmeraldas-Pacific Colombia eco-region (south Colombia and north Ecuador) are recognized as the most structurally complex and best developed mangroves in the Neotropics in terms of leaf area, diameter, height and species diversity (West 1956; Suman 2007); and (4) mangroves of the Guayas estuary (Gulf of Guayaquil, Ecuador) cover an area of 130000 ha with coastal development and shrimp aquaculture as the main drivers of mangrove loss. Quantitative studies of mangrove fish assemblages in these areas will benefit the understanding of the zoogeographic patterns along the entire TEP region, opening the door to more detailed comparisons as already attempted for fish faunas in other habitats of the region (i.e. Edgar et al. 2011).

ACKNOWLEDGEMENTS

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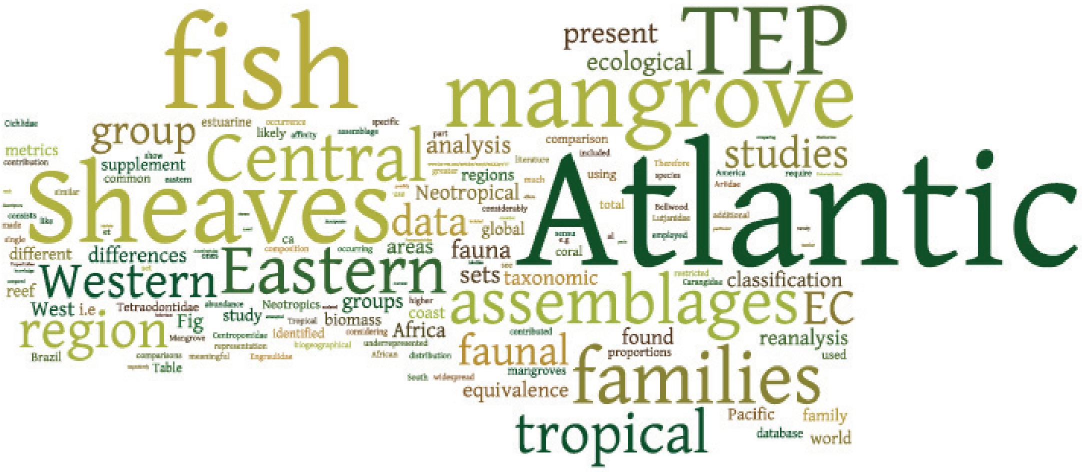
Chapter V. Mangrove fish assemblages from under-represented regions and the measurement of ecological equivalence: Comment on Sheaves (2012)

Gustavo A. Castellanos-Galindo, Uwe Krumme



Cite as: Castellanos-Galindo G.A., Krumme U. (2013) Mangrove fish assemblages from data-sparse regions and the measurement of ecological equivalence: Comment on Sheaves (2012). *Marine Ecology Progress Series* 474:299-302.

ABSTRACT

The global comparison of mangrove fish assemblages and their ecological equivalence by Sheaves (2012; Mar Ecol Prog Ser 461:137–149) presents useful novel information for this specific ecosystem faunal assemblage. This comparison, however, included only a single study from the tropical Eastern Pacific region (TEP), which was assigned to an Eastern Central Atlantic group. Here, we present data that supplement the analysis made by Sheaves and show that the taxonomic composition (at the family level) of the TEP mangrove fish fauna is considerably different from the Eastern Central Atlantic and warrants a different classification. To characterize TEP mangrove fish fauna, we used the same descriptors in Sheaves (2012) (i.e. % of families with widespread vs. restricted distributions and their affinity with families characteristic of coral reefs). Based on our analysis, the estuarine mangrove fish assemblages from the Neotropical region (TEP and Western Central Atlantic) substantially differ — both taxonomically and functionally — from the ones at the West African coast (tropical Eastern Atlantic) so that overall, Sheaves´ (2012) Eastern Central Atlantic group likely consists of 3 groups: TEP, Western Central Atlantic and tropical Eastern Atlantic. An examination of the relative abundance and biomass of fish families revealed striking differences in their representativeness, especially between Neotropical and tropical Eastern Atlantic assemblages. Therefore, further comparisons of ecological equivalence should use metrics with a higher ecological resolution (i.e. biomass) than the ones employed by Sheaves (2012) giving a more meaningful basis to compare mangrove fish assemblages worldwide.

Keywords: Mangrove fish assemblages, Ecological equivalence, Tropical eastern Pacific, Neotropics

Introduction

There have been attempts to synthesize our current knowledge of global mangrove fish assemblages from a taxonomic perspective (e.g. Blaber 2000), but no specific studies have attempted to increase our understanding of the composition and ecological equivalence of these assemblages until Sheaves (2012). Sheaves (2012) analysed the similarities and differences of mangrove fish assemblages from studies around the world by using the proportions of the total species pool contributed by each fish family for each study. He acknowledged that the inclusion of only one study from the tropical Eastern Pacific (TEP) as part of an Eastern Central (EC) Atlantic group has to be interpreted with caution. However, this clear bias may have severe effects on the interpretation of taxonomic and possibly functional relationships among mangrove fish assemblages in different biogeographical areas. Sheaves' (2012) EC Atlantic group classification was based on data from South America and Africa, considering only 4 data sets from Brazil and 13 from the West African coast. Data from major mangrove regions of the EC Atlantic that are underrepresented in the literature were not included, making the global comparison of Sheaves (2012) incomplete. Here, we present a reanalysis using additional studies on mangrove fish assemblages from the TEP and the Western Central Atlantic (French-Guyana, Brazil; see the supplement at www.int-res.com/articles/suppl/m474p299_supp.pdf). In our reanalysis (following the approach of Sheaves 2012), the EC Atlantic category has been split into 3 regions, namely the TEP, the Western Central Atlantic and the tropical Eastern Atlantic, emphasizing that considerable differences exist in the mangrove fish assemblages between these regions.

Tropical eastern Pacific mangrove fish assemblages

The TEP is considered the most isolated tropical marine biogeographical region of the world, with fish fauna endemism estimated at ca. 80% (Robertson & Cramer 2009). The mangrove areas in this region comprise ca. 27% of the total mangroves in the Neotropics and ca. 8% of the world (Lacerda et al. 2002). Mangrove fish assemblage studies in the TEP are lacking from the peer-reviewed literature (Faunce & Serafy 2006). Yet, this underrepresentation has been partially overcome through a recently published review by Castellanos-Galindo et al. (2012) of 9 mangrove fish fauna studies. The database of Sheaves (2012) contained a single TEP study from a Mexican coastal lagoon system (Warburton 1978), which was grouped with the EC Atlantic.

For the mangrove fish studies from the TEP region, we found 8 fish families (Heterenchelyidae, Lophiidae, Microdesmidae, Ophidiidae, Rajidae, Torpedinidae, Triakidae and Urotrygonidae) that were absent from the data sets of Sheaves (2012). Of the 41 families that were present in all 4 faunal groups identified by Sheaves (2012), 9 were not present in the TEP in our analysis (Figure 28). When comparing the families in common between the TEP region and EC Atlantic faunal group, we found differences that will likely alter the faunal groups identified in Sheaves (2012).

A definitive classification will require a reanalysis of the data set used by Sheaves (2012) together with the data provided here. Tetraodontidae, Engraulidae, Lutjanidae, Atherinopsidae, Cichlidae and Centropomidae showed contrasting representation (% of studies within a region where families occurred) between the TEP in our analysis and Sheaves´ (2012) EC Atlantic faunal group (our Figure 28). The contribution from families with widespread distribution (recorded as occurring in most parts of the world where mangroves are found; sensu Sheaves 2012) in the TEP (88%) was much higher than the contribution from families with restricted distribution (i.e. only present in the TEP or the Neotropical region) (12%). These proportions more closely resemble those found by Sheaves (2012) for the EC Atlantic faunal group.

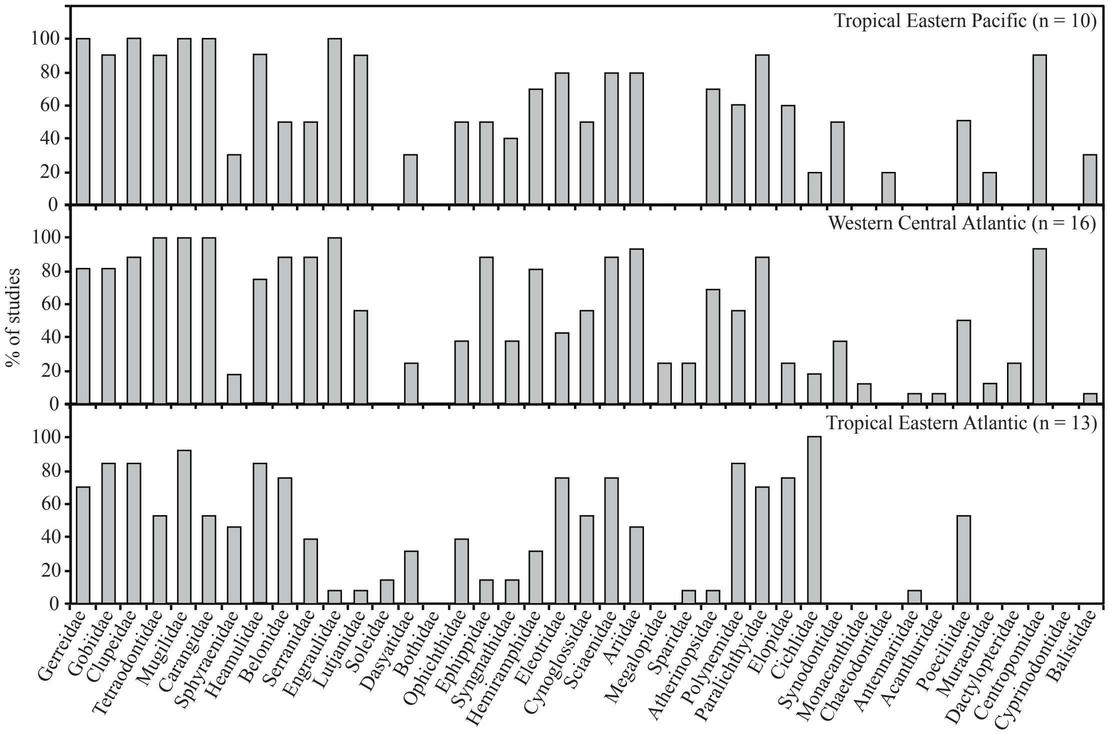


Figure 28. Percentage of data sets analyzed from the tropical Eastern Pacific region (including the data set of Warburton 1978), the Western Central Atlantic and the tropical Eastern Atlantic (see the supplement at www.int-res.com/articles/suppl/m474p299_supp.pdf for a list of references) in which fish families common to all faunal groups identified by Sheaves (2012) occurred. These 3 biogeographical regions constitute the EC Atlantic faunal group identified by Sheaves (2012). Family order on x-axis follows Fig. 5 in Sheaves (2012).

To investigate the degree of overlap of mangrove fish families with coral reef families in the TEP, we compared the occurrence of the 10 fish families in Bellwood's (1996) consensus list of coral reef fish families. We only identified Carangidae and Labridae occurring in >25% of samples of the TEP region (100% and 30% of occurrence in data sets, respectively). The rest of Bellwood's (1996) reef fish families had <20% representation in studies of the TEP (Chaetodontidae, Apogonidae, Mullidae, Pomacentridae) or were not part of the mangrove fish fauna of the region (i.e. Acanthuridae, Blenniidae, Holocentridae, Scaridae). Thus, a very low reef affinity characterized the mangrove fish fauna of the TEP region, similar to what Sheaves (2012) found for the EC Atlantic and Australasian faunal groups.

Neotropical versus tropical Eastern Atlantic fish assemblages

The taxonomic classification of Western Central Atlantic and tropical Eastern Atlantic mangrove fish assemblages as Sheaves´ (2012) EC Atlantic faunal group is potentially problematic. Even though most indicator families for the EC Atlantic faunal group (sensu Sheaves 2012) are present in Brazil, the family Claroteidae (freshwater catfishes), for example, is only present in tropical Eastern Atlantic mangroves (Table 19). Likewise, Cichlidae and Elopidae are rarely reported in studies from the Western Central Atlantic (Figure 28). Moreover, common families in the Western Central Atlantic like Tetraodontidae, Carangidae, Engraulidae, Lutjanidae, Ephippidae, Ariidae and Centropomidae are clearly less common in the tropical Eastern Atlantic region (Figure 28). Therefore, Sheaves' (2012) grouping of mangrove ichthyofaunas of these 2 regions could be an artifact of considering a greater number of data sets from the tropical Eastern Atlantic (13) than from the Western Central Atlantic (4). Our reanalysis includes 16 data sets from the Western Central Atlantic region (see Annex II, Supplemental Table A4). In addition, further differences between Neotropical estuarine areas and West Africa (tropical Eastern Atlantic) emerge when abundance or catch mass metrics are employed: our preliminary analysis employing such metrics shows that TEP and Western Central Atlantic mangrove fish assemblages are considerably more similar to each other, and very different from West Africa (Table 19, Figure 28). In particular, the families Tetraodontidae and Ariidae are only marginally represented in West Africa in terms of biomass, whereas in the TEP and the Western Central Atlantic these two families have top ranking (Table 19).

Conclusion

The starting point to test hypotheses regarding taxonomic and ecological equivalence of mangrove fish assemblages has been set by Sheaves (2012). We supplement the analysis made by Sheaves (2012) with additional data sets from the Neotropics and show that the EC Atlantic group of Sheaves (2012) likely consists of 3 faunal groups: the TEP, Western Central Atlantic (Atlantic coast of South America) and the tropical Eastern Central Atlantic (Atlantic coast of Africa). An ultimate classification would require a reanalysis using the whole database used by Sheaves (2012) and the database presented here. In the future, more meaningful global comparisons need to incorporate studies that are available from underrepresented mangrove areas (e.g. the TEP, estuarine areas of the Caribbean) and also consider the use of metrics like biomass (Magurran & Henderson 2012) that are of much greater ecological significance than the proportions of the total species contributed by each fish family.

Supplementary data is given in Annex II

Table 19. Comparison of different metrics from mangrove fish assemblages from 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 for indicative families (sensu Sheaves 2012) in the Eastern Central (EC) Atlantic faunal group. *: Information on ecologically important families in the Neotropics based on studies not included in Sheaves (2012).

Family	**Tropical Eastern Pacific**[a]			**Western Central Atlantic**[b]			**Tropical Eastern Atlantic**[c]		
	% no. of species	% no. of ind.	% B[d]	% no. of species	% no. of ind.	% B	% no. of species	% no. of ind.	% B
Ariidae	6.67	3.98	19.14	7.41	31.53	32.41	4.29	1.31	3.39
Cichlidae	0.95	0.01	0	0	0	0	4.29	0.02	0.06
Claroteidae	0.00	0.00	0	0	0	0	4.29	0.47	1.45
Clupeidae	2.54	15.41	6.93	2.36	2.35	0.37	5.71	46.54	27.20
Eleotridae	2.54	0.79	0.61	0.77	0.05	0.07	1.43	0.01	0.01
Elopidae	0.32	0.14	0	0.85	0.03	0.04	1.43	0.28	0.41
Engraulidae*	5.40	9.48	0.01	9.95	18.24	7.39	0	0	0
Gerreidae*	4.13	20.41	1.61	2.91	1.56	0.75	2.86	0.11	0.11
Mugilidae	1.27	8.67	1.31	4.56	8.46	8.70	7.14	2.23	2.74
Polynemidae	0.63	0.65	0	0.67	0.02	0.03	4.29	1.69	3.39
Pristigasteridae	0.95	0.21	0	0.83	0.04	0.01	0	0	0
Sciaenidae	12.38	3.07	0.26	16.62	10.43	9.07	8.57	39.65	50.40
Tetraodontidae*	2.86	3.02	19.53	3.94	9.21	21.93	1.43	0.07	0.10

[a] Data from Castellanos-Galindo et al. (2013)

[b] Data from Giarrizzo & Krumme (2008)

[c] Data from Albaret et al. (2004)

[d] Data from a single study where biomass data are available (authors' unpubl. data)

Chapter VI. Long-term stability of tidal-related patterns in mangrove creek fish assemblages in North Brazil.

Gustavo A. Castellanos-Galindo, Uwe Krumme

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ABSTRACT

Intertidal fishes are thought to respond to tidal and diel rhythms since early geological times. However, the assumption that tidal and diel patterns in intertidal fish assemblages are stable over long time scales (> 1 year) is largely untested. Testing the validity of this assumption is crucial to assess whether short-term temporal patterns, once established, can be extrapolated over time and assist in a better understanding of the temporal dynamics of fish assemblages in coastal habitats. Here, we compare the fish assemblage structure from two intertidal mangrove creeks in North Brazil (Bragança Peninsula, Caeté estuary) sampled with the same methodology (block nets), the same sampling effort (two lunar cycles) and same sampling design (accounting for the combination of tidal and diel cycle) in the rainy seasons of 1999 and 2012 to evaluate the persistence, stability and recurrence of short-term patterns in the fish community organization. The interaction of tidal and diel cycles (inundations at spring tide-night, spring tide-day, neap tide-night, neap tide-day), found to be stable after 13 years, resulted in recurrent and stable intertidal mangrove fish assemblage compositions. The intertidal mangrove creek fish assemblage consisted of a persistent number of dominant species (seven). However, there were remarkable changes in fish catch mass, abundance and species dominance between the samplings in 1999 and 2012. The most severe drought in North Brazil since 30 years, linked to lower precipitation and river runoff in the rainy season of 2012, likely resulted in (1) lower abundance of small juveniles of several dominant species in this assemblage (especially Ariidae - *Cathorops agassizii* and *Sciades herzbergii*) and (2) increased dominance of large-sized specimens of the tetraodontid *Colomesus psittacus*. Our findings highlight: (1) the overriding importance and stability of the interactive pulse of the tidal and diel cycles in determining short-term temporal patterns in intertidal mangrove fish assemblages in neotropical macrotidal estuaries despite the occurrence of extreme events (i.e. major decrease in rainfall) and (2) the dramatic influence that these extreme events can exert on recruitment processes in tropical estuarine fish assemblages.

Keywords: Mangrove fish assemblage, persistence, stability, tidal dynamics, precipitation, Brazil, Tropical Western Atlantic

INTRODUCTION

Mangroves are widely referred to as nursery sites for nekton (e.g. Robertson & Duke 1987, Laegdsgaard & Johnson 1995). While equivocal evidence has been presented supporting this claim depending on the geographical area, it is clear that mangroves constitute an important habitat for a specific portion of coastal fish assemblages in the tropics and subtropics. Mangrove fish assemblages worldwide show a certain degree of taxonomic and functional equivalence, indicating some spatial uniformity on large geographical scales (within and between marine provinces) (Sheaves 2012, Castellanos & Krumme 2013). However, the extent to which faunal and functional characteristics persist over time in specific estuarine mangrove fish assemblages is less clear, at least over time scales > 2 years (reviewed in Faunce & Serafy 2006, but see Lorenz 1999, Blaber et al. 2010, Ecoutin et al. 2010).

Persistence and stability are two common descriptors of assemblage variability in time, which form central questions in community ecology (Connell & Sousa 1983). Persistence is considered as the continuous presence of species within assemblages over time, and stability is defined as the degree of constancy in the numbers and/or relative abundances of species within assemblages (Meffe & Minckley 1987). These two concepts have been addressed directly or indirectly in a variety of faunal groups including freshwater and marine coastal fishes (e.g. Oberdorff et al. 2001, Garcia et al. 2012). However, few studies have examined these two ecological properties in intertidal mangrove fish assemblages. Intertidal habitats are unique with respect to the short temporal dynamics that characterize them (e.g. only accessible for fish at high tides during daytime or at night), and therefore constitute a relatively complex system challenging the testing of the persistence and stability of community structure.

An often overlooked source of variability in mangrove fish dynamics in meso- and macro-tidal coasts is the tidal pulse (Gibson 2003). In combination with the diel cycle, tides can control the community organization of tropical intertidal fishes (reviewed in Krumme 2009). This has been shown in fish assemblages migrating with the macrotides to intertidal mangroves in the Bragança Peninsula in North Brazil (Krumme et al. 2004). The number of fish species, abundance and biomass were generally greater at spring tides than at neap tides. A major implication of these results is the need to carefully account for the scales of variation when designing the sampling/data collection and interpreting results from mangrove fish assemblages of meso- or macrotidal coasts (Krumme & Saint-Paul 2010).

The mangroves of North Brazil are a rare example of a tropical coastal area where fish assemblages have been relatively well documented (studies dating back to the late 90s; see Giarrizzo & Krumme 2008, Krumme & Saint-Paul 2010). This area, known as the Amazon Macrotidal Mangrove Coast, is recognized as the largest continuous mangrove area of the world (7424 km^2, 57% of Brazil's mangrove cover; Nascimento Jr et al. 2013). The study of fish assemblages in this region has included both the subtidal main channels of the estuarine system (i.e. Caeté estuary; Barletta et al. 2005) and the intertidal mangrove creeks (Barletta et al. 2003, Krumme et al. 2004, Giarrizzo & Krumme 2007), generating baseline information for these relatively "pristine" ecosystems (Blaber in press). Whereas in channels of a single estuarine system, assemblages comprise ca. 80-90 species (Barletta et al. 2003), in intertidal mangrove creeks this number is reduced to 34-75 species in different localities depending primarily on the size of creeks and sampling intensity (Giarrizzo & Krumme 2008, Krumme & Saint-Paul 2010). Intertidal mangrove creeks are visited by at least 115 fish species along the Amazon macrotidal coast, and constitute an important habitat for estuarine fishes in the area. Creek systems in the Amazon macrotidal coasts are dominated by the same families (i.e. Tetraodontidae, Engraulidae, Sciaenidae, Mugilidae, Haemulidae and Ariidae), but with varying proportions (catch mass) as a function of the proximity to the Amazon mouth (Giarrizzo & Krumme 2008).

While these studies have advanced our understanding of the spatial variability of these assemblages, their long-term persistence and stability in time remains to be tested. Barletta et al. (2003) and Giarrizzo and Krumme (2007) investigated the monthly and seasonal dynamics of mangrove creek fish assemblages in two relatively close estuarine areas (Caeté and Curuça estuary) for a one year period. Both studies found no significant differences in overall fish density between seasons (dry and rainy seasons), but significant seasonal changes in density and biomass for selected dominant species. However, the variability between the sampled creeks was always greater than the temporal variability. Only in Barletta et al. (2003) in the Caeté region did the species-specific seasonal changes in biomass result in significantly higher overall fish biomass during the rainy season.

In the present study, the aim was to examine long-term changes (after 13 years) in the fish assemblage structure of intertidal mangrove creeks in a locality of the Amazon macrotidal mangrove coast (Bragança Peninsula). We specifically assessed if (1) tidal-related patterns were persistent between sampling intervals and if (2) the assemblage showed persistency and stability over time. To avoid spatial and temporal confounding effects common in other studies, we sampled the same intertidal mangrove creeks during the rainy season for two complete lunar cycles in 1999 and 2012. The results obtained here provide a better understanding of the long-term dynamics in mangrove fish assemblages of this region, highlighting that tidal dynamics are a fundamental and stable pulse shaping the distribution of species in macrotidal mangrove creek areas.

MATERIALS AND METHODS

This study took place in the mangroves of the Bragança Peninsula, North Brazil (0º 52’ S, 46º 38’W; Figure 29). This peninsula (about 8 km wide, 25 km long, covering ca. 180 km^2), lies between two of the 23 estuaries characterizing the Amazon macrotidal mangrove coast (Caeté and Taperaçu estuaries; Souza Filho et al., 2009). Up to 90% of the peninsula is covered with mangrove forest dominated by *Rhizophora mangle*, *A. germinans* and *R. racemosa* while *R. harrisonii* and *A. schaueriana* are less abundant (Menezes et al. 2008). Semi-diurnal tides have a tidal range of 3->4 m at spring tides and 2-3 m at neap tides. Mean annual precipitation is 2500 mm; approximately 75% falls during the rainy season (January-June). The dry season starts in July and ends in December. Various large tidal channels (locally called “Furos”) enter into the Bragança Peninsula inundating vast areas at high tide (especially at spring high tides). One of these tidal channels is the “Furo do Meio”, that extends ca. four km into the peninsula (Figure 29). The Furo do Meio is permanently inundated, even at low tide. The tides enter the mangrove forest through large drainage systems (first-order creeks) that have several branches inside the mangroves (second and third-order creeks) (Figure 29b).

Within the Furo do Meio, two second-order creeks (0° 52’ 35” S, 46° 38’ 45” W; *ca.* 100 m in length and 3 m wide at the entrance; detailed creek maps in Krumme et al. 2004) were blocked in the rainy seasons of 1999 and 2012 at slack high tide with fishing nets of equal mesh-size (12 mm, stretched; size of the net in 1999: 10 x 3 m; in 2012: 12 x 4 m). This fishing method is locally called “tapagem” and regarded as highly efficient in recording the fish fauna using vegetated intertidal habitats (Bozeman & Dean 1980). In both sampling campaigns, fishes were sampled in both creeks during two consecutive lunar cycles at spring and neap tides and during day and night (namely spring-day (SD), spring-night (SN), neap-day (ND) and neap-night (NN)), thus accounting for the four most important tidal and diel cycle combinations that result from the disparate duration of tidal *vs* diel periods (24 h 50 min *vs* 24 h). The approximate times of slack high water at spring and neap tides were similar between samplings in 1999 and 2012 (*ca.* 06:00 and 18:00 h at spring tides and *ca.* 00:00 and 12:00 h at neap tides). To further ensure complete comparability between the 1999 and 2012 samples, fish collections were made during the respective rainy periods of both years (with a one month delay in 2012 to account for the maximum decrease in salinity during the rainy season of this year; Figure 30). The mangrove creeks were surveyed in 1999 by one of the authors (U. Krumme). In 2012, an inspection of the same creeks revealed no changes in the overall topography (see Annex III, Supplemental Figure A4), emphasizing that intertidal mangrove creeks exhibit an unexpectedly stable configuration over time. In 1999 creeks were sampled between February and April (n=17 block net catches), whereas in 2012, creeks were sampled between March and May (n=17 block net catches).

