Community structure and patterns of diversity in reef fish communities in the Tropical Western Atlantic and Tropical Eastern Pacific

Dissertation zur Erlangung des Doktorgrades

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Angefertigt am

Zentrum fϋr Marine Tropenökologie

Innerhalb de Fachbereichs 2

Der Universität Bremen

2006

Zentrum für Marine Tropenökologie

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Abstract

The Isthmus of Panama (IOP) is located in Central America and is the narrowest and lowest part of the land bridge that links North and South America. The two regions came together to separate the tropical seas between 1.8 to 3.5 million years bp. The results have been faunal isolation, extinction and extensive turnover in reef fish assemblages.

This thesis identifies factors that can explain differences in taxonomical structure, abundance, functional characteristics and relations with habitat observed among reef fish communities at local and regional scales on both sides of IOP. It describes the taxonomic composition and parameters of diversity of reef fishes, correlating coral coverage, substrate complexity and substrate diversity with fish diversity parameters and abundance. A determination of predominant trophic and mobility groups, their size classes is included, as well as a consideration of oceanographic-physical parameters (e.g. currents, temperature, salinity) and their influence on reef fish assemblages. Habitat preferences in some geminate species were determined in order to understand the principal effects of the closure of IOP on ecological adaptations displayed by a recently divided reef fish assemblage.

The thesis consists of an introduction, four publications and a synopsis. The first publication compares the community-structure of reef-fish over different spatial scales, levels of exposure, and physical complexity in 12 study zones at Bocas del Toro, in the Tropical Western Atlantic (TWA). 288 visual censuses were conducted on 48 benthic transects from April to September 2002. A total of 128 fish species of 38 families were found with increasing species richness from sheltered to exposed and from low-complexity to intermediate and high-complexity zones. Gobies and pomacentrids were most abundant in sheltered areas; labrids were most abundant in exposed zones. Species-richness and diversity were high in exposed zones and in massive-coral reefs and significantly correlate with certain types of complex substrates. Highly mobile fish were more abundant in exposed rocky zones while sedentary fish were more abundant in sheltered massive and foliaceous corals zones. The number of mobile invertebrate-feeding fish species greatly increased along a gradient of increasing exposure, while territorial herbivores were more common in sheltered zones. Demersal zooplankton feeders were common in sheltered areas and oceanic planktivores in exposed areas. Omnivores were more abundant in zones of rubble and sand. Carnivores were less frequent, but accounted for the largest number of species. General species richness and diversity increased with habitat complexity. This increase was more pronounced in exposed zones.

A second publication compares the community structure of reef fish in Bahía Honda, Gulf of Chiriquí, Tropical Eastern Pacific (TEP), based on the results of survey carried out from February to July 2003. 126 fish species of 44 families were found. Plankton feeding pomacentrids and labrids, along with haemulids that feed on mobile invertebrates, were the most abundant families present. Highly mobile and site-attached genera were abundant in most shallow, wave-exposed zones particularly on exposed rocky substrates. Planktivores were the most abundant group, followed by carnivores, mobile invertebrate feeders and piscivores. Herbivores and sessile invertebrate feeders were less abundance. The number of species in all trophic groups increased in exposed complex zones. Carnivores accounted for the largest number of species. Species richness found in the study zone exceeded that of any other studied region close to the mainland in the TEP and correlated with substrate diversity, increasing size-heterogeneity of holes and structural complexity.

A third publication compared the reef-fish communities on both sides of IOP. The numbers of families and species do not differ markedly but species richness/sampling area was found to be higher in the TEP. These results suggest that the species diversity of reef fishes derives from recruitment success related to local oceanographic conditions and the connectivity and diversity of habitats, rather than coral cover-diversity. Herbivores predominate in the TWA; planktivores and piscivores in the TEP. Most reef fish reach larger sizes in TEP. In both zones, the number of species is highest in exposed rocky zones with highly complexand diverse substrates. Massive coral reefs are the second most diverse habitat in both cases. Individuals are smaller on low-complexity substrates in the TWA and in coral branches and holes in the TEP, which provide refuge areas from predation and strong water movements. Better swimmers are typical of exposed zones in TWA and have a wide spatial distribution in TEP. Geminate species show strong habitat plasticity on both sides of the of the IOP, but keep similar habitat preferences in terms of morphology and depth regardless of the taxonomy of present-day, unrelated benthic fauna and flora.

A fourth publication dealt with trophic strategies and spatial use habits of fishes in the Atlantic. It reported the results of research undertaken to determine if the diversity and abundance of fishes that use low-caloric food resources are higher in the tropics. The results supported the hypothesis of differential use of food resources among tropical and higher latitude reef fish. The density of herbivorous fishes in the western Atlantic decreases from tropical to temperate latitudes. Spatial use and mobility vary with latitude and consequently reef type and complexity.

The conclusion is that both sides of IOP have been characterized by a history of decline and loss of species and present conditions in both oceans are the result of these changes. Reef fishes defy simple definition, since coral reefs may have acquired lineages of existing non-reef fauna, acting as sanctuary for the maintenance of diversity without having played a specific role on the origin of this diversity; or they may have provided the physical environment where fish lineages arose, playing a critical role in the both origin and maintenance of extant reef fish taxa. The plasticity of reef fish is demonstrated by their recent shift from corals to rocky reef environments in TEP, but still on highly diverse benthic substrates, following the rise of the geographical barrier. Fish assemblages are relatively resilient in the face of change, as shown by the similarities in familial composition and relative species richness at global scale. The distribution of fish trophic groups may be related to latitudinal gradients; however, similar patterns may also be found at a local scale, within areas of the same latitude in TEP, where temperature gradients occur at the site of coastal upwellings. Temperature can also affect growth parameters, fish size generally increasing in relatively colder regions, such as TEP. More data are necessary to understand the extent to which ecosystem function is shaped by species richness and regional history, and to determine at what point declining species richness begins to compromise ecosystem function. Key questions in this regard is whether ecosystem function is wholly or largely dependent on biogeographical location, or whether peripheral regions on both sides of IOP are more vulnerable to human and natural impacts than others which lie closer to high-diversity areas.

Goals for management of resources as reef fish are far reaching: in many cases, the need for site-specific conservation measures is overlooked because over-generalized methods are used to determine ecosystem health. Examples of this are the use of coral cover instead of substrate diversity and complexity to determine reef health and the use of members of the family Chaetodontidae, which are characterized by extreme habitat plasticity, as indicators of coral presence and ecosystem health. Another problem is the lack of attention paid to the oceanography and geography of the regions being studied. Reef fish assemblages may follow assembly rules, but these assembly rules may not apply directly to functional groups, which can be strongly variable depending on variations on temperature and currents that are related also to atmospherics changes. An extensive database is urgently required to determine future impacts of global warming on the trophic structure and growth patterns in fish communities worldwide

Zusammenfassung

Der Isthmus von Panama (IOP) liegt in Zentralamerika und stellt den engsten und am tiefsten gelegenen Teil der Landbrücke dar, die Nord- und Südamerika miteinander verbindet. Als diese zwei Kontinente vor ungefähr 1,8 bis 3,5 Millionen Jahren zusammentrafen, trennten sie das tropische Meer. Das Resultat war die Isolierung der Faunen, Artensterben und eine ausgeprägte biologische Erneuerung der Gemeinschaften von Rifffischen.

Diese Arbeit identifiziert Faktoren, die Unterschiede in der taxonomischen Struktur, in der Abundanz und in den funktionalen Charakteristika bedingen, die zwischen Rifffischgemeinschaften auf lokaler und regionaler Ebene beiderseits des IOP beobachtet werden können, und versucht die Beziehung zwischen Habitaten zu erklären. Dabei werden die taxonomische Zusammensetzung der Rifffischgemeinschaft und Diversitätsparameter beschrieben, sowie Korallenbewuchs, Substratkomplexität und –diversität mit Parametern der Fischdiversität und –abundanz korreliert. Ebenso beinhaltet diese Arbeit die Definition vorherrschender, trophischer Gruppen und von Fischgruppen gemeinsamer Mobilitätscharakteristika. Die Größenklassen dieser funktionalen Gruppen werden bestimmt, ebenso wie physikalisch-ozeanographische Parameter (z. B. Strömung, Temperatur und Salinität) und der Einfluss dieser Parameter auf die Rifffischgemeinschaften. Um die prinzipiellen Effekte der Schließung des IOP auf ökologische Anpassungen, die von kürzlich getrennten Rifffischgemeinschaften aufgezeigt werden, verstehen zu können, wurden die Habitatpräferenzen einiger Geschwisterarten bestimmt.

Die erste Veröffentlichung dieser dissertation vergleicht die Gemeinschaftsstruktur von Rifffischen über verschiedene, räumliche Skalen, Expositionslevel, und physikalische Komplexität in 12 Untersuchungsgebieten in Bocas del Toro, im tropischen Westatlantik (TWA). 288 visuelle zahluegen wurden über 48 benthischen Transekten von April bis September 2002 durchgeführt. Insgesamt wurden 128 Fischarten aus 38 Familien ermittet; der Artenreichtum stieg dabei von geschützten zu exponierten Standorten an, sowie von Zonen niedriger Komplexität über solche von intermediärer Komplexität zu solchen von hoher Komplexität. Grundeln und Riffbarsche waren in geschützten Gebieten am häufigsten, während Lippfische in exponierten Zonen häufiger waren. Artenzahl und –diversität sind hoch in exponierten Zonen und in Riffen, die von Korallen mit massiver Wuchsform gebildet werden. Beide Parameter korrelieren signifikant mit bestimmten Typen von komplexen Substraten. Äußerst mobile Fischarten waren häufiger in exponierten Felszonen, während Fischarten, die nahe am Substrat leben, in geschützten Zonen mit massiven und verzweigt wachsenden Korallen vermehrt auftraten. Hin zu den am stärksten exponierten Gebieten, stieg die Anzahl der mobilen Fischarten, die sich von Invertebraten ernähren, stark an; im

Gegensatz dazu nahm die Zahl territorialer, herbivorer Arten in geschützten Zonen zu. Demersale Zooplanktonfresser waren in geschützten Gebieten häufiger und ozeanische, planktivore Arten in exponierten Gebieten. Omnivore Arten waren häufiger in Zonen mit Sand, feinem Geröll und Korallenbruchstücken. Karnivore Fische waren weniger häufig anzutreffen, trugen aber erheblich zur Gesamtanzahl der Arten bei. Grundsätzlich war zu beobachten, dass die Artenanzahl und -diversität mit der Habitatkomplexität anstieg. Dieser Anstieg war deutlicher in den exponierten Zonen.

Eine zweite Veröffentlichung vergleicht die Gemeinschaftsstruktur von Rifffischen in Bahía Honda, im Golf von Chiriquí, im tropischen Ostpazifik (TEP), von Februar bis Juli 2003. 126 Fischarten aus 44 Familien wurden hier identifiziert. Plankton fressende Riffbarsche und Lippfische sowie Süßlippen, die sich von mobilen Invertebraten ernähren, waren am häufigsten. Hoch mobile aber auch ortsgebundene Gattungen waren in den meisten Zonen häufig, die flachen Wellen ausgesetzt sind, besonders aber über exponierten Felssubstraten. Nach trophischen Charakteristika geordnet waren planktivore Arten am zahlenreichsten, gefolgt von karnivoren Fischarten, mobilen Invertebratenfressern und Piscivoren. Herbivore Arten und sessile Invertebratenfresser traten seltener auf. Die Artenanzahl aller trophischen Gruppen stieg in exponierten, komplexen Zonen an. Karnivore stellen die höchste Artenzahl. Der Artenreichtum übersteigt alle anderen Regionen, die bisher nahe der amerikanischen Küste des TEP untersucht worden sind, und korreliert mit Substratdiversität, ansteigender Größenheterogenität von Löchern und Höhlen und struktureller Komplexität.

Die Rifffischgemeinschaften auf beiden Seiten des IOP wurden in einer dritten Veröffentlichung miteinander verglichen, wobei sich die Anzahl von Familien und Arten nicht besonders stark zwischen den Regionen unterscheidet, der Artenreichtum pro Untersuchungsgebiet im TEP jedoch höher ist. Diese Ergebnisse lassen darauf schließen, dass Rifffische stärker vom Rekrutierungserfolg in Bezug zu lokalen, ozeanographischen Gegebenheiten und von der Kontinuität und Diversität von Habitaten abhängen als von der Diversität des Korallenbestandes. Herbivore Arten herrschen im TWA vor; Planktivore und Piscivore Arten im TEP. Im TEP erreichen die meisten Rifffische größere Körpermaße. In beiden Regionen nimmt die Anzahl von Arten zu den exponierten, felsigen Zonen des Riffs mit hoher Komplexität und Substratdiversität hin zu. Diese werden in ihrer Artenzahl gefolgt von Riffen mit massiven Korallenblöcken. Individuen sind kleiner in Substraten niedriger Komplexität im TWA; im TEP dagegen in Untersuchungsgebieten mit vielen Korallenverzweigungen und –löchern, die vermutlich als Rückzugsgebiete vor Fraßdruck und starker Wasserbewegung dienen können. Gute Schwimmer sind typisch für exponierte Zonen im TWA, haben aber eine breite räumliche Verteilung im TEP.

Geschwisterarten zeigen eine starke Habitatplastizität auf beiden Seiten des IOP, behalten jedoch unabhängig von Taxonomie und Verwandtschaft der gegebenen benthischen Fauna und Flora ähnliche Habitatpräferenzen in Bezug auf Morphologie und Tiefe bei.

In einer vierten Veröffentlichung wurden Nahrungserwerbsstrategien und Raumnutzungsgewohnheiten von Rifffischen im Atlantik untersucht. Dabei sollte herausgefunden werden, ob die Diversität und die Individuenzahl von Fischen, die Nahrungsressourcen mit niedrigem kalorischen Wert nutzen, in den tropischen Gebieten des Atlantiks höher sind. Die Ergebnisse stützen die Hypothese einer differenziellen Nutzung von Nahrungsressourcen zwischen tropischen Riffischen und Rifffischen aus höheren Breiten. Die Dichte herbivorer Fische vermindert sich vom tropischen Westatlantik zu den gemäßigten Breiten hin. Raumnutzung und Mobilität verändert sich mit den Breitengraden und der dazugehörigen Veränderung bezüglich des Rifftyps und der Riffkomplexität.

Die allgemeine Schlussfolgerung ist, dass beide Seiten des IOP durch einen Rückgang der Vielfalt und durch Artenverlust gekennzeichnet sind, und dass die gegenwärtigen Bedingungen in beiden Ozeanen ein Resultat dieser Veränderungen sind. Der Begriff „Rifffische" entzieht sich einer einfachen Definition, da Korallenriffe oftmals zum Lebensraum für Fischgruppen geworden sind, die nicht ursprünglich in Riffen beheimatet waren. In diesem Fall können Riffe dann als Schutzgebiet für die Erhaltung der entstandenen Artendiversität fungieren, ohne bei der Entstehung dieser Diversität eine spezifische Rolle gespielt zu haben. Im Gegensatz dazu haben Korallenriffe viel zur Evolution anderer Abstammungslinien beigetragen, indem sie die physikalischen Bedingungen gestellt haben, unter denen diese Fischarten entstehen konnten. In diesem Fall haben Riffe die entscheidende Rolle sowohl für den Ursprung als auch für die Erhaltung der gegenwärtigen Rifffischtaxa gespielt. Die Plastizität von Rifffischen wird durch den kürzlich erfolgten Wechsel von Korallenhabitaten zu Felsriff-dominierten Lebensräumen im TEP belegt. Aber auch hier, nach der Anhebung der geographischen Barriere, bewohnen sie hoch diverse benthische Substrate. Angesichts von Veränderungen zeigen sich Fischgemeinschaften als relativ resilient, was auch durch die Ähnlichkeiten in der Zusammensetzung von Fischfamilien und den relativen Artenreichtum im globalen Vergleich belegt wird. Die Verbreitung von trophischen Gruppen innerhalb der Rifffische mag generell in Verbindung mit latitudinalen Gradienten stehen. Eine Ähnlichkeit zu Verbreitungsmustern in temperierten Regionen kann aber auf lokaler Ebene auch innerhalb von Gebieten derselben geographischen Breite im TEP bestehen, wenn diese durch Kaltwasserauftrieb im Küstenbereich beeinflusst sind. Parameter wie Temperatur können hier Wachstumsparameter beeinflussen und auch dazu führen, dass die Körpergröße von Fischen im

Allgemeinen in kälteren Regionen wie dem TEP zunimmt. Um zu verstehen, in welchem Ausmaß die Funktionen eines Ökosystems durch Artenreichtum und regionale Historie eines Gebiets gestaltet werden, und von welchem Punkt an ein Niedergang des Artenreichtums dazu führt, ob und in welchem Ausmaß Ökosystemfunktionen gefährdet sind, werden weitere Daten benötigt. Dies hängt insbesondere von der biogeographischen Lage des betreffenden Ökosystems ab. Gleiches gilt, wenn festgestellt werden soll, ob periphere Regionen beiderseits des IOP verletzlicher auf humane und natürliche Einflüsse reagieren als solche, die näher an Gebieten mit hoher Artendiversität liegen.

Die Ziele des Managements von Riffressourcen wie Fisch reichen weit: In vielen Fällen wird der gebietsspezifische Bedarf an Konservationsmaßnahmen nicht erkannt, da stark generalisierte Methoden angewandt werden um die Gesundheit des Ökosystems zu ermitteln. Beispiele dafür sind die Nutzung von Korallenbedeckung anstelle von Diversität und Komplexität, sowie die Nutzung der Familie der Chaetodontidae als Indikatorarten für Korallenpräsenz, die durch extreme Habitatplastizität charakterisiert ist. Ein weiteres Problem ist die mangelnde Beachtung der Ozeanographie und Geographie der untersuchten Regionen. Rifffische können Gruppierungsregeln folgen, welche nicht unbedingt auch für funktionelle Gruppen gelten müssen. Da funktionelle Gruppen stark variieren können und von Temperatur- und Strömungsschwankungen abhängen, welche ihrerseits mit atmosphärischen Änderungen zusammenhängen. Daher wird dringend eine umfassende Datenbank benötig, um zukünftige Einflüsse der globalen Erwärmung auf die trophische Struktur und die Wachstumsmuster von Fischgesellschaften weltweit erfassen zu können.

Resumen

Panamá (Istmo de Panamá, IDP) está ubicado en América Central y es la sección mas delgada y de más bajo relieve que une a ambas Américas y emergió hace unos 1.8 a 3.5 millones de años.

El resultado de las aguas tropicales que bordean el continente Americano es el aislamiento e intercambio de la fauna, la cual estuvo sometida a extinciones masivas en sus estructuras arrecifales. La estructura biogeográfica de los peces de arrecife, su hábitat y las interacciones energéticas que existen actualmente en los mismos, son el resultado de una larga y compleja historia geológica y oceanográfica.

Esta tesis identifica los factores que pueden explicar diferencias en la estructura taxonómica, abundancia, características funcionales y relación con los distintos tipos de hábitat en las comunidades de peces de arrecife a escala local y regional a ambos lados del IDP, describiendo la composición taxonómica, los parámetros de diversidad y abundancia correlacionando dichas variables con la cobertura de coral, complejidad y diversidad del substrato.

Se mencionan además ciertos patrones de organización funcional (grupos tróficos, clases de tamaño, grupos de movilidad) en conjunto con un análisis de la influencia de los parámetros físicos y oceanográficos (Ej. corrientes, temperatura, salinidad) sobre los peces. Se determinaron también las preferencias de hábitat en ciertas especies relacionadas filogenéticamente con el objetivo de entender los principales efectos del levantamiento del Istmo sobre la adaptación ecológica adquirida por la comunidad de peces recientemente dividida por esta barrera geográfica.

La primera publicación trata sobre la comparación de la estructura de la comunidad de los peces de arrecifes a diferentes escalas espaciales, niveles de exposición y complejidad en 12 zonas de estudio en Bocas del Toro, Atlántico Tropical Occidental (ATO, Mar Caribe). 288 conteos visuales fueron realizados en 48 transecto fijos al substrato durante los meses de abril a septiembre 2002. La cobertura del substrato y su complejidad también fue documentada. Se encontraron un total de 128 especies pertenecientes a 38 familias con un incremento en la riqueza de especies gradualmente de las zonas protegidas hacia las zonas expuestas al oleaje y de la misma manera de las zonas de baja, intermedia a alta complejidad.

Gobiidae y Pomacentridae fueron las familias más abundantes en las zonas protegidas y Labridae en las zonas expuestas. La riqueza de especies y diversidad se incrementa en las zonas expuestas y en arrecifes de coral masivo, correlacionándose significativamente con una serie de substratos complejos. Los peces con mayor movilidad fueron más abundantes en zonas rocosas expuestas mientras que los más sedentarios predominaban en zonas protegidas. En las zonas más expuestas,

se incrementa el número de peces que se alimentan de invertebrados móviles; en las zonas protegidas, aumenta el número de herbívoros territoriales. Los zooplanctívoros demersales fueron comunes en áreas protegidas mientras que los zooplanctívoros oceánicos eran más abundantes en áreas expuestas al oleaje. Los peces omnívoros fueron más abundantes en zonas arenosas mezcladas con coral muerto. Los peces carnívoros fueron poco comunes, pero contribuyeron al mayor número de especies de la región.

Se realizó una segunda publicación que compara la estructura de la comunidad de los peces de arrecife en Bahía Honda, Golfo de Chiriquí, Pacìfico Oriental Tropical (POT) durante los meses de febrero y Julio del 2003. 126 especies pertenecientes a 44 familias fueron encontradas. Pomacéntridos y lábridos fueron los más abundantes en esta región en conjunto con los haemúlidos. Los géneros con mayor capacidad de movilidad y peces asociados intensamente al substrato fueron más abundantes en la mayoría de las zonas expuestas y poco profundas, sobre todo en los arrecifes rocosos. Después de los peces que se alimentan de plankton oceánico y los carnívoros, los que se alimentan de invertebrados móviles y los piscívoros fueron los más representativos. Los peces herbívoros y los que se alimentan de invertebrados sésiles estuvieron poco representados. La riqueza de especies de esta región en el Pacifico Oriental excede todas las otras zonas conocidas, particularmente las cercanas a tierra firme. Dicha riqueza se correlaciona con la diversidad del substrato y se incrementa con la heterogeneidad y el tamaño de los orificios. Esta región es posiblemente un centro o refugio de especies de peces que evolucionaron previamente en los arrecifes de coral y posteriormente se adaptaron a hábitats rocosos.

La estructura de la comunidad de los peces de arrecifes de ambos lados del IDP fue comparada en una tercera publicación y se encontró que el número de familias y especies no fue muy distinto, sin embargo, el número de especies por área de muestreo fue mayor en el POT. Los peces de arrecife dependen del grado y éxito de reclutamiento larval, el cual està relacionado a las condiciones oceanográficas, conectividad y diversidad de hàbitats de determinada región en lugar de la cobertura y diversidad de coral vivo. Los herbívoros predominan en el ATO, mientras que los planctívoros predominan en el POT. La mayoría de los peces encontrados en este estudio comparativo alcanzan mayor tamaño en el POT. Como regla general, el número de especies se incrementa en zonas de arrecifes rocosos expuestos a corrientes y oleaje y con alta complejidad de substrato, así como también en arrecifes de coral masivo caracterizados por su complejidad y diversidad béntica. Dicho patrón se repite en ambas regiones. A micro escala, los individuos más pequeños son encontrados en substratos de baja complejidad en el ATO y en ramas de coral y orificios entre las rocas en el POT, áreas en las cuales es sugerido que los mismos pueden protegerse de la depredación y de las intensas corrientes típicas de dicha región. Los peces que tienen mayor capacidad de natación son habitantes de áreas expuestas en el ATO y tienen una distribución más homogénea en el POT. Las especies relacionadas filogenéticamente muestran una marcada plasticidad de selección de hábitat, sin embargo hay similaridad de preferencia en términos de morfología y profundidad independientemente del componente taxonómico de la fauna y flora béntica.

Una cuarta publicación incluye datos de todo el Atlántico. En ella las estrategias tróficas fueron investigadas para determinar si la diversidad y abundancia de los peces que utilizan alimentos de bajo contenido calórico es más alta en los trópicos. Los resultados obtenidos soportan la hipótesis de una utilización diferencial de los recursos alimenticios entre regiones tropicales y templadas. La densidad de herbívoros decrece gradualmente de las zonas tropicales a las templadas.

Podemos concluir que los arrecifes han actuado como santuario para el mantenimiento de la diversidad sin jugar un papel importante en el origen de dicha diversidad íctica. Los arrecifes aportaron un medio ambiente físico en donde los distintos linajes fueron creados, jugando sin embargo un papel importante tanto en el origen como en el mantenimiento de los distintos grupos taxonómicos en los peces arrecifales. La plasticidad de los mismos es demostrada por el reciente cambio de arrecifes de coral a arrecifes rocosos. Se puede decir que las comunidades de peces arrecifales son resistentes a cambios drásticos a largo plazo, prueba de ello es la gran similaridad en la composición de familias y riqueza de especies e ambas regiones del IDP. La distribución de los grupos tróficos podría estar relacionada a gradientes latitudinales; sin embargo, ciertos patrones encontrados en zonas templadas pueden darse a escala local en el POT, debido al marcado efecto del afloramiento costero típico de dicha región. Ciertos parámetros físicos como la temperatura pueden también influir sobre el crecimiento y probablemente en aguas más frías los peces alcanzan una mayor longitud.

Se necesitan más datos e investigaciones para entender hasta qué punto el funcionamiento del ecosistema es determinado por la riqueza de sus especies e historia regional, y si el decrecimiento de la riqueza de especies empieza a comprometer el funcionamiento de dicho ecosistema. Es necesario también determinar si estos resultados son completamente dependientes en la localización biogeográfica o si estas regiones periféricas son o han sido más vulnerables al impacto natural y humano en comparación con otras áreas de mayor diversidad.

Las metas para el manejo de recursos como los peces de arrecifes están lejos de ser alcanzadas: en muchos casos, la necesidad de medidas de conservación en regiones específicas son subestimadas con la utilización de métodos generalizados para la determinación de la salud de los ecosistemas, como ejemplo tenemos el uso de el porcentaje de cobertura de coral como indicador de buena salud en lugar de la diversidad y complejidad del substrato y utilización de peces de la familia Chaetodontidae, cuyos miembros se caracterizan por una extrema plasticidad de preferencia de hábitat, como indicadores de arrecifes saludables y presencia de corales. Otro problema es la falta de atención a la oceanografía y geografía de determinados sitios de estudio. Las estructuras de los peces arrecifales pueden seguir reglas de organización, pero dichas reglas no se aplican necesariamente a los grupos funcionales, los cuales pueden variar marcadamente dependiendo de la temperatura y patrones de corrientes marinas. Dichos factores están relacionados a cambios atmosféricos. Es necesaria la recopilación de una base de datos urgente para determinar futuros impactos del calentamiento global sobre la estructura trófica y patrones de crecimiento en las comunidades de peces a nivel mundial

1 Introduction

1.1 *General taxonomic structure*

The diversity of coral reef fish communities has always been considered to be higher than that of other marine habitats (Emery 1978). However the factors responsible for the community organization of coral reef fishes are not well understood. Data is sparse and there are many contradictory points of view. One of the factors thought to be related to reef fish diversity is coral diversity: It has been argued that the high coral diverse Indo-Pacific region contains the highest diversity of coral reef fishes; and there is a general concordance between geographic gradients of species richness among fishes, corals and other coral reef biota, all of which indicate latitudinal and longitudinal declines in diversity away from an Indo-Philippine "center" (Erlich 1975; Goldman & Talbot 1976; Springer 1982; Myers 1991a; Vernon 1995). The main question is whether there is an interdependent relationship between fishes and corals. The evolution and development of modern reefs may have been dependent on the presence of modern fish groups, particularly herbivores, controlling growth of algae thus creating the space for development and evolution of corals (Bellwood and Wainwright 2002).

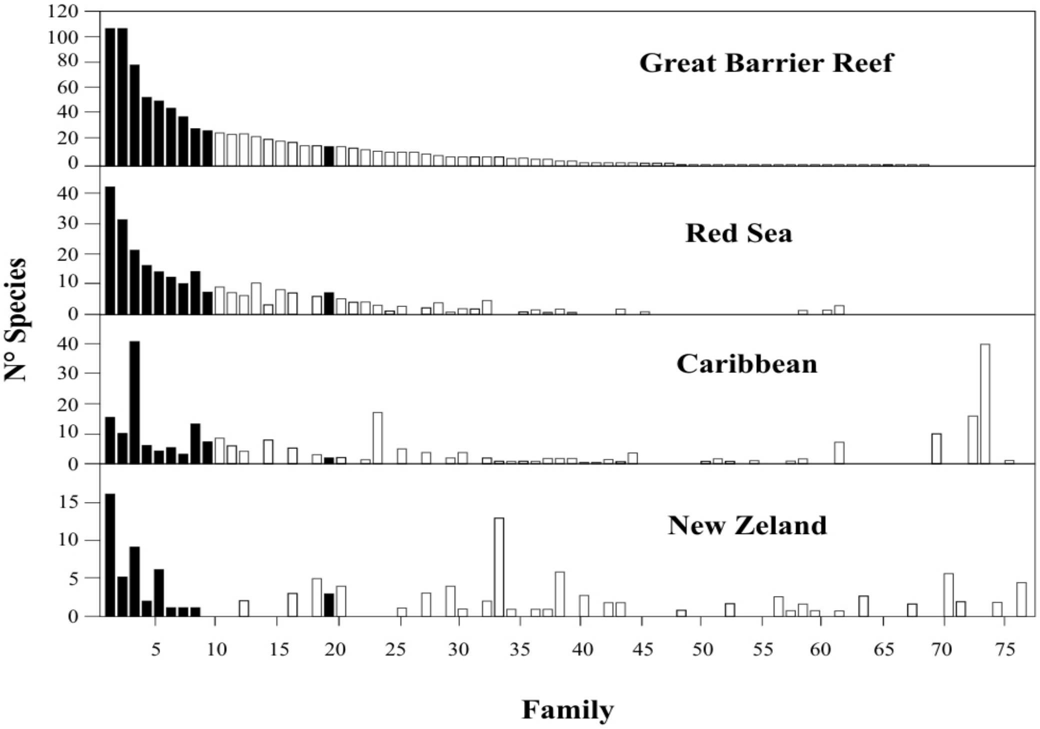


Figure 1: Species richness by ranking of families at four sites. Characteristic reef families are indicated in solid bars (Modified from Bellwood and Wainwright 2002)

How do these concepts relate to fish communities in New World regions, where geological perturbations have led to massive extinction of coral communities in recent geological times, but where reef fishes still live? Are cross-regional comparisons possible between these fish faunas in marginal regions?