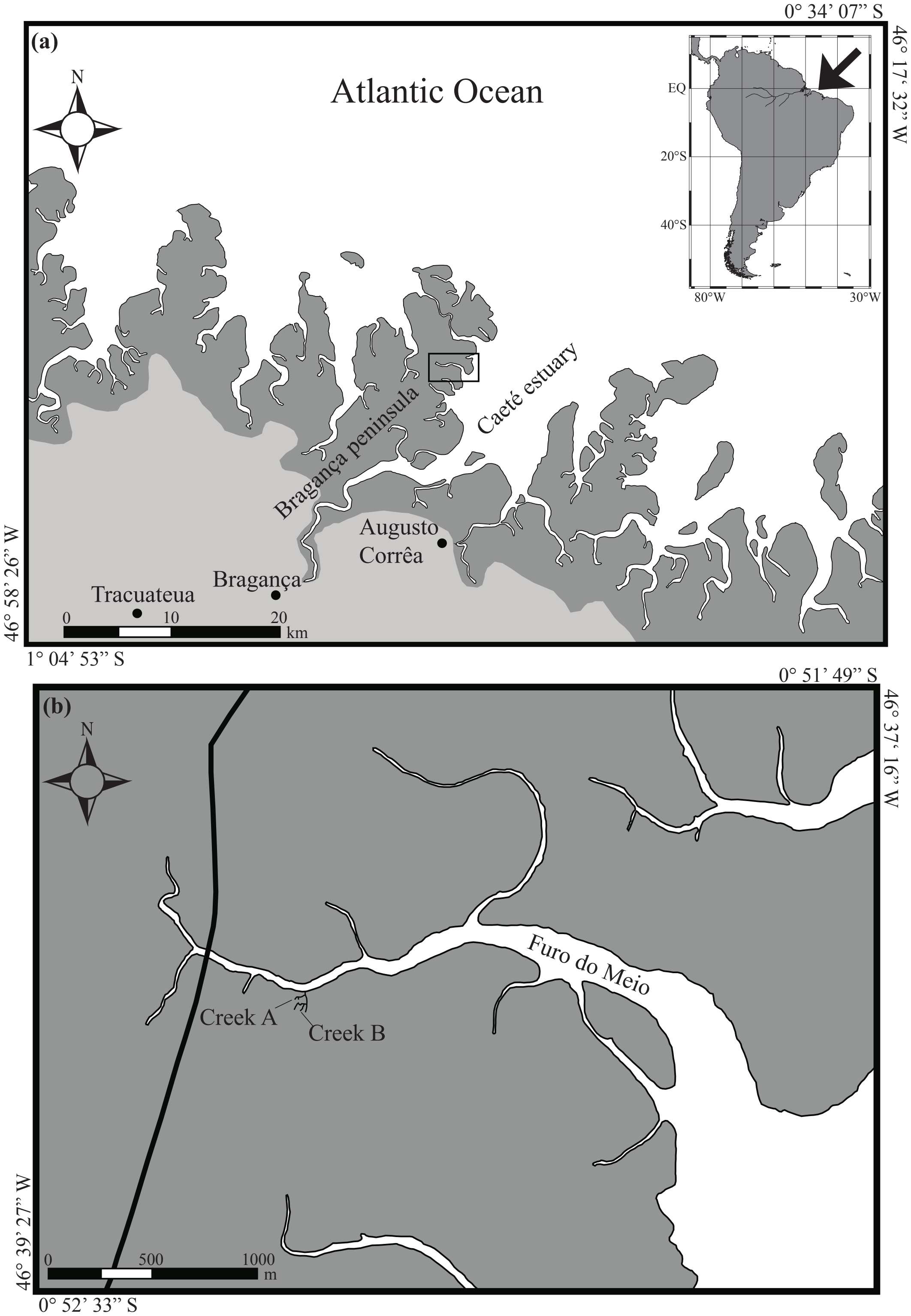

Figure 29. (a) Bragança Peninsula and the Caeté estuary south of the mouth of the Amazon River, (b) The Furo do Meio and location of creeks A and B, sampled in 1999 and 2012; black line: street to the beach.

Rainfall data from the sampling months in 1999 and 2012 were obtained from the nearest station to the sampling site (Tracuateua INMET station, 36 km from the sampling site; Figure 30) and salinity was recorded *in situ* at high tide during both sampling periods (using the Practical Salinity Scale). Mean tidal heights at the entrance of the creeks were smaller during samplings in 2012, but significant differences between sampling periods were only found between tidal heights at spring tides of one creek (see Annex III, Supplemental Figure A4). Lower tidal heights in 2012 may be related to a significant drought that took place in North Brazil during that year, resulting in reduced freshwater discharge into the estuary.

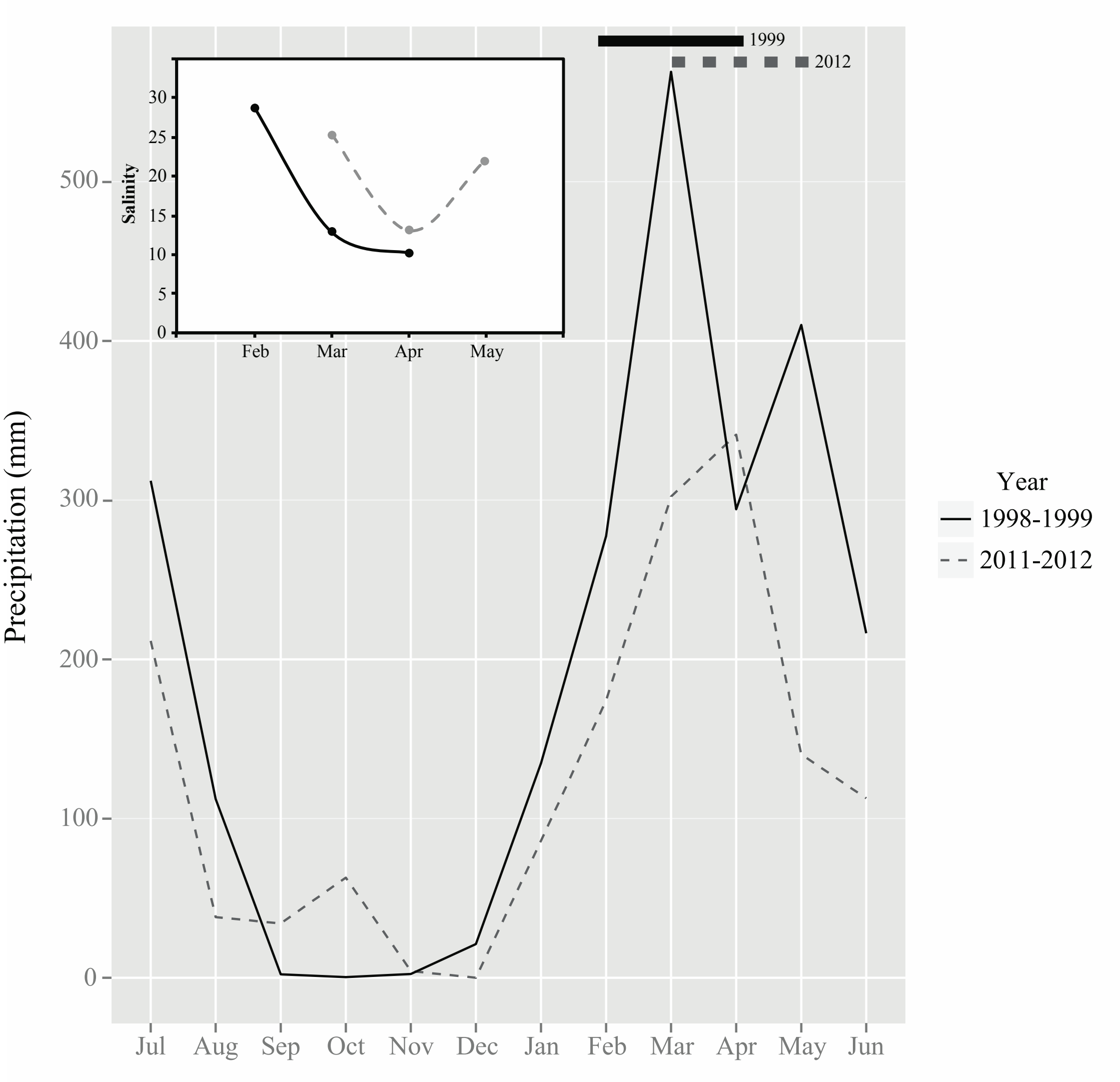

Figure 30. Total monthly precipitation in the study area during 1998-1999 and 2011-2012. Data from INMET, Tracuateua station (see Figure 29). Horizontal bars indicate fish sampling periods in 1999 (black; February to April) and in 2012 (grey; March to May). The small plot shows the recorded salinity values in the Furo do Meio during sampling periods.

Fish caught during samplings in 1999 and 2012 were transported on ice to the laboratory, identified with taxonomic keys for the area (FAO species identification sheets: Cervigón et al. 1993, Carpenter 2002a, 2002b), measured (Total Length-TL) and wet-weighed (±0.01 g). Species abundance distribution plots were constructed to obtain a general description of the fish communities sampled in 1999 and 2012. A three-way PERMANOVA model was used to test whether there were differences in fish composition between the treatments (1) Creeks (random, two levels: creek A and B), (2) Tide-time of day (fixed, four levels: SD, SN, ND, NN), and (3) Sampling year (fixed, two levels: 1999 and 2012). Only species representing > 1% of the total catch weights were used in the analyses (10 species). Since comparisons between years included the same creeks (same spatial units without visible changes in topography and mangrove cover) and the same tide-time of day combinations, catch mass data were used for analyses. Samples between time intervals were considered independent, as there was not a significant decrease of fish catch mass per sampling event with time (see Annex III, Supplemental Figure A4). Analyses were performed on squared-root transformed data and based on Bray-Curtis distances. Since PERMANOVA is sensitive to differences in multivariate dispersion among groups, a test of homogeneity of multivariate dispersions (PERMDISP) was performed. To visualize the multivariate patterns shown in the PERMANOVA test, a PCO (principal coordinate analysis, unconstrained ordination technique analogue to nMDS) was performed. Species responsible for the observed patterns shown in the PERMANOVA were identified using correlations with the PCO axes ($|r| > 0.4$). Routines were performed using PERMANOVA+ for PRIMER software (Anderson et al. 2008).

A two-sample Wilcoxon test was used to statistically test for differences in mean fish lengths (TL) between sample years. Pooled length data (cm) from the whole fish assemblages observed in each sampling interval (1999 and 2012) were used to produce length-frequency distributions. Length-frequency distributions were also generated for the three most important fish species (in terms of catch weight) and compared between sampling times, using a Kolmogorov-Smirnov (KS) two samples test (Zar 1999).

RESULTS

In 2012 the total precipitation during the rainy season (January-June) in the Bragança Peninsula was substantially reduced (40% less rain) compared to the precipitation in the rainy season in 1999 (Figure 30.). This change was reflected in the salinities recorded during the rainy seasons of 1999 and 2012. During 2012 in the Furo do Meio minimum salinities of 13 occurred only in April, when the precipitation reached the annual peak. After April, salinity values returned relatively fast to the former values (> 20). In contrast, in 1999 reduced salinities were observed already in March and continued at 10-12 at least until April, thus reflecting the greater precipitation in 1999 that already had increased in February with peaks in March and May (Figure 30).

Overall, 45 fish species (without discriminating *Mugil* spp.), distributed in 24 families, were identified in the two intertidal mangrove creeks during the two sampling periods (Table 20). A more speciose (40 species) and even assemblage in 1999 (see slopes of Figure 31) contrasted with an assemblage poorer in species (28 species) in 2012, which was strongly dominated by a single species (*Colomesus psittacus*, Tetraodontidae; Figure 31). Of the 10 most abundant species (representing > 90% of the total abundance) in each sampling year, seven were shared (Figure 31), indicating that these species constituted the core part of the fish assemblage. These seven fish species represented ca. 84% and 89% of the total catch weight in 1999 and 2012, respectively (Table 20). Likewise, the same dominant families in terms of catch weight (Ariidae, Tetraodontidae) were observed in 1999 and 2012, accounting for > 65% of the total catch during both samplings. The proportions of the contribution of these families, however, varied remarkably between the two periods. In 1999, the contribution to the total catch weight by Ariidae (*Cathorops agassizii* and *Sciades herzbergii*) and Tetraodontidae (*C. psittacus*) was ca. 50% and ca. 20%, respectively. In 2012, the contribution of Ariidae was relatively low (only 15%) whereas the contribution of Tetraodontidae was high (60%). Abundance and catch weight of mullets (Mugilidae) in 1999 were almost ten-fold and two-fold higher than in 2012, respectively (Table 20). Overall, the sampling in 2012 yielded substantially less fish than the 1999 sampling (ca. 40% in terms of abundance and ca. 80% less in terms of weight). This reduction involved all abundant species found during both sampling periods (Table 20).

Table 20. List of species captured in two intertidal mangrove creeks in the Furo do Meio, Bragança Peninsula, North Brazil during sampling campaigns in 1999 and 2012. The seven core species of this fish assemblage in bold. (-) species not present in survey.

Species	**Weight (g) (%)**		**Abundance (No. Ind) (%)**		**Mean TL (cm) (range)**	
	1999	2012	1999	2012	1999	2012
***Cathorops* sp. (Ariidae)**[a]	23408 (37.4)	3142.8 (8.0)	1030 (26.7)	99 (10.6)	12 (3-23)	14.8 (3.6-23.0)
***Colomesus psittacus* (Tetraodontidae)**	12081 (19.3)	23534.9 (59.9)	417 (10.8)	268 (28.7)	7 (1-27)	12.4 (4.3-29.4)
***Sciades herzbergii* (Ariidae)**[b]	6312 (10.1)	3146.7 (8.0)	441 (11.4)	60 (6.4)	10 (3-34)	17.7 (7.0-26.7)
***Pseudauchenipterus nodosus* (Auchenipteridae)**	3851 (6.2)	1602.2 (4.1)	426 (11.0)	211 (22.6)	9 (5-13)	9.1 (6.4-16.6)
***Anchovia clupeoides* (Engraulidae)**	3034 (4.8)	2035.3 (5.2)	248 (6.4)	98 (10.5)	10 (5-17)	13.9 (8.6-17.5)
***Mugil* spp. (Mugilidae)**[c]	2605 (4.2)	1396.4 (3.6)	446 (11.6)	53 (5.7)	6 (2-29)	14.4 (7.5-20.6)
Anableps anableps (Anablepidae)	2320 (3.7)	442.1 (1.1)	75 (1.9)	15 (1.6)	13 (1-25)	15.2 (9.5-19.3)
***Lycengraulis grossidens* (Engraulidae)**	1354 (2.2)	131.4 (0.3)	348 (9.0)	15 (1.6)	7 (3-14)	10.4 (4.3-13.1)
Batrachoides surinamensis (Batrachoididae)	1025 (1.6)	2265.1 (5.8)	4 (0.1)	6 (0.6)	20 (8-30)	24.6 (9.6-38.1)
Stellifer naso (Sciaenidae)	984 (1.6)	161.0 (0.4)	50 (1.3)	5 (0.5)	12 (6-14)	14.4 (11.1-17.1)
Stellifer stellifer (Sciaenidae)	788 (1.3)	-	89 (2.1)	-	7 (3-14)	-
Pterengraulis atherinoides (Engraulidae)	588 (0.9)	411.4 (1.0)	28 (0.7)	19 (2.0)	12 (2-20)	16.0 (11.3-20.3)
Macrodon ancylodon (Sciaenidae)	553 (0.9)	98.7 (0.3)	46 (1.1)	4 (0.4)	8 (2-23)	15.3 (14.3-16.0)
Cynoscion leiarchus (Sciaenidae)	525 (0.8)	-	80 (1.9)	-	7 (2-16)	-
Cynoscion acoupa (Sciaenidae)	485 (0.8)	216.5 (0.6)	41 (1.0)	12 (1.3)	9 (2-19)	12.6 (8.9-19.3)
Bairdiella ronchus (Sciaenidae)	333 (0.5)	-	8 (0.2)	0 (0)	13 (7-18)	-
Stellifer rastrifer (Sciaenidae)	304 (0.5)	125.6 (0.3)	31 (0.7)	6 (0.6)	8 (3-14)	11.0 (9.4-17.8)
Hyporhamphus roberti (Hemiramphidae)	283 (0.5)	-	35 (0.8)	-	12 (9-16)	-
Genyatremus luteus (Hamulidae)[d]	280 (0.4)	137.7 (0.4)	30 (0.7)	7 (0.7)	6 (2-12)	9.6 (5.5-15.2)
Micropogonias furnieri (Sciaenidae)	199 (0.3)	40.1 (0.1)	114 (2.7)	6 (0.6)	5 (3-9)	9.1 (8.1-11.2)
Oligoplites saurus (Carangidae)	197 (0.3)	19.1 (< 0.1)	97 (2.3)	6 (0.6)	5 (1-9)	7.4 (6.8-8.2)
Achirus achirus (Achiridae)	167 (0.3)	-	4 (0.1)	-	13 (8-15)	-
Lutjanus jocu (Lutjanidae)	143 (0.2)	-	2 (< 0.1)	-	(10-19)	-
Guavina sp. (Eleotridae)	139 (0.2)	-	5 (0.1)	-	12 (10-14)	-

Table 20. (continued)

Species	**Weight (g) (%)**		**Abundance (No. Ind) (%)**		**Mean TL (cm) (range)**	
	1999	**2012**	**1999**	**2012**	**1999**	**2012**
Sciades passany (Ariidae)	138 (0.2)	-	1 (< 0.1)	-	24	-
Centropomus parallelus (Centropomidae)	126 (0.2)	-	6 (0.1)	-	11 (11-14)	-
Diapterus auratus (Gerreidae)	115 (0.2)	174.4 (0.4)	10 (0.2)	15 (1.6)	9 (7-13)	9.3 (5.3-12.2)
Chaetodipterus faber (Ephippidae)	69 (0.1)	40.3 (0.1)	47 (1.1)	8 (0.9)	3 (1-7)	5.5 (4.1-6.2)
Cetengraulis edentulus (Engraulidae)	64 (0.1)	50.6 (0.1)	5 (0.1)	5 (0.5)	10 (6-14)	10.3 (8.3-13.9)
Rhinosardinia amazonica (Clupeidae)	34 (0.1)	14.1 (< 0.1)	18 (0.4)	2 (0.2)	6 (4-7)	10.4 (10.1-10.6)
Anchoviella lepidentostole (Engraulidae)	26 (< 0.1)	-	20 (0.5)	-	4 (2-8)	-
Anchoa spinifer (Engraulidae)	25 (< 0.1)	-	16 (0.4)	-	5 (4-8)	-
Cynoscion steindachneri (Sciaenidae)	25 (< 0.1)	-	1 (< 0.1)	-	14	-
Odontognathus mucronatus (Pristigasteridae)	17 (< 0.1)	5.0 (< 0.1)	8 (0.2)	2 (0.2)	7 (5-9)	8.6 (8.1-9.0)
Bryconamericus sp. (Characidae)	8 (< 0.1)	-	1 (< 0.1)	0 (0)	9	0
Selene vomer (Carangidae)	7 (< 0.1)	7.6 (< 0.1)	2 (< 0.1)	3 (0.3)	(5-6)	5.5 (4.5-6.3)
Poeciliidae	3 (< 0.1)	-	2 (< 0.1)	-	(2-5)	-
Strongylura timucu (Belonidae)	1 (< 0.1)	-	2 (< 0.1)	-	(7-8)	-
Chloroscombrus chrysurus (Carangidae)	0.6 (< 0.1)	-	1 (< 0.1)	-	3	-
Sphoeroides testudineus (Tetraodontidae)	0.1 (< 0.1)	-	1 (< 0.1)	-	1	-
Cynoscion microlepidotus (Sciaenidae)	-	38.9 (0.1)	-	2 (0.2)	-	12.0 (9.0-14.9)
Pellona harroweri (Pristigasteridae)	-	14.7 (< 0.1)	-	5 (0.5)	-	6.5 (6.3-6.7)
Cynoscion virescens (Sciaenidae)	-	12.8 (< 0.1)	-	1 (0.1)	-	13.3
Trichiurus lepturus (Trichiuridae)	-	4.3 (< 0.1)	-	1 (0.1)	-	-
Gobionellus oceanicus (Gobiidae)	-	9.9 (< 0.1)	-	1 (0.1)	-	-
Total	62613	39279.5	4236	935	9.1 (1-34)	12.4 (3.6-38.1)

[a] Catfish locally known as uricica branca and according to Marceniuk et al. (2012) should be *Cathorops agassizii*

[b] Identified as *Hexanematichthys herzbergii* in Krumme et al. (2004)

[c] Juvenile mullets of *Mugil curema*, *M. hospes*, *M. incilis* and *M. curvidens*

[d] The correct name for this species is *Genyatremus cavifrons* according to Tavera et al. (2011)

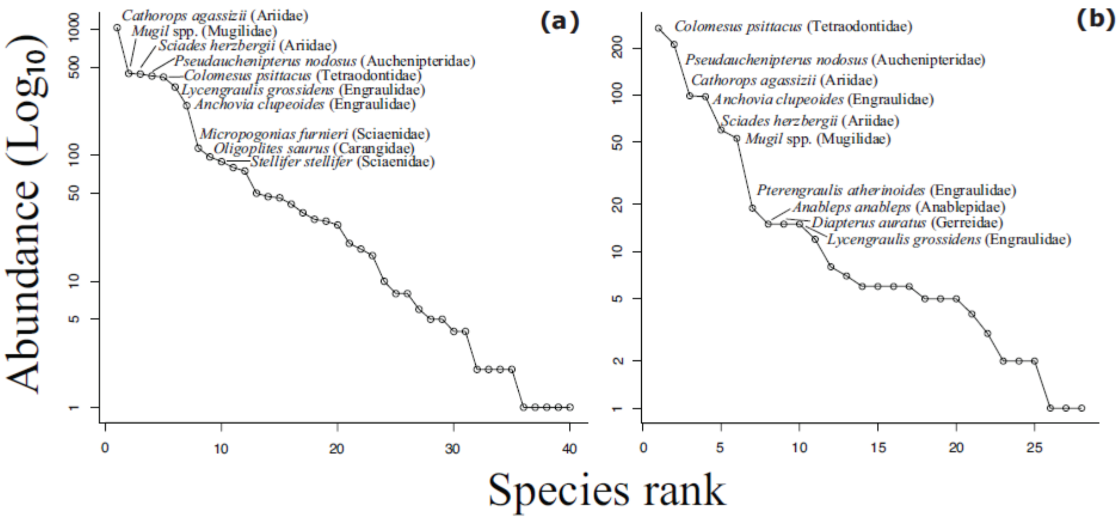

Figure 31. Species abundance distribution models (rank-log abundance plots) for fish communities sampled from the same intertidal mangrove creeks in the Furo de Meio, Bragança Peninsula, Pará, North Brazil in (a) 1999 and (b) 2012. Note different y and x axes.

The PERMANOVA test showed significant differences in fish assemblages for both fixed factors tide-time of day and year, but not for the factor creek. None of the interactions were found to be significant (Table 21). The interaction between tide-time of day was non-significant indicating that tide-related patterns were consistent and stable between both sampling periods (Figure 32). The variation in multivariate dispersion was significant for the factor tide-time of day but not for the factor year (PERMDISP test, Table 22). Further pairwise comparisons between levels of the factor tide-time of day showed that most of the variability in dispersions occurred between samples coming from spring-day and neap-night. The rest of the pairwise comparisons were either non-significant or near the significance level (i.e. 0.05, Table 22).

The PCO ordination showed that ca. 65% of the total variation was explained by the first two PCO coordinate axes (Figure 32). The PCO1 tended to differentiate samples collected in 2012 from samples in 1999. These samples corresponded generally to samples with few individuals of a single or very few species, which were more common in 2012 during neap-day.

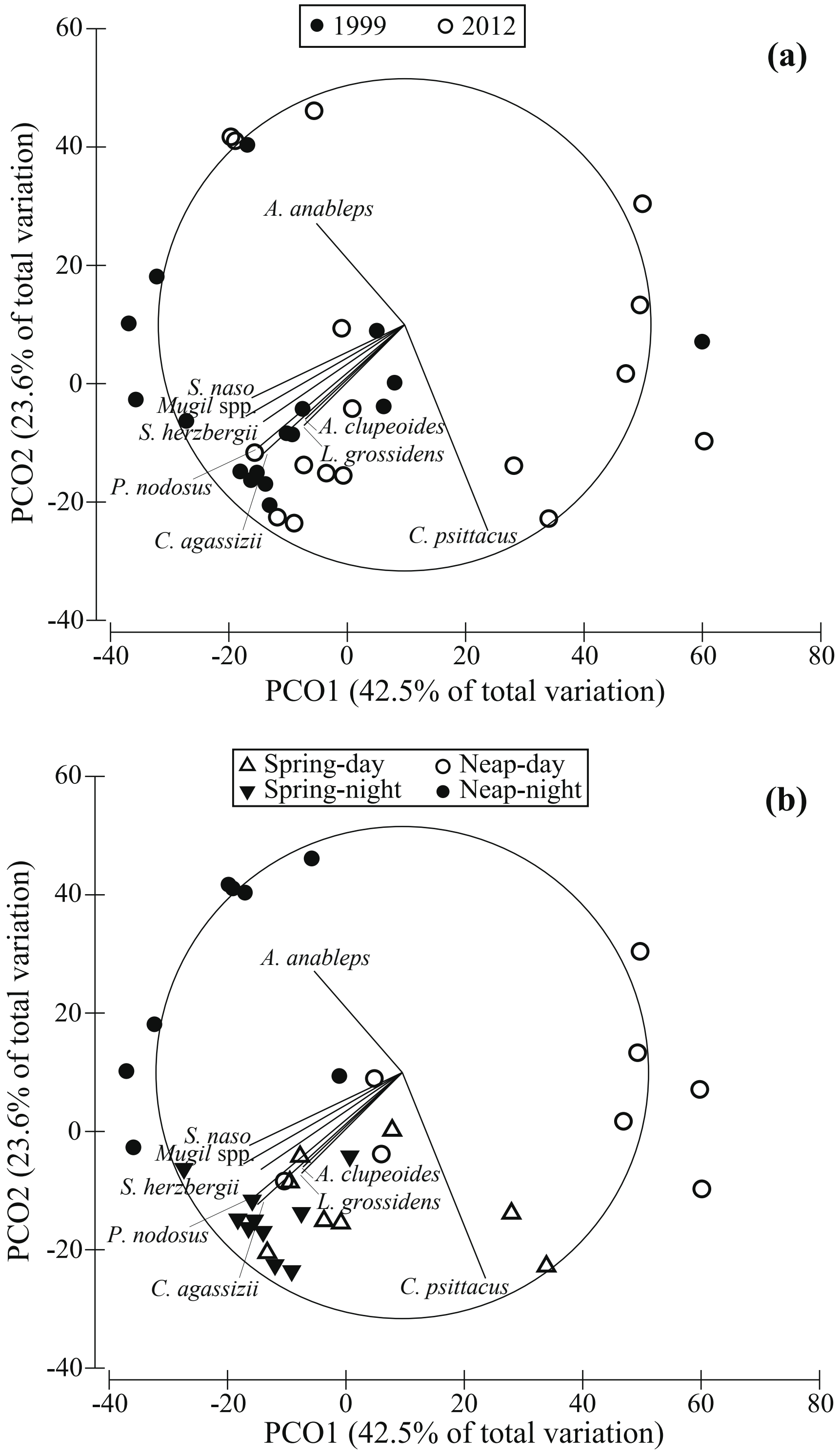

Figure 32. Principal coordinate analysis (POC) ordinations of intertidal mangrove creek fish assemblages in the Furo do Meio, North Brazil sampled in 1999 and 2012 (combined). (a) PCO showing differences between sampling times (1999 *vs* 2012) and (b) PCO showing differences between the four tide-time of day combinations. Species with greatest Spearman correlation (|r| > 0.4) with PCO axes are shown.

Table 21. Results of a three-way mixed model PERMANOVA testing the effects of the factors year (1999 *vs* 2012), tide-time of day combination (spring-day, spring-night, neap-day, neap night) and creek (A *vs* B) on the intertidal mangrove fish assemblages in the Furo do Meio, Bragança Peninsula, North Brazil.

Source	**df**	**SS**	**MS**	**Pseudo-F**	**P**
Creek	1	1531.2	1531.2	1.9698	0.088
Tide-time of day	3	25582	8527.4	10.97	0.001
Year	1	6030.2	6030.2	7.7577	0.001
(Creek) x (tide-time of day)	3	2271.9	757.29	0.97423	0.488
(Creek) x (year)	1	619.82	619.82	0.79738	0.563
(Tide-time of day) x (year)	3	3171.8	1057.3	1.3601	0.159
(Creek) x (tide-time of day) x (year)	3	3020.2	1006.7	1.2951	0.217
Residual	18	13992	777.32		
Total	33	56164			

Table 22. Results of the permutational tests of multivariate dispersions (PERMDISP) for the factors tide-time of day combination (SD, SN, ND, NN) and time (1999 *vs* 2012). Pairwise comparisons for the tide-time of day factor are shown.

Factor	**df**	**Pseudo-F**	**p**
Tide-time of day	3,30	7.1843	0.001
Year	1,32	3.5367	0.137
		Pairwise comparisons	
Groups	**t**		**p**
Spring-day, spring-night	1.6722		0.122
Spring-day, neap-day	2.2256		0.049
Spring-day, neap-night	2.6334		0.028
Spring-night, neap-day	3.5138		0.06
Spring-night, neap-night	3.9529		0.04
Neap-day, neap-night	0.2337		0.831

Samples from the different tide-time of day combinations were distinguishable, either by the presence of *C. psittacus* or by the presence of a relatively species-rich assemblage (Figure 32). For example, samples from neap-day were very poor in the number of species and individuals and were clearly separated from the rest of the tide-time of day combinations. In contrast, samples from both neap-night and spring-day were characterized by the presence of specific fish species. *Anableps anableps* was abundant in samples collected during neap-night, whereas *C. psittacus* was associated with samples collected during spring-day (Figure 33). This pattern can be observed by looking at the strength of the correlation between these species' vectors and the PCO2 axis (Table 23). Finally, samples collected at spring-night were always characterized by samples with the largest number of species illustrated by the number of species' vectors associated with this tide-time of day combination (Figure 32).

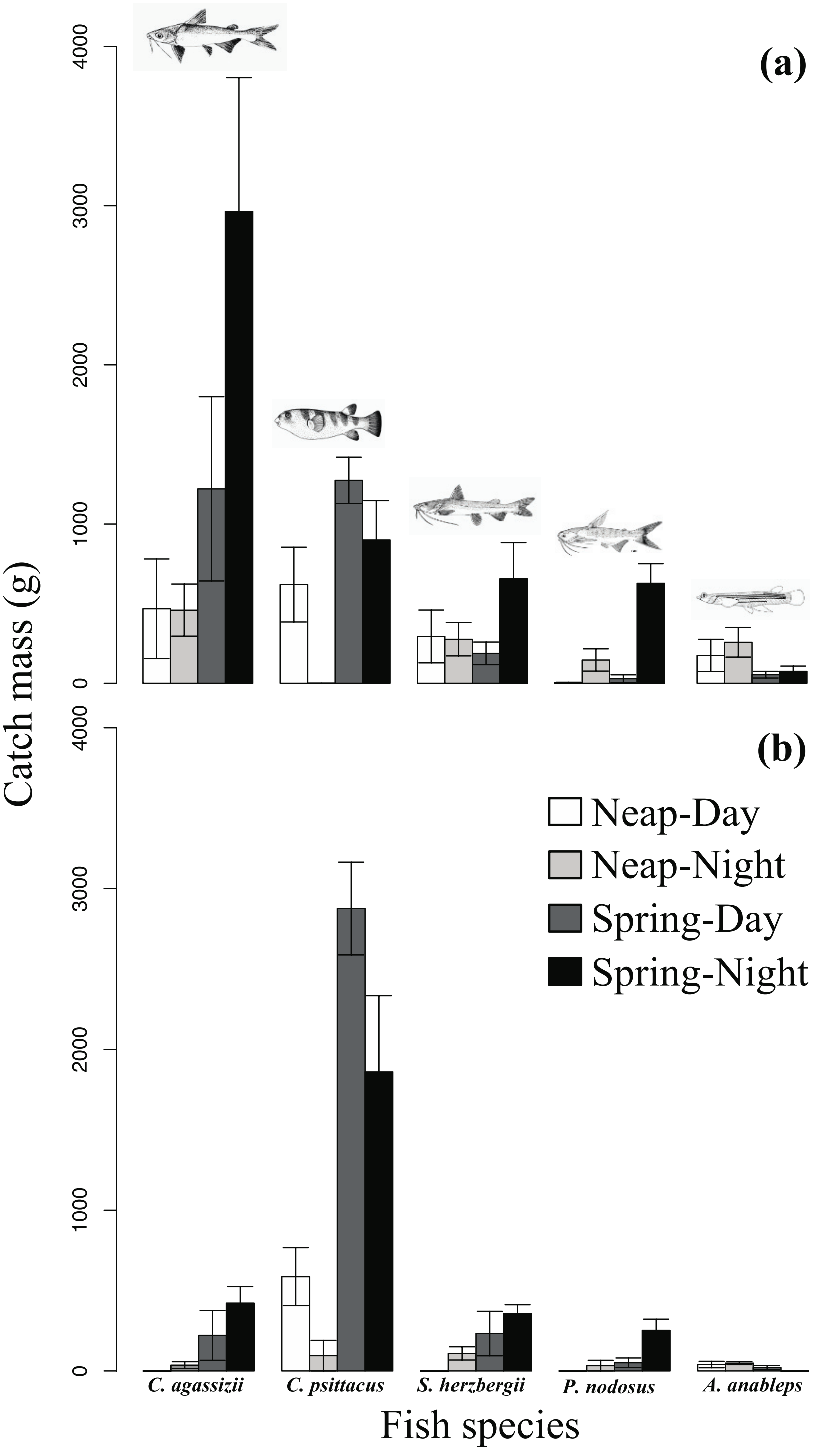

Figure 33. Mean catch mass (±SE) of fish species responsible for differences between levels of the tide-time of day factor in the Furo do Meio, North Brazil in (a) 1999 and (b) 2012.

Table 23. Correlation coefficients for the species (|r|> 0.4) with PCO axes for the effects of the factor tide-time of day.

Species	PCO1	PCO2
Cathorops agassizii	-0.5881	-0.5364
Colomesus psittacus	0.3380	-0.8369
Sciades herzbergii	-0.5745	-0.3941
Pseudauchenipterus nodosus	-0.5955	-0.5006
Anchovia clupeoides	-0.4036	-0.3838
Mugil spp.	-0.6452	-0.3718
Anableps anableps	-0.3583	0.4127
Lycengraulis grossidens	-0.4092	-0.4095
Batrachoides surinamensis	-0.3250	-0.1467
Stellifer naso	-0.6212	-0.2966

Mean overall fish length (±SD) in 1999 (X=9.1 ± 4.3) was significantly lower than in 2012 (X= 12.4±5.2; Wilcoxon test-W= 2605414, p<0.0001). Length frequency distributions were also significantly different between sampling periods (KS test, D=0.966, p<0.0001). The mean lengths of the three principal species (in terms of catch weight) were all significantly lower in 1999 than in 2012 (Table 20, W=70387.5 p<0.0001 for *C. agassizii*, W=85901.5 p<0.0001 for *C. psittacus* and W=22812.5 p<0.0001 for *S. herzbergii*). The comparison of the length distributions of these three species, which constituted > 65% of the total fish catch mass, also revealed significant differences between the sampling periods (KS test D=0.4143 p<0.0001 for *C. agassizii*, D=0.4458 p<0.0001 for *C. psittacus* and D= 0.6946 p<0.0001 for *S. herzbergii*).

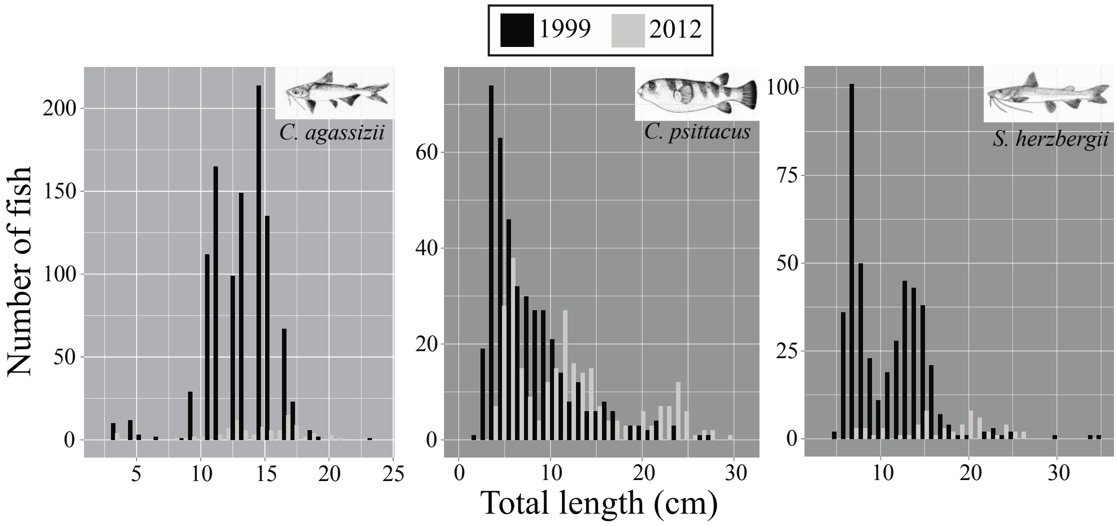

Figure 34. Length distribution of three most important fish species (in terms of catch weight) using intertidal mangrove creeks of the Bragança Peninsula, North Brazil during the rainy seasons of 1999 and 2012. Note different y axes.

For *C. agassizii*, the mode in length composition was slightly higher in 2012 than 1999 (17 cm and 14 cm, respectively). However, in 2012, there were almost no individuals less than 13cm, whereas in 1999 these size classes were abundant. *C. psittacus* in 1999 was mostly represented by small size classes with a mode at 4 cm. In 2012 this species was represented by larger-sized individuals with modes at 6 cm, 12 cm and 24 cm. Finally, a clear absence of smaller size classes (<7 cm) of *S. herzbergii* was observed in 2012 with modes of 15 and 20 cm, whereas in 1999 small size classes were the most abundant (modes at 7 cm and 12 cm, Figure 34).

DISCUSSION

The intertidal mangrove fish assemblage examined here (Furo do Meio in the Bragança Peninsula, North Brazil) has been studied over the course of the last 16 years (Barletta et al. 2003, Krumme et al. 2004 and this study), thus providing a unique opportunity to assess the stability and persistence of a mangrove fish assemblage and its structuring forces over scales usually not covered in fish ecology studies. Our results suggest that tidal-related patterns in the organization of this assemblage are stable in time and predictable, with the same set of species occupying the intertidal mangrove according to specific tide-time of day conditions. In spite of the dramatic reduction in fish biomass reported in 2012, the tidal-diel pulse explained the organization of this intertidal assemblage. We also were able to identify a temporally persistent set of seven species dominated by puffer fishes and catfishes that inhabit intertidal areas in this region (see Table 20, Figure 31). The stability of this assemblage, however, was influenced by unpredictable climatic phenomena that operate over mid- (seasonal) and long-term scales (e.g. El Niño Southern Oscillation - ENSO). These phenomena can drastically reduce local and regional precipitation and alter freshwater discharge into estuaries. Ultimately, these changes may be largely responsible for the fluctuations in the dominance of species during the years examined.

The number of fish species (45) found in second-order creeks of the Furo do Meio in 1999 and 2012 was similar to that found in the same area by Barletta et al. (2003) in larger first-order creeks sampled at diurnal neap tides during one year (49 species from 26 families). This indicates that the rainy season samplings in 1999 and 2012 were sufficient to obtain an accurate picture of this fish assemblage and that sampling during different tide-time of day combinations can appropriately represent the whole fish assemblage using intertidal mangrove creeks. In previous surveys in the Furo do Meio, *C. agassizii* and *C. psittacus* had been identified as the dominant species in intertidal mangroves (ca. 60% or more of the total catch mass; Barletta et al. 2003, Krumme et al. 2004). This was also observed in 2012, where both *C. agassizii* and *C. psittacus* accounted for 39% of the total abundance and 68% of the total catch mass. The seven core species identified in 1999 and 2012 were also the most important components (in catch weights) of the fish assemblage in Barletta et al. (2003), and therefore constitute the dominant species of intertidal mangrove fish assemblages in the region. This can be corroborated by studies in an adjacent mangrove estuarine system where the same dominant species have been recorded (Curuça estuary, ca. 130 km north-west of the Bragança Peninsula; Giarrizzo & Krumme 2007). The persistence of dominant species in both space and time has also been found in estuarine fish assemblages of West Africa and the UK and in freshwater fish assemblages of the Amazon region (Ecoutin et al. 2010, Magurran & Henderson 2003, Hercos et al. 2013). This property of assemblages (dominant species common in both space and time) can be useful in the opportune identification of species that deserve urgent conservation action in megadiverse areas where comprehensive surveys are economically and logistically unfeasible (Hercos et al. 2013).

Persistent fish assemblages over relatively long periods of time have been found in tropical and subtropical estuaries and coastal areas (James et al. 2008, Blaber et al. 2010, Robinson & Yakimishyn 2013). Although persistent in time, the intertidal mangrove fish assemblage in the Bragança Peninsula showed high interannual variation in the overall abundance, catch mass and species dominance. This may indicate low stability (degree of constancy in the numbers and/or relative abundances of species within assemblages) over time in this fish assemblage. This was also observed in the East Kleinemonde Estuary, south-eastern coast of South Africa, where the most dominant species (*Rhabdosargus holubi*-Sparidae) varied in its relative catch composition from 92% to 34% during a ten-year sampling program (James et al.2008). In those years where the catch of this species was severely reduced (2004), the catch of *Myxus capensis* (Mugilidae) reached 52% of the total assemblage. Similarly, on the British Columbia coast in Canada, Robinson and Yakimishyn (2013) found a persistent fish assemblage in eelgrass meadows, but observed that the dominance (rank abundance position) of half of the core species varied over time, indicating instability in relative fish abundances. These changes in the relative abundance or catches of core species over time were not observed by Blaber et al. (2010) in the Embley estuary in tropical Australia. There, the authors did not identify changes over time (1987-1989 *vs* 2005) in catch rates of the most abundant species. Reasons for these contrasting results may include the failure to record a major environmental change during the sampling in 2005 by Blaber et al. (2010), or that the Embley estuary is a “very low impacted” region in Australia, as the authors suggested. However, in areas such as the East Kleinemonde Estuary in South Africa or the Caeté estuary in North Brazil, strong environmental fluctuations (e.g. timing of mouth opening, or reduced rainfall) may severely affect the stability of fish assemblages.

On most meso- and macro-tidal coasts the movements of coastal organisms are synchronized with the interactive tide and diel cycles (Gibson 2003, Krumme 2009). The evidence presented here for a mangrove fish assemblage indicates that this synchronization is remarkably stable, occurring over large (>10 years) temporal scales and which is also observable in macrotidal mangrove systems of other biogeographical provinces (e.g. the Panamic province of the Tropical Eastern Pacific region), further highlighting that fish assemblages in these areas segregate their niches on the temporal axis according to the interaction of tidal and diel rhythms (Castellanos-Galindo & Krumme, in press). Understanding of these spatially and temporally recurrent patterns with regard to the design of fish sampling protocols and fish ecology in macrotidal mangrove coasts, is vitally important. The concept of a very dynamic system over short-temporal scales implies that care should be taken, for example, when static modeling approaches are proposed which do not account for such variability. Sampling only at neap tides during daytime in intertidal areas, for example, may lead to a considerable underestimation of the fish assemblage biomass and diversity. As seen in the Furo do Meio, the intertidal fish assemblage was greatly impoverished during this specific tide-time of day combination. In contrast, sampling at spring tides during nighttime would yield the most diverse assemblage in an intertidal mangrove area and probably the largest catch mass (Krumme and & Saint-Paul 2010). Ultimately, a complete understanding of how mangrove fish use an intertidal area would only be possible by examining all the feasible tide-time of day combinations, and exploratory biodiversity surveys in macrotidal habitats should aim at covering this variation (Krumme 2009). Understanding these short-term tidal-diel dynamics can substantially help to better assess the nursery value of intertidal mangroves for fish, which in turn contributes to better decision making in fisheries management in tropical estuaries.

The drastic decline in fish abundance and catch mass found in the mangrove creeks sampled in 2012 could be attributed to the severe reduction in rainfall in 2012 (Figure 30), that caused lower water levels and reduced recruitment, or to the effect of overfishing in the Caeté estuary. Environmental variability can dramatically affect fish reproductive and recruitment success (e.g. Poizat et al. 2004, Brander 2007, Garcia et al. 2012). Particularly, changes in rainfall patterns can have a sizeable effect on estuarine fish population dynamics (e.g. recruitment, growth, survival). In Queensland - Australia, decreases in rainfall associated to El Niño events (1991-1992, 1993-1995, 1997-1998) coincided with decreased catch per unit effort of estuary-dependent species (Meynecke et al. 2006). The association between climatic events like ENSO, rainfall and fish catch mass could explain the considerable reduction of fish abundance and catch mass observed in the Furo do Meio system. During the austral summer in 2012, the most severe drought affecting North Brazil in recent hydroclimatic history was associated with the South Atlantic high-pressure system (Marengo et al. 2013). This climatic force was likely causative for the low recruitment of common estuarine species in intertidal mangrove creeks of the Furo do Meio in 2012. In the specific case of the catfish *C. agassizii* and *S. herzbergii*, Giarrizzo and Krumme (2009) indicated that these species have their peaks in gonadal maturity at the end of the dry season and high biomass and densities of juveniles are observed during the wet season. During a weak rainy season such as in the year 2012, it is very likely that the recruitment of *C. agassizii* and *S. herzbergii* was low. This was corroborated by the near absence of smaller size classes of these two species during the sampling in 2012 compared to 1999 (Figure 34). Given the reduced abundance of these two dominant catfish species in the tidal creeks of the Furo do Meio in 2012, *C. psittacus*, which is thought to occur throughout the year in mangroves of the region (Giarrizzo & Krumme 2007), could thrive in intertidal mangrove creeks, including individuals of larger size classes. In times of global change, an increase in droughts in North Brazil could result in the overall reduction of fish biomass in the estuarine systems and lead to a shift in fish assemblage structure from one dominated by catfishes to one dominated by puffer fishes.

Although overexploitation of fisheries resources is often presented as a primary cause for declines in fish productivity (i.e. Ecoutin et al. 2010), in the case of the Caeté system we found little evidence to suggest that the artisanal fishery is responsible for the observed decline in fish productivity. Fishing is not large-scale within the mangrove creeks and Furos (own observations) and most of the fish species found in the mangroves contribute little to the overall reported catches in the region, which are dominated by species captured outside the estuary (i.e. *Lutjanus purpureus*; Barletta et al. 1998, Isaac et al. 2010). Small-scale fisheries within the Caeté estuary are considered a low impact activity and ecologically sustainable (Isaac et al. 2009). The situation in the Caeté estuary contrasts with what is reported in the Sine Saloum estuary in Senegal by Ecoutin et al. (2010), where fishing activities (number of fishermen, canoes and fishing gears) substantially increased in a period of 10 years (1990-2010).

Comparing different mangrove systems contributes to the identification of patterns that can be generalized across regional or global scales. This enhances the ability not only to react but also to plan accordingly to protect these natural systems. Our results highlight that comparisons between mangrove systems (particularly on the meso- and macro-tidal coasts) should take careful account of documented short-term temporal scales. Tides and diel cycles not only strongly influence how fish use intertidal mangroves, but also affect results of research investigations into fish diversity and productivity (and the nursery function) in mangroves. Comparisons should also factor the effect of climatic variation on fish productivity, and incorporate an effective means of distinguishing between the influence of climatic effects and overexploitation (Brander 2007).

Supplementary data is given in Annex III

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Chapter VII. Fish habitat use in macrotidal mangroves of the Neotropics: tidal, salinity and biogeography effects on assemblage structure and function

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ABSTRACT

Aim. To assess how the structure of intertidal mangrove fish assemblages vary temporally (according to tidal and diel rythms) and spatially (along salinity gradients) in macrotidal systems of different biogeographical provinces and to test if general assembly rules apply to these assemblages.

Location. Bahía Málaga-Colombia (Panamic province in the Tropical Eastern Pacific-TEP) and Caeté estuary-Brazil (Brazilian province in the Western Atlantic-WA); both locations with similar tidal regimes (semi-diurnal macrotides of $\geq$ 4 m).

Methods. Mangrove fish were sampled in the same habitat (intertidal creeks), with the same methodology (blocknets) for 11-12 months in each location along a salinity gradient between 2009-2012. Taxonomic and functional (trophic) composition, density and biomass were compared between regions. Fish abundance and catch mass data were used to investigate if different tidal (spring and neaps) and diel combinations produced the same predictable response in community structures in both communities.

Results. Similar total fish species richness (*c*. 50 species in each region) mirrored the regional species richness of coastal fishes in the TEP and WA. Pufferfishes (Tetraodontidae) and catfishes (Ariidae) dominated the fish assemblages in both regions. Closely related species within the two families responded in similar ways to tidal-diel changes suggesting the existence of a phylogenetic signal in temporal niche use. The strength of the influence of tidal and diel forces in fish intertidal use was related to the mangrove topography of the two sites. Differences in the taxonomic and functional composition between regions were related to differences in seascape configuration and the biogeography of the adjacent freshwater fish fauna.

Main conclusions. Our results highlight (1) the important role that tidal and diel dynamics play in structuring intertidal mangrove fish assemblages in macrotidal areas of the Neotropics, (2) the imprint that biogeographical history has left in mangrove fish faunas of now isolated regions and (3) the importance that the seascape configuration (mangrove topography and adjacent habitats) can have in determining the composition and structure of intertidal fish assemblages

Keywords: Assembly rules, Bahía Málaga, Brazil, Caeté estuary, Colombia, mangrove fish, Neotropics, phylogenetic signal, tidal dynamics, Tropical Eastern Pacific, Western Atlantic.

(Please note that abstract format is provided as required from the *Journal of Biogeography*)

INTRODUCTION

As a coastal ecosystem dominating *c.* 25% of the tropical shores, mangroves are fundamental habitats for a wide array of shallow water organisms. Although the relative importance of mangroves (e.g. role as nurseries, relationship to fisheries yields) for fish and crustaceans has been highly debated during the last 15 years (Beck et al. 2001, Manson et al. 2005b), it is clear that within or in close proximity to these coastal ecosystems many commercial and non-commercial fisheries resources spend part or their whole life cycle and benefit from increased shelter and/or food resources. Our understanding of how fishes use mangroves is biased by the common assumption that systems in more widely studied areas (e.g. Caribbean Sea or Australia) are representative of systems where few studies have been carried out. Fortunately, during the last 25 years, studies carried out in different tropical coasts have widened the understanding of the role of mangroves as habitat for fishes (see Blaber 2000, Blaber in press). Global comparisons evaluating different aspects of mangrove equivalence across regions start to appear in the literature (see Sheaves 2012, Igulu et al. 2013), but caution needs to be taken especially when comparisons do not adequately account for differences of the systems being compared or when similar sampling methodologies have not been put in place.

Tidal rhythms have affected life in the Oceans for millions of years. Tides, interacting with the diel cycle, modulate the behavior of coastal organisms (Wilcockson & Zhang 2008), including fishes, such as the home range movements and/or feeding activity (Krumme 2009). Tidal and diel cycles, however, vary across geographic areas. Thereby their influence in modulating the organization of fish assemblages may vary in strength depending on the specific interaction of tides and diel cycles. In areas where tides are negible (microtidal; e.g. in the Caribbean, Red or Mediterranean Seas), the diel cycle (day-night) is a primary cue triggering fish movement across habitats. Early observations by Hobson (1973) documented the importance that diel feeding migrations had for a number of tropical reef fish families (Vermeij & Nagelkerken 2007). This has been corroborated in recent years with the use of new technologies improving the accuracy of observations (e.g. Hitt et al. 2011). Most observations have been made in the clear waters of microtidal coasts (i.e. Caribbean Sea). In meso- and especially macro-tidal coasts, intertidal habitats (sand- and mud-flats, rocky shores and mangroves) become available for fish during high tide providing shelter or food for a limited period of time (Sheaves 2005). These intertidal movements can be considered small-scale migrations which are recurrent and to some extent predictable according to the tidal pulse in combination with the diel cycle (Gibson 2003, Krumme 2009). Evidence from macrotidal tropical systems is found in mangroves (e.g. Krumme et al. 2004) and rocky shores (e.g. Castellanos-Galindo et al. 2010). Yet the universal role of tide and diel cycles in shaping the distribution of coastal fishes in intertidal habitats across biogeographical regions has not been tested.

Salinity has been identified by numerous studies as a major force shaping the distribution of fish assemblages in tropical estuarine environments (e.g. Sosa-López et al. 2007). Fishes in estuaries have to cope with the physiologic osmotic stress produced by high variation in salinity; therefore generally most estuarine resident species are considered euryhaline (Fiol & Kültz 2007). Nevertheless, patterns in fish species richness in estuarine habitats are affected by the presence of freshwater species able to colonize estuaries during wet seasons when salinity decreases, but also by marine species that use estuaries when salinities increase or as part of an ontogenetic habitat shift in a juvenile phase (Aburto-Oropeza et al. 2009). Sosa-Lopéz et al. (2007), suggested for a tropical lagoon (Terminos Lagoon in the Gulf of Mexico) a low salinity (5-10‰) ecotone zone where freshwater, estuarine and marine species mixed, and the highest fish species richness could be found. This example, however, may not be applicable to all tropical estuarine systems since fish species richness patterns in these environments may be ultimately dependent on the balance between freshwater species richness and marine species richness. The potential contribution of freshwater fish faunas to the species richness gradients in tropical estuaries is rarely taken into consideration (but see Baran 2000).

The coastal areas in the Neotropics include two warm biogeographical regions (*sensu* Briggs & Bowen 2012): the Western Atlantic (WA) and the Eastern Pacific (EP) regions. Mangroves in the Neotropics are only distributed in six provinces (Carolina, Caribbean and Brazilian in the WA, and Cortez, Panamic and Galapagos in the EP) within these regions, mainly constrained by the 20ºC seawater isotherm during winter times (Duke et al. 1998, Woodroffe & Grindrod 1991). These limits are largely influenced by the presence of cold and warm currents (i.e. Humboldt Current in the EP and the southward flowing Brazilian western boundary current in the WA). Tidal regimes are very variable among the provinces where mangroves occur in the Neotropics. In the Tropical Eastern Pacific (TEP), macrotidal regimes (> 4 m tidal amplitudes) are common in the Panama Bight and the northernmost part of the Gulf of California. Elsewhere, mesotidal regimes are predominant. In the Western Atlantic, the Carolina and the Caribbean region in the WA are microtidal whereas the Brazilian province is macrotidal in its northern part and becomes microtidal towards its southern limit. Neotropical coastal fish and mangrove tree species richness is low compared to the center of biodiversity in the Indo-West Pacific region. The number of shore fishes in the Indo-West Pacific is at least two times higher than in any of the provinces in the Neotropics (*c.* 3000 in the Indo-Pacific vs *c.* 1200-1500 in the TEP, Caribbean or Brazilian provinces, Carpenter & Springer 2005, Zapata & Robertson 2007, Miloslavich et al. 2010, Miloslavich et al. 2011). The same pattern is repeated for mangrove tree species (four times higher in the Indo-West Pacific (58 spp.) than in the Neotropics (13 spp.); Duke et al. 1998). Given the similar characteristics in regional species richness between the Brazilian province of the WA and the EP, similar patterns in species richness at the local level (mangrove fish assemblages) could be expected.

If the ability to exploit intertidal habitats via tidal migrations is considered a trait, and if phylogenetically related species, genera or families are found to undertake tidal migrations across biogeographical regions, then it could be hypothesized that ecological niche conservatism has occurred in some groups of mangrove fish assemblages (inter-continental congruence). Despite much work has been devoted to understand the history of extinction and diversification occurring in the Caribbean as a consequence of the rise of the Isthmus of Panama in the Miocene

(Leigh et al. in press), little is known about the ecological relicts of shared fauna that persisted in the North Brazilian coast.