There are relatively few examples of comparative approaches towards the study of these questions, and few of these discuss ecological data. Gladfelter et al (1980) studied similarity and diversity among new coral reef fish communities in TWA and Tropical Central Pacific fish communities. A principal result of this study was that equal levels of predictability are apparently exhibited by the two different fish faunas, despite the 46% difference in average species richness (Shulman 1983). There have been some taxonomic reviews of fish composition in different habitats and regions (Rubio 1986; Bellwood 1998; Robertson 1998), but there has not been much research in the TEP, which has always been considered a region of low fish species richness (Zapata & Morales 1997; Arburto-Oropeza 2001 Dominici-Arosemena et al 2005). In fact, this perception seems largely to reflect inadequate large-scale sampling of the reef fish fauna of this region (Robertson 1998) - although the similarity of overall taxonomic structures of the fish faunas of the TEP and the TWA has been recognized before (Rosenblatt 1967; Thresher 1991). The co-existence of these apparently conflicting ideas is explained by the fact that the coral rich TWA has a larger area of reef habitat than the TEP, and a much greater abundance of offshore islands and reefs (Robertson 1998). The TEP has been under-evaluated: data from the Gulf of Chiriqui, the largest archipelago in the region, which contains a complex set of ecosystems and probably a highly diverse benthic fauna, has not so far been considered.

1.2 *Energetics and reef fish*

Recent research (at the end of the '90s and beginning of the present decade) suggests that the high diversity of fishes observed on present-day coral reefs is partly related to sustained higher temperatures in the tropics over geological time, and to the more efficient use and transfer of energy permitted by long-term temperature stability. High temperatures and environmental stability have influenced evolutionary processes from the molecular to the community level of organization (Harmelin-Vivien 2002). When looking at the trophic structure of fish faunas, a drastic decrease is observed in the number of species and abundance of herbivores and sessile invertebrate feeders from tropical to temperate reefs. It is suggested that this is because these foods are easier to digest in higher temperatures; however, this analysis has so far only been carried out in the Indo-Pacific region (Harmelin-Vivien 1989), characterized by strongly marked latitudinal temperature gradients, stable currents and the absence of major oceanographic events affecting temperature, salinity and productivity values. Further research is required to confirm the existence of these latitudinal patterns in the Atlantic Ocean; similar patterns should be also looked for in marginal regions where changes of temperature - not related to latitude - occur in specific locations. An example is the understudied Tropical Eastern Pacific (TEP). Any differences that may be found between the Atlantic and in the Tropical Eastern Pacific will be strongly related to oceanographic changes that have occurred since the closure of the Isthmus of Panama (IOP), reflecting the impact of this geographical barrier on the world's oceans (Bellwood and Wainwright 2002).

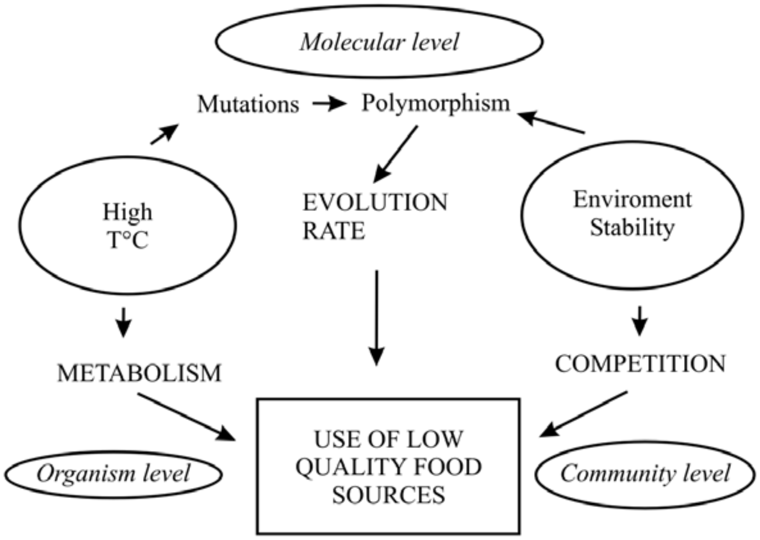


Figure 2: Schematic representation of the hypothetical effects of high temperature and environmental stability to explain the higher consumption of low quality food sources by fishes in tropics compared to those in temperate zones (Modified from Harmelin-Vivien 2002)

Fish in tropical and temperate zones exhibit marked physiological and metabolic differences and these can lead to ecological speciation. These differences are observed not only in trophic guilds but also within single families encountered both in tropical and temperate waters (Harmelin-Vivien 2002). What can we expect on the two sides of IOP?. If there is a synergy between thermodynamics and ecological constraints, the abundance of herbivores and their diversity will be higher in any region with stable high temperatures and low environmental seasonality, especially if these parameters are constant over geological time. High temperatures will increase the rate of mutations, which are related to metabolism rates, and thus speciation in low caloric food feeders (Harmelin-Vivien 2002).

Alongside the study of feeding strategies, the comparative analysis of age and growth in fishes across their geographical range will enable the assessment of systematic trends in life history parameters in response to latitudinal and local gradients in environmental conditions (Choat and Robertson 2002). Fish growth will all also be affected by temperature (Pandian and Vivekanadan 1985). According to Pauly (1998), fishes from warmer waters have smaller asymptotic sizes and higher mortality rates than their colder water counterparts. It is expected that fishes in any colder region will reach larger size classes. On the other hand, if the reduction in growth rates is determined by increased competition as well as by high temperatures, there will be a decrease in asymptotic size if territorial herbivores are abundant (Choat and Robertson 2002).

1.2 *Mobility groups*

Factors such as water motion have been linked to the distribution of fish species from local to regional biogeographic scales (Bellwood et al 2002; Fulton et al 2005). Wave energy and currents and their correlation with distribution patterns of fish species have been well documented and identified as the cause of major variations in community structure (Fulton et al 2005). Wave energy may also directly influence the structure of reef fish assemblages through interactions between wave-induced water motion and different swimming performances (Bellwood et al 2002). According to Fulton et al (2005), this functional relationship is a widespread phenomenon that applies to the majority of the fishes found on coral reefs and wave-induced water motion appears to be important in both ecological and evolutionary terms (O'Dea et al. 2002). What have been the consequences for different mobility groups at local and regional scales since the closure of IOP? In comparison to TWA, TEP is characterized by more intermittent currents and a wider range of tidal variation ; consequently, these two regions can be expected to show marked differences in the relative abundance of different mobility groups.

1.3 *The influence of habitat structure on fish diversity*

While it is true that coral diversity is always related to the diversity of fishes, some other elements of the physical habitat must be involved since there is no clear evidence that long-term association with coral reefs has led to the development of distinctive taxonomic characteristics among coral reef fish species (Robertson 1998).

One of the factors thought to be related to coral reef fish diversity is the heterogeneity of the organic and inorganic substrate that might be used by fish. Coral diversity and substrate

heterogeneity can affect reef fish diversity by offering different opportunities for shelter, which directly influences larval recruitment and rates and patterns of colonization. Some researchers have found variation in species compositions with depth, or more generally among differing habitats (Gosline 1965; Jones 1968; Talbot & Goldman 1972; Harmelin-Vivien 1977; Gladfelter & Gladfelter 1978; McGehee 1994; Dominici-Arosemena et al 2005). Various studies have indicated that physical variables, in particular substrate, depth, and currents, have an important influence on the distribution of fish and other aquatic organisms (Schlosser 1982; Williams 1982; Russ 1984a b; Green et al 1987; McGehee 1994).
Is the relationship between habitat structure and fish diversity parameters a universal rule for fish assemblages? What role do corals play? The long and complex biogeographical story of reef fishes challenges preconceptions about the way fishes and reefs interact. In both evolutionary and ecological terms, coral reefs may represent only one of a range of suitable habitats and reef associations may be largely facultative (Bellwood and Wainwright 2002). Surface complexity is related to substrate diversity, probably due to the natural occurrence of highly diverse benthic fauna on coral reefs that are also morphologically complex. Conclusions regarding the interaction between coral diversity and fish diversity are mostly based on data obtained from coral-rich regions (Hacker & Steneck 1990).

Most studies use the percentage of cover of coral taxa and other benthic life forms as a measure of habitat complexity (McManus et al 1981; Bell & Galzin 1984; Bouchon-Narvarro & Bouchon 1989; Levin 1991). In a few instances, surface attributes such as hole size, slope, and height have been combined with percentage of cover (Roberts & Ormond 1987; Luckhurst & Luckhurst 1978 b). It has been found that species richness is correlated with substrate heterogeneity, and that fish community parameters were poorly correlated with percentage substrate cover by corals (Luckhurst & Luckhurst 1978a). In other studies, species richness increased with live coral coverage (Bell & Galzin 1984).

The IOP provides a good experimental scenario. The closure of the isthmus 3 million years ago gave rise in the TWA to a region richer in corals and with marked differences between exposed and sheltered zones; and in TEP to a region characterized by rocky reefs and a diverse benthic fauna along with variable currents and tides. These two regions exhibit particular variables that will provide additional tools for understanding how these environmental parameters influence reef fish assemblages.

1.4 *Relationship between fish abundance and habitat structure.*

There are some more recent studies on the relationships between certain kinds of substratum topography and abundance in tropical fish assemblages (McCormick 1994). These studies have found substratum topography to be the factor with the highest average correlation score in relation to total fish abundance, diversity and the abundance of individual species.

Is the relation between total fish abundance and habitat complexity a universal pattern in fish assemblages? How is this reflected in the difference between fish assemblages on each side of IOP? Carpenter et al (1981) demonstrated a strong correlation between fish biomass, abundance and substrate complexity. Luckhurst & Luckhurst (1978b) found that fish abundance and substratum complexity were strongly correlated only in part of their study sites. These conflicting results may be due to the occurrence of interactions that are strongly related to local biological and environmental conditions. Probably a wide set of size categories, including small visible recruits, may be more or less strongly associated with habitat complexity depending of the density of predators and shelter availability in a given study area (Almany 2004 ab).

1.5 *Ecological barriers, geminate species and relationship with habitat: effect of IOP*

The biogeographic structure of fish habitats and energetic interactions of reef fishes observed in particular regions today are the result of a long and complex geological and oceanographic history, which has probably involved a number of speciation, dispersal, adaptation and extinction events (Bellwood and Wainwright 2002). Speciation events occur in response to environmental and geological changes, which lead to the separation of populations and subsequence diversification of lineages. In some areas, the inhabitants may be completely eliminated, while in others they prosper;, their individual fates being dependent on a complex of interacting factors: Barriers separating marine populations vary widely. They may be permanent or intermittent and range from complete physical barriers such as land bridges to partial barriers resulting from physical distance, currents or ecology (McManus 1985; Springer 1988; Springer and Williams 1994). The major speciation events affecting reef fish taxa have been the Terminal Tethyan Event (12-18 Myrs), the emergence of the East Pacific Barrier (0-65 Myrs) and most recently the closure of the Isthmus of Panama (IOP, 3.1-3.5 Myrs).

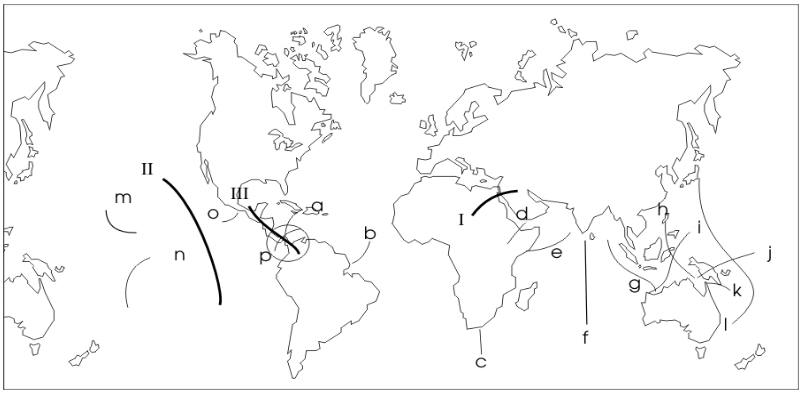


Figure 3 Faunal boundaries and proposed locations of speciation events affecting reef fish taxa. (I) Terminal Tethyan Event (II) East Pacific Barrier (III) Isthmus of Panama. Small letters show intermittent barriers (Modified after Blum 1989 and Bellwood and Wainwright 2002).

The results for the tropical waters bordering the Americas following closure of the IOP have been faunal isolation, extinction and extensive turnover in reef assemblages (Budd 2000; Todd et al 2002). Currently, IOP, like other peripheral regions, is marked by endemism (of survivors) following extensive faunal loss. Even though dispersal and speciation in some species across the IOP started to occur prior to its closure (Barber and Bellwood 2005), the geological time since this event has been relatively short for a drastic shift in fishes' physical adaptations, and there remain about a dozen species that span the isthmus which show little or no morphological differentiation, and several closely related species pairs. Nevertheless, it is interesting to speculate on the subsequent ability of the fish fauna with no marked structural differentiation to adapt to local environments**.** This implies that the degree of diversification or loss of species caused by the recent rise of a geographical barrier may have a profound effect on the functional attributes and short-term adaptation of surviving fauna, particularly in terms of habitat preferences, without strongly affecting the taxonomical composition of fish assemblages in either region**.** Phylogenetic data provide an alternative line of evidence that may give a clearer indication of the history of the reef-fish relationship, providing the basis for examining not only relationships between taxa but also evolution of adaptation to new niches (Winterbottom and McLennan 1993). An examination of habitat preferences among different fish species within the comparative framework provided by molecular based phylogenic studies will open up avenues for future research into biological and ecological changes in fish species and their assemblages over evolutionary times, considering that fish speciation often occurs in conjunction with ecological shifts, particularly in habitats occupied by adults (Tringali et al 1999).

2 Research Objectives

The general objective of this research is to identify factors that can explain differences in the patterns of taxonomical structures, abundance, functional characteristics and relations with habitat types observed among reef fish communities at local and regional scales on both sides of the IOP. The aim is to describe interspecific patterns, elucidate the origin of these patterns, the mechanisms that maintain them and determine the most important ecological consequences.

The general objective will be achieved through the following specific objectives, all of which adopt a comparative approach to the analysis of reef fish assemblages on both sides of IOP:

-To describe the taxonomic composition and parameters of diversity at local and regional scales.

-To correlate coral coverage, substrate complexity and substrate diversity with fish diversity parameters.

-To correlate physical parameters with fish diversity parameters.

-To measure and identify parameters that may have an influence on recolonization, abundance and ontogeny of fishes in different habitats.

-To determine functional organization of reef fish (trophic groups, size classes mobility groups) and analyze the oceanographic and physical parameters (e.g. currents, temperature, salinity) and behavioral interactions that may influence local patterns, discussing the results obtained by the present research in the light of recent energetic theories.

-To determine habitat preferences in geminate species in order to understand the principal effects of the closure of IOP on ecological adaptations displayed by a recent divided reef fish assemblage.

3 Study area

3.1 *Local climatic description*

Panama is located in Central America, bordering both the Caribbean Sea and the East Pacific Ocean, between Colombia and Costa Rica and is the narrowest and lowest part of the land bridge that links North America and South America. It is situated between 7° and 10° Latitude North and 77° and 83° Longitude West and, it encompasses approximately 77,082 square kilometers, is 772 kilometers in length, and between 60 and 177 kilometers in width. The Pacific coastal waters are shallow and wide mud flats extend up to 70 kilometers seaward from the coastline. The tidal range of about 0.7 m between high and low water on the Caribbean coast contrasts sharply with over 7.0 m in some areas on the Pacific coast. The dominant feature of the country's landform is the central spine of mountains and hills that forms the continental divide (Talamanca ridge). Nearly 500 rivers lace Panama's rugged landscape. Rivers flowing into the Pacific are longer and slower running than those on the Caribbean side. Panama has a tropical climate that is governed by the Intertropical Convergence Zone (ITCZ). The convergence zone moves slightly South between January and March, which is the dry season, a period when northeast trade winds predominate (D'Croz and Robertson 1997). Air temperatures are high throughout the year (as is the relative humidity) and there is little seasonal variation (min 24°C max 29°C). The temperature seldom exceeds 32°C. Temperatures on the Pacific side of the isthmus are somewhat lower than on the Caribbean side. Rainfall varies regionally from less than 1.3 meters to more than 3 meters per year. Almost all of the rain falls during the rainy season; which is usually from April to December, but varies in length from seven to nine months. In general, rainfall is much heavier on the Caribbean than on the Pacific side of the continental divide.

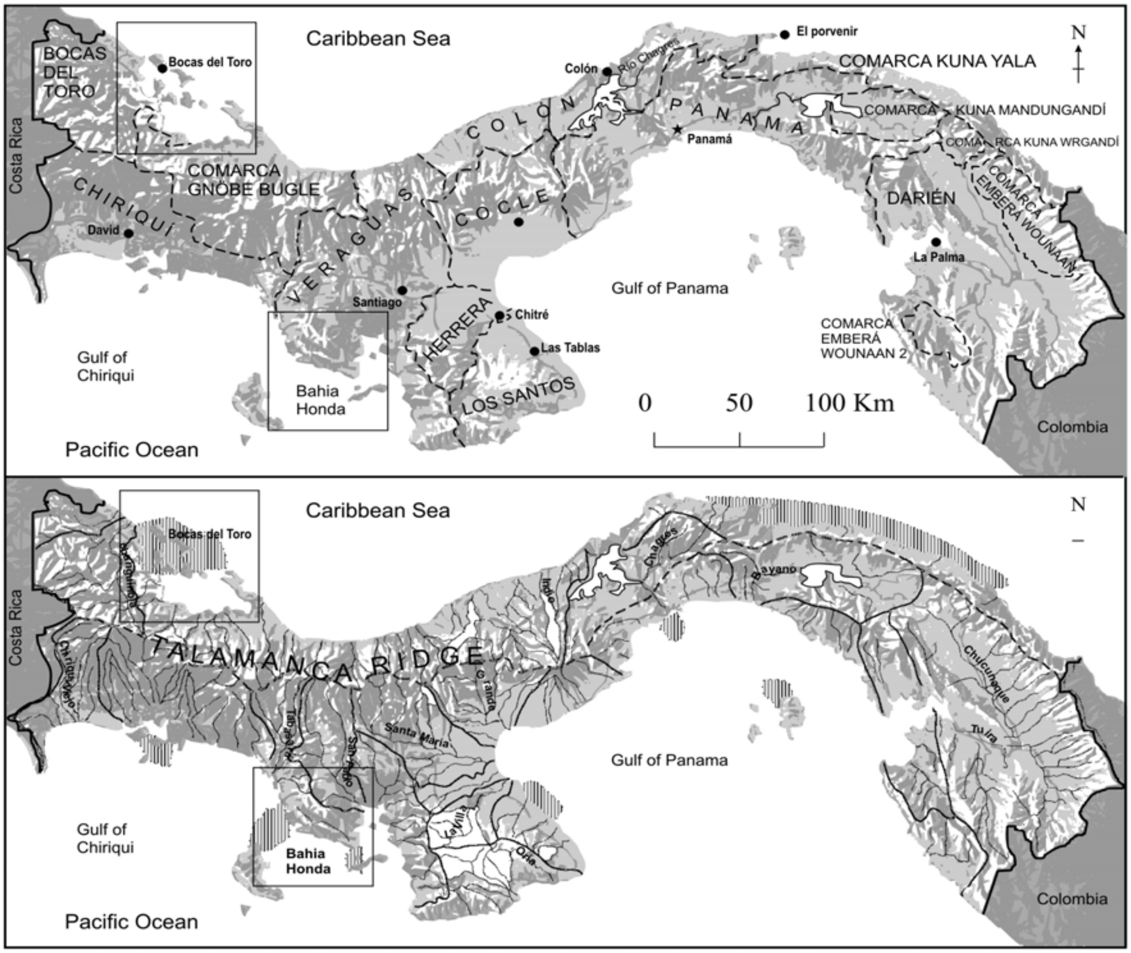


Figure 5: Political and hydrographic map of Panama. Study zones in the squares, major rivers in dark lines over the geographical relief. Dashed vertical lines indicates most important reefs in the region.

3.2 *Tropical Western Atlantic*

The Caribbean is characterized by the absence of coastal upwelling. The runoff from rivers can have a strong influence on the nutrient composition and salinity of coastal waters. The average temperature of the water is 28°C and the salinity is around 33-35 PSU. The rain decreases in the dry season, which is characterized by the northern trade winds, which can produce strong waves, currents and turbulence in exposed reefs. The area is relatively diverse compared to other coastal regions in the Caribbean, with the exception of the Honduras-Belize reef complex (Clifton 1995; 1996).

In the north west of IOP, near the border with Costa Rica in a province called Bocas del Toro, is a chain of islands where reefs cover the old marine sediments, with extended shallow reef habitats (less than 15 meters in depth). Extensive sea grass beds occur, and there are also sandy areas, while mangroves are ubiquitous in sheltered zones. The coral coverage (e.g. *Porites, Millepora, Agaricia Siderastrea, Porites and Montastrea*) is less than 30%, with macroalgae and different genera of soft corals (e.g. *Plexaura, Pseudoplexaura, Eunicea, Gorgonia*) predominating. Encrusting sponges are abundant in the areas of strong current and branching forms in sheltered zones. Sites selected for research were located around protected areas in Bahia de Almirante and in exposed areas of Isla Bastimentos (Wild Cane and Crawl Key).

3.3 *Tropical Eastern Pacific:*

The tropical Eastern Pacific region has historically been characterized as devoid of coral reef. Physical conditions in the region, including low temperatures, variable salinity and high nutrient loads, are apparently not conducive to reef growth. But recent work has identified persistent coral growth in some locations, with relatively high accretion rates, particularly in the Gulf of Chiriqui (Cortés 1997). Coral reefs of the Eastern Pacific are typically small with a discontinuous distribution and low species diversity of corals (mostly *Pocillopora, Pavona* and *Porites)*. In some areas, such as the Gulf of Panama, coastal upwelling occurs during the dry season, caused by the northern trade winds, and during this seasonal event the surface water temperature falls below 20 °C. The salinity varies between 30 to 35 PSU in the dry season, and sometimes descends to 24 to 30 in the rainy season. Light penetration decreases during the dry season due to the rise in plankton density, although this pattern is less marked in the Gulf of Chiriqui, where there is almost no coastal upwelling as a result of the blocking of the northern trade wind by the Talamanca ridge. Compared to other TEP regions, clear waters and less extreme low temperatures are remarkable characteristics of this region (Glynn & Mate 1996).

Located on the Pacific coast, to the southwest of IOP, is the abovementioned Gulf of Chiriqui, an area characterized by strong currents, wide tidal variations and relative stable temperatures and salinity in comparison with other TEP areas, and particularly with the neighboring upwelling zone in the Gulf of Panama, which however influences our study area due to the regional interconnections and cold water intrusions (D'croz 1988; D'croz et al 1991). For this research, sites with different types of substrates, levels of exposure to waves and depth were selected along a gradient from coastal zones in Bahia Honda to more oceanic zones around the island Canal de Afuera. Some exposed coastal zones were also located in Wahoo Rock, a cay on this latter island.

3.4 *Global geological description*

The Isthmus of Panama was formed in the Pliocene. Estimates of the time when two discrete regions came together to definitively separate the tropical seas on either side vary from 1.8 to 3.5 million years (Keller et al 1989; Coates and Obando 1996). The data available suggest a broad division of the region into northern and southern biogeographic provinces with probably more overlap in distribution of fish species in the Caribbean**,** which also contains more discrete patches of suitable habitats in comparison to the East Pacific (Bellwood and Wainwright 2002). The direct impact of the IOP may have been of limited significance for reef fish taxa, probably because the speciation events that have followed the geographical separation are too recent for strong differentiation to emerge among geminate species that have common ancestors (Rocha 2003). The abovementioned east Pacific barrier (see faunal boundaries map) appears to have been a relatively more effective barrier and would have limited the effect of IOP in the Indo-Central Pacific to the isolation of populations along the east Pacific coast. The IOP also prevents recolonization of the East Pacific from the Tropical Western Atlantic. However, there may have been earlier land barriers at this location, in the Paleogene (30-60 Myrs, White 1986) and Cretaceous (100-80 Myrs, Smith et al 1981).

The closure of IOP can be considered a large-scale natural experiment. Through an analysis of the patterns observed we can test general theories regarding the factors that govern the emergence and maintenance of reef fish assemblages. The question thus arises, to what extent are taxonomical and ecological characteristics of reef fishes on both sides of IOP related? (Robertson 1998).

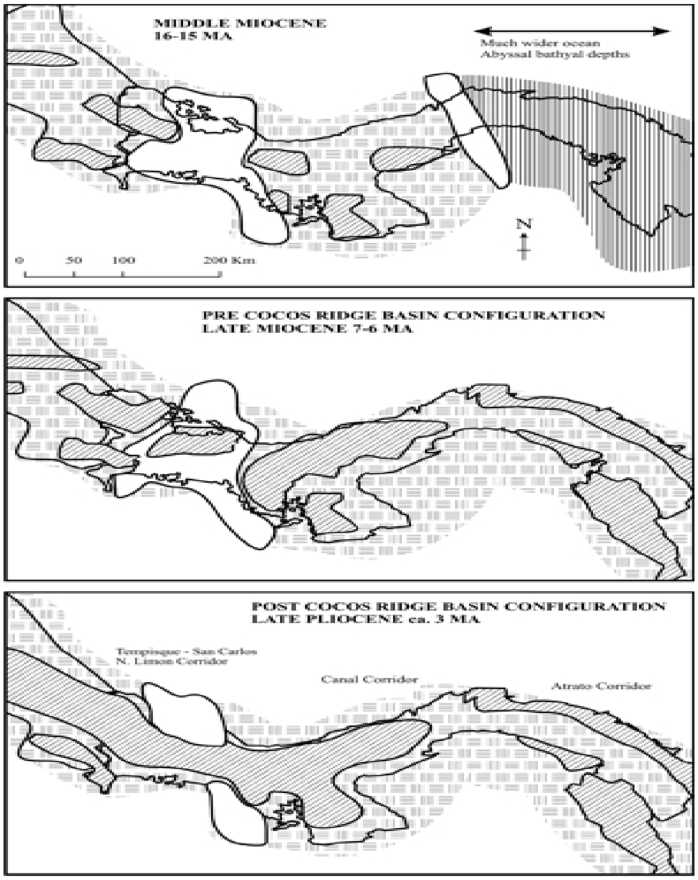


Figure 4: Paleographic reconstructions of the Central American isthmus region. Emergent land represented in grey, shelf sediments by squares, abissal oceanic sediments by vertical lines and interconnections between both sides in white (Modified after Coates and Obando 1996 and Bermingham et al 1997).

4 Organization of the Thesis

This thesis consists of a set of four publications. Each one will constitute a chapter and together these chapters fulfill the objectives of this research. Six hypotheses will be presented and in the Synopsis, the most important results will be discussed.

4.1 Hypothesis 1-*General taxonomic structure*

Although the composition of families is similar in both geographical areas, the taxonomic structure (e.g. predominance of some genera) of reef fishes will show spatial variations, according to differences in habitat characteristics. Species richness per area may be higher in regions more affected by intrusive currents and variable oceanographic conditions.

This hypothesis is supported by the results of comparative studies described in a research paper (Dominici-Arosemena and Wolff, submitted, ***Publication III****). This publication describes and analyses data from research conducted in each of the abovementioned* *geographical regions in IOP (Dominici-Arosemena and Wolff 2005,* ***Publication I****; Dominici-Arosemena and Wolff, 2006,* ***Publication II****). Final conclusions are given in the Synopsis.*

4.2 Hypothesis 2- *Relationship between habitat structure and fish diversity parameters*

Reef fish diversity and species richness will be less correlated to live coral coverage than to substrate diversity and complexity because of the increased availability of shelter and food in a diverse benthic habitat compared with a monospecific coral reef. The role of complexity is stressed: corals are an important structural component along with other substrates, giving rise to habitats composed of a mixture of corals and other benthic components, especially in exposed zones.

The results that support this hypothesis are discussed in detail in two research publications. One deals with the Tropical Western Atlantic (Dominici-Arosemena and Wolff, 2005, ***Publication I****) and the other with the Tropical Eastern Pacific (Dominici-Arosemena and Wolff 2006,* ***Publication II****). Final conclusions are given in the Synopsis.*

4.3 Hypothesis 3 –*Relationship between fish abundance and habitat structure.*

Fish density increases in areas suitable for recruitment and post recruitment. Reef fish density will be more strongly related to substrate complexity when predation is stronger. When predation decreases, populations of territorial families (e.g. pomacentrids and scarids) will also increase. In such a situation we may find juvenile recruitment occurring in edge habitats of low to medium complexity, such as rubble, where small non-territorial species of reef fish may also being found. Coral coverage and substrate diversity will also play an important role, depending of the morphology of the reef frame.

The relationship between fish abundance and habitat parameters are addressed in the detailed discussion of research undertaken in the Tropical Western Atlantic (Dominici-Arosemena and Wolff 2005, ***Publication I****) and in the Tropical Eastern Pacific (Dominici-Arosemena and Wolff 2006,* ***Publication II****). Final conclusions are given in the Synopsis.*

4.4 Hypothesis 4- *Mobility groups*

Better swimmers will be predominant in regions of strong currents and water movement. This pattern may be found at a local scale between exposed and sheltered zones, and at larger scales in any region with a dynamic oceanography , non-homogeneous distribution of currents and wide-variable tides. Most territorial individual (e.g. harvesting algae herbivores) may be more abundant in sheltered areas, or in any case in areas protected from waves. There, we will also find fishes less well adapted to swimming against strong currents.