This study aimed at answering the following questions: (1) Are two estuarine mangrove fish assemblages from two distinct (but previously connected) geographical regions taxonomically and functionally structured in the similar way? (2) Are tidal and diel cycles a persistent force shaping the structure of intertidal mangrove fish assemblages in neotropical macrotidal coasts? (3) Is salinity regulating the structure of these assemblages in the same way? (4) Is there a phylogenetic signal in niche use between members of these two assemblages?

MATERIALS AND METHODS

Study areas

Two estuarine localities within two major neotropical marine regions were selected: the Panamic province in the TEP and the Brazilin province of the WA (Figure 35). These two regions alone comprise 3.7 million ha of mangroves and 81% of the whole mangrove area in the Neotropics (Lacerda 2002). The Caribbean province of the WA was not considered in this study due to the lack of a strong tidal regime (< 1 m tidal range) and estuarine conditions, which are most prevalent in the Panamic and Brazilian provinces. The Panamic and Brazilian provinces were connected in ancient geological times before the formation of the Isthmus of Panama during the Eocene epoch (Montes et al. 2012) in what has been called the “Miocene Caribbean Faunal Province” (Figure 35; Woodring 1974). Both localities are located in estuarine environments and are macrotidal (> 4 m tidal range at spring tides).

The selected study areas were the Caeté estuary (0º 47’ - 0º 59’N and 46º 29’ - 46º 47’W) in the Brazilian province of the WA and Bahía Málaga (3º 56’ - 4º 05’N and 77º 19’ - 77º 21’W) in the Panamic province of the EP (Figure 36). The former locality lies within the Amazon Macrotidal Mangrove Coast-AMCC, considered the largest continuous mangrove belt in the world with an area of 7424 km^2 (Nascimento Jr et al. 2013). This coast in North Brazil extends for *c.* 650 km between Marajó Bay and Sao José Bay and includes 23 estuaries formed by a very jagged coastline. Mangroves in the Caeté estuary have been prograding inland for more than 20km in the last 2000 years (Souza-Filho et al. 2009). The study area in the Panamic province of the EP was Bahía Málaga in the Colombian Pacific, which is part of the largest mangrove area of northwestern South America (West, 1956), named the Panama Bight mangrove ecoregion (Olson & Dinerstein 2002). The Colombian Pacific coast is located in a tectonically active zone where the Nazca plate is subducted under the South American plate.

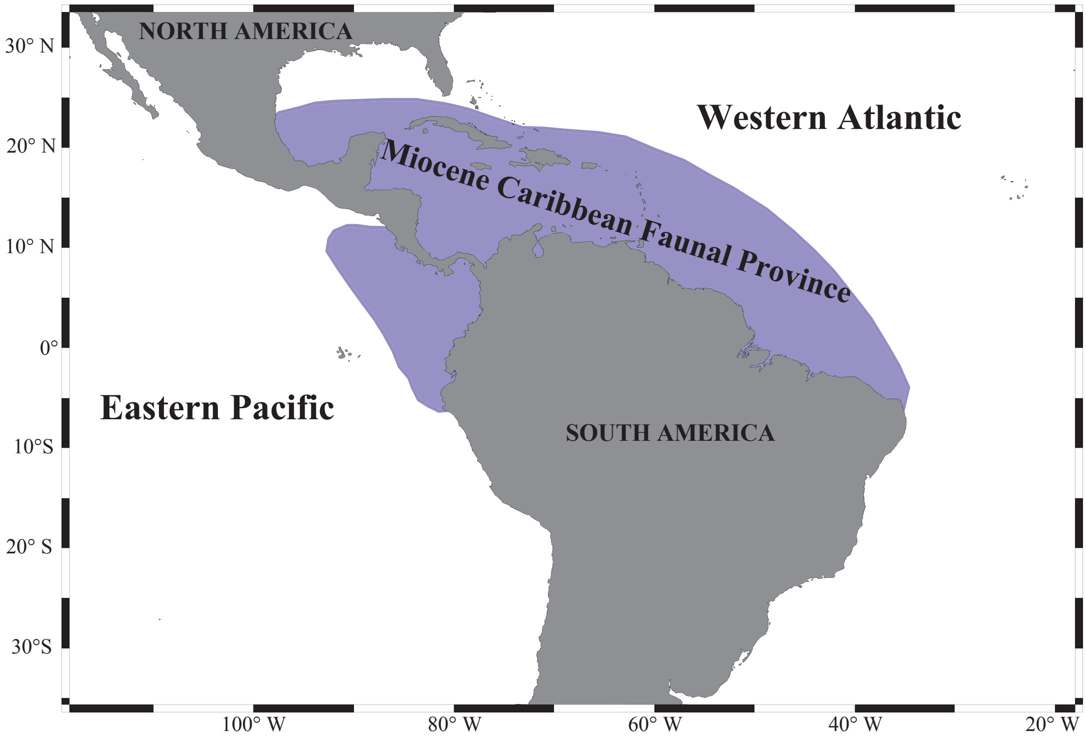

Figure 35. Geographical extension of the Miocene Caribbean faunal province based on the distribution of benthic molluscs [modified after Woodring (1974)].

In the Caeté estuary, a wet season from January to June concentrates *c.* 75% of the total annual precipitation. In Bahía Málaga, a wet season takes places from January to April followed by extremely wet months from May to December (see Annex IV, Supplemental Figure A7). Despite both areas considered humid regions (> 2500 mm year^{-1}), the annual precipitation in Bahía Málaga (*c.* 7500 mm year^{-1}) is three times higher than in the Caeté estuary and it is considered among the wettest areas in the American continent (Poveda & Mesa 2000). Tidal regimes in the Caeté estuary and Bahía Málaga are semi-diurnal and macrotidal, reaching at both sites 4-5 m at spring tides. Red mangroves (*Rhizophora mangle* and *R. racemosa*) are the prevailing intertidal forests in both areas. Other less abundant mangrove trees common to both areas are *Avicennia germinans* and *Laguncularia racemosa* (Cantera et al. 1999, Menezes et al. 2008). The Caeté estuary and Bahía Málaga form part of recently created protection schemes (Reserva Extrativista Marinha-RESEX in Brazil and National Park in Colombia) where human population densities are relatively low (5-25 inhabitants per km^2, Souza-Filho et al. 2009, Etter et al. 2006). These last two features contribute to the relatively undisturbed condition of both systems.

Sampling methods

Fish collections took place from December 2009 to November 2010 in Bahía Málaga-Pacific Colombia, and from October 2011 to August 2012 in the Caeté estuary-North

Brazil. Fish sampling methods were identical at both localities, involvig the use of block nets (15-20 m x 4 m, mesh size 12 mm) set at the entrance of small intertidal creeks (*c.* 3 width and 100 m long; four creeks in Colombia and six creeks in Brazil) during spring and neap tides at daylight and night accounting for the four different conditions when mangrove fish in macrotidal semi-diurnal coasts can access intertidal habitats: at spring tides during daylight (SD), at spring tides during the night (SN), at neap tides during daylight (ND) and at neap tides during night (NN) (details of sampling protocols can be found in Castellanos-Galindo & Krumme, in press). Sampling stations were located across a salinity gradient in both study areas covering ranges from 0 to 22 in Bahía Málaga and 0 to 35 in the Caeté estuary (Figure 36 and Annex IV, Supplemental Figure A8).

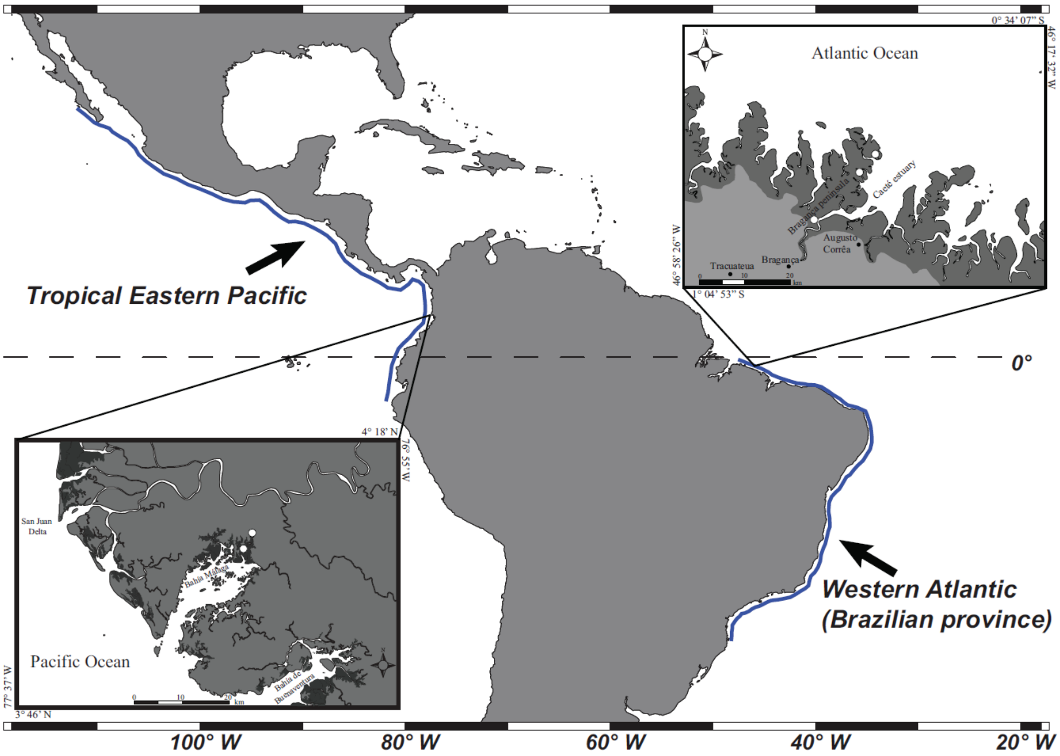

Figure 36. Location of the two macrotidal estuarine systems studied in the Tropical Eastern Pacific and the Brazilian province of the Western Atlantic. Lower panel: Bahía Málaga in the Colombian Pacific coast; upper panel: Caeté estuary in North Brazil. Dark grey areas in both panels represent mangrove areas and white dots indicate the sampling sites along salinity gradients.

Due to the extreme precipitation regime in Bahía Málaga, salinity in the whole estuary rarely exceeded 23 (Cantera et al. 1999). The topography of each creek was surveyed with a GPS, compass and a tape measure to estimate inundated areas and water volumes at high tide and standardize fish catches to density and biomass (see details in Castellanos-Galindo & Krumme in press). Fish collected were identified with taxonomic keys available for the areas (Robertson & Allen 2008, Carpenter

2002a 2002b) and every single individual was measured and wet-weighed. Fish species were assigned to trophic, spatial and estuarine use categories according to Elliot et al. (2007).

Data analyses.
Individual-based rarefaction curves were produced for each of the creeks examined in each region, indicating that sampling intensity adequately represented the intertidal mangrove fish communities of the study sites (see Annex IV, Supplemental Figure A9). Rank species abundance distribution models (SADs), based on biomass and number of individuals, were produced to describe differences in evenness and species richness of the fish assemblages observed along salinity gradients in each of the study sites.

To determine how tide and diel pulses and salinity gradients influenced the composition of intertidal mangrove fish assemblages, a two-way PERMANOVA was implemented with the factors tide-time of day combination as fixed (four levels: SD, SN, ND, NN) and salinity gradient as a fixed factor (two levels: low and high). To assess whether intertidal migrations in time were performed by the same fish families in the Panamic province of the EP and the Brazilian province of the WA, a two-way PERMANOVA model with the factors tide-time of day combination (fixed, four levels: SD, SN, ND, NN) and region (fixed, two levels: Colombia and Brazil) was implemented. For this purpose, species relative catch mass data (%) from both regions were grouped in families and square-root transformed. Constrained canonical analyses of principal coordinates (CAP) and unconstrained principal coordinates analysis – PCO, were used to depict differences in the levels of the factors analyzed and to identify the families that were responsible for the differences observed among levels of a factor. Analyses were conducted with the PRIMER + PERMANOVA software (Anderson et al. 2006).

Trophic analysis.
We used the trophic level index values available in FishBase (Froese & Pauly 2013) to establish the trophic position of each fish species collected in both areas. Mean trophic levels of the two mangrove fish assemblages were compared with a parametric t-test. We constructed fish biomass trophic level spectra after combining the trophic level of species in 0.5 intervals. Cumulative relative biomass spectra were compared between the two biogeographical regions with a Kolmogorov-Smirnov test (Zar 1999).

RESULTS

Intertidal mangrove fish assemblages in macrotidal areas of north Brazil and Pacific Colombia consisted of an approximately equal number of species and families (50 species and 26 families in Pacific Colombia vs 48 species and 27 families in Brazil). The two assemblages did not have any species in common, but 16 (25%) out of 63 genera and 18 (51%) out of 35 families were common between geographic areas (see Annex IV, Supplemental Table A5). Sciaenidae (10 species) and Lutjanidae (6 species) were the most speciose families in North Brazil and Pacific Colombia, respectively. Relative fish abundance was dominated by Auchenipteridae (27%) in North Brazil and by Clupeidae (35%) in Pacific Colombia. Relative biomass was dominated by Tetraodontidae (54%), Ariidae (15%) and Auchenipteridae (9%) in North Brazil; and by Lutjanidae (28%), Tetraodontidae (20%) and Ariidae (19%) in Colombia (Figure 37).

Three spatial guilds in Pacific Colombia (demersal, reef-associated and pelagic) accounted for almost the same relative biomass as the demersal guild in North Brazil (86%, Table 24). In contrast, reef associated species, the second most important spatial guild in Pacific Colombia (32%), was only marginally represented in North Brazil (2%). This was mainly due to the great importance of Lutjanidae in Pacific Colombia, which were not recorded in North Brazil. Estuarine resident species were the most important component of fish assemblages in both mangrove areas. Their relative biomass, however, varied from 84% in North Brazil to 49% in Pacific Colombia. Marine estuarine dependent species were more important in Pacific Colombia than in North Brazil (30% vs 5%).

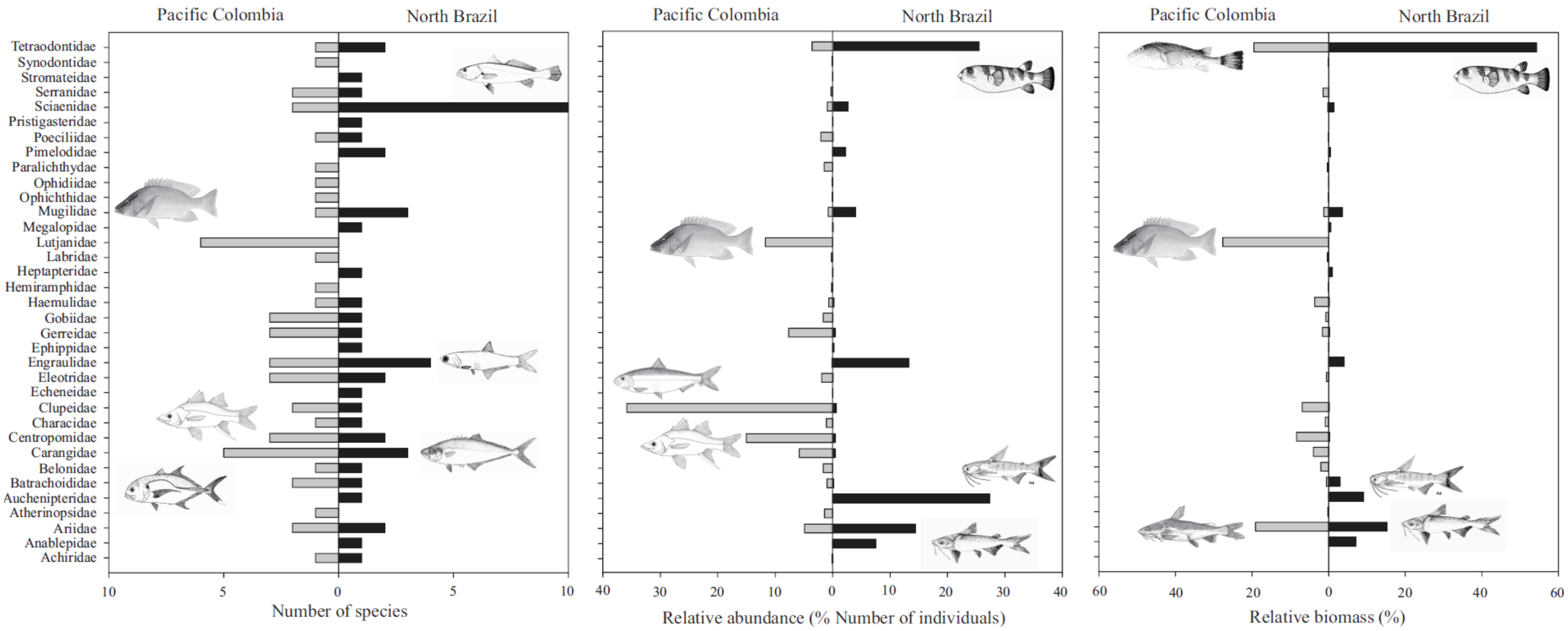

Figure 37. Number of species, relative abundance (%) and relative biomass (%) of 36 fish families found in intertidal mangroves of two neotropical macrotidal estuarine systems (Bahía Málaga, Pacific Colombia and Caeté estuary, North Brazil). Families sorted in descending alphabetical order. Silhouettes of the three principal families for each of the three metrics used in each area are given.

Freshwater migrants were the second most dominant estuarine use guild in Brazil (10%) and only of minor importance in Pacific Colombia (2%). Freshwater catfish families were abundant in number of individuals and biomass in North Brazil, whereas in Pacific Colombia these families were not recorded (Table 25). Fish assemblages in both mangrove regions were largely dominated by zoobenthivores (>75% of the total biomass in both areas). In North Brazil the second and third most important trophic guilds were the detritivores (13%) and herbivores (7%) and were composed of species from the families Anablepidae (*Anableps anableps*) and Auchenipteridae (*Pseudauchenipterus nodosus*), respectively. Herbivores and detritivores in Pacific Colombia only accounted for 3% of the total fish biomass; and Anablepidae and Auchenipteridae were absent in this area. In contrast, zooplanktivores, mainly dominated by Clupeidae, were the second most important trophic group in Pacific Colombia.

Table 24. Relative abundance and biomass of three types of fuctional guilds [proposed by Elliot et al. (2007)] for intertidal mangrove fishes found in two neotropical macrotidal estuarine areas of the Eastern Pacific (Bahía Málaga) and the Western Atlantic (Caeté estuary) regions. Major differences in guilds between regions are underlined.

Guild classification	Bahía Málaga, Colombia		Caeté estuary, Brazil	
	Abundance (%)	Biomass (%)	Abundance (%)	Biomas (%)
Trophic				
Zoobenthivores	53.6	85.2	48.3	76.4
Herbivores	1.1	1.5	18.7	10.6
Zooplanktivores	35.8	5.9	1.4	0.3
Detritivores	2.8	1.4	31.3	12.7
Piscivores	5.5	5.1	0.01	0.03
Other	1.1	0.9	0.3	0.1
Spatial				
Benthopelagic	6.7	6.5	7.8	7.2
Demersal	36.5	50.7	76.0	86.3
Pelagic	40.1	10.5	14.0	4.2
Reef-associated	15.5	31.5	2.1	2.2
Estuarine use				
Estuarine resident	26.5	48.7	61.4	83.8
Marine estuarine dependent	19.1	30.3	6.8	5.4
Marine estuarine opportunistic	48.8	18.2	0.5	0.7
Marine straggler	0.5	1.2	0.8	0.3
Freshwater migrant	5.1	1.6	30.5	9.8

Table 25. Contribution in number of species, relative abundance and relative biomass of freshwater and marine fish families present in intertidal mangrove fish assemblages of two neotropical macrotidal estuarine areas of the Eastern Pacific (Bahía Málaga) and the Western Atlantic (Caeté estuary).

	Bahía Málaga, Colombia			**Caeté estuary, Brazil**		
	No. spp	**Abundance (%)**	**Biomass (%)**	**No. spp**	**Abundance (%)**	**Biomass (%)**
Freshwater fish families	*5*	*5.11*	*1.62*	*7*	*29.85*	*9.71*
Auchenipteridae	-	-	-	1	27.3	9.1
Pimelodidae	-	-	-	1	2.3	0.46
Heptapteridae	-	-	-	1	0.03	0.03
Eleotridae	3	1.90	0.611	2	0.1	0.1
Characidae	1	1.14	0.93	1	0.03	0.003
Poeciliidae	1	2.07	0.078	1	0.1	0.01
Marine fish families	*32*	*68.4*	*49.7*	*27*	*8.1*	*6.4*
Lutjanidae	6	11.9	27.7	-	-	-
Carangidae	5	5.8	4.0	3	0.43	0.07

Mean species richness across salinity gradients changed significantly between salinities in Bahía Málaga in the Colombian Pacific, but not between salinities in the Caeté estuary in North Brazil (Figure 38).

Rank-abundance plots (SADs) showed a dominance of a pelagic species (*L. stolifera* -Clupeidae), in both salinity areas of Bahía Málaga in the Colombia Pacific. The remaining top species were similar between salinity zones in this region with numerical abundance being extremely low in the low salinity area (see differences in y-axes in Figure 39). In the Caeté estuary the greatest overall abundances were observed in the low salinity area (Taperacim) with a very dominant freshwater catfish species (*P. nodosus*) ranking first. This dominance changed across the salinity gradient with *C. psittacus* (Tetraodontidae) dominating in the medium salinity and *A. clupeoides* (Engraulidae) dominating in high salinity zones. The top five species in the three salinity zones always contained three common species (*C. psittacus*, *Cathorops agassizii* and *A. anableps*). Only in the low salinity zone there were two freshwater fish species present in the top five dominating species (Figure 39; see SADs for biomass in Annex IV, Supplemental Figure A10). Mean species richness in Bahía Málaga was significantly lower in low salinities compared to high salinity zones (t=-6.8726, p-value<0.001). In contrast, mean species richness in the Caeté estuary was not significantly different between salinity zones (Krukal-Wallis test, H=1.8874, df=2, p-value=0.3892)

Both individual PERMANOVA tests for Bahía Málaga and the Caeté estuary showed significant main effects for the factors tide-time of day and salinity and their respective interactions (Table 26).

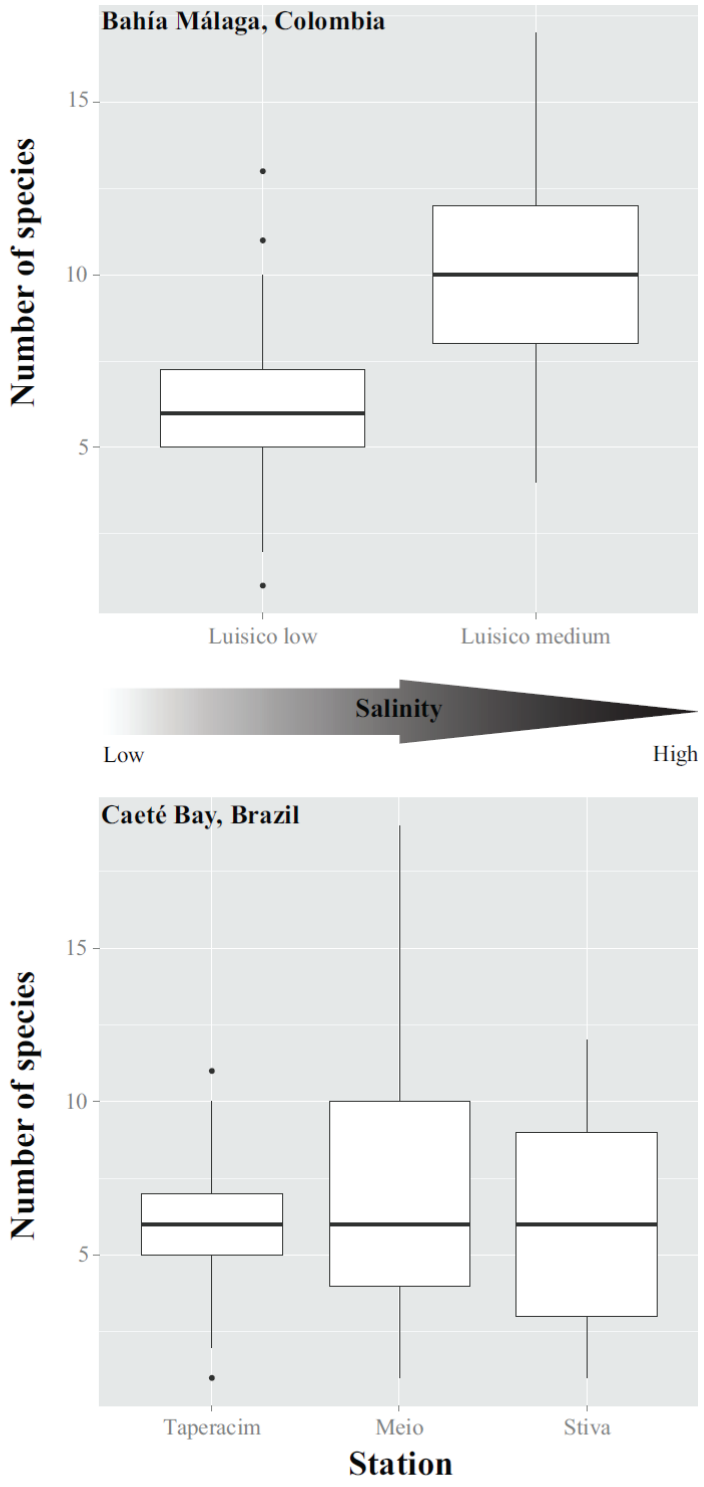

Figure 38. Box-whisker plots showing (median) intertidal mangrove fish species richness across salinity gradients in Bahía Málaga in the Tropical Eastern Pacific and in the Caeté estuary in the Brazilian province of the Western Atlantic.

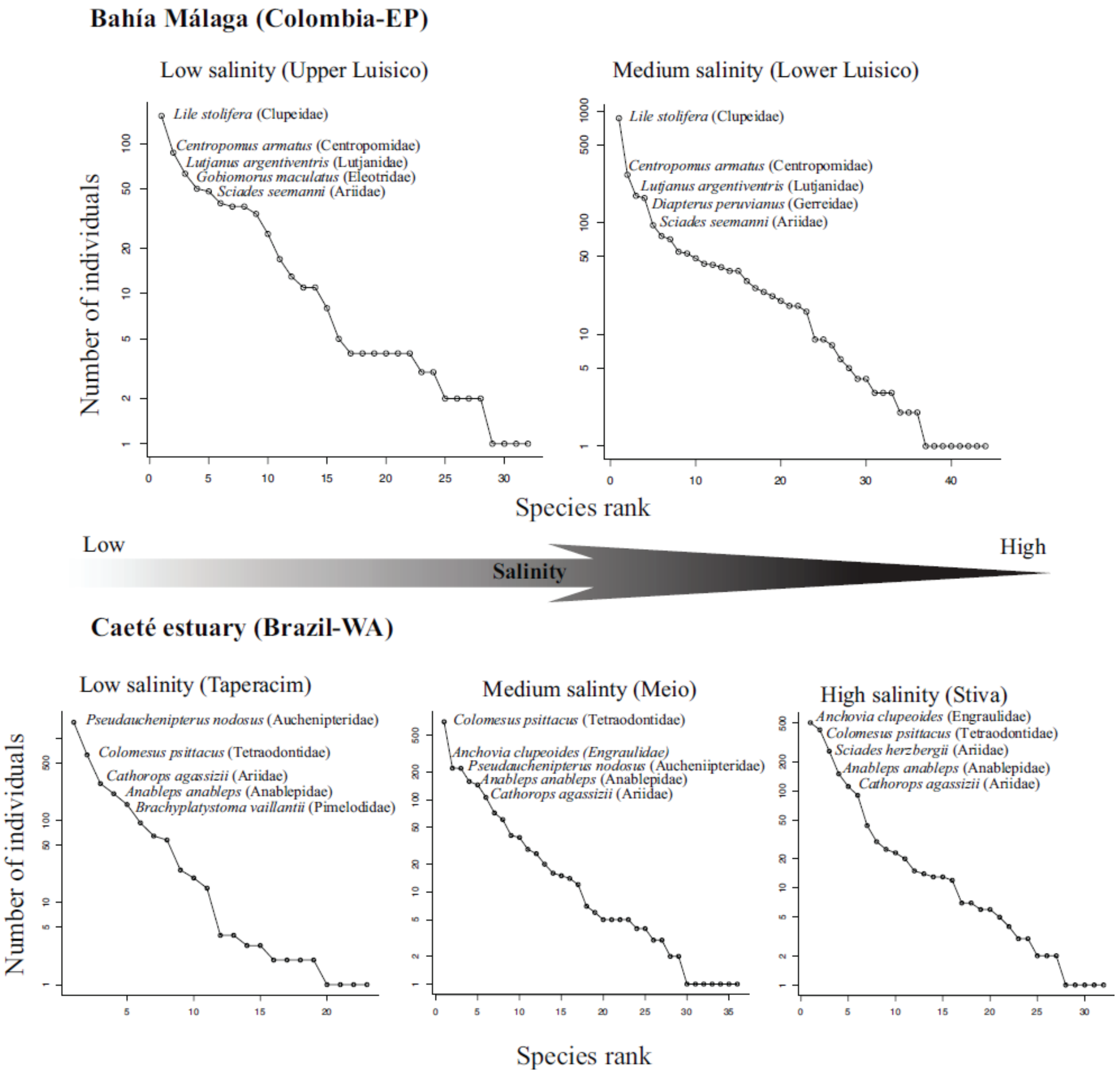

Figure 39. Rank-abundance (biomass) distribution plots ($\log_{10}$ transformed) of intertidal mangrove fish collected along salinity gradients in two localities of the Neotropics (Bahía Málaga, Panamic province of the Eastern Pacific and Caeté estuary, Brazilian province of the Western Atlantic).

The visual inspection of the PCO and CAP grouping data by tide-time of day and salinity (Figure 40 and Annex IV, Supplemental Figure A11) revealed that differences in Bahía Málaga between samples of different tide-time of day combinations were driven by the presence of Clupeidae in samples from spring-day and spring-night, the presence of Tetraodontidae in samples from spring-day and neap-day, and the preference of families such as Ariidae and Centropomidae for neap-night and spring-night conditions. In the Caeté estuary, most indicative species were related to samples from spring tides (day and night), where the greatest number of species was always found.

Table 26. One-way PERMANOVA model testing the effects of the factors: tide-time of day combination (Spring-day, spring-night, neap-day, neap-night) and salinity zone (low-high in Bahía Málaga and low-medium-high in Caeté estuary) on intertidal mangrove fish assemblages of Bahía Málaga (Panamic province of the Tropical Eastern Pacific) and the Caeté estuary (Brazilian province of the Western Atlantic).

Source	df	SS	MS	Pseudo-F	P
Bahía Málaga, Colombia					
Tide-time of day	3	30025	10008	4.9135	0.001
Salinity zone	1	19090	19090	9.3724	0.001
(Tide-time of day) x (salinity zone)	3	14579	4859.7	2.3859	0.001
Residual	84	1.711 x 10^{-5}	2036.9		
Total	91	2.349 x 10^{-5}			
Caeté estuary, North Brazil					
Tide-time of day	3	62313	20771	13.053	0.001
Salinity zone	2	19348	9673.8	6.0792	0.001
(Tide-time of day) x (salinity zone)	6	15610	2601.7	1.6349	0.007
Residual	99	1.575 x 10^{-5}	1591.3		
Total	110	2.569 x 10^{-5}			

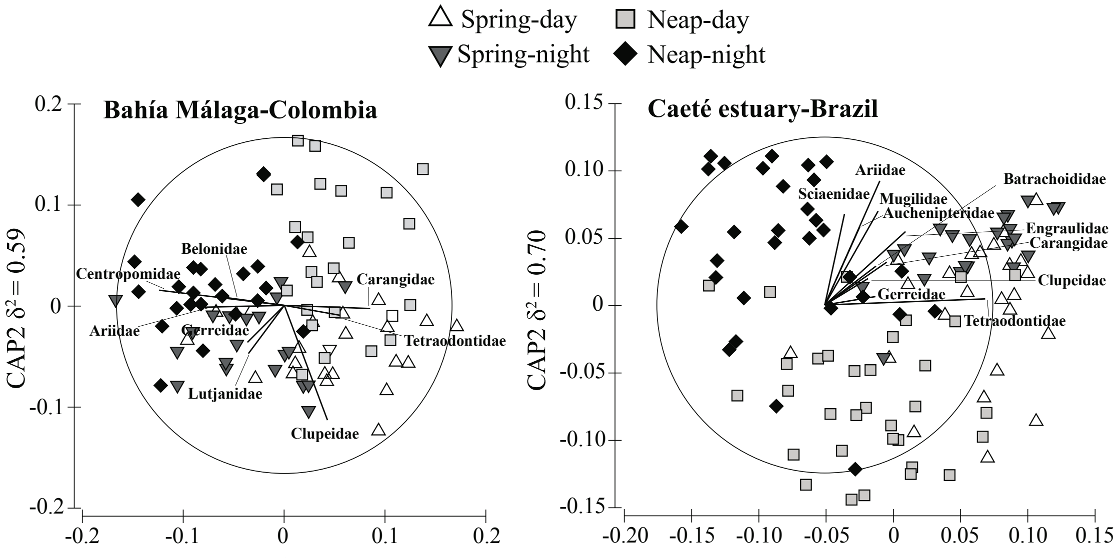

Figure 40. Constrained canonical analysis of principal coordinates (CAP) of neotropical fish families found in intertidal mangroves at specific tide-time of day combinations in the Panamic province of the Tropical Eastern Pacific (left plot) and in the Brazilian province of the Western Atlantic (right plot). Vectors represent fish families with correlations with the canonical axes > 0.4 (Spearman correlations). δ^2 = Square canonical correlation.

Tetraodontidae and to a minor extent Gerreidae, however, were related more to samples coming from the spring-day combination. In the case of salinity, differences in Bahía Málaga were driven by the presence of species of Eleotridae in the low salinity zone and species of Lutjanidae and Tetraodontidae in the high salinity zone. However, other families, such as Ariidae, Centropomidae and Carangidae were associated to both low and high salinity zones. In the Caeté estuary, two freshwater fish families were associated to low salinities (Pimelodidae and Auchenipteridae) in the Taperacim site. Samples from medium and high salinities were difficult to distinguish, but families like Centropomidae and Ephippidae were more characteristics of the high salinity zone (Furo da Stiva). Mugilidae in turn, was more common in samples coming from medium salinity area (see Annex IV, Supplemental Figure A11).

Table 27. Two-way PERMANOVA model testing the effects of the factors: tide-time of day and region (both factors are fixed) on intertidal mangrove fish assemblages of Bahía Málaga (Panamic province of the Tropical Eastern Pacific) and the Caeté estuary (Brazilian province of the Western Atlantic).

Source	**df**	**SS**	**MS**	**Pseudo-F**	**P**
Tide-time of day	3	56529	18843	10.935	0.001
Region	1	1.47 x 10^{-5}	1.47 x 10^{-5}	85.577	0.001
(Tide-time of day) x (region)	3	22888	7629.4	4.4277	0.001
Residual	195	3.36 x 10^{-5}	1723.1		
Total	202	5.66 x 10^{-5}			

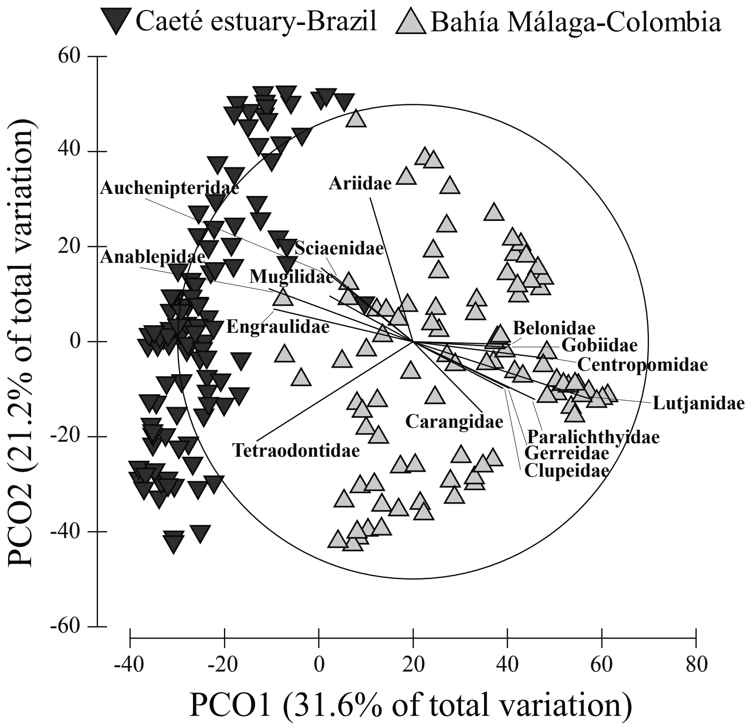

Figure 41. Principal coordinate analysis (PCO) ordination of fish families found in intertidal mangrove areas of two macrotidal estuarine localities of the Neotropics. Vectors represent fish families with correlations with the PCO axes > 0.4 (Spearman correlations).

The PERMANOVA test, where the pooled data of relative biomass from both study areas was used, returned significant main effects: for tide-time date and region (Table 27). The PCO plot clearly separated the samples from the two regions and indicated that such differences were mainly driven by Anablepidae and Auchenipteridae, only present in North Brazil, and by Lutjanidae (only present in samplings in Colombia) and Centropomidae in Pacific Colombia. Vectors from the families Ariidae and Tetraodontidae were somehow split in the two regions (with a different angle from the rest of the vectors) indicating that these two families were dominant in biomass in both regions (. Especially in the case of Tetraodontidae, the vector pointed in the direction of samples from North Brazil due to the great dominance of this family (*c.* 55% of total biomass) during samplings in the Caeté estuary in 2011-2012 (Annex IV, Supplemental Table A5). The CAP plot for the factor tide-time of day showed that Ariidae represented samples coming from night times (especially neap tides). Lutjanidae was especially associated to samples from spring-night. Tetraodontidae represented samples from daytime samples (during neap and spring tides). Finally, Anablepidae, present only in Brazil was associated to samples from neap tides (especially samples coming from daytime; Figure 42).

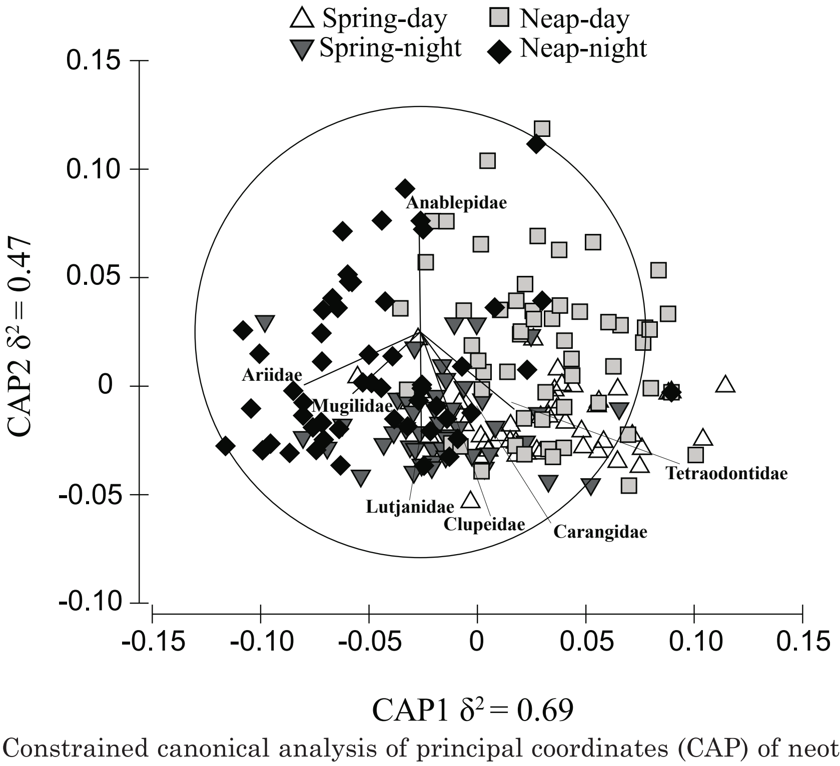

Figure 42. Constrained canonical analysis of principal coordinates (CAP) of neotropical fish families found in intertidal mangroves at specific tide-time of day combinations in two macrotidal estuarine localities of the Neotropics. Vectors represent fish families with correlations with the canonical axes > 0.4 (Spearman correlations). δ^2 = Square canonical correlation.

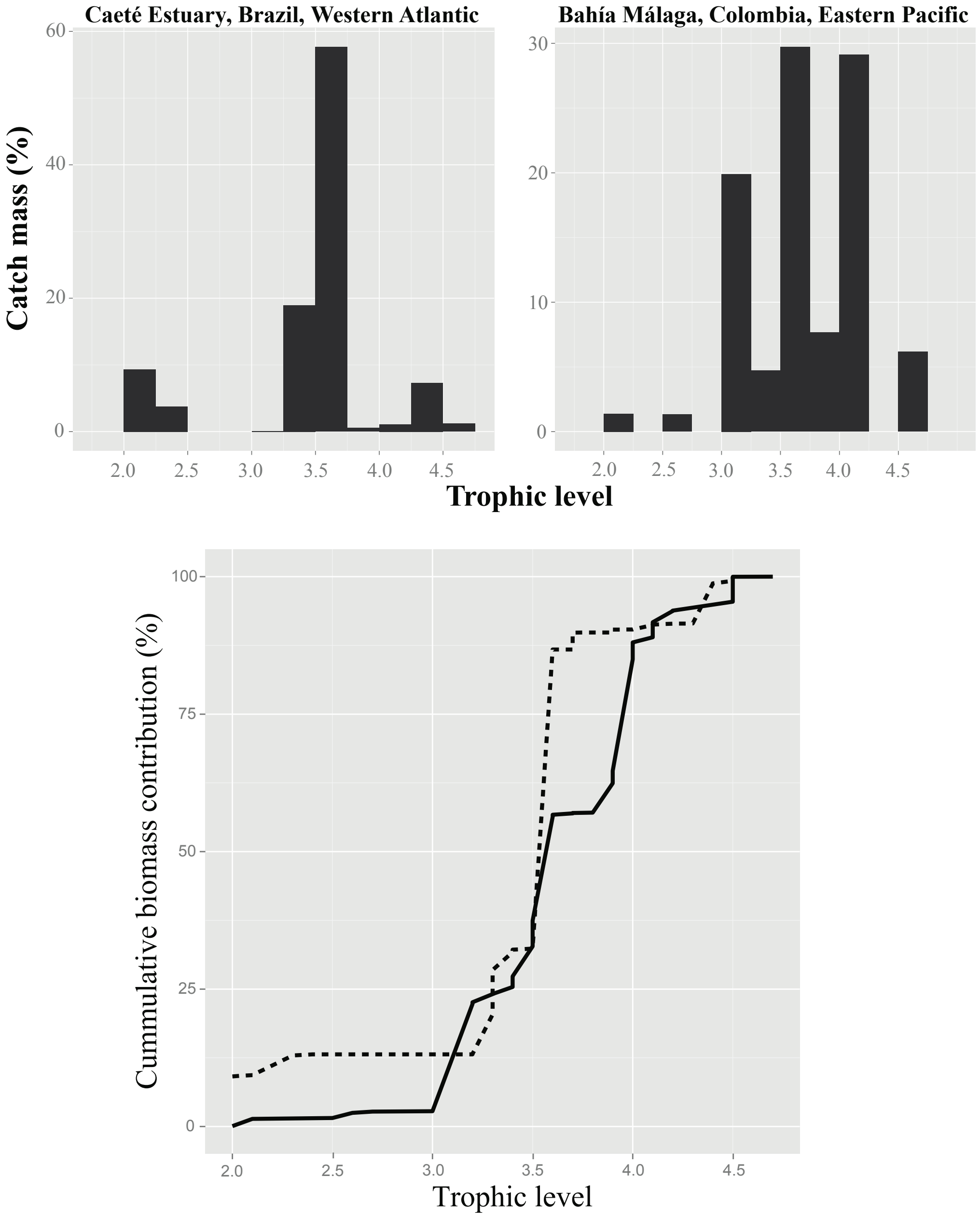

Figure 43. Biomass distribution along trophic levels and cumulative relative biomass trophic level spectra (CBTLS) of intertidal mangrove fish assemblages in two macrotidal estuarine localities of the Neotropics [Bahía Málaga in the Panamic province of the Eastern Pacific (continuous line) and the Caeté estuary in the Brazilian province of the Western Atlantic (dashed line)].

Mean trophic level was equal in both systems (TL=3.64, t=0.0725, p=0.9424). The biomass distribution according to trophic levels, however, was very close to significance level indicating differences between the two systems (Figure 43; KS test, K=0.2756, p=0.05). Species belonging to the trophic class 3.5-3.75 accounted for almost 60% of the total biomass in the mangrove system of North Brazil, whereas in

Pacific Colombia three peaks were observed in the distribution of biomass across trophic levels (3.0-3.25, 3.5-3.75 and 4.0-4.25). These three classes accounted for almost 80% of the total biomass. In North Brazil, the presence of an abundant detritivorous species with low trophic level contrasted with the lack of low trophic levels in Pacific Colombia where 85% of the biomass was allocated to species in trophic levels between 3-4.

DISCUSSION

Intertidal mangrove fish assemblages in the Brazilian province of the Western Atlantic and the Panamic province of the Eastern Pacific comprised an equal number of species that clearly resemble the similarities in the number of species of coastal fishes in both regions (local-regional diversity relationship). Similarities in taxonomic composition and in the dominance (in biomass) of specific fish families in both assemblages reflect the ancient links of coastal faunas of both regions. The tidal and diel pulse were identified as clear drivers of community organization in mangrove fish assemblage composition in both areas, indicating that in macrotidal mangroves of the Neotropics these pulses segregate the temporal use of intertidal habitats by fishes. The same temporal use of intertidal habitats by phylogenetically-related taxa in both areas indicates that there is a signal in the niche preferences dating back to ancient geological times. Differences in taxonomic and trophic composition between areas reflect the effect of: (1) local landscape and environmental characteristics of the estuaries, (2) historical biogeographic processes dating back to the Mesozoic (e.g. allopatric speciation, extinction) and (3) dissimilarities in the regional richness of freshwater fish capable to successfully colonize estuarine habitats.

Relationships between local and regional species richness have been widely documented for a number of taxonomic groups (e.g. Ricklefs 2000). The pattern found for intertidal mangrove fish assemblages in regions that share similar numbers of coastal fish regional diversity is therefore not surprising. Equally expected and partly explained by the historical biogeography of the Neotropics is the similarity at higher taxonomic levels (genera and families) encountered between the two regions. Leigh et al. (in press), claimed that the marine tropical biotas of the Americas and the Eastern Atlantic (West Africa and the Mediterranean) share a common Oligocene (33.9-23.03 mya) heritage forming the Atlantic Eastern Pacific realm (AEP), which was already taxonomically distinct in the Late Oligecene from the Indo-West Pacific (Renema et al. 2008). Both Bahía Málaga in the Colombian Pacific and the Caeté estuary in North Brazil also formed part at least since the early Miocene of Woodring's (1974) so-called Miocene Caribbean faunal province (Gatunian province according to Landau et al. 2008; see Figure 35). More recently, the rise of the Isthmus of Panama, referred to as the Great American Schism for marine biota inhabiting the Eastern Pacific and the Western Atlantic Oceans (Lessios 2008), prompted new and different evolutionary trajectories for organisms inhabiting the now isolated two Oceans. Our results show the influence that ancestral fish groups, widespread in the region back in the Miocene, can have in explaining the extant composition of mangrove fish assemblages in the Panamic and the Brazilian provinces. Two common dominant families in intertidal areas of the two regions, Tetraodontidae and Ariidae, have species that are phylogenetically closely related and whose ancestors date back to Miocene times (see Marceniuk et al. 2012 for Ariidae and Santini et al. 2013 for Tetraodontidae). These indications highlight the great importance that biogeography plays in explaining the extant composition of mangrove fish assemblages in the Neotropics.

Records of the existence of tides and diel cycles date back to the Precambrian (Coughenour et al. 2009). Evidence of marine organisms adapting to these cycles are also well documented (Tessmar-Raible et al. 2011). In tropical coastal fish assemblages both tidal and diel cycles can play a major role in determining the short-term dynamics of intertidal habitat use (Krumme 2009). Our comparative approach in macrotidal estuarine areas of the Neotropics show that fish in these two intertidal mangroves segregate their temporal niche axis according to the interaction of the tidal and diel cycle. In mangroves of the Colombian Pacific specific tide-time of day combinations resulted in a predictable subset of fish species occupying intertidal areas, but higher biomasses or number of species were not necessarily related to a specific tide-diel combination (see datails in: Castellanos-Galindo & Krumme in press). In North Brazil, fish assemblages also segregated in their niche preferences according to tidal and diel dynamics, and also the biomass and number of species using intertidal mangroves changed according to these dynamics.

Differences in the strength of tide-diel related patterns in mangrove fish may be associated to the physical conditions that fish encounter in different mangrove habitats: mangroves in Pacific Colombia are erosional systems where accumulation of sediment within the system is considered low (Pilkey 2006). As a consequence, during spring and neap tides, the mangrove forest is almost equally inundated. Therefore, migrating at spring tides provides no significant increase in feeding grounds to fish. In North Brazil, mangroves have developed in an accretional environment and the higher intertidal zones are only inundated during spring tides. In this type of environments, migrating to the intertidal at spring tides is linked to increased access to foraging grounds for fishes and therefore higher biomasses of fishes.

The fish assemblages analyzed here corresponded to the same habitats: intertidal mangroves in two macrotidal coasts. Despite having equal mean trophic levels, biomass distributions along the trophic levels can tell important differences about the two systems: The Caeté estuary in North Brazil contained a low trophic level group that was almost absent in Bahía Málaga in the Colombian Pacific. The

Caeté estuary is a system dominated by herbivores and detritivores where plant food sources and plant detritus are abundant and remain in the system since high intertidal areas are only inundated during spring tides (Koch & Wolff 2002). The system in the Colombian Pacific is a megahumid area with an annual precipitation almost three times higher than in North Brazil. Moreover, the particular topography of the mangroves, where the intertidal substrate is inundated almost equally during spring and neap tides (see Annex IV, Supplemental Figure A12), produces a system where most mangrove plant material and detritus is flushed away. Consequently, detritivory might not have the same importance as a trophic pathway in this system as it has in the Caeté estuary.

The mean trophic levels observed in these two systems are higher than those obtained in another tropical estuarine system of the Neotropics, Laguna de Terminos in the Gulf of Mexico. In this locality mean trophic levels were generally lower than 3.5 in samplings carried out in the 80s and end of the 90's and 2003-2004 (Sosa-López et al. 2005, Villéger et al. 2008). Similarly, a biogeographic comparison of the estuarine fish assemblages in South Africa indicated that in warm-temperate and subtropical zones most species belonged to trophic levels <3.5 and that in cool-temperate estuaries trophic levels were <2.5 (Harrison & Whitfield 2012). The differences observed may be attributed to the characteristic environments sampled in the different estuarine areas. In Laguna de Terminos, samplings were conducted with trawls in non-vegetated habitats within a lagoon. Similarly, in South African estuaries, sampling included the use of gillnets in open areas within estuaries. These sampling methods and the open environments sampled may be selective towards low trophic level species such a mullets (Mugilidae). In the two localities sampled in the present study, block nets were able to capture the fish that enter intertidal mangroves to feed on the rich prey available in these habitats. Most of the species captured in both mangrove systems were zoobenthivorous species. Especially in the Colombian Pacific, mangrove fish species were composed of a significant proportion of marine estuarine dependent species that have predatory feeding habitats and belong to high trophic levels (Lutjanidae and Carangidae).

Salinity plays a major role in the distribution of fishes in estuarine environments (Sosa-López et al. 2007). Total species richness in the two estuarine systems evaluated here was lower in low salinity sites compared to the higher salinity sites. However, mean species richness displayed different trends between the two systems. Whereas mean species richness was lower in the low salinity areas of Bahía Málaga, mean species richness was relatively uniform across salinity gradients in the Caeté estuary. Low salinity environments in Bahía Málaga display harsh conditions for marine estuarine fish species. The extremely high precipitation regime in this area (*c.* 7 m year^{-1}) implies that mangroves face fast and relatively permanent changes in the hydrological regime leading to very low salinities in the upper reaches of estuaries. The lack of a diverse regional freshwater fish fauna in the Pacific lowlands of Colombia (Trans-Andean/Magdalenean province; Léveque et al. 2008) greatly contributes to the reduced number of species found in low salinity mangrove sites. The isolation of this area due to the rise of the Andes cordillera and the presence of relatively small rivers draining to the Pacific coast results in a highly endemic freshwater fauna which is very poor in species numbers (*c.* 186 species). In contrast, the diverse freshwater fish fauna of the Amazonian province and the coastal rivers of North Brazil, could have promoted that some of these fish groups (especially freshwater Siluriformes - catfishes) colonize the low salinity upper reaches of estuaries like the Caeté estuary and extend further into parts of these estuaries during the rainy seasons (Barletta et al. 2005). Our results indicate that fish species richness patterns across salinity gradients in estuarine areas can be contrasting between regions of the Neotropics. Whereas in areas like Laguna de Terminos in the Gulf of Mexico or North Brazil species richness is negatively correlated with salinity (Barletta et al, 2005, Sosa-López et al. 2007), in the Eastern Pacific this relationship is positive. The ultimate causes for such a discrepancy may lie in the relative contribution of richer or poorer freshwater fish faunas of the regions examined.

In conclusion, this comparison provides for the first time evidence of the crucial role that tides and diel cycles play in shaping patterns of organization in intertidal mangrove fish assemblages in macrotidal coasts of different marine biogeographical regions. For the dominant taxonomic groups (Ariidae and Tetraodontidae) found in the Eastern Pacific and Western Atlantic tide-influenced niche preferences may be deeply rooted in common ancestors (i.e. phylogenetic signal exists). Further analyses with appropriate tests (see Losos 2008), may prove valuable in testing the phylogenetic niche conservatism of intertidal movements for mangrove fishes in macrotidal areas. Seascapes adjacent to mangroves proved crucial in shaping the structure and function of intertidal mangrove fish assemblages. Finally, the role of historical biogeography and the productivity of the systems analyzed seem to be largely responsible for the contrasting effects of salinity on mangrove fish species richness and for the lack of some important taxonomic (Anablepidae) and trophic groups (detritivores and herbivores) in the Eastern Pacific and Western Atlantic.

Supplementary data is given in Annex IV

ACKNOWLEDGEMENTS

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Chapter VIII. Synoptic discussion and Outlook

The present dissertation contains three main findings that contribute to the global understanding of how fish assemblages are distributed in mangrove ecosystems. *Chapters II and III*, provided evidence that fish tidal movements are generally part of the home-range movements of a variety of coastal fish assemblages, but that different intertidal habitats (rocky vs mangroves) may provide different functions for these assemblages. *Chapters II*, *VI* and *VII*, indicated that the combination of tidal and diel cycles are a strong force that regulates intertidal fish assemblages in macrotidal mangrove habitats across geographical areas, and also that the patterns arising from these cycles can be highly stable over time (*Chapter VI*). Finally, *chapters IV*, *V* and *VII* revealed important insights that historical biogeography can provide to our understanding of the present distribution an organization of mangrove fish assemblages in the Neotropics. These findings will contribute to a better understanding and thoughtful comparison of mangrove fish assemblage structures on a global scale.