To support this hypothesis, reef fishes recorded by surveys for this study were classified in to different mobility categories according to their swimming capability in the Tropical Western

Atlantic (Dominici-Arosemena and Wolff 2005, ***Publication I****) and in the Tropical Eastern Pacific (Dominici-Arosemena and Wolff 2006,* ***Publication II.****) Subsequently a comparison of mobility patterns was carried out (Dominici-Arosemena,* ***Publication III****). The classification of reef fishes into mobility guilds and analysis of the influence of mobility on the organization of fish communities had been undertaken using the results of research on latitudinal variations in functional characteristics of reef fishes in the Atlantic* (**Publication IV***, Floeter et al 2004).*

4.5 Hypothesis 5- *Abundance of trophic groups and size classes among reef fish families*

The relative abundance of typical coral reef fish families can vary according to physical conditions (e.g. temperature) and oceanographic ones (e.g. currents, tides, upwelling). Differences in the densities of planktivores, invertebrate feeders and carnivores may be due on the one hand to variations in primary productivity, in regions influenced by coastal upwelling, currents and cold water intrusions; and on the other hand to variations in the densities and diversity of herbivores, in regions which are more stable in terms of temperature and oceanography. Variations in temperature will have an effect on size classes: larger fishes will be relatively more common in colder waters. If there is an increase in productivity, the trophic chain will also be affected. In natural conditions, the abundance of highly energetic food sources will result in larger sizes, greater abundance of top predators and feeders on high protein sources of food. In warmer waters, lower quality food sources and increased competition between (for example) territorial herbivores and other fishes will result in decreased asymptotic sizes in most families.

To support this hypothesis, a paper on latitudinal variation in trophic groups was prepared covering the entire Atlantic Ocean (Floeter et al 2004, ***Publication IV****). Data obtained on the study region in the TEP will be discussed in a comparative review, not only of the results obtained in the study sites but also of these results in comparison with data available from other regions in the TEP (Dominici-Arosemena and Wolff* ***submitted Publication III).***

4.6 Hypothesis 6- *Geminate species: relationship with habitat and effect of IOP*

Taxonomical similarities between IOP fish faunas may be a consequence of the fact that reef fishes have marked habitat plasticity, as confirmed by non-reef habitat utilization during coral extinction. It is expected that speciation of fish may occur in conjunction with ecological shifts; and related species considered as habitat and feeding generalists may show different habitat preferences depending on local oceanographic conditions, the availability of alternative habitats for shelter and specific interrelations (predation, territorialism) within particular fish assemblages. Fishes that share eco-adaptations to some specialized types of food (adaptations from former coral reef environments, reef algae, plankton, sessile invertebrates), depth range, structural similarities in habitat and swimming capacity may show congruent patterns of habitat utilization on both sides of IOP. These tendencies persist over geological-evolutionary time.

To test this hypothesis, representative geminate species belonging to reef fish families were selected for quantitative analysis and analysis of their relationship with habitat on both sides of IOP. This analysis was based on surveys of selected fish species undertaken in each region. The results were described and compared in a research paper. (Dominici-Arosemena and Wolff, submitted, ***Publication III****).*

5 General experimental design and methods overview

5.1 *Survey application*

Before collecting any data, a 6 month-long pilot study (three months in each geographical area) was conducted to test the feasibility of the design and to identify the factors which should be taken into account in the research. An analysis of the pilot study data was used to refine the sampling units and methods (Oxley 1994; Samoilys 1997), and to ensure that the methodology was suitable for a comparative analysis of different habitats in both geographic regions (Andrew & Mapstone 1987).

A species visual census technique was used for studies of the species composition, species diversity and relative abundance of different coral reef fish assemblages in different regions (Jones & Thompson 1978). We review other comparative ecological studies of the fish assemblages associated with natural and artificial reef sites, using a visual transect method similar to Brock (1954).The chosen transect methods permit the measurement of coverage of benthic organisms, and the description of reef topography and its associations with reef fish assemblages using multivariate analysis (Carpenter et al 1981; Luckhurst & Luckhurst 1994 Roberts & Ormond 1987 McCormick 1994). (McCormick 1994).

The relationship between fish size and habitat structure was assessed after determining bias among the observers *sensu* Bellwood & Alcala (1988). All surveys involved visual counts of juveniles, sub-adults and adults (Doherty 1987). Data from transects were also used to asses the scale dependence of correlations between substratum and fish parameters.

Most of the surveys were carried out under ideal conditions and the census techniques employed enabled the identification of individuals from most species encountered. However, environmental conditions imposed some limitations in a few areas. Some censuses were carried out under conditions of poor visibility and/or strong wave surge. The assessment of substrate coverage on these areas demanded an extreme physical effort. It is also important to consider the inherent limitation of the visual census methodology due to the high variance of the estimations (Brock 1982). All the observations and measurements used SCUBA diving equipment, and were carried out at intervals of approximately 8 months in each geographical area with the assistance of a group of marine ecologist trained in the identification of fishes from both regions of IOP. Detailed methodologies will be found in each publication.

5.2 *Data analysis*

Many of the data on physical and biological parameters do not meet the criteria for parametric statistics (normality and homogeneity of variances). These data were evaluated to detect differences within and among reefs using nonparametric analyses including Spearman rank correlation coefficients and the Kurskall Wallis test. The results were also analyzed using multivariate statistic to examine associations of the fishes and their habitats (James & McCulloch 1990; Osborne & Thompson 1997).

6 Core publications

6.1 *Publication list and contribution of authors*

Publication I

Dominici-Arosemena A, Wolff M (2005) Reef fish community structure in Bocas del Toro (Caribbean, Panama) along spatial scales and gradients in habitat complexity. Caribbean Journal of Science 41:613-637

The first author originated the conceptual approach and methods forconducting the fieldwork in Bocas del Toro, managed the data obtained and wrote the first manuscript draft. The second author improved the style of the manuscript, amended the research objectives to incorporate some ideas from transference of energy approaches, suggested the elaboration of a graphic reef profile and developed the idea of performing the Log series model on patterns of diversity in reef fish, to facilitate visualization and interpretation of fish diversity parameters. Both authors provided ideas and inputs for the discussion

Publication II

Dominici-Arosemena, A, Wolff M (2006) Reef fish community structure in the Tropical Eastern Pacific (Panama): Living on a relatively stable rocky reef environment Helgoland Marine Research DOI 10.1007/s10152-006-0045-4

As in the first publication, the first author originated the conceptual approach and methods for conducting the fieldwork in Gulf of Chiriqui, managed the data obtained and wrote the first manuscript. The second author improved the style of the manuscript and the research objectives, suggested the elaboration of a graphic reef profile and developed the idea of performing the Log series model on patterns of diversity in reef fish. The second author also suggesed a new format of graphic visualization of most abundant fish species contributed ideas on trophic interactions, energetic exchange and interactions among trophic groups. Both authors provided ideas and inputs for the discussion

Publication III

Dominici-Arosemena, A, Wolff M Comparing reef fish community structure between the Pacific and the Caribbean side of the Isthmus of Panama. Coral Reef (summited)

The first author conceived the idea of a comparative study of fish communities on both sides of Isthmus of Panama. , He conduct the fieldwork and data management in both regions and wrote the initial manuscript. The second author collaborated with many ideas for graphic visualization of the data obtained, for example data on the number of species per family per region. He suggested the use of the comparative size-abundance per family approach and the application of the Log series model on a regional scale, he also improved the style of the manuscript. The application of multivariate analysis for comparing habitat preferences among geminate species was an idea of first author.

Publication IV

Floeter SR, Ferreira CEL, Dominici-Arosemena A, Zalmon I (2004) Latitudinal gradients in Atlantic reef fish communities: trophic structure and spatial use patterns. Journal of Fish Biology Vol 64:1680-1699

The first author developed the idea of a comparative approach of trophic groups in the Atlantic, drawing on ideas of Dr. Harmelin-Vivien. The third author provided data from Bocas del Toro Panama and obtained much of the information and literature that was not available in libraries at the University of Bremen and Alfred Wagner Institute (AWI). The third author contributed to the discussion of structural reef parameters affecting diversity and mobility groups, and the discussion on the biogeographical comparisons of fish assemblages and their trophic groups.

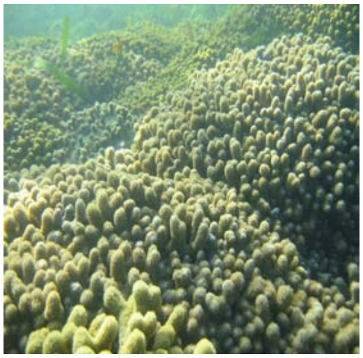
6.2 *Overview of publications content*

Publication	**Title**	**Topics addressed**
I	"Reef fish community structure in Bocas del Toro(Caribbean, Panama) along spatial scales and gradients in habitat complexity."	-General taxonomic structure TWA -Relationship between habitat structure and fish diversity parameters in TWA -Relationship between fish abundance vs. habitat structure in TWA. -Spatial variation in trophic groups TWA -Mobility groups TWA
II	"Reef fish community structure in the Tropical Eastern Pacific (Panama): Living on a relatively stable rocky reef environment".	-General taxonomic structure TEP -Relationship between habitat structure and fish diversity parameters in TEP -Relationship between fish abundance vs. habitat structure in TEP. -Spatial variation in trophic groups TEP -Mobility groups TEP
III	"Comparing reef fish community structure between the Pacific and Caribbean side of the Isthmus of Panama."	-General taxonomic structure TWA vs. TEP -Relationship between habitat structure and fish diversity parameters TWA vs. TEP -Relationship between fish abundance and habitat structure TWA vs. TEP -Trophic groups TWA vs. TEP -Mobility groups TWA vs. TEP -Abundance trophic groups and size classes among reef fish families. -Geminate species, relationship with habitat and effect of IOP.
IV	"Latitudinal gradients in Atlantic reef fish communities: Trophic structure and spatial use patterns."	-Abundance and latitudinal variation in trophic and mobility groups among reef fish families in the Atlantic ocean. -Energetic theories

6.3 Publication I

REEF FISH COMMUNITY STRUCTURE IN BOCAS DEL TORO (CARIBBEAN, PANAMA) ALONG SPATIAL SCALES AND GRADIENTS IN HABITAT COMPLEXITY.

Arturo Dominici-Arosemena and Matthias Wolff



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Caribbean Journal of Science, Vol. 41, No. 3, 613-637, 2005

Reef Fish Community Structure in Bocas del Toro (Caribbean, Panama): Gradients in Habitat Complexity and Exposure

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ABSTRACT.—We compared the community-structure of reef-fish over different spatial scales, levels of exposure, and physical complexity in 12 study zones of Bocas del Toro, Panama. Two hundred and eighty-eight visual censuses were conducted on 48 benthic transects from April to September 2002. Substrate coverage and surface complexity was also recorded. We found 128 fish species in 38 families with increasing species richness from sheltered to expose and from low-complexity to intermediate and high-complexity zones. Only 7% of the species occurred in all zones. Gobies and pomacentrids were most abundant in sheltered areas and labrids at exposed zones. Eleven species showed significant size-segregations between zones, suggesting ontogenic movements, with smaller sizes in low-complexity zones, and larger-sizes in intermediate to high complexity areas. Species-richness and diversity are high in three of the four exposed zones and in the main areas of massive-coral reefs and significantly correlate with certain types of complex substrates. Highly mobile fish were more abundant in exposed rocky zones while sedentary fish were more abundant in sheltered massive and foliaceous corals zones. Towards the most exposed areas, the number of mobile invertebrate-feeding fish species greatly increased, while territorial herbivores increased in sheltered zones. Roving herbivores (scarids and acanthurids) showed lower frequency than territorial herbivores in all zones. Demersal zooplankton feeders were common in sheltered areas and oceanic planktivores in exposed areas. Omnivores were more abundant in zones of rubble and sand. Carnivores were less frequent, but contribute to the majority of species. We concluded that the species' richness in Bocas del Toro relates to the structural complexity of the substrate rather than substrate type. While some species change their preferred habitat during ontogeny, general species diversity increased with habitat complexity. This increase was more pronounced in exposed zones. It seem that water current strength and waves, which select for swimming capacity, play an important but still little understood role in the organization of fish assemblages in rocky and coral reefs.

KEYWORDS.—Fish diversity, distribution, fish mobility, trophic groups, exposure level, lagoonal system, Mesoamerican Caribbean

INTRODUCTION

It has been widely stated that there are geographic gradients in the richness of fish species, corals and other coral reef biota, with a general decrease in diversity with increasing latitude and distance from the Indo-Philippine 'centre' (Goldman and Talbot 1976; Veron 1995). In the Atlantic Ocean, the Caribbean is thought the diversity centre for both fishes and corals (Briggs 1995; Veron 1995; Floeter and Gasparini 2000). The present study focuses on Bocas del Toro, which forms part of the Southern Caribbean biogeographic province. For this area, and the Caribbean Mesoamerican region in general, only a few studies exist that address variation in the community-structure of reef-fishes (Sierra and García 1996; Clifton and Clifton 1998), and most of these were conducted along Caribbean islands away from the mainland (McGehee 1994; McKenna 1997). Generally, species composition varies among different habitats (Talbot and Goldman 1972; McGehee 1994) and it appears that a strong taxonomic division between reef and non-reef faunas is difficult. "Reef fishes" may thus be characteristic of—but not restricted to—coral reefs (Robertson 1998; Bellwood

1998). Support for this assertion can be found in different geographical regions, such as the south-western Atlantic, where the most diverse fish faunas are along rocky shores with low coral coverage (Floeter et al. 2001).

Studies concerning reef fish have focused almost exclusively on coral reefs, not including a wide spectrum of reef habitats (Robertson 1998). They usually compare either diverse living coral-reef areas or rocky shores. The structural complexity of a habitat is very important for the community organization, since it provides physical structure for juvenile and adult animals (Jones 1988; Beck 1997 1998); it plays an important role in the regulation of foraging patterns (Dolmer 1998; Erlandsson et al. 1999) and predation (Hixon and Beets 1993); it also plays an important role in habitat selection (Levin and Grimes 2002), and in some cases relaxes competition (Diehl 1988). The role of complexity seems clear for most researchers, but whether its difference among areas is due to the degree of coverage of living coral or other habitat characteristics should be studied on a spatial scale that includes different habitats and levels of exposure to waves and currents. The presence of currents may affect larval dispersal and retention, thus influencing the populations' connectivity (Cowen 2002). The relative contribution of population growth, mortality, food requirements, metabolic level to fitness, as well as the role of habitat structure and selection, requires further investigation (Jones and McCormick 2002), In this context, *edges* of habitats have often been severely under sampled (Sagarin and Gaines 2002). Swimming ability and trophic behaviour are also important properties of species that may influence community organization. More studies are necessary in this field.

We compared the community-structure of reef-fish in the Bocas del Toro region of the Tropical western Atlantic, which exhibits one of the highest diversity and abundance of corals in shallow Caribbean waters (Guzmán and Guevara 1998a,b 1999). This Mesoamerican or "isthmian" Caribbean is a peculiar region due to the many geological changes it has been subjected to, including the emergence of the Isthmus of Panama.

The study aimed to characterize fish assemblages (including taxonomical composition, abundance and species richness) along spatial scales and gradients of substrate complexity to determine the relative importance of the physical structure provided by corals, rocks and benthic sessile substrate-building organisms. We also determined characteristics such as mobility, home range, size, territoriality, and feeding behaviour responsible for the selection of habitats by certain species and/or guilds along gradients of wave exposure, reef type (i.e., Coral reef vs. rocky reef) and general substrate complexity.

MATERIALS AND METHODS

Study site

The study was conducted from April to September 2002 in sheltered areas of Almirante Bay and the exposed areas around Isla Bastimentos at the Province of Bocas del Toro (8°30′09°40′N, 82°56′081°08′W), (Fig. 1).

Intense rain and irregular seasonal patterns characterise Bocas del Toro. The most important coastal current comes from an easterly direction of Nicaragua and Costa Rica (Greb et al. 1996). Waves and currents have a strong effect outside of the archipelago, but the major islands act as a barrier, decreasing wind-strength, wave-height, and tidal amplitude for the inner water bodies (Bahía de Almirante and Laguna de Chiriquí). A sheltered semi-lagoonal system with tidal amplitudes < 0.5 m is created, which supports mangrove forests. Changes in oceanic conditions of the southern Caribbean during the late Miocene, due to the progressive constriction of the Atlantic-Pacific seaway weakened the westward circulation and the southern Caribbean flow (Collins et al. 1996). All these changes resulted in a well-defined semi-lagoonal system that is connected to the southern reef areas of the Caribbean from Costa Rica (Cortés 1984).

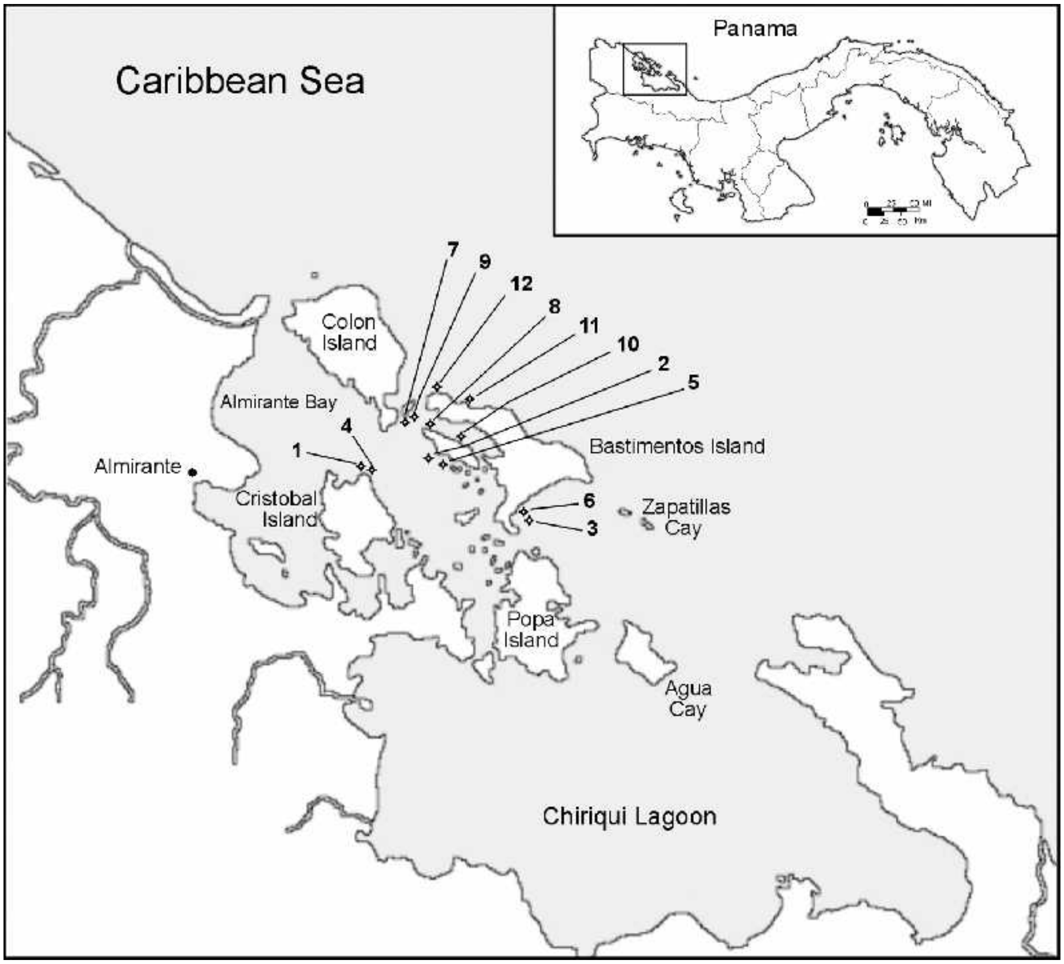


FIG. 1. Sampling zones in Bocas del Toro, Caribbean. 1: North east of Cristóbal Island; 2: South of Solarte Island; 3: Crawl Key, west side of Bastimentos Island; 4: Northeast of Cristóbal Island; 5: South of Solarte Island; 6: Crawl Key; 7: Carenero Island; 8: Hospital point, northeast of Solarte Island; 9: Carenero Key; 10: Northwest of Solarte Island; 11: Wild Cane Key, north of Bastimentos Island; 12: Bastimentos Point, east of Isla Bastimentos.

The selection of study sites was based on a preliminary-survey that identified areas with different but nevertheless characteristic habitats of the region. From this survey, 12 characteristic zones were classified in terms of depth, substrate type, topography and cover. Within each of the 12 zones, four benthic 30 m transects were set up parallel to the shore at approximately the same depth. Substrate coverage and surface complexity was estimated using a link-chain methodology (CARICOMP 2001; Rogers et al. 1994). The benthic surface measures were taken along the chain that would lay limp following the surface contour of the substrate. In this way the structural complexity of the substrate was estimated as the ratio between the length of the chain laid over the substrate and the direct linear length from the beginning to the end of each transect. The number of links outlining the surface of the substrate was counted, noting the kind of substrate under each segment of the chain; the length of the contour for each portion was then estimated at 1.6 cm per chain-link.

A detailed description of the benthic regions is in Guzmán and Guevara (1998a,b

1999). We classified the zones in ascending order of complexity (1 to 12) along with the following general description (Fig. 2):

Zones of sand and rubble SRU (1-2): Found in deeper areas adjacent to patches of the branching coral *Porites furcata*.

Zones of turf-algae and dead branching coral TA (3): A mixture of eroded skeletons of foliaceous and branching corals, with a dense cover of different species of turf-algae. These zones were found below the exposed reef-slope of fire-coral zones.

Zones of madreporic branching coral BC (4-5): Patchy zones dominated by the finger-like coral *Porites furcata*.

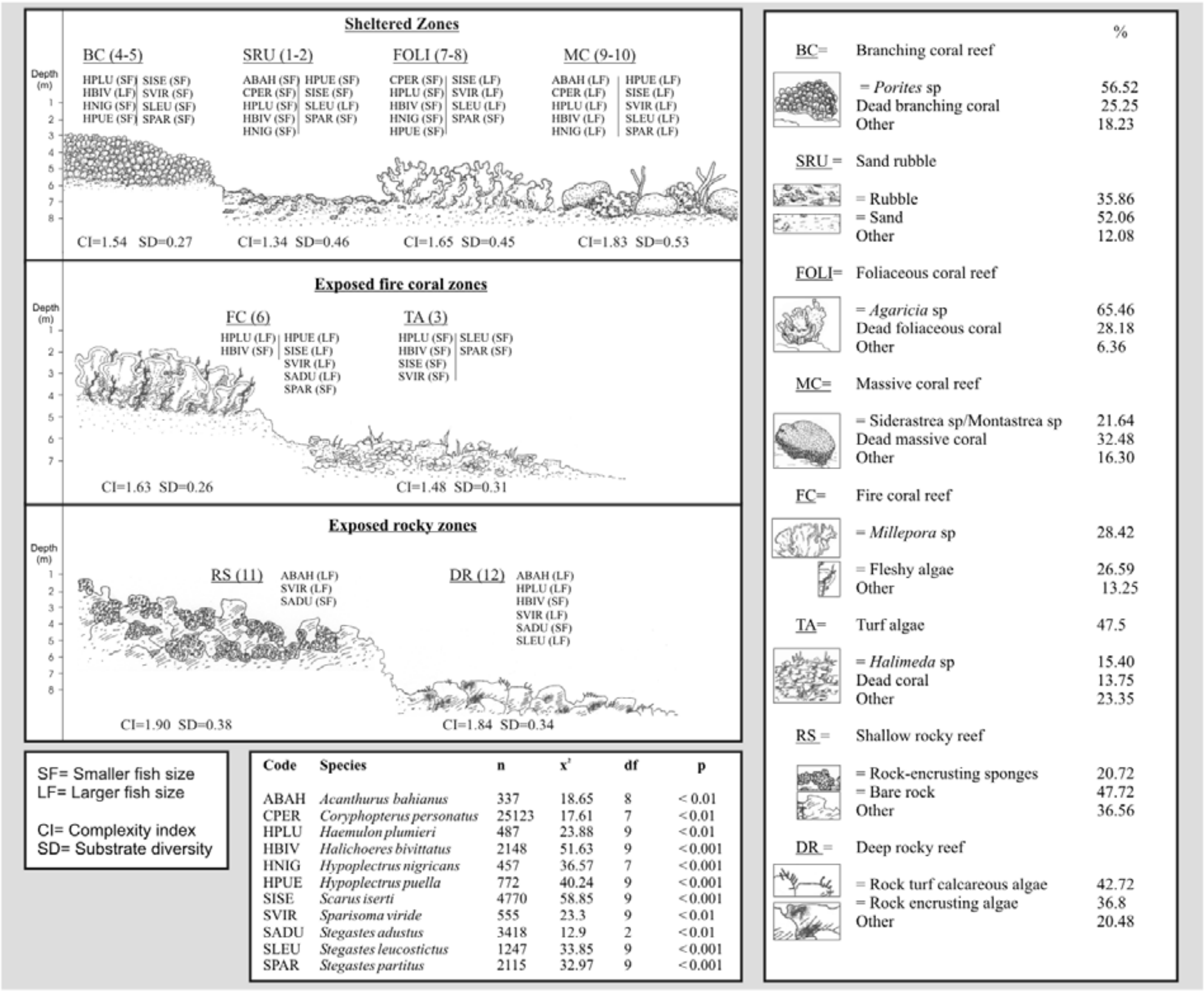
Zones of fire-coral FC (6): Continuous shallow zones (reef flat) exposed to wave influence and characterised by the presence of the fire coral *Millepora complanata*, macroalgae and other benthic components.

Zones of foliaceous coral FOLI (7-8): Sheltered deeper reefs covered with living and dead colonies of the scleractinean coral *Agaricia tenuifolia*.

Zones of massive coral MC (9-10): Coral-reef zones separated by sand, with a mixture of living and dead massive coral of different genera including *Montastraea cavernosa*, *Siderastrea siderea;* also erect sponges and sand.

Zones of massive volcanic rocks: Not common in Bocas del Toro and virtually absent in sheltered areas (pers. obs.). This kind of habitat was found on a single deeper profile (11) and in a single shallow one (12). It has a component of sessile organisms (e.g., encrusting sponges and algae) that tend to predominate in areas of high disturbance and strong currents and waves (Dethier 1994; Steneck and Dethier 1994).

The species and abundance of fish was assessed using standard methodology for underwater visual-survey with SCUBA diving equipment (English et al. 1994; Khalaf and Kochzius 2002; McKenna 1997). The fixed benthic transects (30 * 5 m) used for the study of the benthos were also used for the fish census. Monthly sampling was conducted at all transects (six census per transect), amounting to 288 on 48 benthic transects. Two to three observers swam along the transects, recording data for fishes (including small cryptic individuals)



Code	Species	n	x^2	df	p
ABAH	*Acanthurus bahianus*	337	18.65	8	< 0.01
CPER	*Coryphopterus personatus*	25123	17.61	7	<0.01
HPLU	*Haemulon plumieri*	487	23.88	9	<0.01
HBIV	*Halichoeres bivittatus*	2148	51.63	9	<0.001
HNIG	*Hypoplectrus nigricans*	457	36.57	7	<0.001
HPUE	*Hypoplectrus puella*	772	40.24	9	<0.001
SISE	*Scarus iserti*	4770	58.85	9	<0.001
SVIR	*Sparisoma viride*	555	23.3	9	<0.01
SADU	*Stegastes adustus*	3418	12.9	2	<0.01
SLEU	*Stegastes leucostictus*	1247	33.85	9	<0.001
SPAR	*Stegastes partitus*	2115	32.97	9	<0.001

Fig 2. Summary of habitat structure variables and results of the frequency analysis (χ^2) to test the differences in size distribution of species and habitat type, only the species that had significant differences of small and larger individuals are showed.

encountered within 2.5 m on both sides and 5 m above. The standard length (SL) of the fishes was estimated to the nearest centimetre with a PVC ruler. From these data, abundance (indiv./150 m^2) and Shannon-Wiener diversity (H′) were calculated based on relative abundance (Pielou 1975).

Each species was included in one of three mobility /home range size categories, as applied by Floeter et al. 2004: Category 1 represents high mobility, including wide horizontal displacement species (e.g., roving herbivores, mullids). Category 2 is represented by relatively sedentary and demersal species in close association with the reef substrate (e.g., serranids, haemulids, chaetodontids). Category 3 includes species with a small home range and a site attachment also expressed by territorial behaviour (e.g., gobies, damselfishes).

Fish species were trophically classified following Ferreira et al. (2004) and Jones et al (1991) as: roving herbivores: fish that feed on detritus, turf algae and macroalgae (scarids and acanthurids); territorial herbivores: fish that feed on farmed turf-algae within their territories; mobile-invertebrate feeders: fish that feed primarily on crabs, molluscs and other benthic mobile invertebrates on hard and soft substrates; sessile-invertebrate feeders: fish that eat sessile benthic invertebrates; piscivores: fishes that prey on living fishes; carnivores: fish that feed on mobile benthic organisms and also fishes; planktivores: fish that consume primarily macro and micro-zooplankton; omnivores: fishes that feed on a variety of organisms, including both animal and plant material.