8.1. The ecological significance of tidal migrations for fish in macrotidal coastal habitats (rocky shores vs mangroves).

Tidal migrations (*sensu* Gibson 2003) constitute an overlooked part of the home-range movements of coastal organisms. The study of these movements in two tropical coastal ecosystems (rocky shores in *Chapter III* and mangroves in *Chapter II*, *V* and *VI*) revealed that fish (inter) tidal movements are important for a considerable number of species within local subtidal fish assemblages. In rocky shores of northern Colombia, >70% of subtidal rocky-coral reefs fish species used intertidal rocky shores to varying degrees (*Chapter III*). In mangroves of north Brazil, *ca.* 40% of the fish species identified by Barletta et al. (2005) in the main channel of the Caeté estuary were found in adjacent intertidal mangrove creeks during the sampling campaign carried out in 2011-2012 (*Chapters VI* and *VII*). Nevertheless, the relative importance of intertidal habitats as feeding or shelter areas for fish assemblages can vary. In rocky shores of the Tropical Eastern Pacific, only a few species were found to permanently depend on intertidal zones as feeding or resting areas (e.g. the banded wrasse *Halichoeres notospilus*). In contrast, in macrotidal systems of Pacific Colombia and North Brazil, intertidal mangroves were consistently important for the ecologically dominant fish in the adjacent areas (e.g. catfishes, pufferfishes and snappers). The area available for intertidal migration and the distribution of prey resources in these intertidal habitats might explain this difference. Whereas in rocky shores, the inundated area at high tide may be in the order of 10s of meters (with the edge of the low water level as a reference), in the mangroves systems under study, the intertidal habitat available at high tide easily extends for 100s of meters inland through the ramification of several intertidal creeks forming a dendritic (branching like a tree) system. Similarly, prey distribution in intertidal areas may affect the distribution of predators (fish). Higher prey abundance in lower than in high intertidal areas of rocky shores (Lubchenco et al. 1984, Rilov & Schiel 2006) indicate no additional advantage for fish in migrating to higher intertidal areas at spring tides. In contrast, the distribution of prey in mangroves shows higher abundances in high intertidal areas (Koch 1999), which are only available to the fish during spring tides (in North Brazil). Therefore, migrating into intertidal mangroves when larger areas are inundated (i.e. spring tides) may represent a significant advantage for those fish searching for food in this intertidal habitat.

The home-range of many coastal fish includes temporally available habitats like intertidal areas, which form important part of the coastal ecosystem mosaic – CEM (Sheaves 2009). The results presented here, show that different intertidal habitats in macrotidal coast may provide different functions to the fish assemblages that visit them at high tide. Intertidal mangroves therefore may not be just “another shallow-water habitat” where fish shelter from predation (Sheaves 2005), but a rich source of food for fish at high tide. Intertidal rocky shores, conversely, may represent only an alternative habitat for the majority of the diverse reef fish community, where shelter and not feeding is the main function for most species. These observations have profound implications for identifying and prioritizing the protection of fish nursery (intertidal) habitats within the CEM in macrotidal tropical areas.

8.2. Tides and salinity regimes as major forces structuring local community structure in mangrove fish assemblages

Tidal-related movements, despite being ubiquitous in meso- and macrotidal coasts, are often ignored as an important mechanism determining the distribution of estuarine fishes. The results presented here indicate that spring-neap tide in combination with day-night cycles can explain the organization of fish assemblages using intertidal mangroves in neotropical macrotidal coasts. Defined fish assemblages in the Colombian Pacific and in North Brazil were found to use the intertidal habitats depending on the specific tide-time of day combination (*Chapters II*, *VI*, *VII*), suggesting that these cycles may shape how fish communities use resources in intertidal areas. The finding that related fish species from isolated biogeographical regions used the intertidal zone during the same tide-time of day combination may indicate that the division in niches according to tides-diel cycles has already been in place for long time (geological time scales).

In mangroves of North Brazil (the Caeté estuary), the influence of diel-tidal cycles was found to exert a more direct influence on mangrove fish productivity (fish catch mass) in the intertidal areas than in the system of the Colombian Pacific (Bahía Málaga). Higher fish catch mass during spring tides in the Caeté estuary were considered to be the result of the characteristic geomorphology of the mangrove system. Larger areas inundated during spring tides allowed fishes (mostly zoobenthivores) to access extensive intertidal forest rich in prey resources that were not available during inundations at neap tides. The accretionary area where mangroves develop in North Brazil is therefore likely responsible for a stronger control of tidal-related forces on intertidal mangrove fish production. In sharp contrast to North Brazil, in the Colombian Pacific coast, mangroves develop in erosional conditions, mainly as a result of a tectonically active area (Pilkey 2006) and an extreme precipitation regime. Consequently, mangrove topography in the Colombian Pacific is less elevated (see Figure in S7 of Chapter VII) causing the difference between inundated areas at spring and neap tides to be not as high as in the accretionary type of mangroves (North Brazil). Fishes under this condition may not benefit from increased prey resources during greater inundations at spring tides. Fish productivity in this type of intertidal mangroves therefore may not be extremely regulated by the tidal mangnitude.

In conclusion, the controlling force of tides on intertidal mangrove fish is, on one side, clear when regulating the niches in time (i.e. along the tide-time of day combination) of assemblages, but on the other side, is dependent on the specific local geomorphologic setting that modulates fish productivity.

Two contrasting estuarine systems with respect to precipitation regimes and salinity fluctuations were encountered in the Eastern Pacific and the Western Atlantic. On one side, Bahía Málaga in the Colombian Pacific is located probably within the wettest region of the whole American continent (Poveda & Mesa 2000), where mean annual rainfall reaches 7-8 m. The amount of rainfall and subsequent high river runoff into the Ocean in this area is clearly mirrored in the oceanographic conditions of the whole Panama Bight area where salinities are the lowest in the whole TEP (Fiedler & Talley 2006). These conditions have been probably in place since the formation of the Isthmus of Panama (Haug et al. 2001). Most estuaries in the whole Colombian Pacific coast have salinities < 28 even in their lower reaches/mouths (Cantera et al. 1999) and the presence of an extremely wet season (May-December), with monthly precipitations reaching up to 1000 mm, severely decreases salinity within estuaries (see *Chapter II*). Hence, fish assemblages in these extreme environments have adapted to such conditions.

In North Brazil, the precipitation in the Caeté estuary does not exceed 4 m year^{-1}. The dry season, which normally extends from July to December, presents average monthly rainfall values below 100 mm, whereas during the rainy season (January-June), these values reach 400 mm month^{-1}, the same values observed during the “dry season” (called wet season in *Chapter II*) in Bahía Málaga. The

Caeté estuary has salinities that reach 35 in the lower estuary during the dry season and that can decrease in this same area to 10-20 during the wet season (see *Chapter VII*). In this system, Barletta et al. (2005) observed different assemblages along salinity gradients in the main channel of this estuary. Since salinity fluctuates as a function of freshwater discharge, the distribution of freshwater fish species extended during the rainy season in the main channel of the Caeté estuary (Barletta et al. 2005). In mangrove creeks of the Caeté system, it was also observed that different salinity zones were characterized by different assemblage structures. It was also observed that the distribution of an estuarine species (*Pseudauchenipterus nodosus*) extends to medium salinity zones (Furo do Meio) during the rainy season It is worth noting that 2011-2012 was an atypical period in the Caeté system where precipitation during the wet season decrease 40% with respect to other years (see *Chapter VI*)

Salinity was therefore a major controlling factor in the distribution of estuarine mangrove fish assemblages in the two estuarine areas examined in this thesis. Nevertheless, the effect of these salinity gradients was strikingly different between the two systems. The lack of a dominant and abundant freshwater fish assemblage in the system in the Colombian Pacific (Bahía Málaga) produced an extremely depauperate mangrove creek assemblage in low salinity zones. Furthermore, the extremely reduced salinities during the very wet season in the area did not promote the colonization of new areas within the estuary by the few freshwater fish species encountered in this system. In sharp contrast to this pattern, intertidal creeks in low salinity areas in the North Brazilian system were not depauparate in species richness or in biomass. The increase in rainfall and decrease in salinity in the estuary during the rainy season increased the distributional range of freshwater species, which colonized other areas (Furo do Meio). The explanation for these contrasting results with respect to salinity are most likely linked to the biogeography of freshwater faunas (discussed in the next section).

8.3. Biogeographical patterns of estuarine mangrove fish assemblages in the Neotropics

The number of fish species associated to mangroves in both geographical regions analyzed (TEP and the Brazilian province of the Western Atlantic) is influenced by the regional coastal fish diversity. In the Tropical Eastern Pacific and the Brazilian province of the Western Atlantic, the number of fish species associated to mangrove fishes was 315 and 327, respectively. These numbers represent ca. 25% of the total coastal fish fauna in both regions (*Chapters IV* & *V*). This pattern is similar to what was found in coral reef fish assemblages in the Neotropics. In the Southwestern Atlantic (mouth of the Amazon River to Santa Catarina, Brazil), Floeter et al. (2008)

identified 471 reef fish species, whereas in the Tropical Eastern Pacific the number of reef-associated fish reached 341 (Zapata & Robertson 2007). The surveys in intertidal mangroves of Bahía Málaga and the Caeté estuary, using equal sampling methods and intensity, yielded similar species numbers (ca. 50 in each locality, *Chapter II* and *Chapter VI*), supporting the well-established pattern where regional diversity influences local diversity (Ricklefs 2000).

When compared to other mangrove fish assemblages in the world, another clear pattern, previously shown in coral reef fish, is observed. Mangrove fish assemblages in the Indo-West Pacific contain ca. 600 species (Blaber 2007). This number is almost half the number of fish species found in any of the neotropical regions examined here. This pattern recurred at the family level: 135 fish families are found in the Indo-West Pacific (Australasian and Central Indo-Pacific regions in Sheaves (2012)) and approximately half this number was found in the Tropical Eastern Pacific or in the Brazilian province of the Western Atlantic (68 and 80 families, respectively).

Similar patterns in species richness gradients across fish communities from different ecosystems (and across taxonomic groups, see Tittensor et al. 2010) suggest that the same forces could explain these patterns. Historical geographical factors, available habitat and temperature have been hypothesized as the principal factors predicting species richness in marine organisms (Tittensor et al. 2010). For coral reef fishes, the interaction between biogeographical history and environmental predictors such as coral reef area has been identified as a very good predictor of species richness (Parravicini et al. 2013).

Consequently, for mangrove fish assemblage in the Neotropics the same environmental and biogeographical predictors may apply and explain lower species richness. Diverse families represented in mangroves of the Indo-West Pacific (e.g. Ambassidae, Siganidae), are not present in the Neotropics, whereas the common fish families in mangroves of the two regions have considerably more species in the former region (e.g. Gobiidae). The mangrove fish assemblages in the Neotropics are therefore formed by a group of families that are widespread in mangroves around the world (e.g. Mugilidae) and groups of fishes that have diversified and adapted to life in mangroves in the Neotropics after the appearance of major biogeographical barriers isolating this region (e.g. *Centropomus* genus within Centropomidae).

8.3.1 Phylogenetic signal and the possibility for niche conservatism in neotropical estuarine mangrove fishes

A species' niche, as defined by Hutchinson (1957), is considered to be the set of conditions (biotic and abiotic) where species are able to persist. Tetraodontidae and Ariidae have been especially adapted to life in mangroves of the Neotropics. It appears that there is a phylogenetic signal and/or niche conservatism (i.e. retention of ecological traits in related species) in the capacity of closely related species from these families to migrate with the tides to intertidal areas. In this context, both families have adapted to migrate with tides especially under specific tide-time of the day combinations. Whereas species of Ariidae in both geographical areas are adapted to migrate to intertidal mangroves at spring-night tides, Tetraodontidae species have adapted to migration during spring-day and neap-day tides.

The phylogenetic relationships within the family Ariidae (marine catfishes) have been scrutinized in recent times both from a morphological and molecular point of view and different biogegraphical hypothesis have been proposed to explain the distribution of extant species (Betancur-R et al. 2007, Betancur-R et al. 2009, Marceniuk et al. 2012). Compared to these advancements, very little is known about the ecology of the species conforming these phylogenetic trees. In the present comparison, two pairs of related species from Ariidae (*Sciades herzbergii* and *Sciades seemanni*, and *Cathrops agassizii* and *C. steindachneri*, Figure 44) have been found to constitute an important part of the intertidal mangrove fish fauna in both regions. Similar ecological traits (ability to migrate with the tides) in these species may be the product of phylogenetic relatedness. This means that migrating to intertidal areas in these species is a trait that has been present in ancient lineages and it is preserved in the extant species.

Sphoeroides rosenblatti and *Colomesus psittacus* from Tetraodontidae were among the most important species (in catch mass) found in the two systems examined in the Tropical Eastern Pacific and the Western Atlantic, respectively. According to Santini et al. (2013), *Colomesus* is a genus deeply nested within *Sphoeroides* that share a common ancestor. The split between the two genera is calculated to have occurred 12.9 Ma ago in the Miocene (Santini et al. 2013; Figure 44). A phylogenetic signal in this species could explain why they have similar ecological characteristics. In *S. rosenblatti*, intertidal migrations and predation on littorinid gastropods, barnacles and oysters have been recorded (Duncan & Szelistowski 1998, Castellanos-Galindo & Krumme *in press*). Similar behavior for *Colomesus psittacus* in mangroves of north Brazil has been documented (Giarrizzo et al. 2010). It is therefore very likely that these closely related species retain traits from the common ancestor that allow them to dominate in intertidal mangrove habitats of these two regions of the Neotropics.

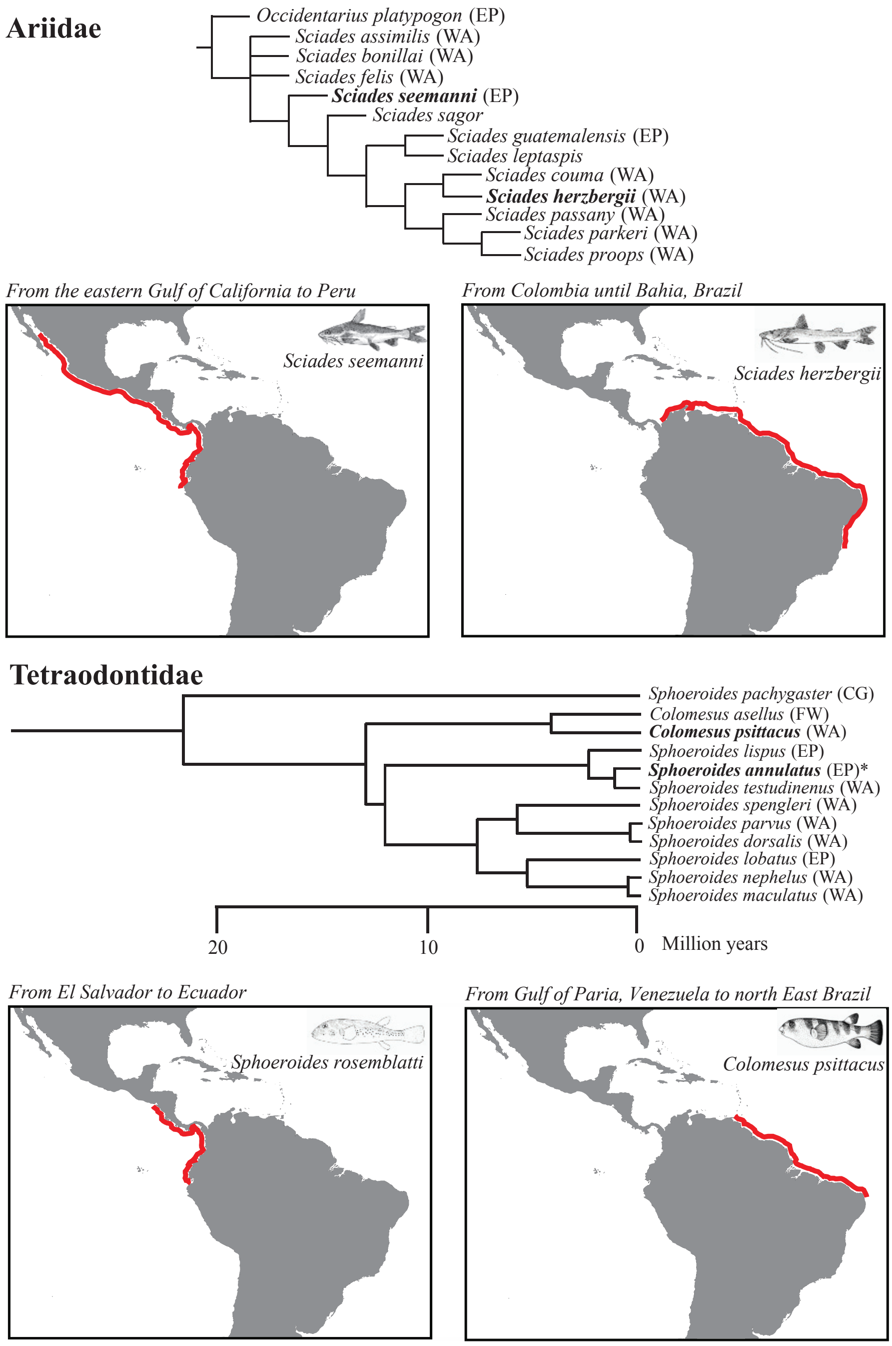
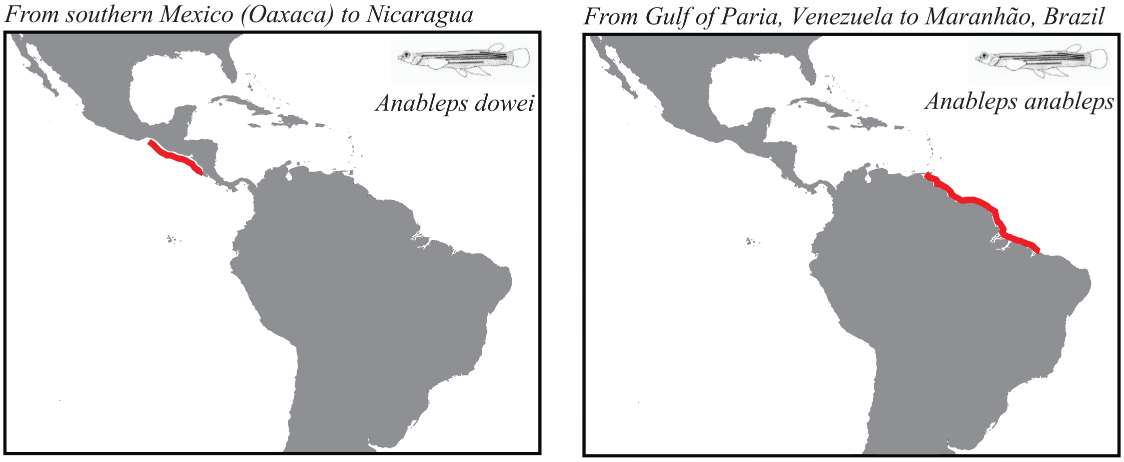


Figure 44. Geographical distribution of species found in intertidal mangroves of Bahía Málaga in the Eastern Pacific (EP) and the Caeté estuary in the Western Atlantic (WA). Recent phylogenetic trees of Ariidae and Tetraodontidae are shown according to Marceniuk et al. (2012) and Santini et al. (2013), respectively. * *Sphoeroides annulatus*, distributed also in the EP, is thought to be a related species to *S. rosenblatti* (Walker & Bussing 1996, the latter species is not shown in the available phylogenetic tree).

8.3.2 The effect of major biogeographic events in the Neotropics

The presence of an abundant member of the family Anablepidae in intertidal mangroves of North Brazil (*Anableps anableps*) contrasted with the absence of this family in the Colombian Pacific. Anablepidae that is restricted to the Neotropics is a sister family to the Poeciliidae (Nelson 2006) and has representatives in the Tropical Eastern Pacific. A sister species of *A. anableps*, which is though to be more related to the ancestral form of *Anableps*, occurs in a restricted part of Central America (southern Mexico to Nicaragua, see Figure 45). *Anableps dowei* is found in coastal areas, including mangroves of this part of Central America and penetrates rivers up to 200 km upstream (Miller 1979). This species has been also found to migrate with the tides to intertidal areas in El Salvador (John Burns, personal communication). The disjoint distribution of this two sister species (*A. anableps* and *A. dowei*) has been observed for other fish groups and might be the consequence of the geological history of the Caribbean region. Rosen (1975) hypothesized that this discontinuous distribution of closely related taxa is the result of remnants of ancestral biota that suffered geographical fragmentation, in this case due to the Antillean land movement from the current day position of Central America to the west in the late Mesozoic. After fragmented, the low dispersal capability of Anablepidae (viviparous), and the specific characteristic of the coastal habitats in the Eastern Pacific might have prevented the ancestor of *A. dowei* to move north or south to Panama or Colombia.


From southern Mexico (Oaxaca) to Nicaragua

From Gulf of Paria, Venezuela to Maranhão, Brazil

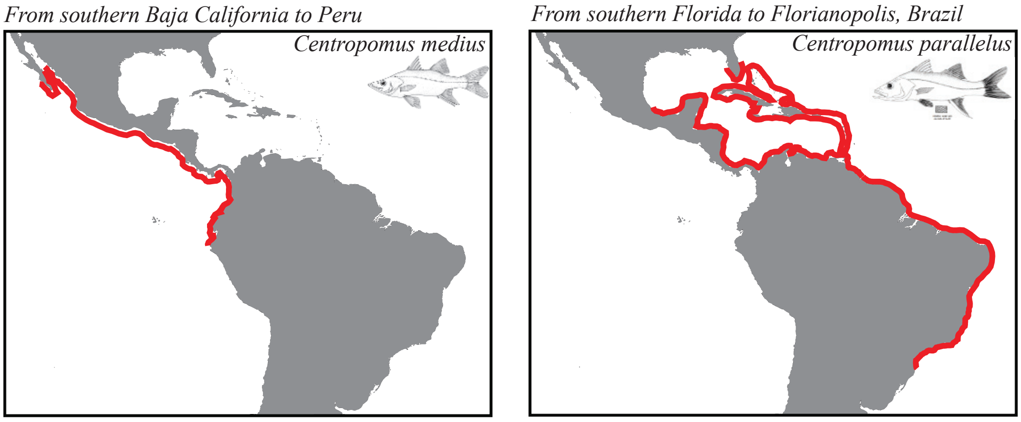
Figure 45. Distribution of two of three members of the genus *Anableps* in the Western Atlantic (right) and Eastern Pacific (left). A third species, *A. microlepis*, with the same distributional range as *A. anableps* occurs in the Western Atlantic.

8.4. The Effect of local environmental conditions (rainfall and seascape configuration) and freshwater fish biogeography

However, the phylogenetic signal and possible niche conservatism has not occurred in all groups. The configuration of landscape can have an overwhelming influence in the structure of mangrove fish communities in the Neotropics. This is the case for species of the family Lutjanidae. In the Tropical Eastern Pacific, specifically at the study site in Pacific Colombia (Bahía Málaga), mangroves occur in relatively close proximity to hard bottoms (see *Chapter II*). The landscape configuration in this area facilitates ontogenetic movements of the yellowtail snapper (*Lutjanus argentiventris*), which therefore constitutes a dominant species in this specific mangrove setting. In other areas in the Colombian Pacific (e.g. Sanquianga National park near the border with Ecuador) where hard bottoms do not occur in proximity to mangroves, Lutjanidae occurs in much lower abundances than those observed in Bahía Málaga (G. Castellanos-Galindo, unpublished data). Similarly, in the study site of the Brazilian province (Caeté estuary), hard bottoms are rare and so was the presence of Lutjanidae in mangroves. In adjacent systems to the Caeté, the presence of *Lutjanus jocu* in mangroves has been recorded, due to a more diverse adjacent landscape containing subtidal rocks and bedrock (Giarrizzo & Krumme 2007). This fish species has similar ecological requirements as *L. argentiventris* in the Tropical Eastern Pacific. Moura et al. (2011) documented in an estuarine-reef complex system in Brazil (Abrolhos Shelf) ontogenetic habitat shifts in *L. jocu* similar to those shown in *L. argentiventris* in the Gulf of California in Mexico (Aburto-Oropeza et al. 2009). *Lutjanus jocu* belongs to a complex of species within Lutjanidae in the Western Atlantic that includes *L. griseus*, *L. apodus* and *L. alexandrei* (Gold et al. 2012). *Lutjanus apodus* and *L. argentiventris* have been suggested to be geminate species (Lessios 2008), however, the former species does not occur in the Brazilian province (Moura & Lindeman 2007). Given the ecological similarities between *L. jocu* and *L. argentiventris*, it would be relevant to examine the phylogenetic relationships of these two species in the future.

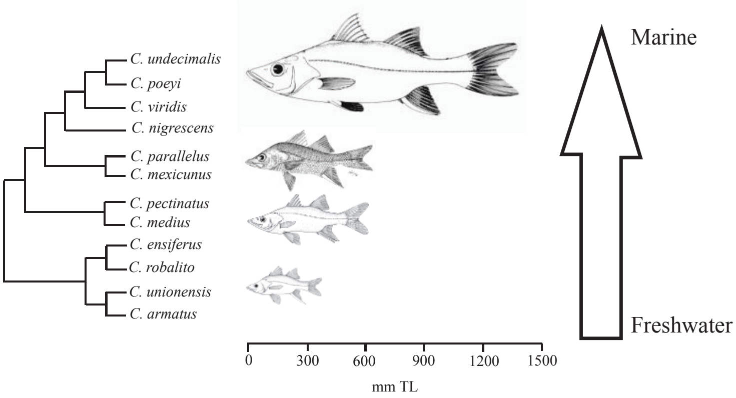
A particular difference between the systems examined was the importance (in terms of abundance and catch mass) that Centropomidae have in Bahía Málaga and in the whole Tropical Eastern Pacific (see *Chapters II and IV*) compared to the scarcity of this family in mangrove areas of the Caeté estuary (*Chapter V and VI*) and most areas of the Brazilian province (Vilar et al. 2013). According to Tringali et al. (1999), Centropomidae underwent ecological diversification ca. 10 Ma ago (mid- to late Miocene). The most basal lineage (*C. ensiferus* group, Figure 46), which includes the smallest species of the family, thrives in low salinity and freshwater environments during all life stages. Members of the intermediate sized species (*C. pectinatus* and *C. parallelus* groups) are known to live in estuarine areas, but do not occur in fully marine environments. Finally, the species of Centropomidae attaining the largest sizes (*C. undecimalis* group) are commonly recorded in fully marine conditions with little or no freshwater influence (Tringali et al. 1999; see Figure 46). Under this scenario, the high abundance of *C. armatus* and *C. medius* in estuarine areas of the Tropical Eastern Pacific could be explained by a considerable higher precipitation regime in parts of this region (i.e the Panama Bight) compared to the Brazilian province of the Western Atlantic. Estuaries in the Panama Bight present salinities generally below 30 and can dramatically drop to almost freshwater conditions during ENSO years (La Niña, see *Chapter II*, Valiela et al. 2012). In turn, the Caeté estuary presents high seasonal variability in salinity reaching values of 35 within the estuary during the dry season (see *Chapter VI*), and values of 10 during rainy seasons. The stability in low salinity conditions in estuaries of the Panama Bight in the Tropical Eastern Pacific may promote the establishment of these species of Centropomidae that require freshwater and estuarine conditions during their whole life cycle. In the Caeté system, only species from the Centropomidae groups that are associated to marine and estuarine conditions were recorded. These species where always recorded in the high salinity sampling sites (Furo da Stiva). Likewise, a further explanation for the absence of the most freshwater-tolerant Centropomid in the Western Atlantic (i.e. *C. ensiferus*), could be the lack of ecological opportunity to colonize freshwater or low salinity areas in estuaries of this region. This is likely due to an already established and diverse freshwater fish fauna in the Amazonia have occupied niches in the upper reaches of estuaries, preventing the colonization of these spaces by *C. ensiferus*. In contrast, upper reaches of estuaries in the Tropical Eastern Pacific lack a diverse freshwater fish fauna and therefore have allowed species from the basal lineages of Centropomidae (i.e. *C. armatus*, *C. robalito*) to thrive in this region and exploit this available niche. Similar hypotheses related to the colonization of freshwater environments by marine catfishes (Ariidae) and their rate of diversification depending on the previous presence of diverse freshwater faunas have been recently tested (see Betancur et al. 2012). The indication that radiations of Ariidae in freshwater environments have been facilitated by the lack of competitors in geographical areas where the freshwater fish diversity is low, may also apply in the case of Centropomidae (competitively inferior to well-established freshwater fish fauna) and their inability to colonize low salinity and freshwater areas in the Western Atlantic.