We used the Simpson’s diversity index to estimate the diversity of organic and inorganic habitat categories (Ferreira et al. 2001). The index ranges from zero (highest diversity) to one (monotony). An index value of one indicates coverage by a single kind of substrate. Since much of the data on physical and biological parameters may not meet the criteria for normality and homogeneity of variances, parametric one-way ANOVA or non-parametric Kruskall-Wallis tests (Kruskall-Wallis) were applied to the data after testing for normality. Study sites were then compared for differences in physical conditions (substrate diversity), fish density, mobility pattern groups and index of diversity (H′) of fish assemblages (Zar 1996). An additional Student-Newman-Keuls (SNK) test of multiple-comparisons of means was applied as a *post-hoc* test (Zar 1996). The relationships between diversity indices, species density, and physical parameters were examined using Spearman rank-correlation (Siegel 1970; Peet 1974; Sokal and Rohlf 1980; Zar 1996). Association between the most abundant species, mobility pattern groups and their relationship with the habitat was examined using Canonical Correspondence Analysis (CCA) (Ter Braak and Verdonschot 1995). For this CCA analysis a value for the degree of exposure (score 0 to 4) was determined by general field observations. Differences in size distribution of all species and habitat types were examined based on length frequencies and applying chi-square analysis (χ^2) to the size groups.

Fish abundance for different zones were pooled and visually presented in a rank-order of species according to their corresponding log numbers to easily visualize the species richness and relative importance of live coral coverage and low coral coverage substrates vs. complexity (zone number) at the different study zones (Wolff and Alarcón 1993).

RESULTS

The One-Way ANOVA (Table 1) showed significant differences of the Simpson’s diversity index between some zones. It ranged close to zero (highest substrate diversity) at many of the exposed zones, especially fire corals and rocky reef, and it was close to one (monotony) in the sheltered zones that had similar index values (Fig. 2).

One hundred twenty eight fish species in 38 families were found (Appendix). The total number of fish species increased from sheltered to exposed zones. The number of genera and species found at all locations was not equal; 63% of the genera were restricted to certain zones, and only 7% of the species occurred in all zones. The number

TABLE 1. Results of parametric (One way ANOVA: F, MS) and non-parametric (Kruskal Wallis, H) ANOVA and multiple comparisons (Student Neumann Keuls, SNK) for diversity comparisons (fish and habitat), and mobility groups between study zones in Bocas del Toro. ND = Normal distribution data, NND = Non normal distribution data.

	H	Df	F	MS	p	Multiple comparison (SNK)
Substratum diversity (Simpson's diversity index)	ND	11	7.90	0.04	<0.001	Other zones < 8 = 7 = 5 = 4 = 2 = 1
Fish diversity (H')	ND	11	9.94	0.065	<0.001	12 = 11 = 6 > other zones
Fishes/census	36.52	11	NND	NND	<0.001	5 = 2 = 1 > other zones
Category 1	40.89	11	NND	NND	<0.001	12 > other zones
Category 2	42.57	11	NND	NND	<0.001	12 = 11 = 2 = 1 > other zones
Category 3	32.62	11	NND	NND	<0.001	10 = 9 = 8 = 2 = 1 > other zones

of species per genus increased from low-complexity to intermediate and high-complexity zones in the entire region. Regardless of their densities, many of the genera and species in the families (e.g., Blennidae, Labridae) and species in the genera (e.g., *Halichoeres* spp.) were not overlapping. They showed marked differences in distribution between protected and exposed zones (Appendix).

In the size frequency analysis 27 species were abundant enough to allow segregation by size; all these species were habitat-representative and 11 of them show significant size-segregation between different zones (Fig. 2). Non-territorial species such as *Scarus iseri*, *Halichoeres bivittatus*, *Acanthurus bahianus*, *Sparisoma viride,* and *Haemulon plumierii,* had smaller sizes (juveniles and pre-adults) in low-complexity zones such as sand rubble and turf algae; while larger sizes increase proportionally in zones of intermediate and high-complexity such as those of massive and fire coral, and also in some cases in complex exposed rocky zones. The genus *Hypoplectrus* showed a similar pattern but larger individuals were scarce at any of the exposed zones. Sedentary species such as *Coryphopterus personatus* and *Stegastes partitus* were also present at smaller sizes on sand-rubble areas and at larger sizes in zones of intermediate complexity such as those of branching, foliaceous, and massive coral. Individuals of *Stegastes adustus* were smaller at all rocky zones and larger at fire-coral locations. Individuals of *Stegastes leucostictus* had smaller sizes at zones of branching coral and turf-algae, but the larger sizes were found in zones of different levels of complexity and according to no discernible pattern (Fig. 2).

Gobies and pomacentrids were the most abundant families. The goby *Coryphopterus personatus* was the most common species in sheltered zones along with some labrids, such as *Halichoeres bivittatus*, the scarid *Scarus iseri*, the pomacentrid *Stegastes planifrons,* the serranid *Serranus tortugarum* and the haemulid *Haemulon plumierii* (Fig. 3). On the other hand, the species *Thalassoma bifasciatum, Chromis multilineata*, *Stegastes adustus* along with some acanthurids were common at exposed zones (Fig. 4).

As revealed by the results of Canonical Correspondence Analysis (CCA), (Table 2, 3 and Fig. 5), the association between fish and environmental variables for the 12 study zones show (at the right side of Axis 2) a gradient of exposure. Most exposed zones were associated with rock-encrusting red algae and fire coral (Zone 6, 1.22 m; Zone 11, 8.15 m; Zone 12, 3.88 m). Fishes associated with this axis were: *Thalassoma bifasciatum* (TLUC), *Halichoeres maculipinna* (HMAC), *Chromis multilineata* (CMUL), *Stegastes adustus* (SADU), the acanthurids *Acanthurus bahianus* (ABAH) and *Acanthurus chirurgus* (ACHI) which had a closer association with this group at exposed zones. The positive side of Axis 1 showed sheltered zones with branching corals (Zones 4 and 5, *Porites furcata*, 2.5 m) and zones with foliaceous corals (Zones 7 and 8, *Agaricia tenuifolia* 6.93 m). Here *Stegastes planifrons* (SPLA) and *Scarus iseri* (SISE) predominated, along with *Hypoplectrus* spp. (HPUE, HNIG), and some other species. Zone 3

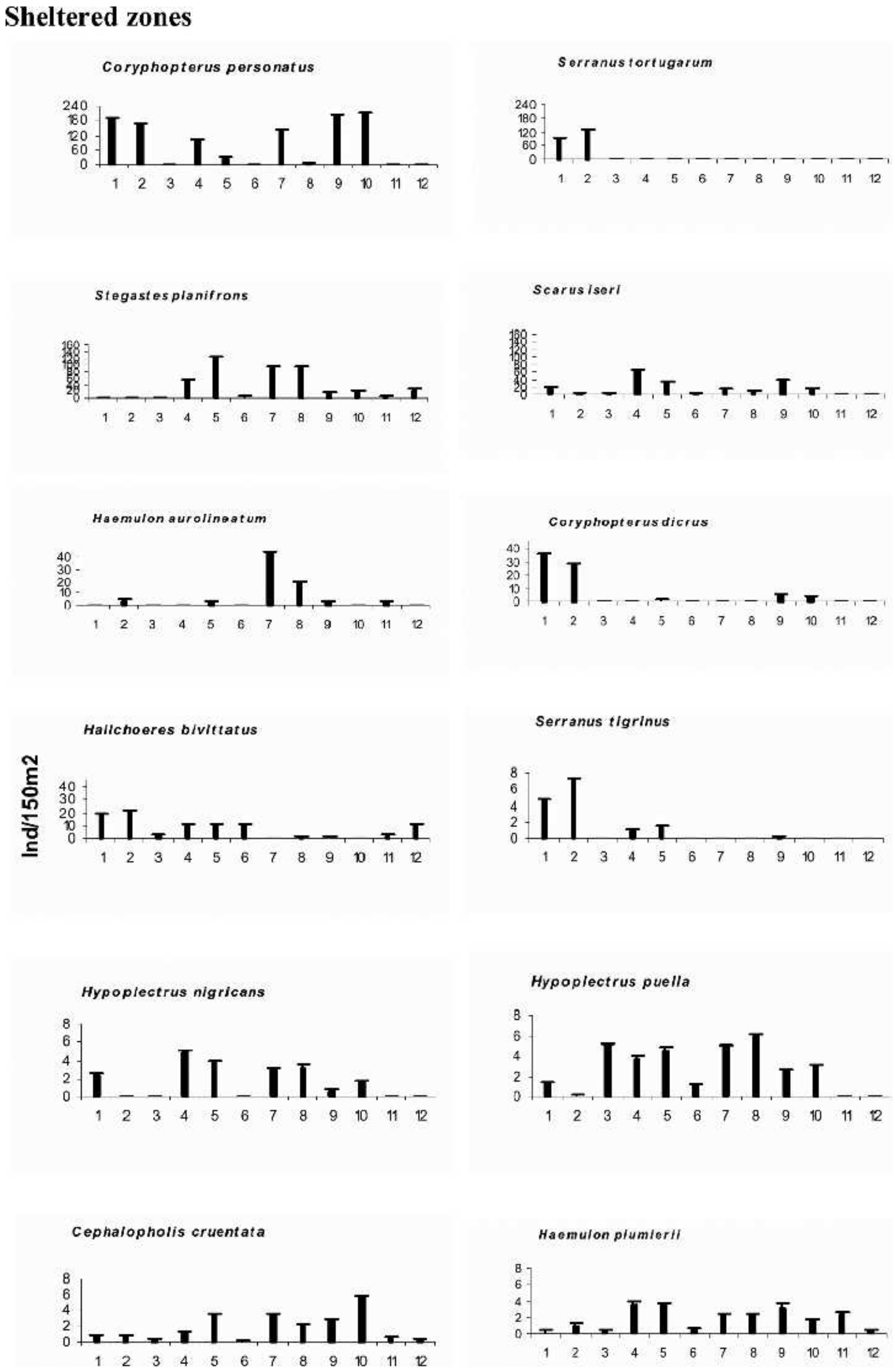


FIG. 3. Density (Ind/150 m^2 ± SE) for the most abundant species found in sheltered zones (1, 2, 4, 5, 7, 8, 9, and 10) in Bocas del Toro, Panama.

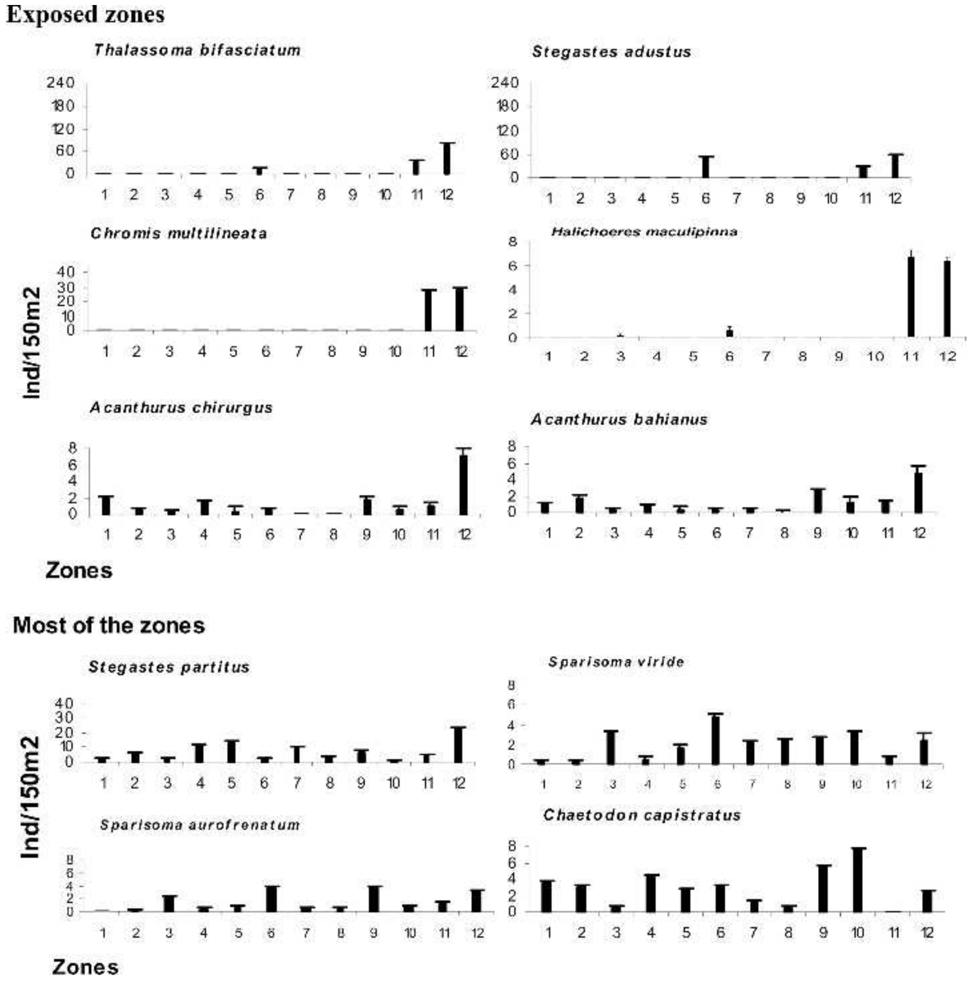


FIG. 4. Density (Ind/150 m^2 ± SE) for the most abundant species found at exposed zones (3, 6, 11, 12) and most of the zones in Bocas del Toro, Panama.

(deeper exposed zone 6.3 m) shows similar habitat composition than 4 and 5, except for the lack of living coral coverage, and had a similar fish fauna as zones 4, 5, 7, and 8. The negative part of Axis 1 shows sand-rubble areas (Zones 1 and 2, 6.36 m), which associate with *Serranus tortugarum* (STOR), *Serranus tigrinus* (STIG), the goby *Coryphopterus dycrus* (CDIC) and the labrid *Halichoeres bivittatus* (HBIV). A fourth group closer to the centre of the ordination diagram is comprised by species found in all study zones: the pomacentrid *Stegastes partitus* (SPAR), the scarids *Sparisoma viride* (SVIR), *Sparisoma aurofrenatum* (SAUR) and the chaetodontid *Chaetodon capistratus.*

The results of One-Way ANOVA and multiple comparisons (Student-Newman Keuls [SNK]) for fish parameters show significant differences in the Shannon-Wiener index (H́) between some zones (Table 1). Fish diversity had higher and similar values in three of the four exposed zones, including the rocky deeper zone (11), followed by shallow rocky zone (12), and shallow fire-coral zone (6). All other zones had a lower diversity.

These differences are appreciated in more detail in the log-series model in Fig. 6. The flatness of the line (greatest evenness) as well as its intersection with the x axis (Species richness) was greatest in the more

TABLE 2. Dominant species. O = Omnivore; C = Carnivore; P = Piscivore; MI = Mobile Invertebrate feeder; SI = Sessile Invertebrate feeder; PL = Planktivore; RH = Roving Herbivore; TH = Territorial Herbivore.

Code	Species	Family	Trophic group
ABAH	*Acanthurus bahianus*	ACANTHURIDAE	RH
ACHI	*Acanthurus chirurgus*	ACANTHURIDAE	RH
CCAP	*Chaetodon capistratus*	CHAETODONTIDAE	SI
CDIC	*Coryphopterus dicrus*	GOBIIDAE	O
CMUL	*Chromis multilineata*	POMACENTRIDAE	PL
CPER	*Coryphopterus personatus*	GOBIIDAE	PL
CCRU	*Cephalopholis cruentata*	SERRANIDAE	C
HAUR	*Haemulon aurolineatum*	HAEMULIDAE	C
HBIV	*Halichoeres bivittatus*	LABRIDAE	MI
HMAC	*Halichoeres maculipinna*	LABRIDAE	MI
HNIG	*Hypoplectrus nigricans*	SERRANIDAE	C
HPLU	*Haemulon plumierii*	HAEMULIDAE	C
HPUE	*Hypoplectrus puella*	SERRANIDAE	C
SADU	*Stegastes adustus*	POMACENTRIDAE	TH
SAUR	*Sparisoma aurofrenatum*	SCARIDAE	RH
SISE	*Scarus iseri*	SCARIDAE	RH
SPAR	*Stegastes partitus*	POMACENTRIDAE	TH
SPLA	*Stegastes planifrons*	POMACENTRIDAE	TH
STIG	*Serranus tigrinus*	SERRANIDAE	C
STOR	*Serranus tortugarum*	SERRANIDAE	PL
SVIR	*Sparisoma viride*	SCARIDAE	RH
TBIF	*Thalassoma bifasciatum*	LABRIDAE	PL

TABLE 3. Canonical Correspondance Analysis. VCP = Variance in cumulative percentage. SEV = Sums of eigenvalues. SACCA = Species association (Fig. 5). MCCA = Mobility groups (Fig. 8).

	SACCA			MCCA	
VCP	41.45	66.30	75.50	62.30	100.0
SEV	0.78	0.46	0.17	0.11	0.07

complex zones 6, 9, 10, 11, and 12, independent of their coral coverage. The lines of zones 1 to 5, 7, and 8 that had predominance of a single type of substrate (e.g., rubble, branching or foliaceous corals) had a higher slope and lower regression coefficient, indicative of a higher dominance within the assemblage and of a less diverse community respectively. All outlier points above the lines (omitted in Fig. 6 for better graphic visualization) correspond to the low and medium complexity sheltered zones and represent the dominant species of pomacentrids, gobiids and serranids (dwarf basses, *Serranus* sp.). More species were in areas with complex massive coral and rocky reef.

The non-parametric ANOVA (Kruskal Wallis) shows that fish abundance differs significantly between zones. Zones of rubble (1 and 2) and branching corals (5) had the higher fish abundance (Table 1, see Fig. 3 and 4 for most abundant species).

The Spearman rank-correlation analysis (Fig. 7) shows significant positive correlation between species-richness and index of diversity with habitat complexity and certain types of substrates such as rocks with encrusting red algae, dead and living massive coral, turf calcareous algae, rock-encrusting sponges. An inverse correlation was significant for species richness and fish diversity with the Simpson's index. Monotony (single type of substrate, value close to 1) was related to a less diverse fish community structure. Inverse correlations were also found with diversity parameters and dead and living branching coral, dead foliaceous coral, and turf-algae, and (on a lower level) for living foliaceous coral, calcareous algae, and rubble.

Fish abundance (indiv./census) seem positively correlated only with substrates like dead massive coral, sand, and erect sponges (Fig. 7), due to the high abundance

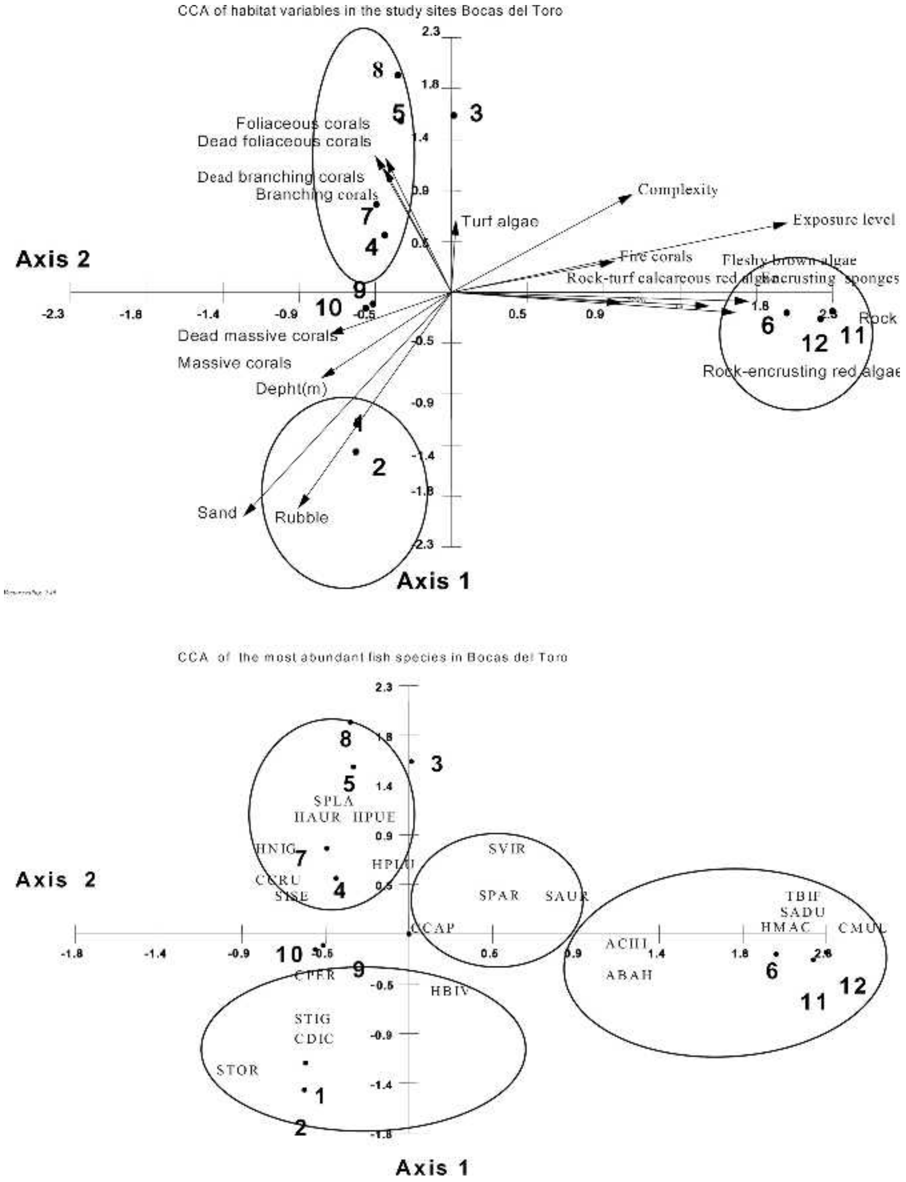


FIG. 5. Canonical Correspondence Analysis (CCA) for fish abundance vs. percentage of substrate coverage and environmental variables associated to respective zones (numbers) in Bocas del Toro, Panama. Species codes are shown on Table 2.

of the gobiid *Coryphopterus personatus* and the serranid *Serranus tortugarum*. Total fish-abundance was inversely correlated with hard substrates as living and dead branching coral, fire-coral with fleshy and turf brown algae (Fig. 7).

As seen in Table 1, the rocky shallow zone (12) had more fishes of high horizontal and vertical mobility (Category 1). Relatively sedentary species (Category 2) had similar abundance in rubble-sheltered zones (1 and 2) and exposed rocky reef (11 and 12). Site attached species (Category 3) were more represented in rubble (1 and 2), foliaceous (7 and 8) and massive coral zones (9 and 10). This association of mobil-

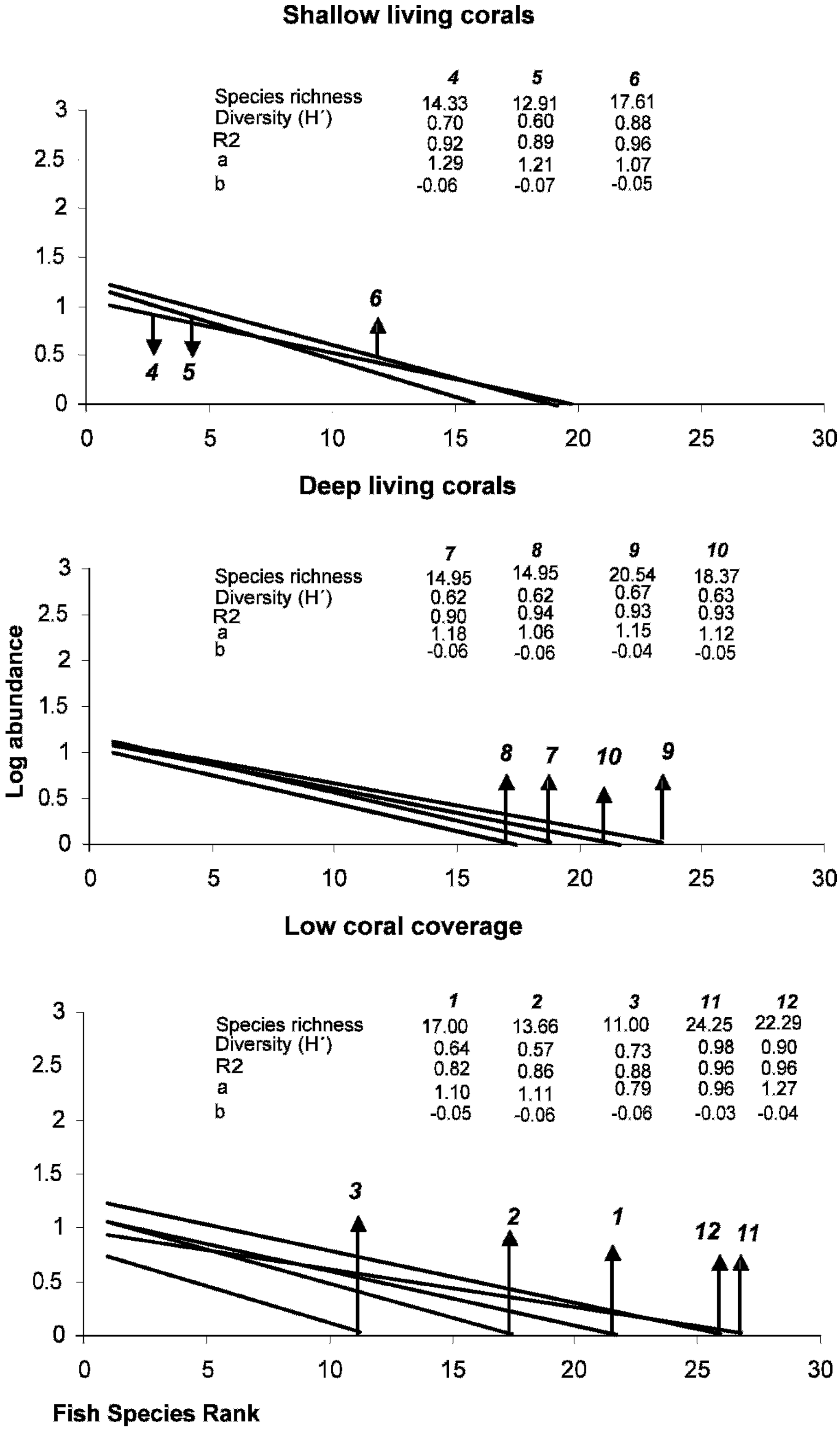


FIG. 6. Species Rank vs. log-abundance (log-series model). Shallow living coral (1.22-3.05 m); Deep living coral (5.9-7.9 m); Low coral coverage (3.8-8.15 m). Outlier points omitted for better graphic visualization.

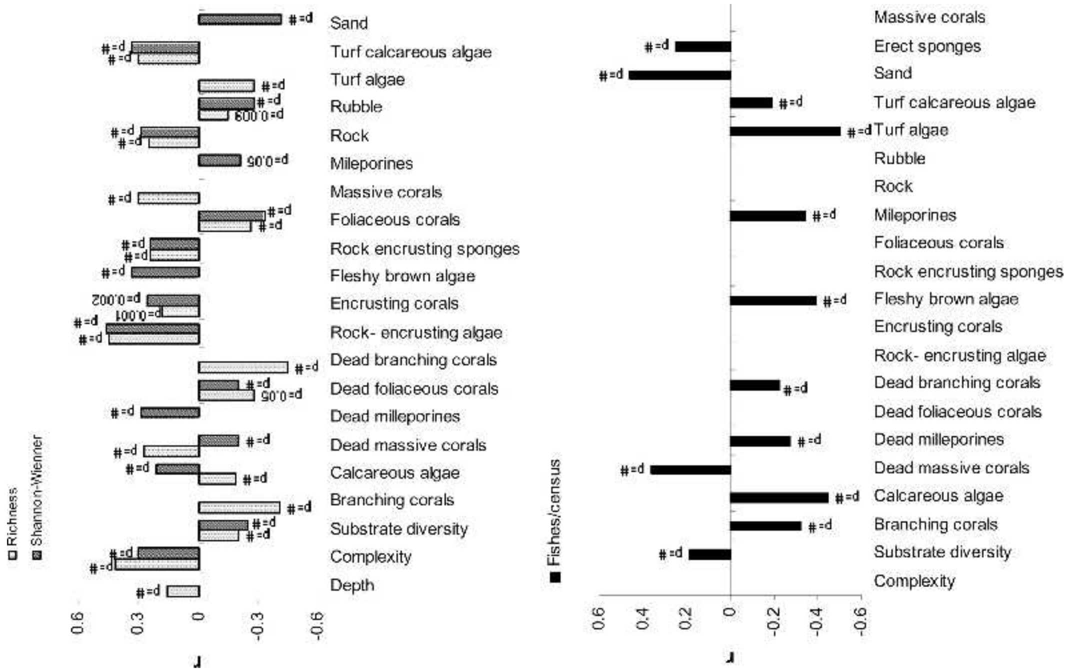


FIG. 7. Spearman rank correlations between fish community structure and habitat variables; n = 288, # = $p < 0.0001$.

ity groups or categories with certain habitat attributes and zones was revealed by the CCA-Analysis (12 zones; all species included Table 3; Appendix and Fig. 8), which shows the environmental variables by arrows and the Categories in the different zones in a single diagram. At the right (positive) side of Axis 2 a gradient of exposure is found (clockwise) with most exposed zones (11 and 12) associated with a habitat of rock-encrusting red algae. Fishes in Category 1 (high mobility species) were associated with this axis mainly by the presence of the planktivorous *Chromis multilineata, Thalassoma bifasciatum* and acanthurids. The area between the negative side of Axis 2 and negative side of Axis 1 shows, in an anti-clockwise direction, the sheltered zones with foliaceous corals (*Agaricia tenuifolia*) and the presence of massive and shallow branching corals reef (*Porites furcata*). Here, the Category 3 (site attached species) is mostly represented by *Coryphopterus personatus* and *Stegastes planifrons*. Category 2 (relatively sedentary species) in rubble-sheltered zones is mostly represented by *Serranus tortugarum* and this category is also related to exposed zones (11 and 12) where relatively sedentary families were more diverse (e.g., Serranidae, Balistidae) (Fig. 3, 4 and 8, Appendix).

As compared to sheltered areas, in most exposed and complex areas, such as Punta Bastimentos (12), Wild Cane (11), and Crawl Cay (6), fish of specific trophic groups (e.g., mobile-invertebrate feeders) increase in abundance and species numbers Herbivores accounted for 77% of the relative fish abundance in Bocas del Toro with a predominance of territorial herbivores in almost all zones. Their frequency increased toward sheltered zones; however roving herbivores (scarids and acanthurids) were less frequent in all zones.

Along with herbivores, demersal zooplankton feeders (in sheltered areas) and planktivores that use a larger part of the water column (at exposed zones) were common trophic groups in Bocas del Toro, but of low species numbers. Omnivores were more abundant in zones of rubble and sand; mobile-invertebrate feeders increased

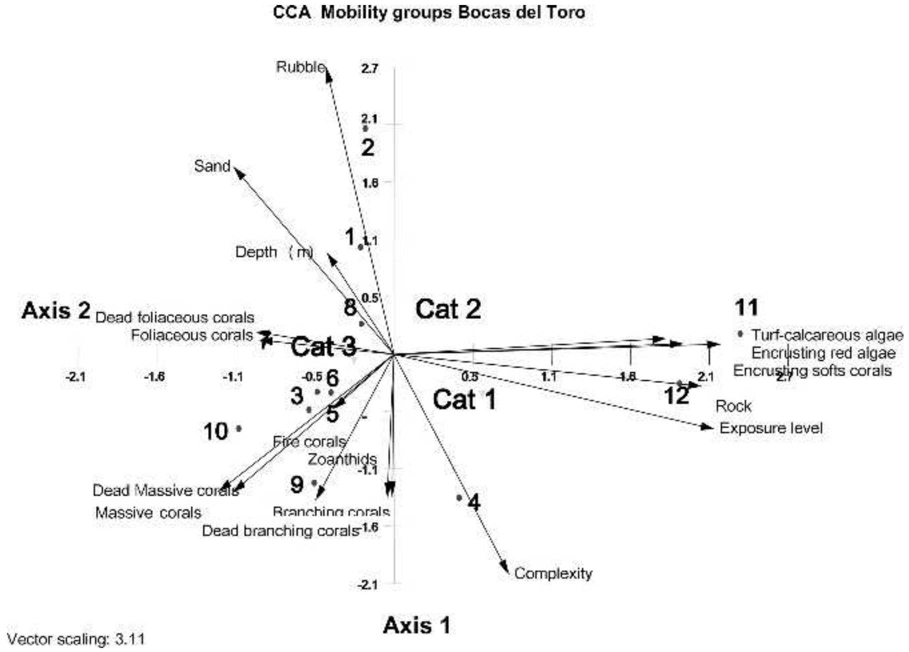


FIG. 8. Canonical Correspondence Analysis (CCA) mobility groups (categories) vs. percentage of substrate coverage and environmental variables associated to respective zone (numbers) in Bocas del Toro, Panama.

in relative abundance and diversity from sheltered to exposed zones.

Carnivores are less frequent compared to the other mentioned trophic groups, but included the majority of species. Their species number did not vary significantly among zones. Sessile-invertebrate feeders and piscivores were represented by few species and were found in low numbers only (Fig. 7).

DISCUSSION

Along with other factors, the distribution pattern of a species varies with ontogenetic morphological changes and shifts in habitat requirements (García-Charton and Pérez-Ruzafa 2001; Nagelkerken et al. 2000a,b). Some species ontogenetic movement between habitats may be directed towards more complex habitats and related to swimming ability of post recruits (see respective section). Few studies have been conducted in this field, but Aburto-Oropeza, and Balart (2001) found spatial variation and size-discrimination for eight of the most abundant species in the Gulf of California. The smaller individuals on low-complexity substrates may be able to hide while predators and other large fish may lack retreats. We consider these patterns also to play an important role for the organization of reef fish assemblage in Bocas del Toro.

Our results indicate that in many fish families species numbers increased toward more complex zones and densities of specialized feeders (e.g., herbivores) increase in sheltered zones. This pattern is marked in Labridae (particularly the genus *Halichoeres)*, Scaridae (*Scarus* sp.) and Pomacentridae (*Stegastes* sp.). Similar to what was found in some southern Caribbean reefs such as in Venezuela (Rodríguez and Villamizar 2000), the scarid *Scarus iseri* and the pomacentrid *Stegastes planifrons* are two of the most common fishes particularly in sheltered zones in Bocas del Toro, feeding on green turf algae that grows between branches or the coral *Porites* spp. and *Agaricia* spp. However, with the exception of *S. iseri*, none of the dominant species in Bocas del Toro are also dominant further North in Honduras (Clifton and Clifton 1998).

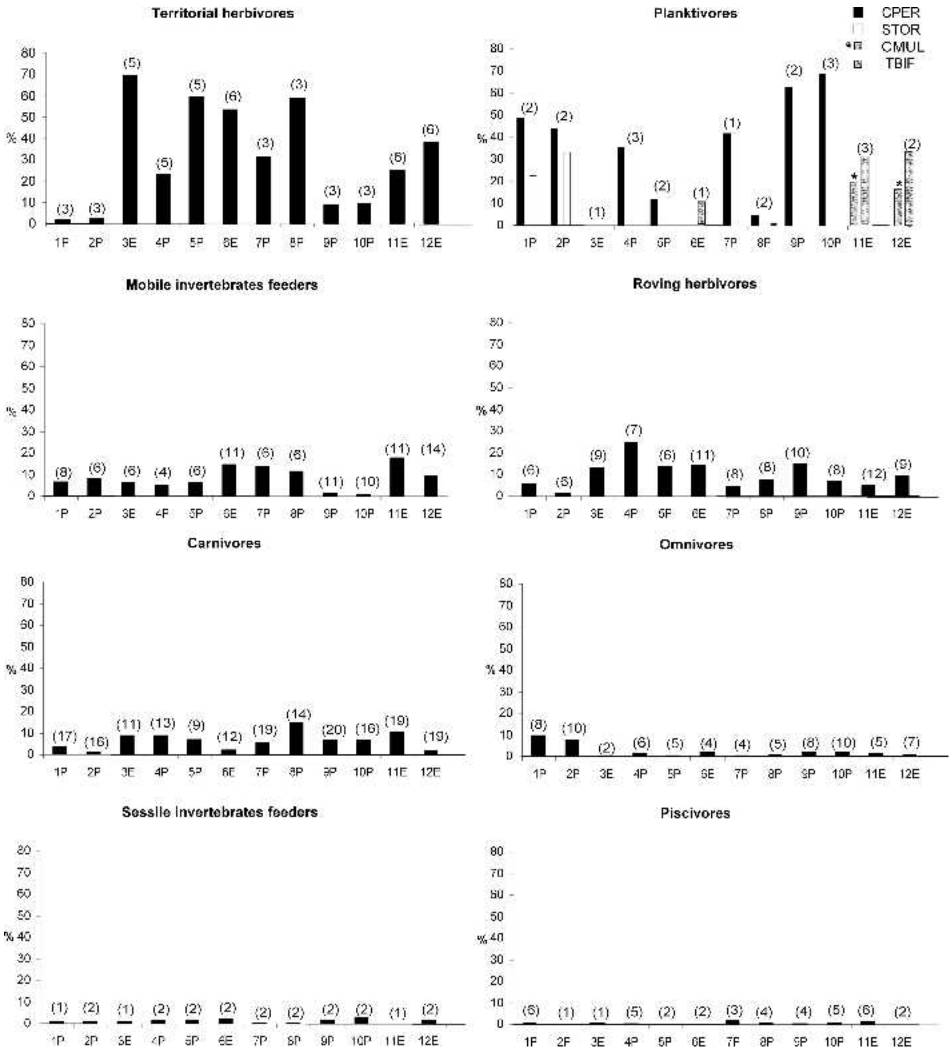


FIG. 9. Frequency, in percent, of the principal trophic groups in the different study zones; numbers in parenthesis indicate the number of species in each group. E = Exposed zone; P = Protected zone.

The species associations at exposed complex rocky shores and fire-coral reefs in Bocas del Toro (right side the CCA diagram) were similar to those of exposed coral reefs in Puerto Rico, but here there are no reported records of invertebrate feeders such as *Halichoeres poeyi* (HPOE) and *Halichoeres maculipinna* (HMAC) at exposed zones and in the same study an association between *Hypoplectrus chlorurus* (hamlets), *Stegastes planifrons* (SPLA), and *Holocentrus rufus* in areas of low water movements were found (McGeehee 1994). In Bocas del Toro, this association is replaced with similar genera but different species of hamlets along with schools of roving herbivores that can overcome the aggressiveness of damselfishes (Robertson et al. 1976). Haemulids were also present, and they may migrate from adjacent areas of mangroves. And the genus *Serranus* spp and *Coryphopterus dicrus* (CDIC) are typical inhabitants of sand-rubble areas. According to Floeter et al (2004), some of the species that were not associated to any particular habitat in our study are considered highly mobile and relatively sedentary *(Sparisoma* spp. and *Chaetodon capistratus* respectively*).* Even

Stegastes partitus is considered as territorial herbivore was in most zones. We believe that this is due to the fact that *S. partitus* is an omnivore that can either feed on zooplankton, small invertebrates and/or benthic algae at different exposed or sheltered zones (Booth and Hixon 1999). Differences in feeding behaviour among species of the same genus are an important factor in defining distributional patterns in Bocas del Toro as well. Randall (1967) found that the two species of blennies *Ophioblennius atlanticus* and *Parablennius marmoreus* have different feeding behaviour; the former feeding on algae growing in rocky shores and the latter, besides feeding on algae, feeds on many soft substrate animals that can often be found on patchy sandy habitats. The same author also found that *Halichoeres bivittatus* shows a higher feeding plasticity compared to other species on the genus and this is indicated by the many prey items found in their stomachs. This may be the reason why it is widely distributed on the different exposed and protected zones in Bocas del Toro. The more specialized foragers of the genus such as *Halichoeres radiatus* and *H. maculipinna* are present in the more complex exposed zones were they feed on particular food resources.

The species richness in Bocas del Toro is intermediate when compared with other studies from the Caribbean (Florida Keys 74 spp. McKenna 1997; Puerto Rico 71 spp. McGhee 1994; South-eastern Brazil 91 spp. Ferreira et al. 2001; Gulf of México 153 spp. Pattengill et al. 1997; Honduras 214 spp. Clifton and Clifton 1998; Colombia 273 spp. Mejía et al. 1998) and similar to that along the Pacific coast of the Isthmus (Gulf of Chiriquí, Dominici-Arosemena and Wolff unpublished data). Many of the regions of similar or lower species richness seem to lie close to the mainland and being affected by the runoff of rivers and environmental seasonality (Venezuela 68 spp. Rodríguez and Villamizar 2000; Costa Rica 48 spp. Sierra and García 1996). This situation also holds for Bocas del Toro.

Besides the consequences of geological changes (Coates et al. 1992), reef structure is regarded as a direct consequence of wave energy, while coral community structure, and to a greater extent fish community structure, seems a complex, indirect and non-linear consequence of reef structure and environmental conditions (Bradbury and Young 1981). In some studies, no correlation was found between fish diversity and habitat complexity (Ault and Johnson 1998; Clarke 1988). Studies in the Red Sea also suggest that coral cover has little influence on the species richness and abundance of fish (Roberts and Ormond 1987; Luckhurst and Luckhurst 1978). These findings are confirmed in Bocas de Toro due to the high abundance of small serranids and gobids in little complex rubble sand areas. We did, however, find positive correlations of species richness with hard substrates (massive corals and rocky complex reefs) along with an inverse correlation with monotony (less diverse substrate). It is suggested that the diverse strata in Bocas del Toro provide more niches and shelter, and thus increase species richness. Coral cover is also important in enhancing the physiographic structure in many of the more complex sheltered coral reefs in Bocas del Toro (e.g., zones 9 and 10). Recent studies on the Red Sea, by Khalaf and Kochzius (2002) also found total fish abundance and species richness to positively correlate with hard substrate and habitat diversity.

Waves and tides may play an important role in modifying the habitat structure (and by this increasing complexity) due to shaping of rocks and morphology of corals (Bradbury and Young 1981). In Bocas del Toro, exposed zones are physically more complex and the fish community is more diverse. But besides the influence of exposure in shaping the habitat, the presence of diverse and abundant food resources (e.g., oceanic plankton) is notorious in these exposed zones. Under these conditions, also sessile invertebrates (e.g., sponges) and algae increase the substrate diversity and allow, along with the rich food supply, for the occurrence of additional fish species.

The variability in reef fish larval transport and settlement is determined by the interaction of water masses and the effects of external forcing such as winds and tides.

In areas of low tidal variation, such as Bocas del Toro, winds may play an important intermittent role in larvae input to inshore sheltered zones while currents may play an important role for settlement and recruitment in exposed zones (Cowen 2002). Many horizontal patterns of community structure were described with respect to shore proximity, including occasional, completely isolated embayment (or lagoonal) assemblages. While water physics is important, larval distribution is not merely the result of passive dispersion by currents and tides. Particularly in areas of low current flow and small tidal range, many studies have found a high concentration of pomacentrid/gobiid larvae (see review by Cowen 2002). There is no information of larvae assemblages in Bocas del Toro, but our results indicate that these aforementioned families are the most abundant post-recruits in sheltered zones. From a comparative Mesoamerican perspective, patterns of spatial variation could markedly differ between Tropical Eastern Pacific (TEP) and Tropical Western Atlantic (TWA), since different oceanographic conditions could lead to differences in spatial patterns diversity. The large tidal fluctuation observed in the TEP (which can be several meters) in comparison with TWA (0.5 m) may facilitate larval transportation, settlement, and recruitment across a wider range of habitats than in the TEP.

Another reason for the spatial difference in the number of genera and species of reef fish in the study area may be the "habitat patchiness effect". Recent studies have found that the degree and the scale of habitat patchiness may be associated with fish diversity. Acosta and Robertson (2002) emphasize that species assemblages of small isolated habitat patches will constitute only a subset of the assemblage of a large patch reef, and the patterns of reef fish diversity may thus be highly scale dependent. In our study area the community differences were clearly marked between exposed and sheltered zones, although the total area per zone included in our sampling units were of the same size (600 m^2 in each habitat). We suggest that, with the exception of the continuous rocky reef (zones 11 and 12) and fire coral fringing reef (zone 6) areas, most of the sheltered zones can be considered as relatively isolated discontinuous patches, separated mostly by sand, sea grass and mangroves (Guzmán and Guevara 1998b). Even if we pool all these zones and count the total number of species, it will be lower than that of massive corals and exposed rocky and fire coral reef ones. This suggests that these types of habitat are vitally important for the fish species richness in Bocas de Toro due to their complexity, level of exposure, and interconnectivity with other substrates. It is also important to mention that in the province of Bocas del Toro we can find a particular "nestedness" of select families of obligated reef fishes in sheltered zones (e.g., aggregation of gobiids and pomacentrids). These nesting patterns seem to be associated with recruitment limitation at the reef scale (McLain and Pratt 1999).

Particular mobility guilds were found in Bocas del Toro, which were specific to certain zones: better swimmers are adapted to exposed rocky zones of strong currents. Small site attached species and territorial herbivores are present in high numbers in sheltered zones of massive and foliaceous coral reefs with little current influence. Most studies regarding these mobility guilds focused only on labrids and tried to link their swimming performance to fin morphology (Bellwood and Wainwright 2001; Bellwood et al. 2002). There is still no knowledge about the swimming ability of many of the other reef fish, however, and questions regarding their ability for vertical and horizontal movements after settlement and recruitment on different types of reef can as yet not be answered. We found a marked difference in the presence/absence of species (within families) between exposed and sheltered zones in Bocas de Toro. Besides labrids, spatial differences were found in species of territorial herbivores and scarids. While improved swimming performance is definitely an advantage in exposed zones with higher structural complexity and shelter availability, there must be a trade of between the energy loss for this high swimming activity and the energy gain through the high food abundance. Further research needs to determine if the distribution of certain species is more related to their swimming performance or/and type of food.

It seems that in the northern part of the Caribbean such as in the Gulf of México (including the Florida Keys), planktivores and invertebrate feeders dominate, while herbivores are low in numbers compared to Bocas del Toro (Bohnsack and Bannerot 1986; Pattengil et al. 1997). Here territorial herbivorous fishes are abundant and the areas they defend can cover over 80% of the surface of some reef habitats (Robertson and Lassig 1980; Ferreira et al. 1998; Ceccarelli et al. 2001). Ferreira et. al. (1998) mentioned that this trophic group may greatly depend on the physical structure of the coral reef and the distribution of the associated benthic organisms. An important part of the diet of some herbivores (e.g., *Scarus iseri*) is detritus and/or calcified material (Randall 1967). Browsing scarids (e.g., *Sparisoma*) that feed on some types of macro algae increase in abundance along with this food source at exposed and heterogeneous complex zones. Roving herbivores such as acanthurids have preference for certain types of algae common in exposed reef flats (Sluka and Miller 2001). Planktivores (e.g., *Serranus tortugarum*) at sheltered areas account for 20 to 70% of fishes in certain zones of rubble-sand. They swim above the bottom to mainly feed on demersal plankton (e.g., amphipods and harpadicoids copepods), found in low current areas (Randall 1967; Morales, Alvaro pers. comm.). This type of habitat is similar to that proposed by Parrish and Boland (2004) who called it "banks with infrequent relief features", where planktivorous are most numerous and benthic carnivores increased with an increased substrate complexity.

Bocas del Toro has been subjected to anthropogenic disturbances in recent years, due to its increasing importance as a popular tourist destination in the Republic of Panama. This will increase the human activities such as artisanal extractions, sport fishing and the use of the environmental landscape due to diving activities. This region lacks previous baseline data that could be used to organize sustainable fishery practices for the region. This study has provided the first description of the reef fish community structure, which can be used to help define areas of protection (Sale 2002). Even though more relevant studies are required to evaluate these ideas, we suggest that Bocas del Toro is an isolated site, where the population are likely to be maintained by self-recruitment and this types of regions needs particular guidelines to establish management plans (Sponaugle et al. 2002). Most of the smallest post recruit and juveniles that we found in our transects in sheltered zones belong to species that may have shorter pelagic larval duration (e.g., Gobiidae, Pomacentridae, Serranidae) in comparison to muraenids, balistids and tetraodontids that are families with the longest larval duration of reef fish families and were present occasionally only in exposed zones or in very lower numbers if not virtually absent in sheltered zones (Floeter and Gasparini 2000; Leis and McCormick 2002; Robertson 2001). In addition, in closed, shallow regions such as the internal sheltered zones of Bocas del Toro with low water circulation and changes in surface salinity may negatively affect the species richness of the Ichthyoplankton (Dominici-Arosemena et al. 2000; Romero 1992). Despite a few interconnected coral reefs in Southern Costa Rica, much of the remaining coastline stretching to the Southern boarder of Nicaragua is unsuitable for reef development due to sandy substrate, coastal marshes in the North, and the input of freshwater by San Juan River (Cortés pers. comm.). The abundance of larvae being transported from the reefs in Southern Nicaragua southwards are likely to decline resulting in low recruitment in Bocas del Toro. Thus, the distance from Northern reef develop areas and the presence of suitable interconnected substrate for larval settlement in neighbouring regions, may constitute an important function of settlement and recruitment in Bocas del Toro. We suggest that as a result of its particular oceanographic regime, larval recruitment may be low in Bocas del Toro and even what would normally be considered an average fishing pressure may be unsustainable. The highest-populated centres of the Bocas region are located at Isla Bastimentos, Isla Colón, and Carenero island, where some of the massive coral and rocky reefs are located. In our study we confirm that rocky zones are rich in species and should be included within the limits of the Bastimentos National Park (e.g., rocky shores of Bastimentos Island and areas of spear or other artisanal fisheries). In other studies, the reduction of three-dimensional structure has been identified as one cause for the shift in species composition (McKenna 1997), a process that is currently underway due to physical destruction of habitat (e.g., reef fishing, anchoring); which will directly or indirectly affect the fish community structure. Our results indicate a negative correlation of fish diversity with either the percentage of dead coral substrates and/or low substrate diversity zones (rubble, dead corals live branching and foliaceous corals) that normally result from habitat destruction or the growing of opportunistic species of corals due to the high sediment deposition (Cortés 1984). Our study supports the need for: 1. the protection of many reef areas and their benthic fauna (especially those zones of massive and fire coral cover) (for delineation of these areas, see Guzmán and Guevara 1998a,b, 1999); 2. the education of tourists to not destroy or extract the benthic flora and fauna; and 3. restrict the fishing activities in coral reef areas. There is also a need to delimit all reef zones to avoid anchorage of boats in reef areas. In addition, other anthropogenic impacts (e.g., sediment deposition from extensive banana plantations) are also affecting this area. For these regions, habitat degradation of the benthic fauna and flora could be faster than expected. The present situation of Bocas del Toro may already represent a fish community structure subject to human induced changes.

Acknowledgments.—This research was sponsored by the World Wildlife Fund (BMZ, Mesoamerican Biological corridor fellowship), with cooperation of the Centre for Marine Tropical Ecology in the University of Bremen (ZMT), The German Academic Exchange Service (DAAD), and the Smithsonian Tropical Research Institute (STRI) at the Bocas del Toro station. We thank Ross Robertson for his advice at STRI; and Carlos L. Ferreira, Sergio Floeter, Marc Kochzius, Matthias Birkicht, Suzanne Lao, Tom Nicolai, Fernando Zapata, Carlos Jiménez, Sabine Dittmann, Jorge Cortés, Hector Guzmán, Jorge Ventocilla, Nélida Gómez, David Kline, Gustavo Alcides Concheiro Pérez, Pedro Alcolado, Carlos Gamboa, Ghislain Rompré, Marc Taylor, Scott Smith, Alexander Schröder, Lukas Schäerer, Werner Ekau, Carlos Guevara, Uta Berger, Christian Jakob and Steve Robert Niedzielski who also contributed with their advice. Juan Gabriel Domínguez and Irving Bethancourt helped on field and data management, Arcadio Castillo and Willie Pomare, also helped on the field. We also thank Sabine Kadler, Christa Müller, Silke Meyerholz, Andreas Hanning, Kai Bergmann, Stefanie Bröhl, Dieter Peterke (ZMT), Harry Barnes, Luis Mou, Adriana Bilgray, Marissa Batista, Ernesto Peña, Edgardo Ochoa, Reynaldo Tapia and Mercedes Denis (STRI), for logistic and administrative support. Map and profile figures drawn by Marco Luque Parigi.

LITERATURE CITED

Acosta, C. A., and D. N. Robertson. 2002. Diversity in coral reef fish communities: the effects of habitat patchiness revisited. *Mar. Ecol. Prog. Ser.* 227:87-96.

Arburto-Oropeza, O., and E. Balart. 2001. Community structure of reef fish in several habitats of a rocky reef in the Gulf of California. *Mar. Ecol.* 22(4):283-305.

Ault, T. R., and C. R. Johnson. 1998. Spatially and temporary predictable fish communities on coral reefs. *Ecol.l Monogr.* 68(1):25-46.

Beck, M. W. 1997. A test of the generality of the effects of shelter bottlenecks in four stone crabs populations. *Ecology* 78:2487-2503.

Beck, M. W. 1998. Comparison of the measurement and effects of habitat structure on gastropods in rocky intertidal and mangrove habitats. *Mar. Ecol. Prog. Ser.* 169:165-178.

Bellwood, D. R. 1998. What are reef fishes? Comment on the report by D. R. Robertson: Do coral reef fish faunas have a distinctive taxonomic structure? (*Coral Reefs.* 17:179-186) *Coral Reefs* 17:187-189.

Bellwood, D. R., and P. C. Wainwright. 2001. Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. *Coral Reefs* 20:139-150

Bellwood, D. R., P. C. Wainwright, C. J. Fulton, and A. Hoey. 2002. Assembly rules and functional groups at global biogeographical scales. *Functl. Ecol*. 16: 557-562.

Bohnsack, J. A., and S. P. Bannerot. 1986. A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. *NOAA Tech. Rep. NMFS Cir*. 41:1-15.

Booth, D. J., and M. A. Hixon. 1999. Food ration and condition affect early survival of the coral reef damselfish, *Stegastes partitus. Oecologia* 121(3):364-368.

Bradbury, R. H., and P. C. Young. 1981. The effects of a major forcing function, wave energy, on a coral reef ecosystem. *Mar. Biol. Prog. Ser.* 5:229-241.

Briggs, J. C. 1995. Global Biogeography. *Developments in Paleontology and Stratigraphy*, 14, Amsterdam: Elsevier.

Caribbean Coastal Marine Productivity (CARICOMP). 2001. Methods Manual Levels 1 and 2. Manual of methods for mapping and monitoring of physical and biological parameters in the coastal zone of the Caribbean. *University of the West Indies Mona, Kingston Jamaica and Florida Institute of Oceanography.* 90 p.

Ceccarelli, D. M., G. P. Jones, and L. J. McCook. 2001. Territorial damselfishes as determinants of the structure of benthic communities on coral reefs. *Oceanogr. Mar. Biol. Annu. Rev.* 39:355-389.

Clarke, R. D. 1988. Chance and order in determining fish species composition on small coral patches. *J. Exp. Mar. Biol. Ecol.* 115:197-212.

Clifton, K E., and L. M. Clifton.1998. A survey of fishes from various coral reef habitats within the Cayos Cochinos Marine Reserve, Honduras. *Rev. Biol. Trop*. 46:109-124.

Coates, A. G., et al. 1992. Closure of the Isthmus of Panamá: the near-shore marine record of Costa Rica and Western Panamá. *Geol. Soc. Amer. Bull.* 104:814-828.

Collins, L. S., A. F. Budd, and A. G. Coates. 1996. Earliest evolution associated with closure of the Tropical American Seaway. *P. Natl. Acad. Sci.* 93:6069-6072.

Cortés, J., and M. J. Risk. 1984. El arrecife coralino del Parque Nacional Cahuita, Costa Rica. *Rev. Biol. Trop*. 32(1):109-121.

Cowen, R. K. 2002. Larval dispersal and retention and consequences for population conectivity. In *Coral reef fishes: dynamics and diversity in a complex ecosystem*, ed. P. F. Sale, 149-170. San Diego, CA.: Academic Press.

Dethier, M. N. 1994. The ecology of intertidal algal crusts: variation within a functional group. *J. Exp. Mar. Biol. Ecol.* 177:37-71.

Diehl, S. 1988. Foragins efficiency of three freshwater fishes: effects of structural complexity and light. *Oikos* 3:207-214.

Dolmer, P. 1998. The interactions between bed structure of *Mytilus edilus* L. and the predator *Asterias rubens* L. *J. Exp. Mar. Biol. Ecol.* 228:137-150.

Dominici-Arosemena A., E. Brugnoli-Olivera, S. Solano-Ulate, and A. Ramírez-Coghi. 2000. Ictioplancton en la zona portuaria de Limón, Costa Rica. *Rev. Biol. Trop.* 48(2):439-442.

English, S., C. Wilkinson, and V. Baker. 1994. *Survey manual for tropical marine resources*. Townsville: Australian Institute of Marine Science.

Erlandsson, J., V. Kostylev, and G. A. Williams. 1999. A field technique for estimating the influence of surface complexity on movement tortuosity in the tropical limpet *Cellana grata* Gould. *Ophelia* 50:215-224.

Ferreira, C. E. L., A. C. Peret, and R. Coutinho. 1998. Seasonal grazing rates and food processing by tropical herbivorous fishes. *J. Fish Biol.* 53:222-235.

Ferreira, C. E. L., J. E. A. Gonçalves, and R. Coutinho. 2001. Community structure of fishes and habitat complexity in a tropical rocky shore. *Env. Biol. Fish* 61:353-369.

Ferreira, C. E. L., S. R. Floeter, J. L. Gasparini, B. P. Ferreira, and J. C. Joyeux. 2004. Trophic structure patterns of brazilan reef fishes: a latitudinal comparison. *J. Biogeogr.* 31:1-13.

Floeter, S. R., and J. L. Gasparini. 2000. The southwestern Atlantic reef fish fauna: composition and zoogeographic patterns. *J. Fish Biol.* 56:1099-1114.

Floeter, S. R., et al. 2001. Geographic variation in reef-fish assemblages along the Brazilian coast. *Global Ecol. Biogeogr.* 10(4):423-433.

Floeter, S. R., C. E. L. Ferreira, A. Dominici-Arosemena, and I. Zalmon. 2004. Latitudinal gradients in Atlantic reef fish communities: trophic structure and spatial use patterns. *J. Fish Biol.* 64:1-20.

García-Chartron, J. A., and A. Pérez-Ruzafa. 2001. Spatial pattern and the habitat structure of a Mediterranean rocky reef fish local assemblage. *Mar. Biol.* 138:917-934.

Goldman, B., and F. H. Talbot. 1976. Aspects of the ecology of coral reef fishes. In *Biology and geology of coral reef,* ed. O. A. Endean, 125-154. New York: Academic Press.

Greb, L., et al. 1996. Ökologie ind Sedimentologie eines rezenten Rampensystem an der Karibikküste von Panama. *Profil Band* 10. Universität Stuttgart, 168 p.

Guzmán, H. M., and C. A. Guevara. 1998a. Arrecifes coralinos de Bocas del Toro, Panamá: I. Distribución,estructura, diversidad y estado de conservacion de los arrecifes continentales de la Laguna de Chiriquí y Bahia Almirante. *Rev. Biol. Trop.* 46(3): 601-622.

Guzmán, H. M., and C. A. Guevara. 1998b. Arrecifes coralinos de Bocas del Toro, Panamá: II. Distribución, estructura, diversidad y estado de conservación de los arrecifes de las Islas Bastimentos, Solarte, Carenero y Colón. *Rev. Biol. Trop*. 46(4): 889-912.

Guzmán, H. M., and C. A. Guevara. 1999. Arrecifes coralinos de Bocas del Toro, Panamá: III. Distribución, estructura, diversidad y estado de conservación de los arrecifes de las islas Pastores, Cristobal, Popa y Cayo Agua. *Rev. Biol. Trop.* 47(4): 659-676.

Hixon, M. A., and J. P. Beets. 1993. Predation, prey refuges, and the structure of coral-reef assemblages. *Ecol. Monogr*. 63:77-101.

Jones, G. P. 1988. Experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of two coral reefs fishes. *J. Exp. Mar. Biol. Ecol*. 123:115-126.