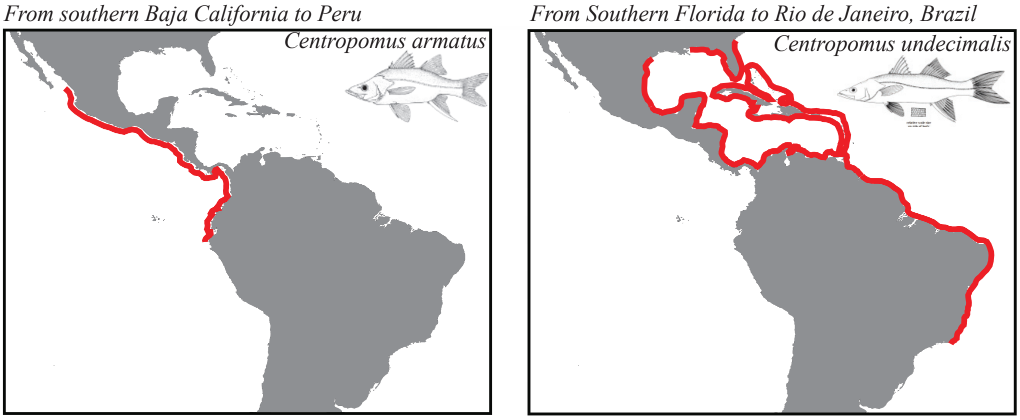
A further effect of the biogeography of freshwater fish fauna in the Neotropics is the presence of a biodiverse Siluriform (catfishes) fauna in Amazonia and a depauperated one in the Pacific lowlands in Colombia. This may explain the dominance of the Neotropical family Auchenipteridae in upper reaches of the Caeté system and a total lack of freshwater catfishes (including Auchenipteridae) in upper estuaries in the Colombian Pacific locality (Bahía Málaga). The cocosoda catfish, *Pseudauchenipterus nodosus*, distributed from southern Trinidad to Brazil (Bahia) is an extremely abundant detritivorous species in low salinity upper reaches of the Caeté estuary (see *Chapter VII*). During the rainy season, as salinity decreases in the estuary, this species becomes especially abundant, to the extent that in overall it was the most abundant species during the sampling campaign in 2011-2012 in mangrove creeks of the Caeté system. No species of freshwater origin was found to extend its range within Bahía Málaga as salinity decreased.



From southern Baja California to Peru

From southern Florida to Florianopolis, Brazil





From southern Baja California to Peru

From Southern Florida to Rio de Janeiro, Brazil

Figure 46. Distribution of the species of the family Centropomidae captured in intertidal mangrove creeks in the Caeté estuary, north Brazil and Bahía Málaga, Pacific Colombia. The phylogenetic tree in the middle indicates the relationship between the twelve species of Centropomidae present in America and the habitat preferences of adults (indicated with the arrow, adapted from Tringali et al. 1999).

8.5. Conclusions and outlook

The results presented here provide an overview of the possible environmental and biogeographical mechanisms that affect the structure of estuarine mangrove fish communities in macrotidal areas of the Neotropics. The consideration of these mechanisms has substantial implications with applications ranging from methodological aspects of future ecological studies on mangrove fishes (see *Chapter VI*) to the management and conservation of mangrove-associated fisheries resources. Additionally, the study of relatively undisturbed systems in the Colombian Pacific and North Brazil provides baseline references to compare with systems within regions where mangrove systems face acute threats or have been already severely affected by anthropogenic actions (e.g. loss of 28-40% mangrove areas in Ecuador in the Eastern Pacific; Hamilton & Stankwitz 2012).

Searching for generality of assembly rules for mangrove fish communities is not an easy task. Examples where ecologists extrapolate patterns found in one ecosystem to the same ecosystem, but in an area with a different setting, are common. Such extrapolations in mangrove ecosystems may proof misleading when conservation and management actions need to be taken (Ewel et al. 1998). Sheaves (2012) suggested recently that the question of ecosystem equivalence should move forward to ask “which limits should be placed on extrapolation from one example of an ecosystem type to other?”. The present thesis provides hints on this discussion by indicating that intertidal mangrove fishes in (neotropical) macrotidal regions respond to tidal and diel dynamics in a predictable way. The search for generality in the role of salinity as a force structuring estuarine mangrove fish assemblages seems more complicated. As it was shown, the biogeographical history of freshwater fish faunas in the regions analyzed played an important role in predicting how salinity influenced the distribution and structure of estuarine fish assemblages. Therefore, further regional comparisons should not overlook this biogeographical component when investigating salinity related patterns and in estuarine mangrove fishes. This approach has been previously useful in analyzing estuarine fish faunas in West African estuaries (Baran 2000).

A promising field of research constitutes the evaluation of how preserved are certain traits of mangrove fish assemblages in the phylogenies of closely related species. Examples in the recent literature document that species retain traits over long evolutionary periods of time (slow evolutionary change; Wiens et al. 2010). However, tests of phylogenetic signal and niche conservatism in related clades need to be carefully designed, since phylogenetic signal and niche conservatism may not be ubiquitous (Losos 2008). The present composition of the most important taxa of intertidal mangrove fishes in North Brazil and the Colombian Pacific could be explained by these phenomena (patterns). However, well-resolved phylogenies using molecular tools and detailed knowledge of the ecological niches occupied by mangrove fish species is needed. Ultimately, identifying group of species that show niche conservatism in their preference for intertidal mangrove habitats may help to identify these species, as the most vulnerable to mangrove degradation. These species may have low flexibility and/or potential to adapt to rapid deterioration of habitats and therefore greater risk to become extinct (Wiens et al. 2010).

Having understood that tidal and diel movements into intertidal areas are important part of the home range of coastal fishes in different habitats, the challenge now lies in identifying how these movements can also help to connect other (intertidal) habitat patches in a seascape nursery area (Nagelkerken et al. *in press*). The seascape nursery concept incorporates not only specific habitats where fish production or aggregation is high, but also migration corridors (such as subtidal mangrove channels) that are critical to the nursery value of a seascape. Fish tidal migrations occur not only to intertidal areas but can connect shelter and feeding habitats through these corridors. Such seascape nursery concept should go beyond the traditionally mangrove-seagrass-coral reef seascape paradigm often described in microtidal areas and incorporate other seascapes that are present in estuarine habitats of many meso- and macrotidal regions (e.g. mangrove-mudflat-sandy bottom continuum) like the ones studied in the present thesis. Only by acknowledging the great variability present in seascape nurseries, real advances in the conservation and management of coastal ecosystems can be made.

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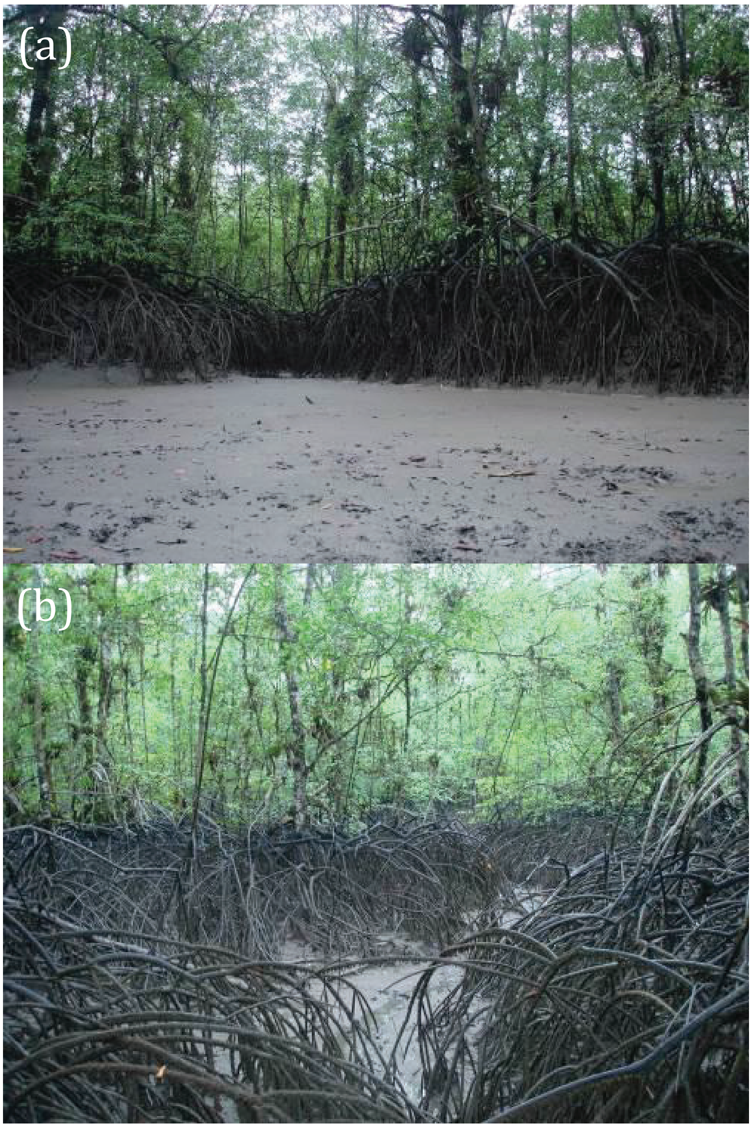
ANNEX

Annex I. Supplements for Chapter II

Supplemental Figure A1. (a) Mouth of intertidal mangrove creek M1 at low water in Bahía Málaga, Colombian Pacific (for location of M1 see Figure 7); (b) inner part of creek at low water (height of above-ground stilt root system: 5-6 m). Note the low level of elevation of the mangrove floor compared to the mudflat. Also note the high density of Bromeliacea indicating megahumid conditions.



Supplemental Table A1. Summary of intertidal fish sampling scheme in four mangrove creeks of the Estero Luisico, Bahía Málaga, Colombia, Tropical Eastern Pacific (December 2009-November 2010). N = number of block net samples.

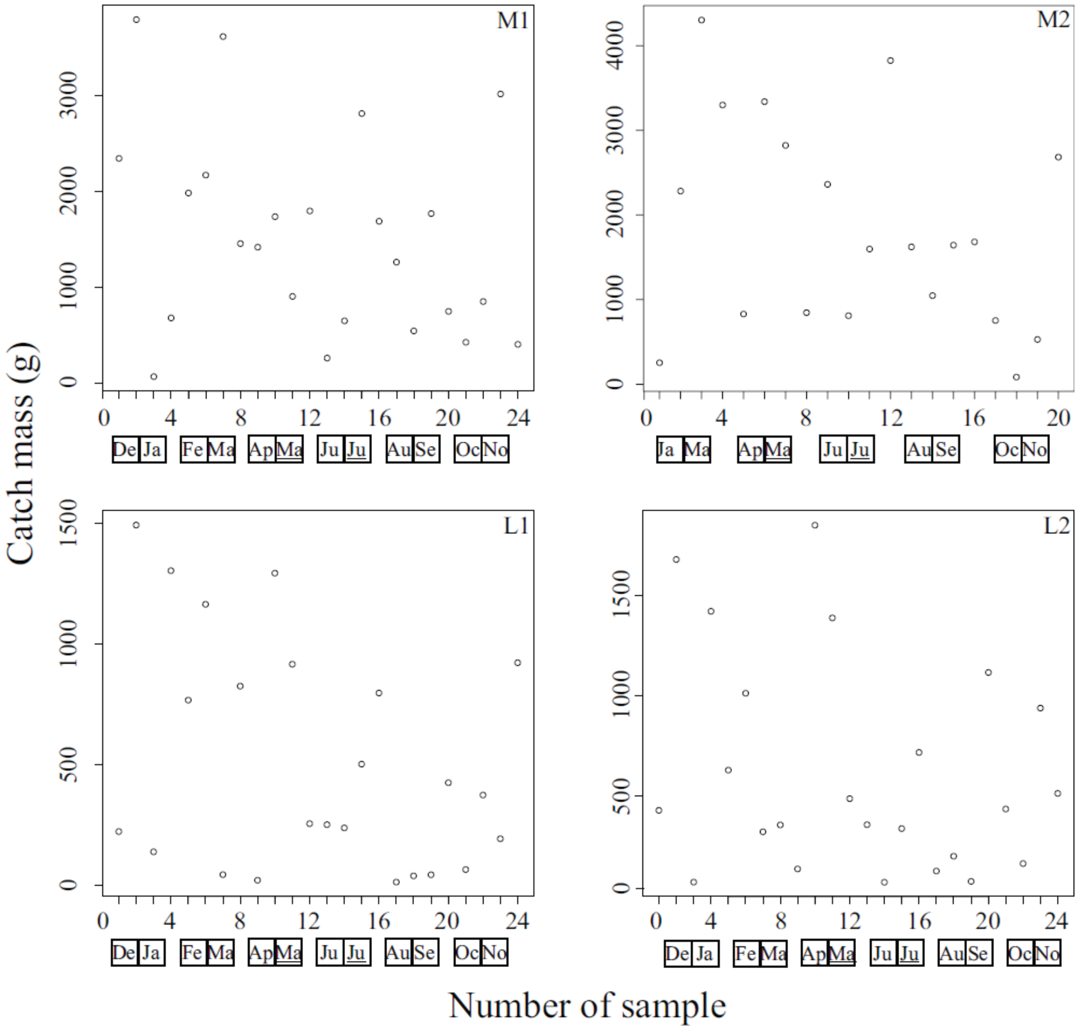
No	**Month**	**Date**	**Tidal magnitude**	**Mean tidal range (m)**	**N**
1	Dec^{vw}	18-20	Spring	3.31	6
2	Jan^{w}	24-25	Neap	2.36	8
3	Feb^{w}	28-2(Mar)	Spring	4.62	6
4	Mar^{w}	26-28	Neap	3.10	8
5	Apr^{w}	23-24	Neap	2.77	8
6	May^{vw}	25-27	Spring	3.51	8
7	Jun^{vw}	6-8	Neap	2.14	8
8	Jul^{vw}	13-15	Spring	4.38	8
9	Aug^{vw}	19-21	Neap	2.25	8
10	Sep^{vw}	25-27	Spring	3.49	8
11	Oct^{vw}	9-11	Spring	4.61	8
12	Nov^{vw}	28-29	Neap	3.13	8

^{vw} very wet season
^{w} wet season

Supplemental Table A2. Mean inundation area and volume of four intertidal creeks during spring and neap tides in Bahía Málaga, Colombia, Tropical Eastern Pacific.

Creek	**Spring tide**		**Neap tide**	
	X Area (m^2)	X Volume (m^3)	X Area (m^2)	X Volume (m^3)
M1	5573.6	3282.4	3344.2	1969.4
M2	9392.8	5481.1	5635.7	3288.7
L1	5139.7	4123.7	3083.8	2474.2
L2	4874.5	3647.6	2924.7	2188.6

Supplemental Figure A2. Correlation plots of catch masses for consecutive block net samplings at four creeks in Bahía Málaga, Colombia, Tropical Eastern Pacific. De: December, Ja: January, Fe: February, Ma: March, Ap: April, Ma: May, Ju: June, Ju: July, Au: August, Se: September, Oc: October, No: November. Kendall (τ) correlations in all cases were not significant (creek M1: T=104, p=0.09679, τ = -0.2463, creek M2: T= 75, p= 0.2086, τ = -0.2105, creek L1: T= 110, p= 0.1743, τ = -0.2028 ; creek L2: T= 120, p= 0.3893, τ = -0.1204).



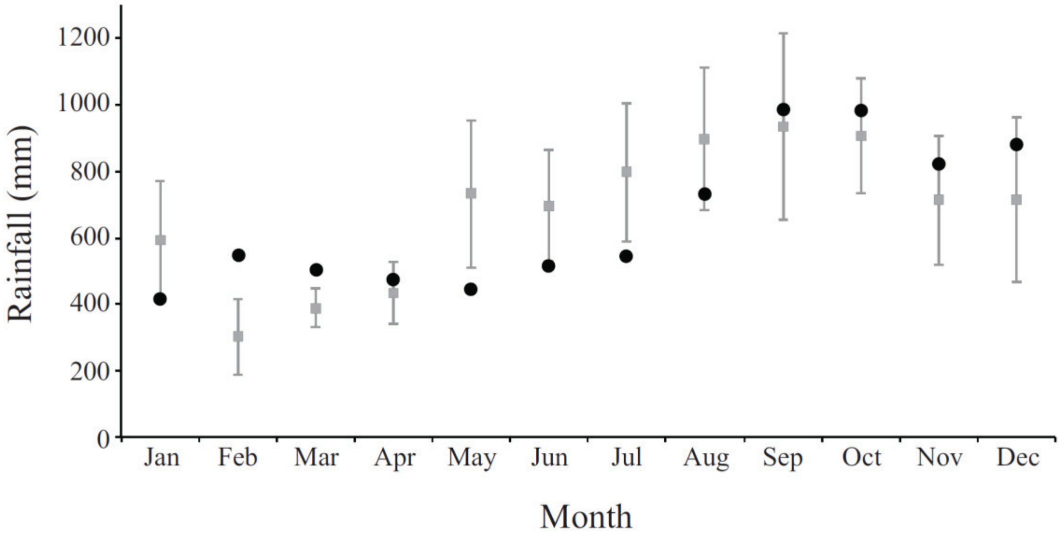
Supplemental Table A3. Common names for fish species collected in mangrove creeks of Bahía Málaga. Sorted in decreasing abundance.

Scientific name	**Common name**
Lile stolifera (Clupeidae)	Pacific piquitinga
Centropomus armatus (Centropomidae)	Armed snook
Lutjanus argentiventris (Lutjanidae)	Yellow snapper
Diapterus peruvianus (Gerreidae)	Peruvian mojarra
Ariopsis seemanni (Ariidae)	Tete sea catfish
Sphoeroides rosenblatti (Tetraodontidae)	Oval puffer
Centropomus medius (Centropomidae)	Blackfin snook
Poeciliopsis turrubarensis (Poecilidae)	Barred livebearer
Caranx caninus (Carangidae)	Pacific crevalle jack
Oligoplites altus (Carangidae)	Longjaw leatherjacket
Caranx sexfasciatus (Carangidae)	Bigeye trevally
Gobiomorus maculatus (Eleotridae)	Pacific sleeper
Lutjanus jordani (Lutjanidae)	Jordan's snapper
Strongylura scapularis (Belonidae)	Shoulderspot needlefish
Lutjanus guttatus (Lutjanidae)	Spotted rose snapper
Bathygobius andrei (Gobiidae)	Estuarine frillfin
Citharichthys gilberti (Paralichthyidae)	Bigmouth sanddab
Atherinella serrivomer (Atherinopsidae)	Bright silverside
Brycon meeki (Characidae)	-
Opisthonema medirastre (Clupeidae)	Middling thread herring
Daector dowi (Batrachoididae)	Dow's toadfish
Bairdiella ensifera (Sciaenidae)	Swordspine croaker
Eucinostomus currani (Gerreidae)	Pacific flagfin mojarra
Mugil cephalus (Mugilidae)	Flathead grey mullet
Pomadasys macracanthus (Haemulidae)	Longspine grunt
Lutjanus colorado (Lutjanidae)	Colorado snapper
Centropomus unionensis (Centropomidae)	Union snook
Chloroscombrus orqueta (Carangidae)	Pacific bumper
Halichoeres aestuaricola (Labridae)	Mangrove wrasse
Lutjanus novemfasciatus (Lutjanidae)	Pacific dog snapper
Rypticus nigripinnis (Serranidae)	Blackfin soapfish
Cathorops steindachneri (Ariidae)	Steindachner's sea catfish
Eleotris picta (Eleotridae)	Spotted sleeper
Hyporhamphus snyderi (Hemiramphidae)	Skipper halfbeak
Eugerres brevimanus (Gerreidae)	Short fin mojarra
Selene brevoortii (Carangidae)	Hairfin lookdown
Achirus mazatlanus (Achiridae)	Mazatlan sole
Epinephelus quinquefasciatus (Serranidae)	Pacific goliath grouper

Supplementary Table A3. (continued)

Scientific name	**Common name**
Synodus scituliceps (Synodontidae)	Shorthead lizardfish
Cynoscion phoxocephalus (Sciaenidae)	Cachema weakfish
Lophogobius sp. (Gobiidae)	Crested-goby
Ophidion fulvum (Ophidiidae)	Earspot cusk eel
Anchoa exigua (Engraulidae)	Slender anchovy
Anchoa sp. (Engraulidae)	
Anchoa spinifer (Engraulidae)	Spicule anchovy
Batrachoides pacifici (Batrachoididae)	Pacific toadfish
Ctenogobius sagittula (Gobiidae)	Longtail goby
Guavina micropus (Eleotridae)	Pacific Guavina
Lutjanus aratus (Lutjanidae)	Mullet snapper
Pisodonophis daspilotus (Ophichthidae)	Marble-toothed snake-eel

Supplemental Figure A3. Mean (±SD) monthly rainfall in Bahía Málaga for the period 2002-2009 (grey squares) and monthly rainfall during 2010 (black circles). Data from IDEAM station Malaguita (No. 5407003).



Annex II. Supplements for Chapter V

Supplemental Table A4. List of studies used to construct Figure 28 in the main article.

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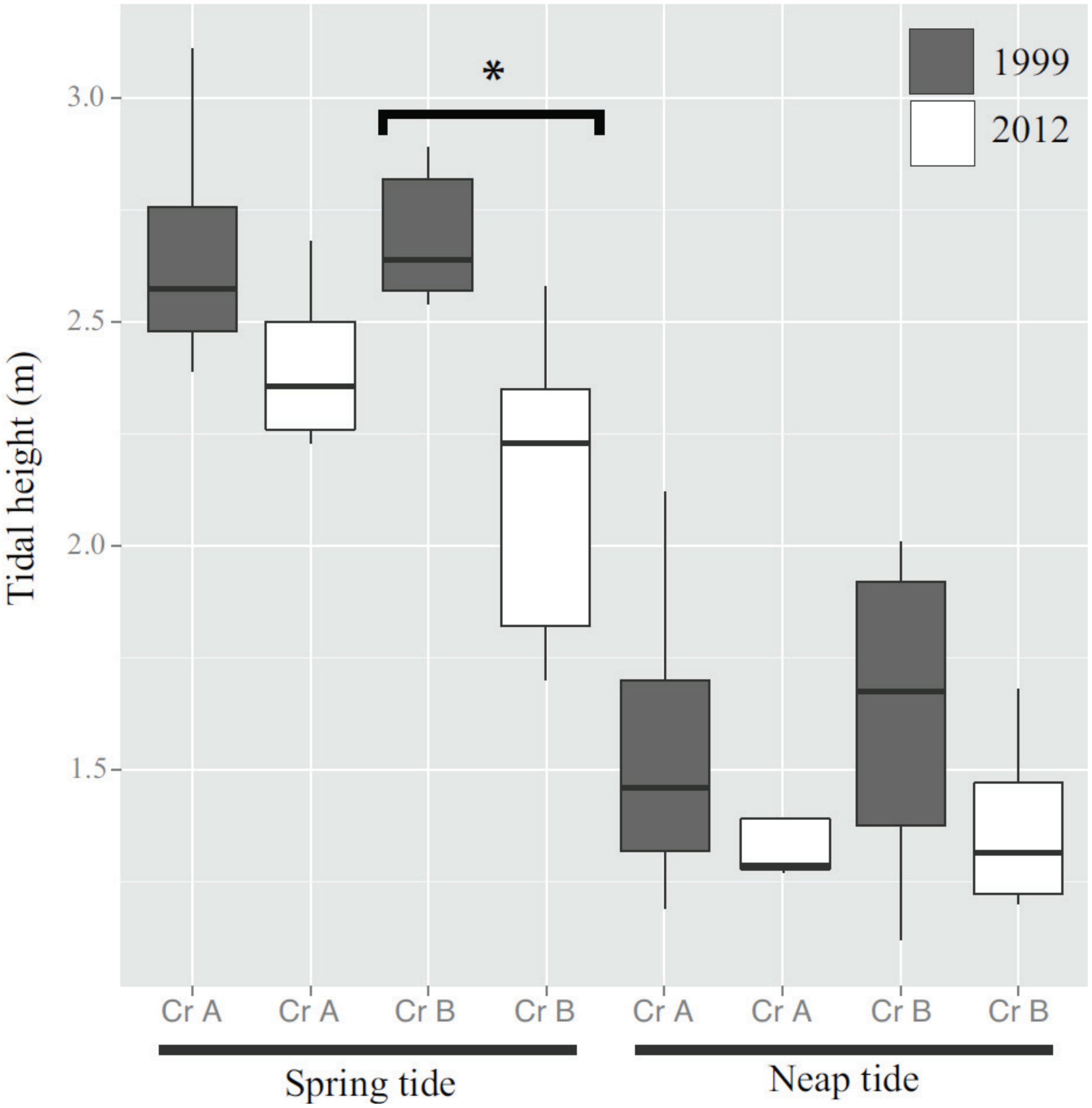
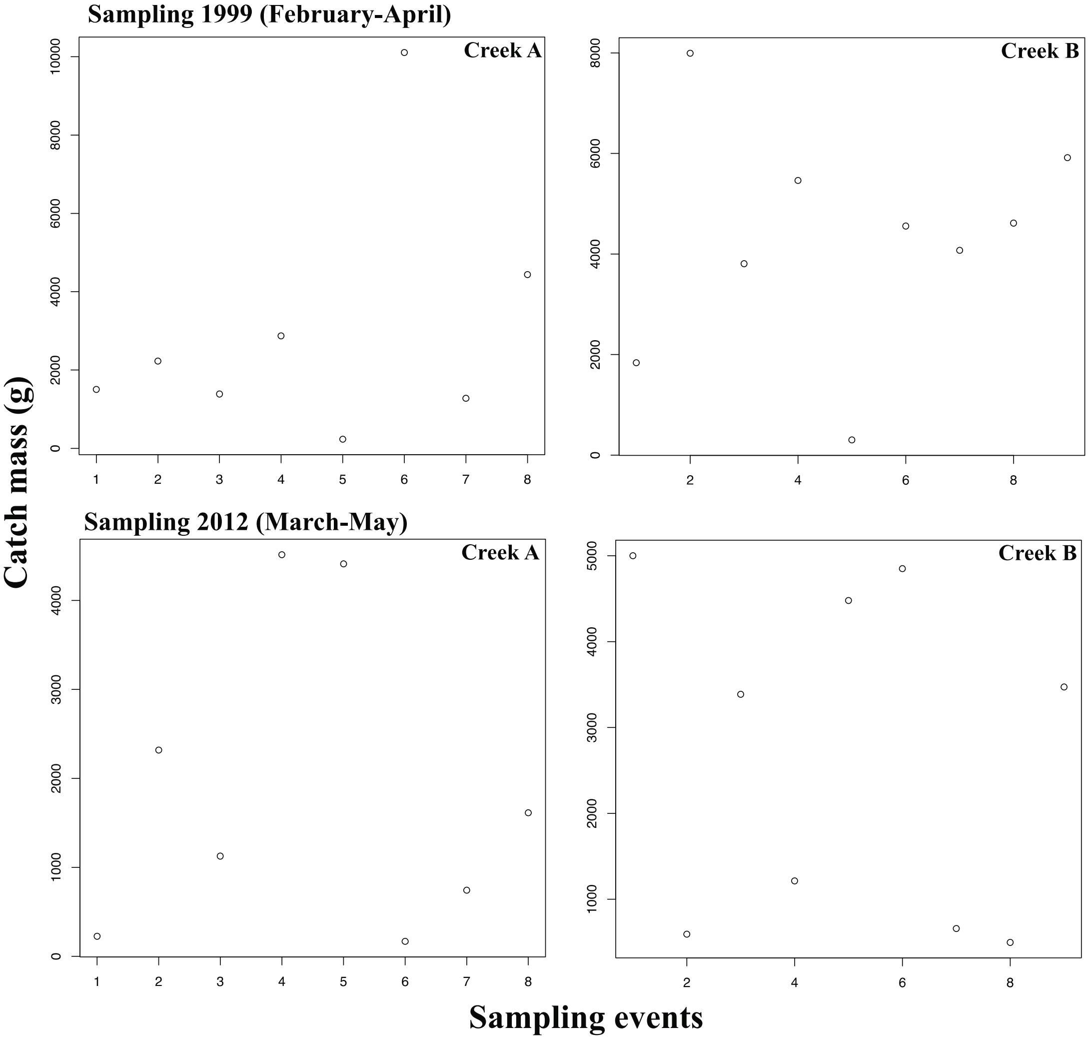
Annex III. Supplements for Chapter VI

Supplemental Figure A4. Entrances of intertidal mangrove creeks A and B sampled in 1999 and 2012 during the rainy season in the Bragança Peninsula, North Brazil. View during low tide from upstream towards the mouth of the creeks.