Jones, G. P., D .J. Ferrel, and P. F. Sale.1991. Fish predation and its impact on the invertebrates of coral reefs and adjacent sediments. In *The ecology of fishes on coral reefs,* ed. P. F. Sale, 156-179. San Diego, CA.: Academic Press.

Jones, G. P., and M. I. McCormick. 2002. Numerical and energetic processes in the Ecology of coral reef fishes. In *Coral reef fishes: dynamics and diversity in a complex ecosystem,* ed. P. F. Sale, 221-238. San Diego, CA.: Academic Press.

Khalaf, M. A., and M. Kochzius. 2002. Changes in trophic community structure of shore fishes at an industrial site in the Gulf of Aqaba. *Mar. Ecol. Progr. Ser.* 239:287-299.

Leis, J. M., and M. I. McCormick. 2002. The Biology, behaviour, and Ecology of the pelagic, larval stage of coral reef fishes. In *Coral reef fishes: dynamics and diversity in a complex ecosystem*, ed. P. F. Sale, 171-199. San Diego, CA.: Academic Press.

Levin, P. S., and C. B. Grimes. 2002. Reefs fish Ecology and grouper conservation and management. In *Coral reef fishes: dynamics and diversity in a complex ecosystem,* ed. P. F. Sale, 377-389. San Diego, CA.: Academic Press.

Luckhurst, B. E., and K. Luckhurst. 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Mar. Biol*. 49:317-323.

McGehee, A. 1994. Correspondence between assemblages of coral reef fishes and gradients of water motion depth, and substrate size off Puerto Rico. *Mar. Ecol. Prog. Ser.* 105:243-255.

McKenna, J. 1997. Influence of Physical Disturbance on the Structure of Coral Reef Fish Assemblages in the Dry Tortugas. *Caribb. J. Sci.*. 33(1-2):82-97.

McLain, D. K., and A. E. Pratt. 1999. Nestedness of coral reef fishes accross a set of fringing reefs. *Oikos* 85:53-67.

Mejía, L. S., J. Garzón-Ferreira, and A. Acero. 1998. Peces registrados en los complejos arrecifales de los cayos Courtown, Albuquerque y los bancos Serrana y Roncador, Caribe occidental, Colombia. *Bol. Ecotrópica* 32:25-41.

Nagelkerken, I., M. Dorenbosch, W. C. E. P. Verberk, E. Cocheret de la Morinière, and G. van der Velde. 2000a. Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution. *Mar. Ecol. Progr. Ser.* 202: 175-192.

Nagelkerken, I., et al. 2000b Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuar. Coast. Shelf Sci.* 51:31-44.

Parrish, F. A., and R. C. Boland. 2004. Habitat and reef-fish assemblages of banks in the North Western Hawaiian Islands. *Marine Biology* www.springerlink.com/index/WY3L2F2VX6U83AQP.pdf

Pattengill, C. V., B. X. Semmens, and S. R. Gittings. 1997 Reef fish trophic structure at the Flower Gardens and Stetson Bank, NW Gulf of Mexico. *Proc. 8th Int. Coral Reef Sym*. 1:1023-1028.

Peet, R. K. 1974. The measurement of species diversity. *Ann. Rev. Ecol. Syst.* 5:285-307.

Pielou, E. C. 1975. *Ecological diversity*. New York: John Wiley and Sons.

Randall, J. E. 1967. Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogr.* 5:665-847.

Roberts, M. R., and R. F. G. Ormond. 1987. Habitat complexity and coral reef diversity and abundance on Red Sea fringing reefs. *Mar. Ecol. Prog. Ser.* 41: 1-8.

Robertson, D. R., H. P. A. Sweatman, E. A. Fletcher, and M. G. Cleland. 1976. Schooling as a mechanism for circumventing the territoriality of competitors. *Ecology* 57:1208-1220.

Robertson, D. R., and B. Lassig. 1980. Spatial distribution patterns and coexistence of a group of territorial damselfishes from the Great Barrier Reef. *Bull. Mar. Sci.* 30:187-203.

Robertson, D. R. 1998. Do coral-reef fish faunas have a distinctive taxonomic structure? *Coral Reefs* 17:1-8.

Robertson, D. R. 2001. Population maintenance among tropical reef fishes: Inferences from small-island endemics. PNAS. 98:5667-5670.

Rodríguez, J., and E. Villamizar 2000. Estructura de la comunidad de peces arrecifales de playa Mero, Parque Nacional Morrocoy, Venezuela. *Rev. Biol. Trop.* 48(1):107-113.

Rogers, C. S., G. Garrison, R. Grober, Z. M. Hillis, and M. A. Franke. 1994. Coral reef monitoring manual for the Caribbean and Western Atlantic. *Southern Regional Office National Park Service. The Nature Conservancy WWF.* 100 pp.

Romero, M. 1992. Ictioplancton de la región nororiental de la plataforma de Cuba (Zona D). *Cienc. Biol.* 8:82-94.

Sagarin, R. D., and S. D. Gaines 2002. The abundance 'Centre' distribution: To what extend is it a biogeographical rule? *Ecol. Lett.* 5:137-147.

Sale, P. F. 2002. The science we need to develop for more effective management. In *Coral reef fishes: dynamics and diversity in a complex ecosystem,* ed. P. F. Sale, 361-376. San Diego, CA.: Academic Press.

Siegel, S. 1970. *Estadística no-paramétrica aplicada a las ciencias de la conducta.,* México, D.F.: Trillas.

Sierra, L. M., R. Claro, J. P. García-Arteaga, and E. Valdés-Muñoz. 1990. Estructura trófica de las comunidades de peces que habitan en diferentes biótopos del Golfo de Batabanó. In *Asociaciones de peces en el Golfo de Batabanó,* ed. R. Claro, 83-95, La Habana, Cuba: Editorial Academia.

Sierra, L. M., and J. P. García. 1996. Estructura de las comunidades de peces y la pesca artesanal en los arrecifes coralinos del Caribe costarricense. *Resúmenes del 8vo simposio de arrecifes de coral*, Panamá, p. 182.

Sluka, R. D., and M. W. Miller. 2001. Herbivorous fish assemblages and herbivory pressure on Laamu Atoll, Republic of Maldives. *Coral Reefs* 20:255-262.

Sokal, R. R., and F. G. Rohlf. 1980. *Biometry*. San Francisco, CA.: Freeman.

Sponaugle, S., et al. 2002. Predicting self-recruitment in marine populations: Biophysical correlates and mechanisms. *Bull. Mar. Sci.* 70(1):341-375.

Steneck, R. S., and M. N. Dethier. 1994. A functional group approach to the structure of algal dominated communities. *Oikos* 69:476-498.

Talbot, F. H., and B. Goldman. 1972. A preliminary report on the diversity and feeding relationships of the reef fishes of One Tree Island, Great Barrier Reef system. *Proc. First Intl. Coral Reef Symp*. 1:425-440.

Ter Braak, C. J. F., and P. F. M. Verdonschot. 1995. Canonical correspondance analisys and related multivariate methods in aquatic ecology. *Aquat. Sci*. 57:255-289.

Veron, J. E. N. 1995. *Corals in space and time*. Ithaca, NY.: Cornell University Press.

Wolff, M., and E. Alarcón 1993. Structure of a scallop *Argopecten purpuratus* (Lamarck, 1819) dominated subtidal macro-invertebrate assemblage in Northern Chile. *J. Shellfish Res.* 12(2):295-304.

Zar, J. H. 1996. *Biostatistical analysis*, 3rd ed. Upper Saddle River, New Jersey: Prentice Hall.

APPENDIX. List of species found and their distribution in the study zones (1-12). TL = Trophic Level; C = Carnivorous; I = mobile Invertebrates; O = Omnivore; P = Piscivore; PL = Planctivore; RH = Roving Herbivore; SI = Sessile Invertebrate feeder; TH = Territorial Herbivore.

Family/Name	TL	1	2	3	4	5	6	7	8	9	10	11	12
ACANTHURIDAE													
Acanthurus bahianus	RH	X	X	X	X	X	X	X	X	X	X	X	X
Acanthurus chirurgus	RH	X	X	X	X	X	X			X	X	X	X
Acanthurus coeruleus	RH	X		X	X	X	X	X		X	X	X	X
APOGONIDAE													
Apogon townsendi	MI										X		
Apogon pseudomaculatus	MI											X	
AULOSTOMIDAE													
Aulostomus maculatus	C			X			X	X	X	X	X		
BALISTIDAE													
Aluterus scriptus	O											X	
Balistes vetula	SI											X	
Cantherhines pullus	O											X	X
BLENNIDAE													
Ophioblennius atlanticus	TH						X					X	X
Parablennius marmoreus	O	X	X					X		X	X		
BOTHIDAE													
Bothus lunnatus	C												X
CARANGIDAE													
Carangoides bartholomaei	P	X								X	X	X	
Caranx crysos	P				X	X		X	X	X	X	X	X
Caranx ruber	P	X	X	X	X		X	X	X	X	X	X	X
Chloroscombrus chrysurus	Pl										X		
Decapterus punctatus	C				X				X	X	X		
Decapterus sp.	C				X			X					
CHAETODOTIDAE													
Chaetodon capistratus	SI	X	X	X	X	X	X	X	X	X	X		X
Chaetodon ocellatus	O	X	X		X		X	X	X	X	X		X
Chaetodon striatus	SI		X		X	X	X	X	X	X	X		X
CIRRHITIDAE													
Amblycirrhitus pinos	C											X	
DASYATIDAE													
Dasyatis americana	O	X	X						X	X	X		
DIODONTIDAE													
Diodon holocanthus	MI									X			
Diodon hystrix	MI										X		X
ELOPIDAE													
Megalops atlanticus	C								X				
GERREIDAE													
Gerres cinereus	MI	X	X								X		
GINGLYMOSTOMATIDAE	MI												
Ginglymostoma cirratum	C	X	X										
GOBIIDAE													
Coryphopterus dicrus	O	X	X			X				X	X		
Coryphopterus personatus	PL	X	X		X	X		X	X	X	X		
Gnatholepis thompsoni	O										X		
Ctenogobius saepepallens	O	X	X										
Elacatinus dilepsis	O										X		
Elacatinus xanthiprora	O	X	X			X				X	X	X	
Elacatinus sp.	O		X										
GRAMMATIDAE													
Gramma loreto	MI											X	

APPENDIX. Continued.

Family/Name	TL	1	2	3	4	5	6	7	8	9	10	11	12
HAEMULIDAE													
Anisotremus surinamensis	C											X	
Anisotremus virginicus	MI	X			X		X	X		X	X	X	X
Haemulon aurolineatum	MI		X			X		X	X	X		X	X
Haemulon carbonarium	MI	X					X			X		X	
Haemulon chrysargyreum	MI						X	X					
Haemulon flavolineatum	MI			X	X	X	X	X	X	X	X	X	X
Haemulon macrostomum	MI			X		X	X				X	X	X
Haemulon parra	C									X			
Haemulon plumierii	C	X	X	X	X	X	X	X	X	X	X	X	X
Haemulon sciurus	C	X					X					X	X
HOLOCENTRIDAE													
Holocentrus adscensionis	C	X	X	X	X	X	X	X	X	X		X	X
Holocentrus rufus	C							X			X	X	X
Myripristis jacobus	C							X	X			X	X
Neoniphon marianus	MI								X				
Sargocentron vexillarium	C										X	X	X
KYPHOSIDAE													
Kyphosus sectator	RH						X		X			X	
LABRIDAE													
Bodianus rufus	MI											X	X
Halichoeres bivittatus	MI	X	X	X	X	X	X		X	X	X	X	X
Halichoeres garnoti	MI							X	X	X	X	X	X
Halichoeres maculipinna	MI	X		X			X					X	X
Halichoeres pictus	MI											X	X
Halichoeres poeyi	MI			X			X					X	X
Halichoeres radiatus	MI											X	X
Lachnolaimus maximus	MI									X			
Thalassoma bifasciatum	PL			X	X	X	X	X	X	X	X	X	X
LABRISOMIDAE													
Labrisomus nuchipinnis	C											X	
Malacoctenus triangulatus	MI		X				X				X	X	X
LUTJANIDAE													
Lutjanus analis	C	X	X				X	X		X	X	X	X
Lutjanus apodus	C	X	X				X		X	X	X	X	X
Lutjanus cyanopterus	C												X
Lutjanus griseus	C	X			X			X		X			
Lutjanus jocu	C	X	X					X					
Lutjanus mahogoni	C	X			X		X			X		X	
Lutjanus synagris	C		X									X	
Ocyurus chrysurus	C	X	X	X	X	X	X	X	X	X	X	X	X
MALACANTHIDAE													
Malacanthus plumieri	C		X										
MULLIDAE													
Mulloidichthys martinicus	MI	X	X			X	X	X		X	X	X	X
Pseudupeneus maculates	C	X	X	X	X	X		X	X	X	X	X	X
MURAENIDAE													
Echidna catenata	C												X
Gymnothorax miliaris	C												X
OPISTOGNATHIDAE													
Opistognathus aurifrons	PL	X	X	X				X				X	
OSTRACIIDAE													
Lactophrys triqueter	O												X

Appendix. Continued.

Family/Name	TL	1	2	3	4	5	6	7	8	9	10	11	12
Pempheridae													
Pempheris schomburgkii	PL						X					X	
Pomacanthidae													
Holacanthus ciliaris	O				X		X			X		X	X
Holacanthus tricolor	O		X						X		X		X
Pomacanthus arcuatus	O		X	X	X	X		X	X	X	X		
Pomacentridae													
Abudefduf saxatilis	O				X	X	X		X		X		X
Chromis cyanea	PL											X	
Chromis multilineata	PL											X	X
Microspathodon chrysurus	TH			X	X	X	X					X	X
Stegastes adustus	TH			X	X	X	X					X	X
Stegastes leucostictus	TH	X	X	X	X	X	X	X	X	X	X	X	X
Stegastes partitus	TH	X	X	X	X	X	X	X	X	X	X	X	X
Stegastes planifrons	TH	X	X	X	X	X	X	X	X	X	X	X	X
Scaridae													
Scarus coelestinus	RH			X			X	X	X	X		X	
Scarus iseri	RH	X	X	X	X	X	X	X	X	X	X	X	X
Scarus taeniopterus	RH									X			
Scarus vetula	RH											X	
Sparisoma aurofrenatum	RH		X	X	X	X	X	X	X	X	X	X	X
Sparisoma chrysopterum	RH	X	X				X	X	X	X	X	X	X
Sparisoma radians	RH			X			X					X	X
Sparisoma rubripinne	RH			X	X		X	X	X	X	X	X	X
Sparisoma viride	RH	X	X	X	X	X	X	X	X	X	X	X	X
Sciaenidae													
Equetus punctatus	MI	X						X	X	X			
Odontoscion dentex	C			X				X	X	X	X	X	
Scombridae													
Scomberomorus maculatus	P	X			X								
Scomberomorus regalis	P	X			X	X			X		X	X	
Serranidae													
Epinephelus adscensionis	C									X	X		
Cephalopholis cruentata	C	X	X	X	X	X	X	X	X	X	X	X	X
Cephalopholis fulva	C									X		X	X
Epinephelus guttatus	C									X		X	X
Epinephelus striatus	C												X
Hypoplectrus aberrans	C							X					
Hypoplectrus guttavarius	C									X			
Hypoplectrus indigo	C		X					X					
Hypoplectrus nigricans	C	X	X	X	X	X		X	X	X	X		
Hypoplectrus puella	C	X	X	X	X	X	X	X	X	X	X		
Hypoplectrus sp.	C	X	X	X	X	X	X	X		X			
Hypoplectrus unicolor	C	X	X	X	X	X		X	X	X	X		
Mycteroperca venenosa	C										X		
Rypticus maculatus	C						X						
Rypticus saponaceus	C												X
Serranus baldwini	MI											X	
Serranus tigrinus	MI	X	X	X	X	X				X	X	X	X
Serranus tortugarum	PL	X	X		X								
Sparidae													
Archosargus rhomboidalis	O	X			X		X						
Calamus penna	MI	X	X			X				X			
Sphyraenidae													
Sphyraena barracuda	P	X			X		X		X			X	

APPENDIX. Continued.

Family/Name	TL	1	2	3	4	5	6	7	8	9	10	11	12
SYNODONTIDAE													
Synodus intermedius	P	X						X		X	X	X	
TETRAODONTIDAE													
Canthigaster rostrata	O	X	X	X	X	X		X	X	X	X	X	X
Sphoeroides spengleri	O	X								X			
UROLOPHIDAE													
Urobatis jamaicensis	C	X											

6.4 Publication II

REEF FISH COMMUNITY STRUCTURE IN THE TROPICAL EASTERN PACIFIC (PANAMA) : LIVING ON A RELATIVELY STABLE ROCKY REEF ENVIRONMENT

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Reef fish community structure in the Tropical Eastern Pacific (Panamá): Living on a relatively stable rocky reef environment

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Abstract: We compared the community structure of reef fish over different physical complexities in 12 study zones of Bahía Honda, Gulf of Chiriquí (BH-GCH), Tropical Eastern Pacific (TEP), Panama, aiming at an analysis of the importance of the physical structure provided by corals, rocks and benthic sessile organisms. This was the first region that emerged in the Isthmus of Panama; it exhibits the oldest benthic fauna and has constant conditions in terms of temperature and salinity. 288 visual fish censuses were conducted on 48 benthic transects from February to July 2003. 126 fish species of 44 families were found. Plankton feeding pomacentrids and labrids along with haemulids that feed on mobile invertebrates were the most abundant, particularly in shallow areas. 14 species showed size-segregations between zones, suggesting ontogenetic migrations (smaller fishes in shallow high-complexity zones, larger-sized fishes in deeper habitats). Highly mobile and site-attached genera were abundant in most shallow-wave exposed zones particularly on exposed rocky substrates. Planktivores were the most abundant, followed by carnivores, feeders on mobile invertebrate and piscivores. Herbivores and feeders on sessile invertebrate were lower in abundance. Species richness exceeds that of any other studied region close to the mainland in the TEP and correlates with substrate diversity, increasing size-heterogeneity of holes and structural complexity. Species diversity increases with habitat complexity and benthic diversity. It seems that water current strength, tides and waves which select for swimming, play an important role in the community organization. The study region has been proposed as a refuge-centre in the TEP, where reef fishes that evolved on coral reefs have shifted their distribution onto rocky reef habitats.

Keywords: Fish diversity, Distribution, Trophic groups, Rocky reef, Tropical Eastern Pacific.

Introduction

Ocean basins may promote speciation within a region during periods of low sea levels, and extensive shallow habitats can reduce faunal losses by acting as a refuge or centre of accumulation (Springer and Williams 1994; Paulay 1996; Wilson and Rosen 1998 ; Palumbi 1997; Bellwood and Hughes 2001). It has been suggested that reef fish have evolved along with the coral communities they are associated with, but that their ancestors have existed even prior to the coral reefs (Bellwood and Wainwright 2002). Thus, the recent reef dwellers would represent derived forms, with ancestors which would have occupied non-reef habitats (Bellwood and Wainwright 2002). In this respect, it should be considered that tropical reef fishes indeed occupy non-coral builded habitats such as rocky shores that are predominant in the Tropical Eastern Pacific (TEP). The fish fauna in this region has a north-south division, and subdivisions can be based on the highly localized endemism of small benthic rocky reef-associated fishes (Hastings and Robertson 2001). In the Central American Isthmus, besides the Golfo Dulce in Costa Rica, a fiord-like tropical embayment with anoxic deep waters (Quesada-Alpízar and Morales-Ramírez 2004; Wolff et al. 1996) and low coral development (Cortés 1990), the first uplifted region where new reef development started is the open area of the Gulf of Chiriquí (GCH). Here are the oldest corals of modern reefs in the TEP displaying maximum thickness and accretion rates (Cortés 1993, 1997). This region comprises the largest archipelago of rocky islands in the TEP (Kwiecinski and Chial 1983; Glynn and Maté 1997). Due to its inaccessibility, detailed biological studies are still lacking. The fish community structure of this region is particularly interesting from the perspective of population biology and biogeography due to its geological history and environmental stability (Kwiecinski and Chial 1983; Glynn and Maté 1997). The GCH forms part of the Panamic province of the TEP, and there is only one recent inventory in the Coiba National Park by Vega and Villarreal (2003), which includes many reef fish with the exception of the cryptic ones (e.g. gobiids, chaenopsids). Some pioneering studies have already addressed variations of the reef fish community structure in the reef areas in TEP (Zapata and Morales 1997;

Arburto-Oropeza and Balart 2001; Dominici-Arosemena et al. 2005). Belonging to the lower Mesoamerica, this region offers unique opportunities for comparative fish community studies (e.g. non-reef vs. coral reef environments; TEP vs. Tropical Western Atlantic, TWA) (Robertson 1998). It is believed that this region has a very diverse fish fauna, and that a significant component of it is made up of resident transpacific fishes that may live on reefs elsewhere in the Pacific (Robertson 1998). There is a sufficient diversity of habitats allowing for meaningful biological comparisons with the lower Mesoamerican TWA.

For comparative purposes we have conducted recently a similar study on the Caribbean west side of the Isthmus in Bocas del Toro (Dominici-Arosemena and Wolff 2005). Both the Caribbean and the Pacific side of Western Panama exhibit a rich landscape, and it was these parts which in geologic times (7-3 million years ago) became first interconnected by a shallow shelf (while Eastern Panama was still lacking a shelf area) when the isthmus started to rise, finally resulting in the fusion of the North and South American continents and the separation of the two oceans (Bermingham et al 1997).

While the Indo-Pacific regions have been suggested as evolutionary source of many reef fish species worldwide (Mora et al. 2003), the TWA is believed to be the centre of diversity for both fish and corals in the Atlantic Ocean (Briggs 1995; Veron 1995; Floeter and Gasparini 2000). However, the available information on the TEP does not allow for the determination of gradients in fish diversity in the Mesoamerican region and for the verification of the basic assumption of higher diversity of reef fish in the TWA compared to the TEP.

The main objective of the present study was thus to characterise the fish assemblages of Bahía Honda (BH-GCH, TEP) along spatial scales and gradients of substrate complexity.

It is hypothesized that due to its environmental stability (as compared to other TEP regions), its relative old age and great habitat diversity, a relatively rich reef fish community has evolved. Since this and other regions of the TEP have been subjected to a massive decrease in coral diversity due to geological changes, we suspect that reef fish may have evolved and diversified on the available rocky substrates with high benthic diversity and complexity in a similar way as have other reef fish communities on (diverse) coral reefs elsewhere. We thus propose that corals do not play the same reef community-structuring role here as in the Indo-Pacific and the Caribbean, and we postulate that reef fish communities may just represent species guilds related to hard substrates of diverse complexity.

The TEP region is the most unstable province in the whole Pacific where reef communities are adapted to geological changes, and to temperature decreases due to coastal upwelling. In the non-upwelling GCH (where temperatures are higher with relatively low seasonality) fishes and benthic fauna that recruit from more unstable regions may be adapted to short scale disturbances, particularly warming events (e.g. ENSO; for disturbance resistance in corals on this region, see D'Croz and Maté 2004). Even though research is pending in this field, the fishes in GCH, TEP may have developed some resistance to environmental changes, and suitable habitats should have promoted their speciation and diversification in the region.

The study thus aims at an analysis of the relative importance of the physical structure provided by corals, rocks and benthic sessile organisms for the reef fish community organization.

Furthermore, we studied the coexistence of subordinate species with dominant species by differential habitat use (i.e. different mobility and home range, size frequencies, territoriality, trophic organization), the importance of wave exposure and current regime for structuring the community, and the role of reef type (i.e. coral reefs vs. rocky reefs) and general substrate diversity and complexity for shaping the fish community.

Materials and Methods

Study area

The Pacific coast of Panama is divided by the Azuero Peninsula into two major areas with notable oceanographic differences: the upwelling Gulf of Panama to the East and, protected from northern trade winds by the mountains, the non-upwelling stable GCH to the West (D'Croz and Robertson 1997; Glynn and Maté 1997). Study sites were located in the latter (7º 50´ N, 81º 35` W; Fig. 1). Sampling was carried out from February to July 2003.

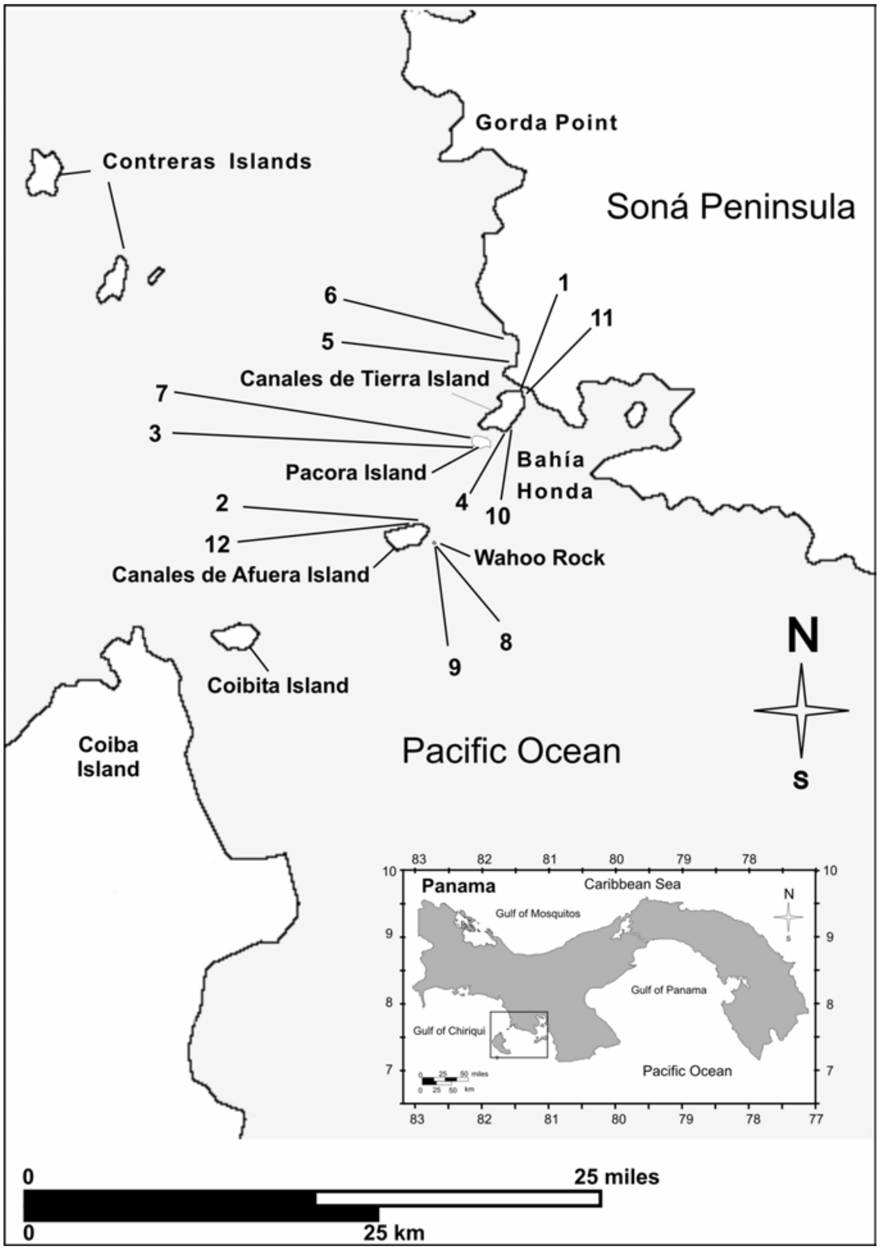


Fig. 1 Sampled reef zones in Bahía Honda , Gulf of Chiriquí. 1. Isla Canales de tierra ; 2. Canales de Afuera; 3. Isla Pacora; 4. Bonsai key; 5. Isla Mona; 6. Punta Gorda; 7. Isla Pacora; 8. Wahoo Rock key; 9. Wahoo rock; 10. Bonsai Cay; 11. Isla Canales de tierra; 12. Isla Canales de afuera

The GCH has a rainy climate compared to the Gulf of Panama. The coverage of living coral decreases with depth due to an increase in turbidity, and the region has large tidal variations of up to 3-4 m (Glynn and Maté 1997; NOAA/NOS 2005). There are fringing pocilloporid patch reefs over rocks between BH and other regions close to the mainland. Coral and rocky reefs are present also off shore on the Canales de Afuera Island, which is part of the Coiba National Park (Cardiel et al. 1997).

12 study zones were classified in terms of depth, substrate topography, cover, kind of benthic organisms and inorganic substrates. The selection of study zones was based on a previous survey aimed at identifying areas of different but characteristic habitats of the region.

Habitat characterisation

In each of the twelve zones, four benthic transects of 30 m length each were set up parallel to the shore. Substrate coverage and surface complexity was estimated using a link-chain methodology (CARICOMP 2001; Rogers et al. 1994). The benthic surface measures were taken along the chain laid out limp to follow the surface contour of the substrate. The ratio between the length of the chain laid over the substrate and the direct linear length from the beginning to the end of each transect was used to estimate the structural complexity of the substrate. The type of substrate under each segment of the chain was recorded and the length of the contour for each portion was then estimated as 1.6 cm per chain-link. Following Ferreira el al. (2001) we considered the number and size of holes as an additional complexity variable. For this, we counted the holes present along both sides of each transect (2.5 m) on all types of habitats and measured their size with a PVC ruler.

Habitat structure

A detailed description of the coral composition of the region can be found in Glynn and Maté (1997). The substrate codes assigned for substrate categories are found in Table 1, and according to the indexes obtained for surface complexity, we classified the zones as follows: 1 to 3 low complexity, 4 to 6 intermediate, and 7 to 12 high complexity (Fig. 2).

Sand and rubble (SRU; 1–2): Found in deeper areas adjacent to patches of the branching coral *Pocillopora* sp., and with a mixture of dead pieces of coral and sand.

Table 1 Substrate codes

Code	Category
BDC	Branching dead corals
DMC	Dead massive corals
DYC	*Dictyota* spp
EBA	Rock-Encrusting brown algae
EC	Rock-Encrusting corals
ERA	Rock-Encrusting red algae
ECS	Rock-Encrusting sponges
ES	Erect sponges
FBA	Fleshy brown algae *(Padina spp)*
FRADBC	Fleshy red algae/dead branching corals
MC	Massive corals
PD	*Pocillopora damicornis*
PE	*Pocillopora elegans*
BRIO	Rock-bryozoans
RU	Rubble
RUEA	Rubble-encrusting red algae
RFRA	Rubble fleshy red algae
TBA	Turf brown algae
TCA	Turf calcareous algae
TCRA	Turf-calcareous red algae
TRA	Turf red algae

Deep zone of middle size rocks and sand (DRS; 3): A mixture of middle size rocks (around 30-50 cm) covered by fleshy algae of the genus *Padina*, encrusting-turf red algae and sand.

Deep rocky wall (DRW; 4): Rock walls covered by encrusting red algae and some small colonies of erect and encrusting sponges. Vertical crevices were also present.

Deep rocky reef (DR; 8): Continuous rocky zones exposed to oceanic currents. It is similar to DRW, but DR has more heterogeneous complex rocks and more sand, and is partially covered by fleshy brown algae of the genus *Sargassum* and calcareous red algae *Galaxaura*.

Exposed shallow rocky reef (SR; 7–9–10): Rocky shallow reefs that are strongly wave-exposed and harbour living colonies of the scleractinian corals *Pocillopora elegans* and *P. damicornis*; they are tightly covered by encrusting, turf and calcareous red algae along with turf brown algae of the genus *Dyctiota*. These zones feature numerous cavities and crevices.

Zones of massive coral (MCR; 5–6): Coral-reef zones separated by sand, with a mixture of living and dead massive coral of two different genera including *Pavona gigantea* and *Porites lobata;*

also turf brown algae, rubble and sand. These zones feature many crevices.

Zones of madreporic branching coral (BCR; 11–12): Patchy zones dominated by the branching corals *Pocillopora damicornis* and *P. elegans*, and characterised by an absence of rocks.

Estimation of fish abundance

The species of fish present and their abundance was assessed using standard methodology for underwater visual surveys with SCUBA diving equipment, e.g. English et al. (1994). The fixed transects used for the study of the benthos were also used for the fish censuses (30 x 5 m). Monthly sampling was conducted at all transects (six censuses per transect). A total of 288 visual censuses were conducted on 48 benthic transects. Three same observers during the whole study period swam along the transects, recording data for fishes (including small cryptic individuals) encountered within 2.5 m on both sides and 5 m above for 45 min/transect. The standard length (SL) of the fishes was estimated to the nearest cm with a PVC ruler. From these data, abundance (individuals/150 m^2) and Shannon-Wiener diversity (H') were calculated based on relative abundance (Pielou 1975).

Spatial use, mobility and trophic groups

Each species was included in one of three mobility and home range size categories, as applied by Floeter et al. 2004: Category 1 = wide horizontal displacement, high mobility; category 2 = sedentary and demersal species in close association with the substrate; category 3 = small home range and a side attachment and/or territorial behaviour.

Fish species were classified trophically according to Ferreira et al. (2004) as carnivores (fish that feed on mobile benthic organisms and fish); mobile-invertebrate feeders (fish that feed primarily on crabs, molluscs and other benthic mobile invertebrates on hard and soft substrates); omnivores (fishes that feed on a variety of organisms, including both animal and plant material); piscivores (fishes that prey on living fishes); planktivores (fish that consume primarily macro- and micro-zooplankton); roving herbivores (fish that feed on detritus, turf algae and macroalgae, e.g. scarids and acanthurids); sessile-invertebrate feeders (fish that eat sessile benthic invertebrates); territorial herbivores (fish that feed on farmed turf-algae within their territories).

Data analysis

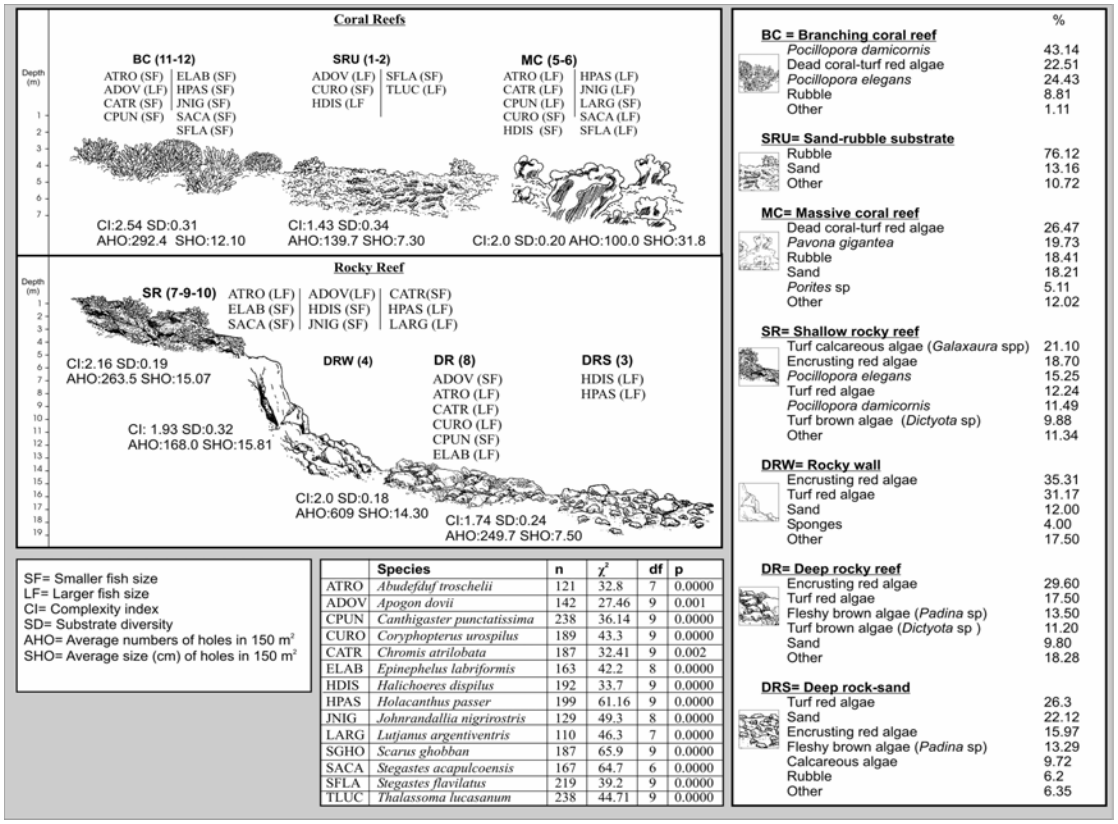
Simpson's diversity index was used to estimate the diversity of organic (e.g. corals, algae) and inorganic (bare rocks, sand-rubble) habitat categories (modified classification from Ferreira et al. 2001). It ranges from zero (highest diversity) to one (monotony); thus an index value of one indicates coverage by a single kind of substrate. Since much of the data on physical and biological parameters may not meet the criteria for normality and homogeneity of variances, parametric one-way ANOVA or non-parametric Kruskall-Wallis tests (Kruskall-Wallis) were applied to the data after testing for normality. Study sites were then compared for differences in physical conditions (substrate diversity), fish density, mobility pattern groups and index of diversity (H′) of fish assemblages (Zar 1996).

An additional Student-Newman-Keuls (SNK) test of multiple-comparisons of means was applied as a *post-hoc* test (Zar 1996). The relationships between diversity indices, species density, and physical parameters were examined using Spearman rank-correlation (Zar 1996). Association between the most abundant species, mobility pattern groups and their relationship with the habitat was examined using Canonical Correspondence Analysis (CCA). The method operates on field data on abundances of species and data for environmental variables at zones and extract from the measured environmental variables synthetic gradients (ordination axes, fit given by weighted variance) that maximize niche separation (given by eigenvalues) (Ter Braak and Verdonschot 1995). Habitat-related differences in size distribution were examined for all species based on length frequencies and applying chi-square analysis to the size groups. Fish abundances for different zones were pooled and presented in a rank-order of species according to their corresponding log numbers in order to easily visualise species richness and the relative importance of live coral coverage and low coral coverage substrates vs. complexity (zone number) at the different study zones (Log series model) (Wolff and Alarcon 1993).

Results

Substrate diversity

One-way ANOVA (Table 2) reveals significant differences between some zones with respect to Simpson’s diversity index. It is close to zero (highest substrate diversity) for all shallow rocky zones that are more exposed to waves (7, 9, 10), for one of the complex deep rocky zones (8) and for the massive coral reefs (5, 6). It is close to one (monotony) for the rubble (1, 2), the deep sandy rocky zone (3), deep rocky walls (4) and pocilloporid branching coral reefs (11, 12).



	Species	n	χ^2	df	p
ATRO	*Abudefduf troschelii*	121	32.8	7	0.0000
ADOV	*Apogon dovii*	142	27.46	9	0.001
CPUN	*Canthigaster punctatissima*	238	36.14	9	0.0000
CURO	*Coryphopterus urospilus*	189	43.3	9	0.0000
CATR	*Chromis atrilobata*	187	32.41	9	0.002
ELAB	*Epinephelus labriformis*	163	42.2	8	0.0000
HDIS	*Halichoeres dispilus*	192	33.7	9	0.0000
HPAS	*Holacanthus passer*	199	61.16	9	0.0000
JNIG	*Johnrandallia nigrirostris*	129	49.3	8	0.0000
LARG	*Lutjanus argentiventris*	110	46.3	7	0.0000
SGHO	*Scarus ghobban*	187	65.9	9	0.0000
SACA	*Stegastes acapulcoensis*	167	64.7	6	0.0000
SFLA	*Stegastes flavilatus*	219	39.2	9	0.0000
TLUC	*Thalassoma lucasanum*	238	44.71	9	0.0000

	%
BC = Branching coral reef	
Pocillopora damicornis	43.14
Dead coral-turf red algae	22.51
Pocillopora elegans	24.43
Rubble	8.81
Other	1.11
SRU= Sand-rubble substrate	
Rubble	76.12
Sand	13.16
Other	10.72
MC= Massive coral reef	
Dead coral-turf red algae	26.47
Pavona gigantea	19.73
Rubble	18.41
Sand	18.21
Porites sp	5.11
Other	12.02
SR= Shallow rocky reef	
Turf calcareous algae (*Galaxaura* spp)	21.10
Encrusting red algae	18.70
Pocillopora elegans	15.25
Turf red algae	12.24
Pocillopora damicornis	11.49
Turf brown algae (*Dictyota* sp)	9.88
Other	11.34
DRW= Rocky wall	
Encrusting red algae	35.31
Turf red algae	31.17
Sand	12.00
Sponges	4.00
Other	17.50
DR= Deep rocky reef	
Encrusting red algae	29.60
Turf red algae	17.50
Fleshy brown algae (*Padina* sp)	13.50
Turf brown algae (*Dictyota* sp)	11.20
Sand	9.80
Other	18.28
DRS= Deep rock-sand	
Turf red algae	26.3
Sand	22.12
Encrusting red algae	15.97
Fleshy brown algae (*Padina* sp)	13.29
Calcareous algae	9.72
Rubble	6.2
Other	6.35

Fig. 2 Summary of habitat structure variables and results of the frequency analysis (χ^2) to test for habitat-related differences in the size distribution of species; only species that had significant differences in size are shown

Table 2 Results of parametric (one-way ANOVA: F, MS) and non-parametric (Kruskal Wallis, H) ANOVA and multiple comparisons (Student Neumann Keuls, SNK) for comparing diversity (fish and habitat) and mobility groups (categories) between study zones in Bahía Honda; ND= normal distribution of data, NND= no normal distribution of data

	H	Df	F	MS	p	Multiple comparisons (SNK)
Substrate diversity (Simpson index)	31.26	11	NND	NND	0.001	Other zones < 1=2=3=4=11=12
Fish diversity (H`)	ND	11	11.76	0.101	0.001	Other zones>1=2=11=12
Fish abundance	23.61	11	NND	NND	0.014	Other zones > 1=2=3=4=5=6
Category 1	31.77	11	NND	NND	0.001	Other zones > 1=3=6
Category 2	21.86	11	NND	NND	0.02	Other zones > 7=9
Category 3	39.76	11	NND	NND	0.001	Other zones < 4 =7=9=10

Taxonomic structure of the fish community and its relationship with habitat

126 species of fish belonging to 44 families were found. The total species number increased from rubble over branching coral reef, massive corals, and deep rocky zones to shallow rocky zones with the highest species richness. The number of genera and species differed between all locations, with the greatest difference between shallow and deeper zones; 71 % of the genera were restricted to certain zones, while 18 % of the species occurred in all zones.

30 species were abundant enough to allow for a size frequency analysis, and 14 of them showed a significant size-segregation between zones (Fig. 2). Non-territorial species such as *Canthigaster punctatissima, Chromis atrilobata, Epinephelus labriformis, Halichoeres dispilus, Holacanthus passer, Johnrandallia nigrirostris, Scarus ghobban* and *Thalassomna lucasanum* had smaller sizes (juveniles and pre-adults) in shallow high-complexity zones such as pocilloporid reefs (11, 12) and shallow rocky reefs (7, 9, 10); while the number of larger individuals increase in different deeper habitats of intermediate and high complexity (rubble, massive corals and deep rocky zones). Territorial species such as *Stegastes acapulcoensis, S. flavilatus* and *Abudefduf troschellii* showed a pattern similar to the non-territorial species mentioned above. *Apogon dovii* showed an opposite pattern with smaller sizes over deep rocky reefs and massive corals, and larger sizes over shallow branching corals and rocky reefs. *Lutjanus argentiventris* had smaller sizes at zones of massive corals, while the larger sizes were found in all rocky zones at different depths and different levels of complexity. Larger individuals of *Coryphopterus urospilus* were mostly found

in complex deep rocky zones.

Pomacentrids, labrids, haemulids and apogonids were the most abundant families, the pomacentrid *Chromis atrilobata* and the labrid *Thalassoma lucasanum* being the most common and abundant species. *Chromis atrilobata* was present in most shallow wave exposed zones and even in oceanic-current exposed deep zones (8). *Thalassoma lucasanum* was abundant in most shallow zones while *Halichoeres dispilus* was common on hard and sandy substrates such as massive-coral reefs and deeper rocky sandy zones. Haemulids were dominant in most shallow zones, while apogonids dominated in crevices on deep rocky walls (Table 3, Fig. 3).

Table 3 Dominant species; trophic groups: O = omnivore; C = carnivore; P = piscivore; MI = mobile-invertebrate feeder; SI = sessile-invertebrate feeder; PL = planktivore; RH = roving herbivore; TH = territorial herbivore.

Code	Species	Family	Trophic group
ATRO	*Abudefduf troschelii*	POMACENTRIDAE	O
AHAN	*Acanthemblemaria hancocki*	CHAENOPSIDAE	MI
ADOV	*Apogon dovii*	APOGONIDAE	PL
APAC	Apogon pacificus	APOGONIDAE	PL
BDIP	*Bodianus diplotaenia*	LABRIDAE	MI
CPUN	*Canthigaster punctatissima*	TETRAODONTIDAE	O
CCAB	*Caranx caballus*	CARANGIDAE	P
CATR	*Chromis atrilobata*	POMACENTRIDAE	PL
COXY	*Cirrhitichthys oxycephalus*	CIRRHITIDAE	MI
CURO	*Coryphopterus urospilus*	GOBIIDAE	MI
EPUN	*Elacatinus punticulatus*	GOBIIDAE	SI
HMAC	*Haemulon maculicauda*	HAEMULIDAE	C
HSTE	*Haemulon steindachneri*	HAEMULIDAE	C
HSCU	*Haemulon scudderi*	HAEMULIDAE	C
HDIS	*Halichoeres dispilus*	LABRIDAE	MI
HMEL	*Halichoeres melanotis*	LABRIDAE	MI
JNIG	*Johnrandallia nigrirostris*	CHAETODONTIDAE	O
LARG	*Lutjanus argentiventris*	LUTJANIDAE	C
PCOL	*Paranthias colonus*	SERRANIDAE	PL
PLAT	*Prionurus laticlavius*	ACANTHURIDAE	RH
SGHO	*Scarus ghobban*	SCARIDAE	RH
SPSI	*Serranus psittacinus*	SERRANIDAE	C
SACA	*Stegastes acapulcoensis*	POMACENTRIDAE	TH
SFLA	*Stegastes flavilatus*	POMACENTRIDAE	TH
TLUC	*Thalassoma lucasanum*	LABRIDAE	PL

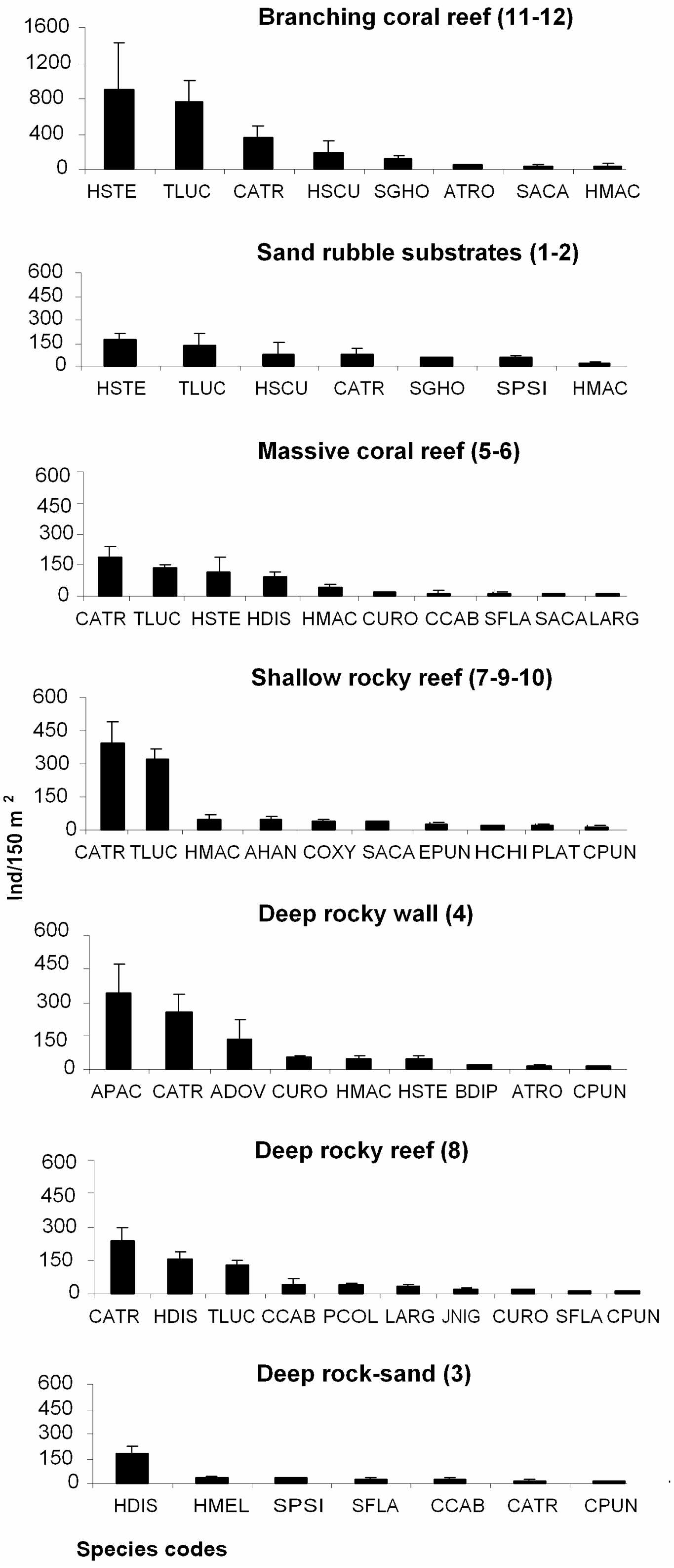


Fig. 3 Density (individuals/150 m^2 ± SE) for the most abundant species on different habitats found in Bahia Honda, Panama (for species codes, see Table 3)

Species associations as related to habitat attributes

The results of the Canonical Correspondence Analysis (CCA; species codes in Table 3, data in Table 4, and species associations in Fig. 4) show that fishes related to shallow branching corals and sand-rubble (negative side of axis 2; 1, 2, 11, 12; HSCU, HSTE and SGHO). The negative part of Axis 1 shows species in shallow rocky wave exposed zones (7, 9 and 10; AHAN, CCAB, COXY, EPUN, PLAT and SACA). There is a depth gradient in the other two rocky-sandy deeper zones with its particular species (3, 8; SFLA, HDIS, HMEL, JNIG, LARG and PCOL). The rock wall zone (4) characterised by sponges and rock-encrusting red algae has another particular group of fish species (APAC, ADOV, BDIP and CURO). A fourth group is comprised by species found in most (mainly shallow) study zones (ATRO, CATR, TLUC, SPSI, HMAC and CPUN).

Table 4 Canonical Correspondance Analysis; VCP= Variance in cumulative percentage; SEV= Sums of eigenvalues

	Species association (Fig. 4)							**Mobility groups** (Fig. 7).	
VCP	32.17	52.12	69.78	80.39	86.12	90.92	94.39	69.85	100
SEV	0.48	0.29	0.26	0.15	0.08	0.07	0.05	0.18	0.07

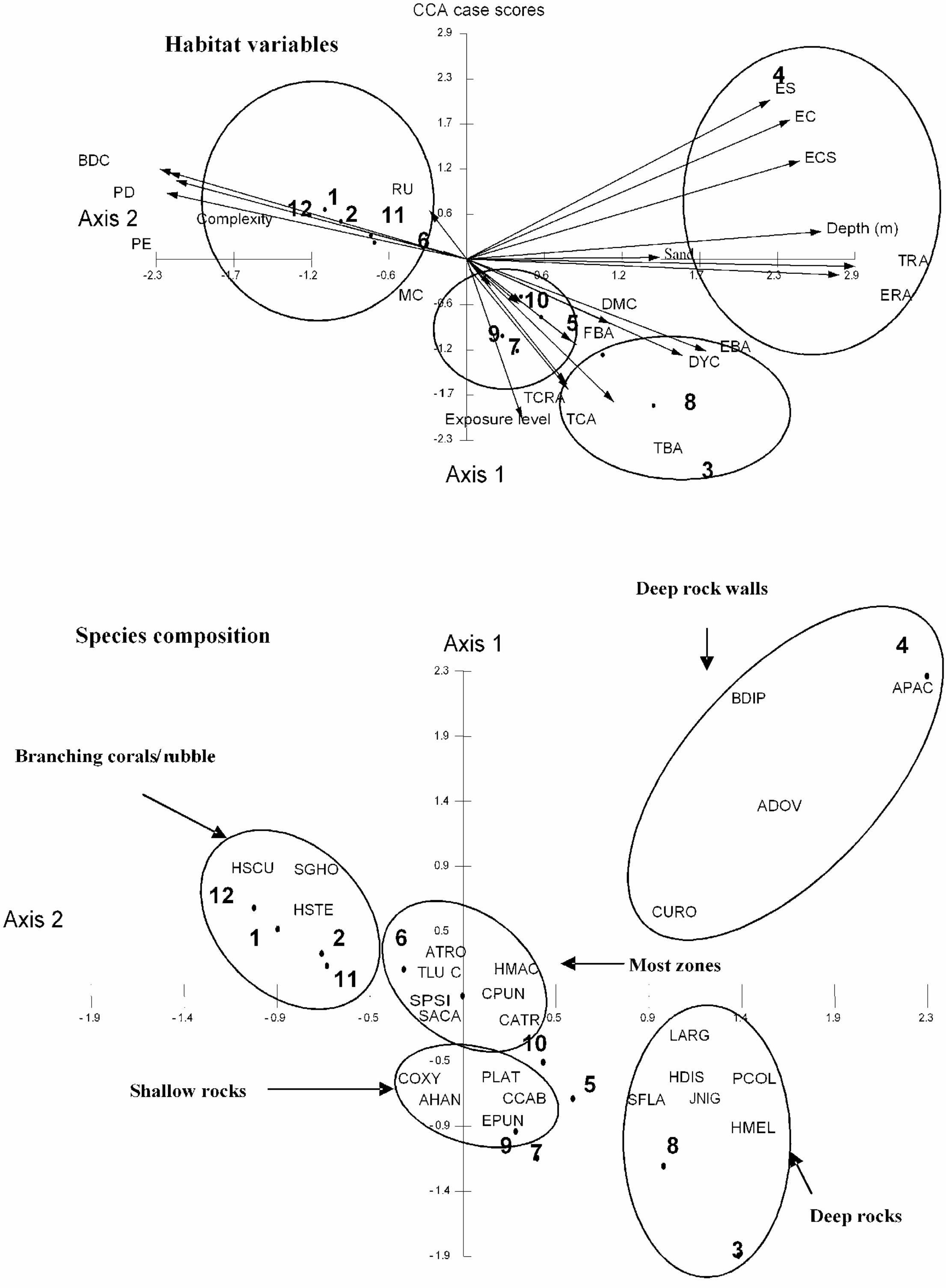


Fig. 4 Canonical Correspondence Analysis (CCA) for fish abundance vs. substrate coverage and environmental variables (codes for substrate categories in Table 1, for species in Table 3)

Fish diversity and abundance

The results of parametric one-way ANOVA and multiple comparisons (Student Neumann Klaus [SNK]) for fish diversity show significant differences between zones. In general, fish diversity was higher in most rocky zones and zones of massive corals, and lower above branching coral reefs (11, 12) and rubble (1, 2).

These differences can be appreciated in more detail in the log-series model in Figure 5. The line is flatter (greatest evenness) and its intersection with the axis (Species richness) is greater in the complex rocky zones (7, 8, 9, 10) and in the massive coral reef (5, 6), independent of their coral coverage or depth. All these zones have a more diverse benthic component (lower Simpson index). The rubble, branching corals and sand zones have higher slopes and lower regression coefficients, indicating a higher dominance within the assemblage and a less diverse community, respectively. All outlier points above the lines (omitted in Fig. 5 for better graphic visualization) represent the dominant species of pomacentrids and labrids. More species were found in areas with complex massive coral and complex rocky reef. The non-parametric ANOVA shows that fish abundance differs significantly between zones; zones of highest complexity (particularly shallow rocky zones and branching corals, 7 to 12) have higher fish abundances, e(?)specially a high number of juveniles of different species.

Summary of correlations

The Spearman rank-correlation analysis (Fig. 6) shows a significant positive correlation between species-richness/index of diversity and the average size of holes (along with their variation in size). The correlation was strongest for most of the substrates from rocky reefs, and was also positive for live massive corals.