Supplemental Figure A5. Boxplots showing tidal heights in creeks A and B at spring and neap tides in 1999 and 2012. Bold lines: medians, boxes: 25th and 75th percentiles, whiskers: minimum and maximum value. Significant differences between tidal heights of 1999 and 2012 were only found in creek B at spring tides (in asterisk in graph; t=-3.113, p=0.024).

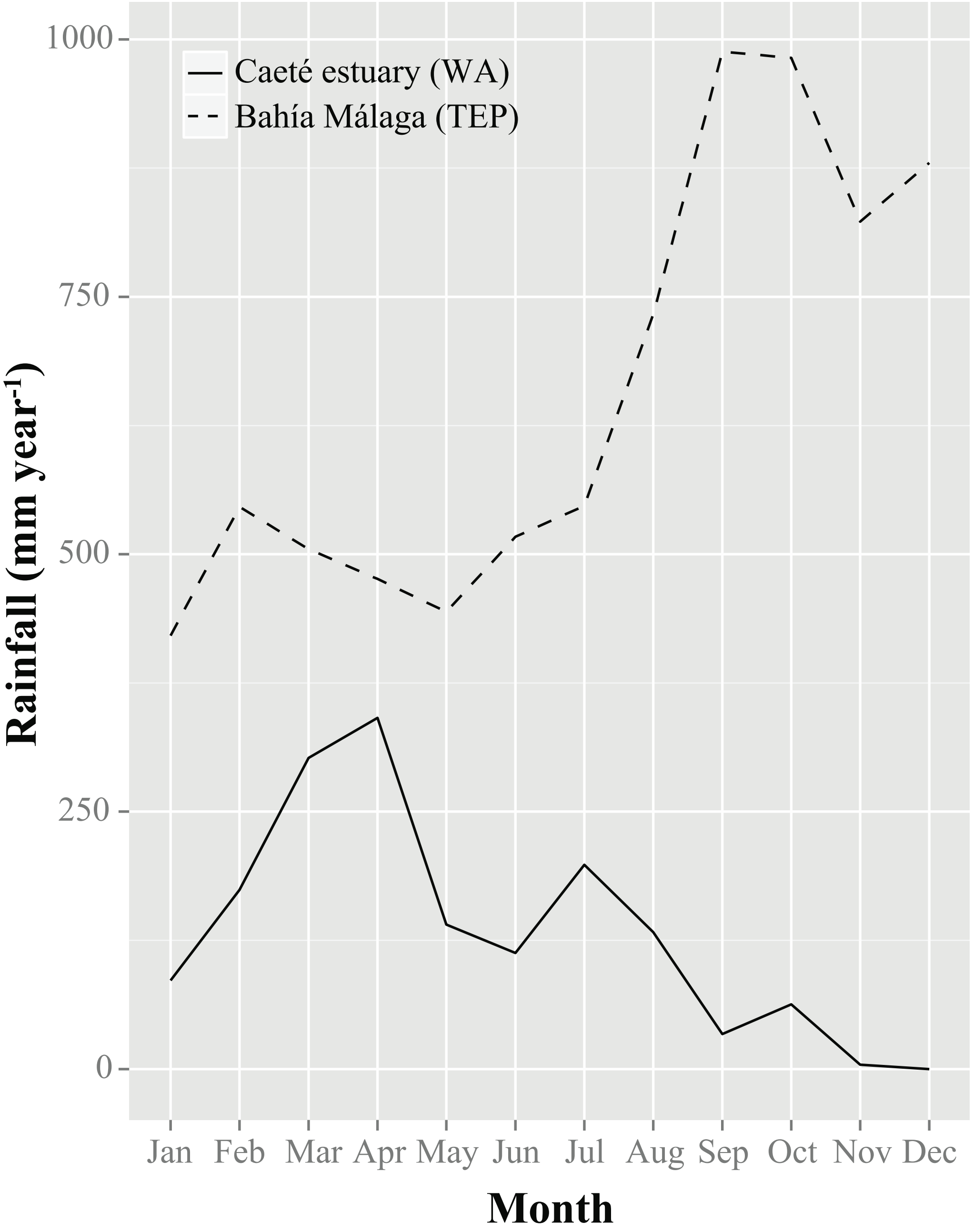


Supplemental Figure A6. Correlation plots of catch masses for consecutive block net samplings (in chronological order) at two second-order creeks in Furo do Meio, Caeté Estuary, North Brazil during 1999 and 2012. Kendall (τ) correlations in all cases were not significant [(1999) creek A: T = 16, p = 0.7195, τ = 0.1428, Creek B: T = 22 , p = 0.4767, τ = 0.2222; (2012) creek A: T = 14, p = 1, τ = 0; creek B: T = 15, p = 0.6122, τ = -0.1667].



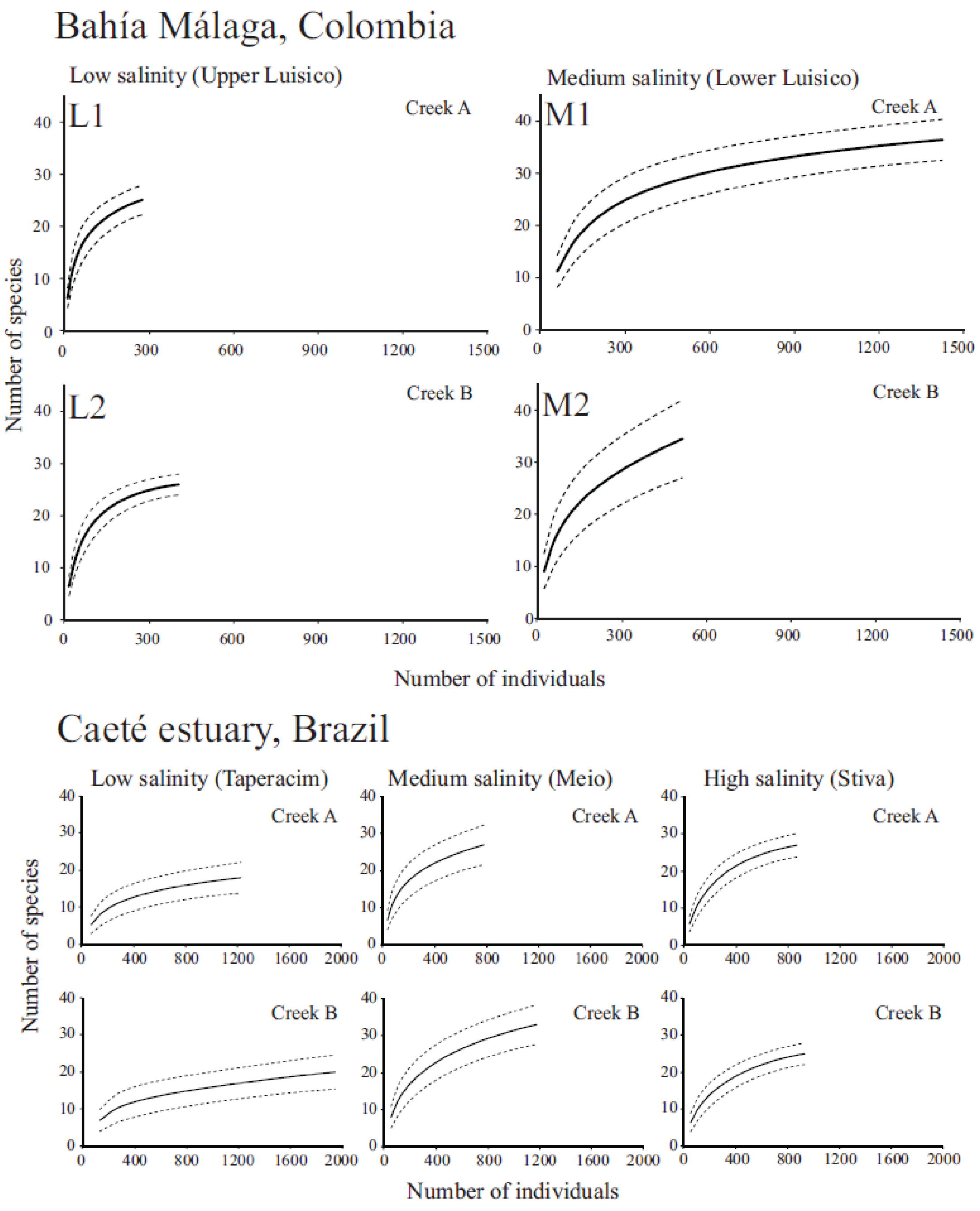
Annex IV. Supplements for Chapter VII

Supplemental Figure A7. Monthly precipitation recorded during sampling periods in the estuarine systems of Bahía Málaga (2009-2010; Colombia) and Caeté (2011-2012; North Brazil). Rainfall data obtain from nearest stations in Malaguita and Tracuateua (IDEAM and INMET Meterological Centers).



Supplemental Figure A8. Salinity measurements at high tide in each of the sampling sites at the Caeté estuary-Brazil (Brazilian province of the Western Atlantic, left side) and Bahía Málaga-Colombia (Panamic province of the Tropical eastern Pacific). Samplings took place from December 2009-November 2010 in Colombia and from October 2011-August 2012 in Brazil.

Supplemental Figure A9. Individual-based rarefaction curves of mangrove creek fish collected along salinity gradientes in localities of the Panamic province of the Eastern Pacific (Bahía Málaga) and the Brazilian province of the Western Atlantic (Caeté estuary). Dashed lines indicate 95% confidence intervals.



Supplemental Table A5. List of fish species (sorted in alphabetical order by fish families) captured during 11-12 month sampling campaigns in intertidal mangrove systems of Bahía Málaga (Colombia, Panamic province of the Eastern Pacific) and the Caeté estuary (Brazil, Brazilian province of the Western Atlantic).

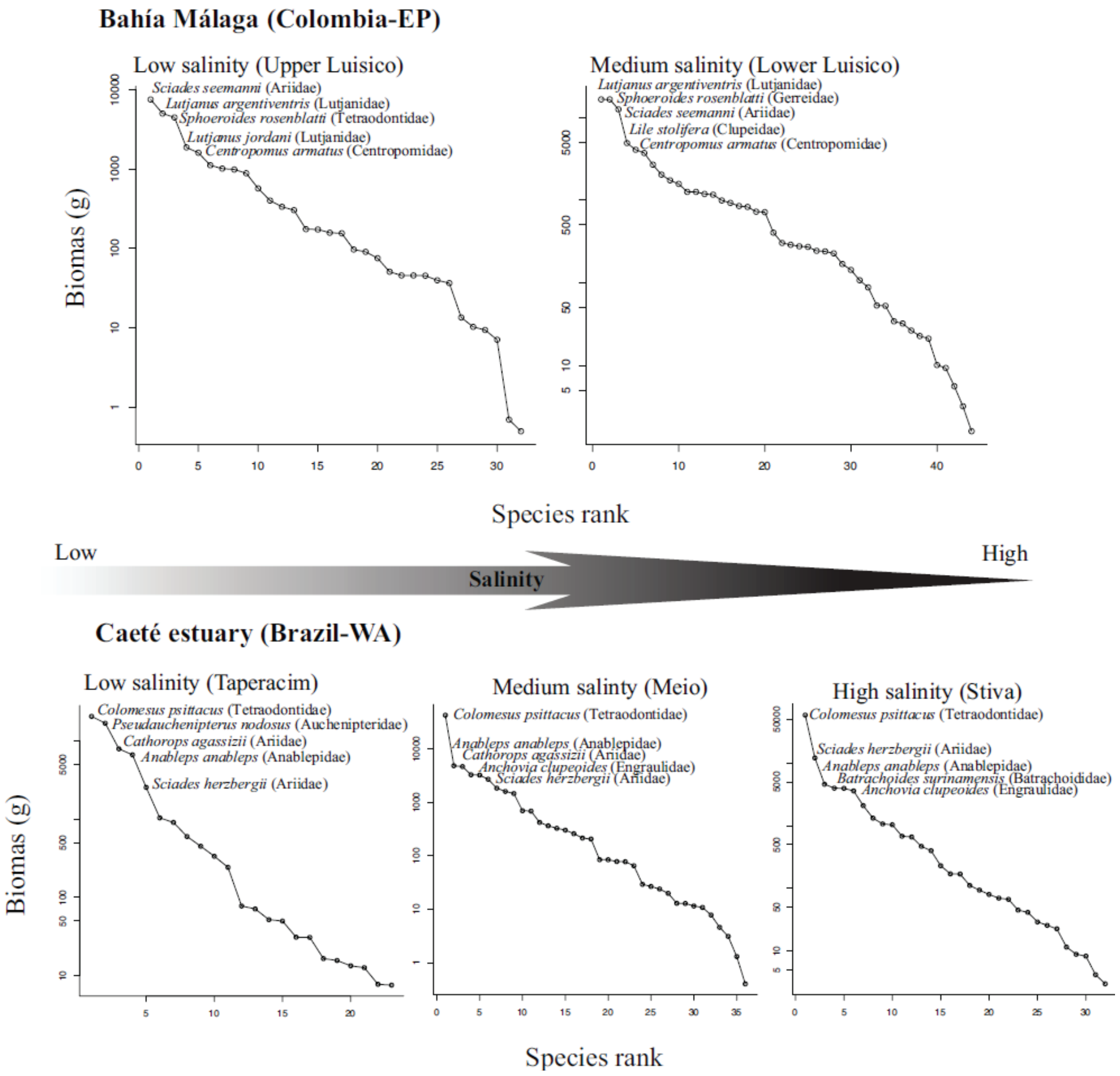
Bahía Málaga, Colombian Pacific				Caéte estuary, North Brazil			
Species	TropL	% Abund.	% Catch mass	Species	TropL	% Abund.	% Catch mass
Achiridae				**Achiridae**			
1. *Achirus mazatlanus*	3.2	0.10	0.009	1. *Achirus lineatus*	3.7	0.03	0.002
Anablepidae (not recorded)				**Anablepidae**			
	-	-	-	2. *Anableps anableps*	3.3	7.56	7.15
Ariidae				**Ariidae**			
2. *Cathorops steindachneri*	4.5	0.17	0.26	3. *Cathorops agassizii*	4.4	7.79	7.20
3. *Sciades seemanni*	3.6	4.78	18.89	4. *Sciades herzbergii*	3.3	6.60	7.96
Atherinopsidae				**Atherinopsidae** (not recorded)			
4. *Atherinella serrivomer*	2.7	1.40	0.23		-	-	-
Auchenipteridae (not recorded)				**Auchenipteridae**			
	-	-	-	5. *Pseudauchenipterus nodosus*	2.0	27.29	9.12
Batrachoididae				**Batrachoididae**			
5. *Batrachoides pacifici*	3.6	0.03	0.38	6. *Batrachoides surinamensis*	3.7	0.16	2.99
6. *Daector dowi*	3.5	0.97	0.19				
Belonidae				**Belonidae**			
7. *Strongylura scapularis*	4.2	1.70	2.05	7. *Strongylura timucu*	4.5	0.01	0.03
Carangidae				**Carangidae**			
8. *Caranx caninus*	3.9	1.84	1.19	8. *Chloroscombrus chrysurus*	3.2	0.04	0.001
9. *Caranx sexfasciatus*	4.5	1.77	1.63	9. *Oligoplites saurus*	4.5	0.32	0.06
10. *Chloroscombrus orqueta*	2.5	0.30	0.16	10. *Seleve vomer*	4.3	0.07	0.01
11. *Oligoplites altus*	4.1	1.80	0.94				
12. *Selene brevoorti*	3.8	0.13	0.05				
Centropomidae				**Centropomidae**			
13. *Centropomus armatus*	3.9	11.89	5.34	11. *Centropomus parallelus*	4.2	0.22	0.18
14. *Centropomus medius*	4.0	2.97	2.96	12. *Centropomus undecimalis*	4.4	0.18	0.09
15. *Centropomus unionensis*	4.0	0.33	0.12				
Characidae				**Characidae**			
16. *Brycon meeki*	2.6	1.14	0.99	13. Characidae sp1	2.8	0.03	0.003

Bahía Málaga, Colombian Pacific				Caéte estuary, North Brazil			
Species	TropL	% Abund.	% Catch mass	Species	TropL	% Abund.	% Catch mass
Clupeidae				**Clupeidae**			
17. *Lile stolifera*	3.5	33.91	5.45	14. *Rhinosardinia amazonica*	3.4	0.63	0.13
18. *Opisthonema medirastre*	3.3	1.00	1.48				
Echeneidae (not recorded)				**Echeneidae**			
	-	-	-	15. Echeneis naucrates	3.4	0.01	0.003
Eleotridae				**Eleotridae**			
19. *Eleotris picta*	3.9	0.17	0.04	16. *Eleotris pisonis*	3.7	0.09	0.08
20. *Gobiomorus maculatus*	3.5	1.70	0.55	17. *Guavina guavina*	4.2	0.01	0.005
21. *Guavina micropus*	3.5	0.03	0.02				
Engraulidae				**Engraulidae**			
22. *Anchoa exigua*	3.3	0.033	< 0.001	18. *Anchovia clupeoides*	3.4	10.47	3.23
23. *Anchoa spinifer*	4.1	0.033	0.002	19. *Cetengraulis edentulus*	2.1	0.68	0.22
24. *Anchoa* sp.	3.7	0.033	0.005	20. *Lycengraulis grossidens*	3.6	0.42	0.11
				21. *Pterengraulis atherinoides*	3.9	1.68	0.52
Ephippidae (not recorded)				**Ephippidae**			
	-	-	-	22. *Chaetodipterus faber*	4.5	0.25	0.09
Gerreidae				**Gerreidae**			
25. *Diapterus peruvianus*	3.4	6.88	1.28	23. *Diapterus auratus*	2.4	0.42	0.22
26. *Eucinostomus currani*	3.2	0.74	0.31				
27. *Eugerres brevimanus*	3.3	0.13	0.02				
Gobiidae				**Gobiidae**			
28. *Ctenogobius sagitula*	3.7	0.03	< 0.001	24. *Gobionellus oceanicus*	3.5	0.03	0.01
29. *Bathygobius andrei*	3.4	1.57	0.72				
30. *Lophogobius* sp.	3.2	0.07	0.006				
Haemulidae				**Haemulidae**			
31. *Pomadasys macracanthus*	3.5	0.67	3.65	25. *Genyatremus cavifrons*	3.5	0.25	0.19
Hemiramphidae				**Hemiramphidae** (not recorded)			
32. *Hyporhamphus snyderi*	3.0	0.17	0.07		-	-	-
Heptapteridae (not recorded)				**Heptapteridae**			
	-	-	-	26. *Rhamdia quelen*	3.2	0.03	0.03
Labridae				**Labridae** (not recorded)			
33. *Halichoeres aestuaricola*	3.5	0.23	0.28		-	-	-

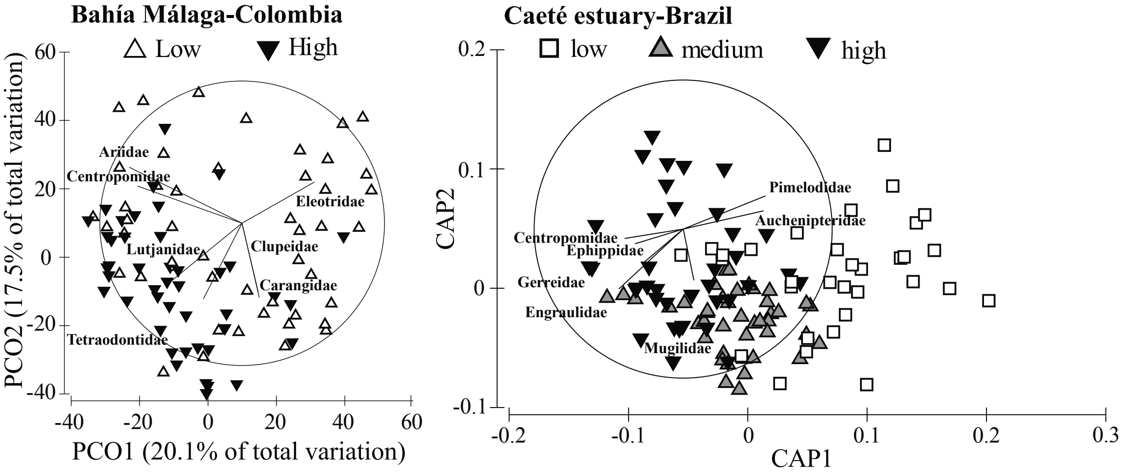
Bahía Málaga, Colombian Pacific				Caéte estuary, North Brazil			
Species	TropL	% Abund.	% Catch mass	Species	TropL	% Abund.	% Catch mass
Lutjanidae				**Lutjanidae** (not recorded)			
34. *Lutjanus aratus*	4.1	0.03	0.23		-	-	-
35. *Lutjanus argentiventris*	4.0	7.92	20.19				
36. *Lutjanus colorado*	3.4	0.40	1.19				
37. *Lutjanus guttatus*	3.9	1.60	0.80				
38. *Lutjanus jordani*	4.5	1.70	4.28				
39. *Lutjanus novemfasciatus*	4.1	0.20	0.97				
Megalopidae (not recorded)				**Megalopidae**			
				27. *Megalops atlanticus*	4.5	0.10	0.59
Mugilidae				**Mugilidae**			
40. *Mugil cephalus*	2.1	0.74	1.31	28. *Mugil curema*	2.0	1.21	1.38
				29. *Mugil hospes*	2.3	2.17	1.53
				30. *Mugil incilis*	2.0	0.48	0.60
				31. *Mugil* sp.	2.3	0.13	0.05
Ophichthidae				**Ophichthidae** (not recorded)			
41. *Pisodonophis daspilotus*		0.03	0.08		-	-	-
Ophidiidae				**Ophidiidae** (not recorded)			
42. *Ophidion fulvum*	3.4	0.07	0.03		-	-	-
Paralichthydae				**Paralichthydae** (not recorded)			
43. *Citharichthys gilberti*		1.50	0.36		-	-	-
Pimelodidae (not recorded)				**Pimelodidae**			
				32. *Brachyplatystoma vaillantii*	4.5	2.27	0.46
Poeciliidae				**Poeciliidae**			
44. *Poeciliopsis turrubarensis*		2.07	0.08	33. Poeciliidae sp1		0.13	0.01
Pristigasteridae (not recorded)				**Pristigasteridae**			
				34. *Pellona harroweri*	4.2	0.06	0.005
Sciaenidae				**Sciaenidae**			
45. *Bairdiella ensifera*	3.7	0.87	0.25	35. *Cynocion acoupa*	4.1	0.84	0.81
46. *Cynoscion phoxocephalus*	4.7	0.07	0.009	36. *Cynoscion leiarchus*	4.1	0.03	0.01
				37. *Cynoscion microlepidotus*	4.1	0.07	0.03
				38. *Cynoscion virescens*	4.0	0.01	0.01

Bahía Málaga, Colombian Pacific				Caéte estuary, North Brazil			
Species	TropL	% Abund.	% Catch mass	Species	TropL	% Abund.	% Catch mass
				39. *Isopisthus parvipinnis*	3.6	0.01	0.003
				40. *Macrodon ancylodon*	3.9	0.04	0.03
				41. *Micropogonias furnieri*	3.3	0.35	0.14
				42. *Stellifer microps*	3.3	0.04	0.01
				43. *Stellifer naso*	3.4	1.17	0.33
				44. *Stellifer rastrifer*	3.5	0.07	0.03
Serranidae				**Serranidae**			
47. *Epinephelus quinquefasciatus*	4.1	0.10	1.18	45. *Epinephelus itajara*	4.1	0.01	0.04
48. *Rypticus nigripinnis*	3.9	0.20	0.26				
Stromateidae (not recorded)				**Stromateidae**			
				46. *Peprilus paru*		0.01	< 0.001
Synodontidae				**Synodontidae** (not recorded)			
49. *Synodus scituliceps*	4.2	0.10	0.05				
Tetraodontidae				**Tetraodontidae**			
50. *Sphoeroides rosenblatti*	3.2	3.64	19.53	47. *Colomesus psittacus*	3.6	25.44	54.25
				48. *Sphoeroides testudineus*	3.2	0.10	0.03

Supplemental Figure A10. Rank-abundance (number of individuals) plot ($\log_{10}$ transformed) for mangrove fish assemblages collected along salinity gradients in macrotidal areas of the Eastern Wacific (Bahía Málaga) and the Western Atlantic. Note the different scales in y-axis en each of the plots.



Supplemental Figure A11 Principal coordinates analysis (left) ordination and constrained canonical analysis of principal coordinates (CAP) of neotropical fish families found in intertidal mangroves at specific different salinity zones in the Panamic province of the Tropical Eastern Pacific (left plot) and in the Brazilian province of the Western Atlantic (right plot). Vectors represent fish families with correlations with the canonical axes > 0.4 (Spearman correlations).



Supplemental Figure A12. Entrance of intertidal mangrove creeks sampled in macrotidal areas of the Eastern Pacific and Western Atlantic biogeographical regions. (A) Mangrove creek in Bahía Málaga at low tide and (B) Mangrove creek in the Caeté estuary at low tide. Arrows indicate the different characteristics of mangrove topography with (A) having low accumulation of sediment around mangrove roots (erosional environment) and (B) showing high acummulation of sediment (accritional environment) and a more defined mangrove plateau (white line).