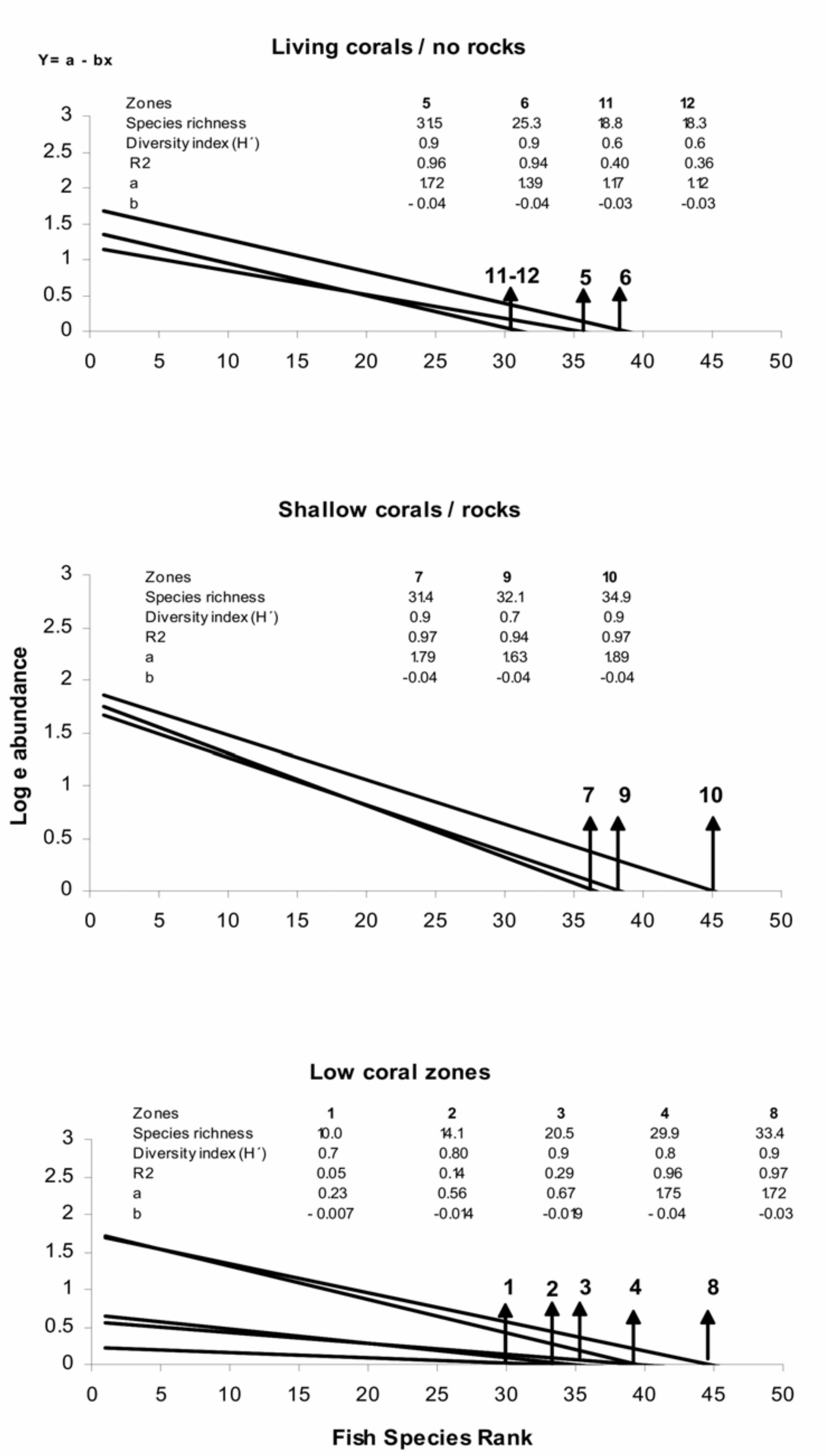


Fig. 5 Species rank vs. log-abundances (Log-series model); zone numbers in bold

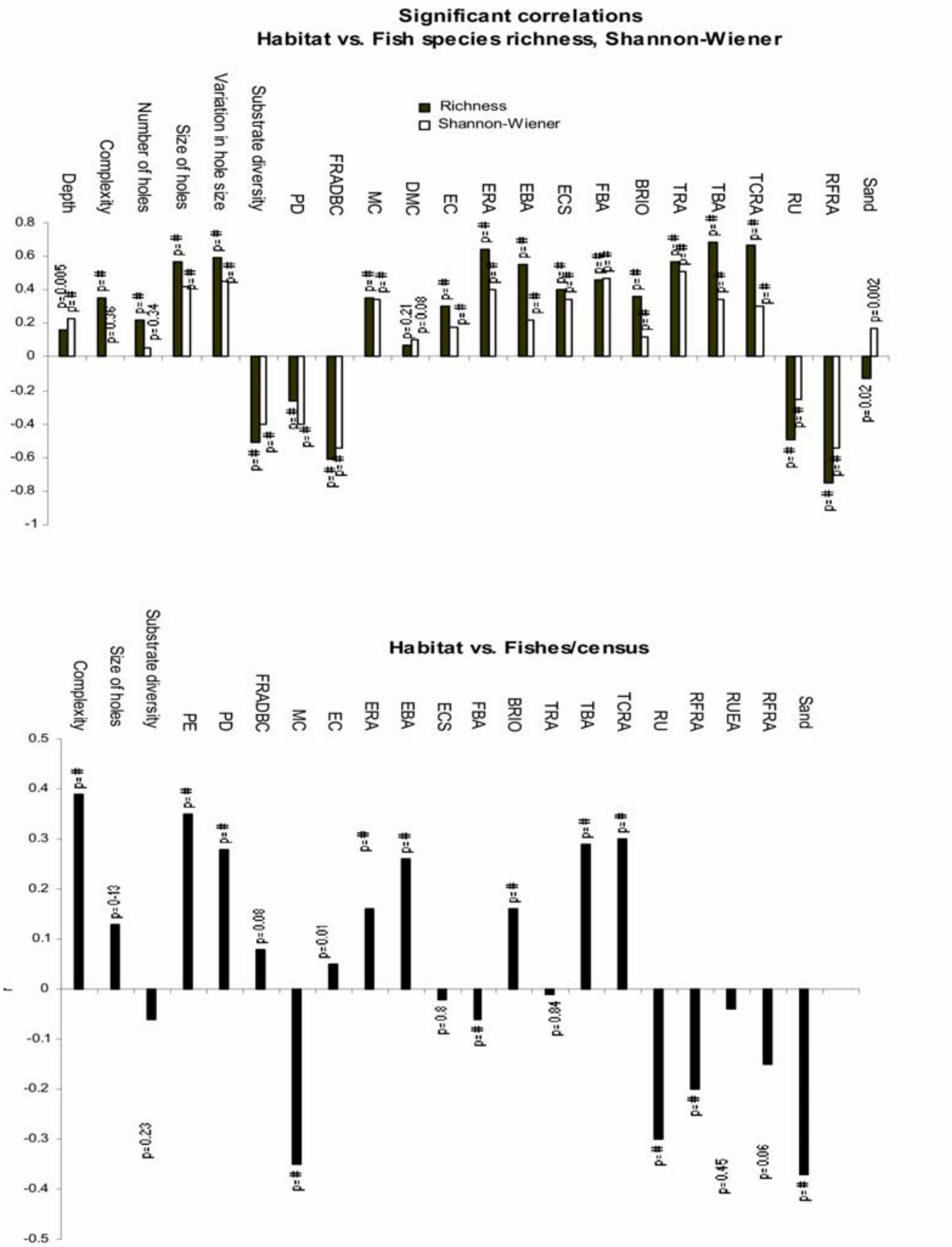


Fig. 6 Spearman rank correlations, fish community and habitat variables; n = 288, # = <0.0001 (substrate codes in Table 1)

Our results show that surface complexity is only positively correlated with species richness and that substrate monotony (Simpson index, value close to 1) is related to a less diverse fish community. Inverse correlations were also found in richness and diversity with dead and living branching coral, and with rubble.

Fish abundance (individuals/census) seems to be positively correlated with complex substrates such as branching corals reef and shallow rocky reef. This is due to the high abundance of pomacentrids and labrids (especially juveniles) in these habitats. Total fish abundance was inversely correlated with all substrates related to rubble zones (Fig. 6).

Mobility and home-range

Most of the shallow wave-exposed zones (7, 9, 10) and the deep zone (8) with strongest exposure to oceanic currents have fishes with high horizontal and vertical mobility (Category 1). The exceptions were for one of the rubble zones (1), the deep rock sand zone (3), and a massive coral reef zone (6). All these zones were closer to the mainland and less exposed to currents and waves. Relatively sedentary species (Category 2) were abundant in most zones except in two rocky shallow zones strongly exposed to waves. Site-attached species (Category 3) were more represented in zones with lower proportion of sand and higher coverage of hard rocky substrate: In shallow rocky zones (7, 9, 10), and on rocky walls (4). This correlation of mobility groups with certain habitat attributes and zones is revealed by the CCA-Analysis (12 zones; all species included, results data in Table 4, associations of categories in Fig. 7). This analysis shows a gradient of exposure (zones 7, 9 and 10). Fishes in Category 3 (site-attached species) are represented by small chaenopsids (e.g. *Acanthemblemaria hancockii*) on small holes in basaltic rocks. In the coral reef deeper sandy zones, fishes of Category 2 (relative sedentary species) are more abundant. Category 1 (fishes of high horizontal and vertical mobility) are more related to rocky reefs.

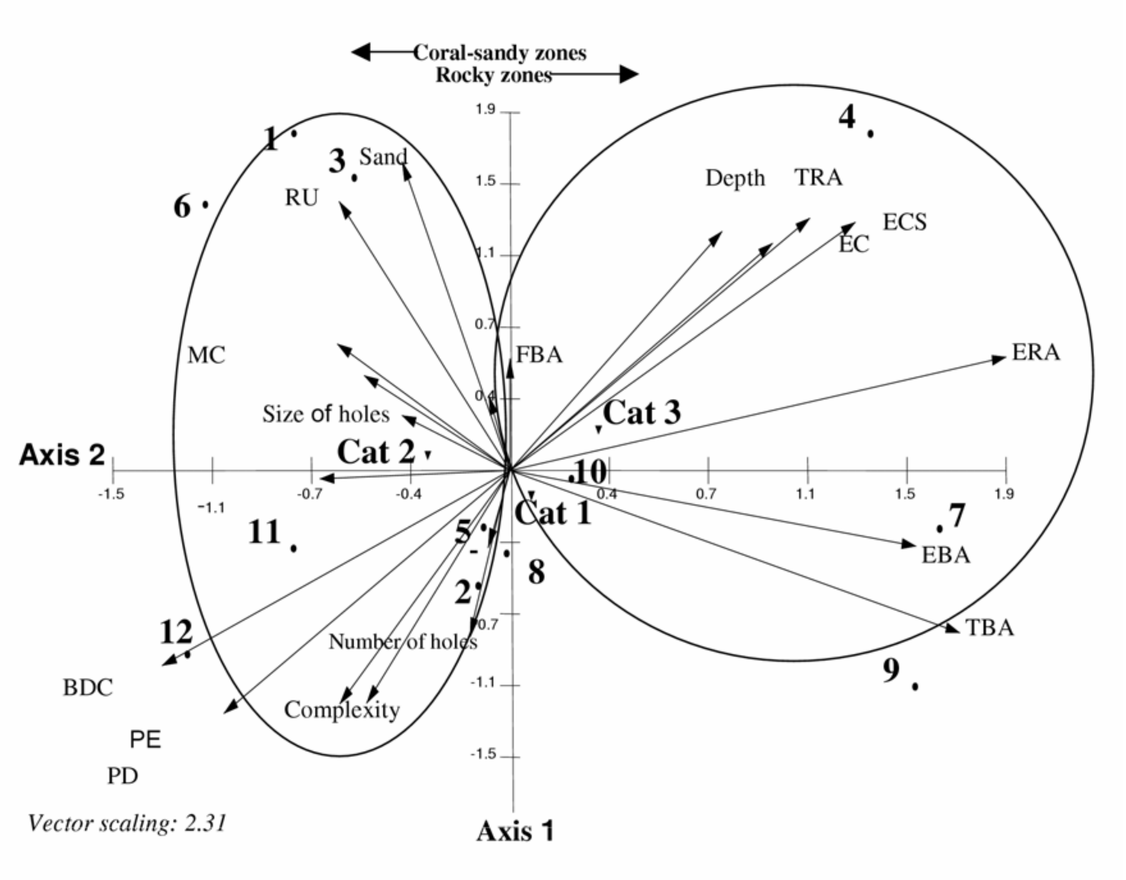


Fig. 7 Canonical Correspondance Analysis (CCA); mobility groups (categories) vs. percentage of substrate coverage and environmental variables associated with the respective zones (zone numbers in bold, substrate codes in Table 1)

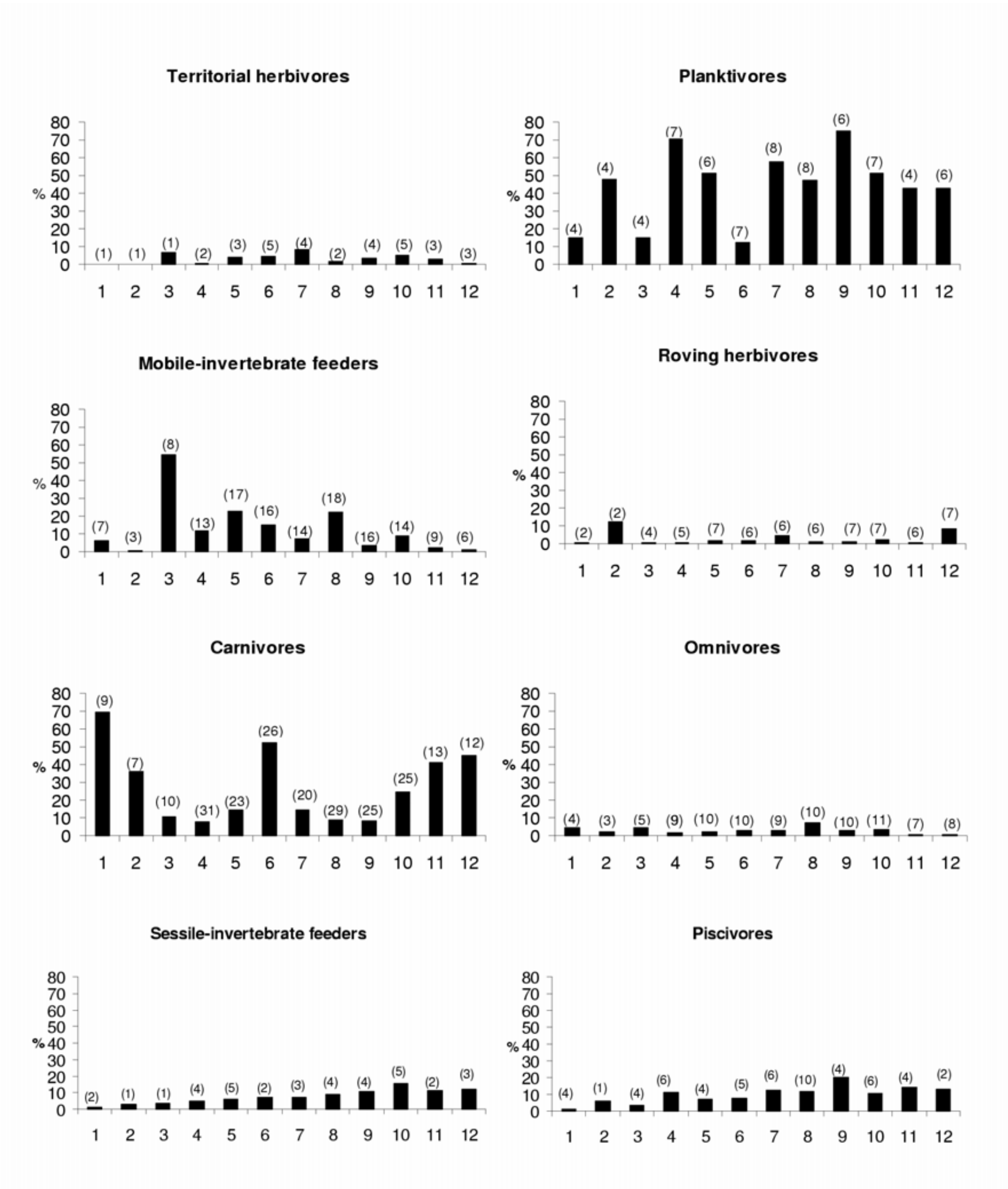
Trophic groups

Planktivores account for more than 50 % of the relative abundance in most zones, and a similar pattern is followed by carnivores with 30 %, mobile invertebrate feeders with 20 %, piscivores with 20 %, and herbivores and sessile invertebrate feeders with a low relative abundance of 10 %. Planktivores have relatively low species numbers compared to other trophic groups: Carnivores account for 32 %, mobile invertebrate feeders for 23 %, and omnivores for 13 % of the species in BH-GCH. In general, the number of species within trophic groups increases towards rocky and massive coral zones (Fig. 8).

Discussion

Distribution patterns as related to water depth

In BH-GCH 71.4 % of the species found have smaller sizes and higher densities in shallow high complex habitats, while larger size classes are mainly associated with complex deep zones with bigger crevices. Small individuals thus hide in between coral branches, complex rocky-reef and small holes in shallow areas, probably as an effective way to avoid the predation encountered in deeper zones (Almany 2004a, b).


Territorial herbivores

Planktivores

Mobile-invertebrate feeders

Roving herbivores

Carnivores

Omnivores

Sessile-invertebrate feeders

Piscivores

Fig. 8 Frequency (%) of the principal trophic groups in the different study zones (1-12); numbers in parentheses indicate the number of species in each group

According to Fulton and Bellwood (2002) this shift in microhabitat use could also largely be due to flow-refuging behaviour, where substrate complexity and boundary layer act as refuges from water flow. Some of the species associations observed in the center of the CCA ordination diagram represent the better swimmers such as the genera *Thalassoma*, *Abudefduf* and *Chromis*, indicative for habitats of stronger currents and greater water movement (Floeter et al. 2004) (see also further discussion below). The distribution of the two territorial herbivores *Stegastes acapulcoensis and Stegastes flavilatus* differ by depth (Dominici-Arosemena et al. 2005; Arburto-Oropeza and Balart 2001; this study). This example confirms that substratum selection alone is insufficient to explain the discrete spatial distribution of adults. Possibly, habitat selection and interspecific aggression combine to determine the adult distribution of these species of *Stegastes* (Bay et al. 2001). Our correspondence analysis suggests many subdivisions and well-composed groups of species in rocky zones, where assemblages vary along a depth gradient, either due to differential food requirements or due to particular habitat adaptations (e.g. oceanic planktivores with higher swimming capacity in shallow zones vs. less mobile species on soft bottom environments in deeper zones).

Species richness, diversity patterns, spatial variation and relationship with habitat variables

As shown in our log series model (Fig. 5), aspects of habitats other than live coral cover-richness are involved in the maintenance of diversity in this region. Massive coral zones (5 and 6) show lower fish abundance than, but similar fish species richness as most rocky zones with high substrate diversity. Reef fish may thus well be characteristic of -but not restricted to- coral reefs as has already been stated by other authors (Robertson 1998; Bellwood 1998). Species richness correlates negatively with monotony (less diverse substrate) and positively with hole variables (numbers, variation and size), similarly as has been described for rocky shores in higher latitudes (Ferreira et al. 2001; García-Charton and Pérez-Ruzafa 2001) and in the Red Sea (Khalaf and Kochzius 2002). As indicated by our research in BH-GCH, and confirmed by other studies, coral cover alone has little influence on the species richness and abundance of fish (Roberts and Ormond 1987; Luckhurst and Luckhurst 1978), and coral reef community structure (in general and fish community in particular) seems to be a complex, indirect and non-linear consequence of reef structure and environmental conditions (Bradbury and Young 1981).

Mobility, home range and local patterns of trophic groups

Better swimmers (Category 1) such as *Thalassoma* sp. are adapted to, and have high densities in exposed upper shallow rocky zones (7, 9 and 10), in shallow pocilloporid reef subjected to intermittent currents due tide variation (11 and 12), and in the oceanic deep zone most exposed to current (8), while mid slope zones are characterized by less efficient swimmers (Category 2) such as the genus *Halichoeres* (Bellwood and Wainwrigt 2001). These patterns are similar among geographical regions (Bellwood et al. 2002). In BH-GCH, small site-attached cirhitids in branching corals (*Pocillopora elegans*) over shallow rocks, and chaenopsids (Category 3) in holes of basaltic rock may better withstand strong waves and currents. Most studies regarding these mobility guilds have been focused on labrids (Bellwood and Wainwright 2001; Bellwood et al. 2002), acanthurids and pomacentrids (Fulton et al. 2005), and further research on these patterns is needed in other reef fish families. The distribution of these mobility groups in BH-GCH may be related to tides and currents, with the good swimmers (Category 1) being more homogenously distributed but with a higher affinity to shallow-rocky-branching coral and deeper zones that are more affected by oceanic currents. Good swimmers are able to withstand strong currents and most of them feed on oceanic plankton. As shown in this study, this pattern varies among sites, with a decreasing abundance of category 1 fish in zones close to the mainland where current intensity is lower. Planktivores indeed account for as much as 80% of all fish in many zones in BH-GCH. Zooplankton reside in a constantly flowing environment, maintaining their depth by swimming against upwelling and downwelling currents. This explains why oceanic fronts become major feeding grounds for planktivores (Genin et al. 2005; Thresher 1983). In BH-GCH roving herbivores are represented by scarids in shallow zones in low frequencies when compared with other trophic groups. Other roving herbivores such as acanthurids seem to prefer certain types of algae common in exposed reef flats such as the zones 7, 9 and 10 (Sluka and Miller 2001), where the surgeon fish *Prionurus laticlavius* was found in incidental aggregations.

The trophic groups that feed on high nutritive food sources (Floeter et al. 2004) such as mobile-invertebrate feeders, carnivores, piscivores and omnivores have a wide spatial distribution and most of them a high relative abundance in BH-GCH: Piscivorous fishes are particularly important here compared to other TEP regions, namely carangids and serranids of large size classes and even top predators such as the great hammerhead sharks *Sphyrna mokarran* that were seen occasionally (pers. observation). Recent studies have pointed to the importance of piscivorous fish as regulators of the abundance of prey species, probably including many small territorial herbivores. This top-down control by piscives may maintain high species diversity due to decreasing the competition among subordinate species by lowering their population densities (Almany 2004a, b; Beukers-Stewart and Jones 2004). A reduction in the recruitment of many fish families due to environmental stochasticity (i.e. phenomena such as ENSO) may in addition provoke a bottom-up regulatory force in balancing the whole community structure (Almany 2004a, b).

Comparison with other regions in TEP

In Southern Baja California (SBC) 40 % of the species that feature significant habitat differences between juveniles and adults are the same as in BH-GCH. Some benthic components such as rodoliths and black corals may also provide protection for juveniles (Arburto-Oropeza and Balart 2001). Only 39.5% of the species considered as dominant (e.g. *Thalassoma lucasanum* and *Chromis atrilobata*) and common in the SBC are present in BH-GCH, and both regions share a similar deep water fish assemblage. Chaenopsids, gobids, damselfishes such as *Stegastes acapulcoensis,* carangids and apogonids are less abundant or considered as rare species in SBC (Arburto-Oropeza and Balart 2001). A similar situation holds for the Galapagos with a large number of species of Peruvian-Chilean origin, which were absent in our surveys (Edgar et al. 2004), and with only 50% of the species shared with BH-GCH. Only 23% of the species that we found in the GCH are of Indo-Pacific or circumtropical origin, and many are shared with the other TEP regions mentioned, but these patterns vary among the mainland and offshore islands (Table 5 and 6). Geographic history and isolation, environmental conditions (e.g. oceanic currents, ENSO events), duration of the pelagic stage of fish larvae, and substrate may play a role in shaping these differences.The species richness in the GCH is higher than in most other areas in the TEP but slightly lower than at the Galapagos and Clipperton Islands (Allen and Robertson 1997; Edgard et al. 2004). The species composition (even if we exclude species that may be over-fished for human consumption) around near shore islands (e.g. Gorgona) and in other warmer regions close to the mainland is similar, but species numbers and abundance are lower compared to the GCH. This may be due to the more constant conditions (e.g. salinity and temperature) along with the presence of a wider set of habitats and greater availability of shelter at our study site, the largest archipelago in the TEP. The higher species numbers reported for oceanic islands (e.g. Galapagos and Clipperton Islands) which are attributed to the larval inputs from different geographical sources (other islands, continental shores of TEP), has motivated authors to suggest that in this region insular and continental components of fish fauna, subjected to habitat fragmentation, should be treated separately when analysing such patterns (Mora and Robertson 2005).

In terms of trophic groups, it seems that in all TEP regions investigated planktivores and invertebrate feeders dominate, while herbivores are low in numbers (Zapata and Morales 1997; Aburto-Oropeza and Balart 2001; Dominici-Arosemena et al. 2005; this study). The predominance of good swimming planktivores (e.g. *Chromis atrilobata* and *Thalassoma lucasanum*) seems to be a common pattern in the whole TEP, but their proportion may vary among regions. The data available shows that their densities increase in regions of higher tide variation: The relative abundance of better swimming planktivores seems to be lower in SBC (tidal variations of about 1.7 m) in comparison with GCH (tidal variations between 3 and 4 m), Gulf of Papagayo, Costa Rica (tidal variation max 2.7 m) and Gorgona Island, Colombia (4 m) (Zapata and Morales 1997; Aburto-Oropeza and Balart 2001; Dominici-Arosemena et al. 2005; Prahl et al 1979; this study). Future research is still necessary to distinguish the effects of food and the effect of currents at global and local scales. Planktivores may be abundant because they swim better and spend their time in the water column, or because there is a high abundance of plankton in such areas. This makes it difficult to separate the two effects that are inextricably interlinked (DR Robertson, pers. comm.; Genin et al. 2005). Comparing studies from different locations, herbivores show low densities in all TEP regions, but in GCH their abundance tends to increase. This may be related to the use of low quality protein content food sources as algae in warmer and stable regions (Floeter et al 2004; Harmelin-Vivien 2002). Further studies on how the relative importance of different trophic and mobility groups in reef fish assemblages varies with latitude in the TEP are still necessary (Floeter et al. 2004).

Conservation issues

BH is close to the former presidium in Coiba Island, an isolated region with low human population density. It has not been subjected to strong anthropogenic disturbances as yet. Due to the closing of the Coiba presidium (August 2004) and the increasing importance as a tourist destination, human activities such as artisanal fishery, sport fishing and diving activities are bound to increase. Fishes of 28 species of commercial interest have been reported in the GCH, particularly in the National Park. Prior to this study, this region had lacked baseline data that could be used to plan and manage a sustainable fishery (Vega and Villarreal 2003). There are plans by the UNESCO to declare the Coiba National Park as a world patrimony. But BH does not form part of the Coiba National Park and, while fishery regulations are being developed by the National Environmental Authority (ANAM) for the National Park, as yet no management measures have been elaborated for the regions close to the mainland (Vega Angel, pers. comm.). The most populated centres of the BH region are around the town Pixvae, but the construction of tourist hotels with a high demand for infrastructure and seafood, and this great impact on the coastline and its habitats is to be expected in the near future. This is expected to go along with the development of tourism in the Coiba National Park.

The reduction of the three-dimensional habitat structure has been identified as one cause for the shift in species composition (McKenna 1997), and there have been few repeated cases of blast fishing (personal observation). BH and the Coiba National Park are isolated but interconnected sites, with probably the most diverse fish communities in the continental TEP, and the importance of this region has as yet not been sufficiently acknowledged. Our results confirm that it may also be the most important refuge for benthic organisms.

Based on the results of this study the following measures are recommended: 1. Pocilloporid reefs and shallow coral-rocky zones should be protected as nursery areas for juvenile fish, and protection should not only be provided for the National Park of Coiba Island but also in regions that are close to the mainland. 2. Tourists and locals should be trained to not destroy or extract the benthic flora and fauna (through destructive fishing or irresponsible diving practices that may increase from low to extreme levels due to missregulations and lack of control). This should include a well organized monitoring by the authorities. 3. A permanent protection should be applied to areas inside and outside of the National Park, with special attention paid to areas of high diversity of predators (also rocky-complex zones) that form part of the secondary and tertiary consumers in the trophic chain. Due to its isolation, the GCH may be one of the few coastal regions of the TEP where the trophic web is still relatively pristine with a balance between herbivorous and carnivorous fish guilds. This fragile equilibrium would be highly affected if fishing pressure was to build up. 4. Reef areas that represent important ecosystems in the region should be delimited to prevent anchorage of boats.

In addition, there may be other anthropogenic impacts to this area in the future, particularly the expected increase in sediment deposition on the reefs caused by the construction of new infrastructure, hotels and houses in the area.

Table 5 List of species found and their distribution to trophic groups (TG; see Table 3) and study zones (1-12; see Fig. 1); *= Indo-Pacific species, **circumtropical species (Atlantic and Pacific),***species from both sides of the Isthmus of Panama (Edgard et al. 2004; Robertson et al. 2004; Robertson and Allen 2002)

Family/Species	**TG**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
ACANTHURIDAE													
*Acanthurus nigricans**	RH				X					X			
*A. xanthopterus**	RH	X	X		X	X	X	X	X		X	X	X
*A. triostegus**	RH												X
Ctenochaetus marginatus	RH		X										
Prionurus laticlavius	RH				X	X	X	X	X	X	X		
APOGONIDAE													
Apogon dovii	PL		X		X	X	X	X	X	X	X	X	X
Apogon pacificus	PL				X			X	X		X		X
AULOSTOMIDAE													
*Aulostomus chinensis**	P												X
BALISTIDAE													
Balistes polylepis	O			X		X			X		X		
*Pseudobalistes naufragium**	O		X	X	X	X	X	X	X	X	X		X
Sufflamen verres	SI	X	X	X	X	X	X	X	X	X	X	X	X
BLENNIIDAE													
Ophioblennius steindachneri	TH						X	X		X	X	X	X
Plagiotremus azaleus	P		X	X	X	X	X	X	X	X	X	X	X
BOTHIDAE													
*Bothus mancus**	MI									X			
CARANGIDAE													
Carangoides otrynter	P				X								
Carangoides caballus	P	X	X	X	X	X		X	X	X	X	X	
*Caranx lugubris***	P								X				
*C. melampygus**	P								X				
*C. sexfasciatus**	P								X				
*Elagatis bipinnulata***	P	X								X	X		
Gnathanodon speciosus	P	X		X	X	X		X			X		
Oligoplites refulgens	P								X				
Selene peruviana	P								X				
*Seriola rivoliana***	P			X	X	X		X	X				
Trachinotus rhodopus	P								X		X		
CHAENOPSIDAE													
Acanthemblemaria exilispinus	MI			X	X	X	X	X	X	X	X		
Acanthemblemaria hancocki	MI				X	X	X	X	X	X	X		
Mccoskerichthys sandae	PL				X	X		X	X	X			
CHAETODOTIDAE													
Chaetodon humeralis	SI	X		X	X	X	X		X		X	X	X
Johnrandallia nigrirostris	O			X	X	X	X	X	X	X	X	X	X
CIRRHITIDAE													
Cirrhitus rivulatus	C				X					X			
*Cirrhitichthys oxycephalus**	C	X	X	X		X	X	X	X	X	X	X	X
DASYATIDAE													
Dasyatis dipterura	MI				X	X							

Family/Species	**TG**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Dasyatis longa	MI	X											
DIODONTIDAE													
*Diodon holocanthus***	MI	X	X	X	X	X			X	X			X
*Diodon hystrix***	MI					X					X		
EPHIPPIDIDAE													
Chaetodipterus zonatus	O									X			
FISTULARIIDAE													
*Fistularia commersonii**	C	X	X		X	X	X	X	X	X	X	X	X
GERREIDAE													
Eucinostomus currani	MI						X						
Diapterus aureolus	MI						X						
GOBIIDAE													
Elacatinus inornatus	MI				X				X				
Elacatinus punticulatus	SI				X	X		X	X	X	X		
Coryphopterus urospilus	MI		X	X	X	X	X	X	X	X	X	X	X
HAEMULIDAE													
Anisostremus caesius	C						X						
A. interruptus	C						X						
A. taeniatus	C				X	X	X		X				
Haemulon flaviguttatum	C				X		X		X		X		
H. maculicauda	C				X	X	X				X		
H. scudderi	C	X									X	X	X
H. sexfasciatum	C					X	X						
*H. steindachneri****	C	X				X	X		X		X	X	X
HOLOCENTRIDAE													
*Myripristis berndti**	PL										X		X
M. leiognathus	PL				X	X		X	X	X			X
Sargocentron suborbitalis	PL					X	X	X			X		X
KYPHOSIDAE													
Kyphosus elegans	O			X		X	X	X	X	X	X		
Sectator ocyurus	MI				X				X				
LABRIDAE													
Bodianus diplotaenia	MI			X	X	X	X	X	X	X	X	X	X
Halichoeres chierchiae	MI			X	X	X	X	X	X	X	X	X	
H. dispilus	MI	X	X	X	X	X	X	X	X	X	X	X	
H. melanotis	MI	X		X	X	X		X	X		X		
H. nicholsi	MI		X	X	X	X	X	X	X	X	X	X	
H. notospilus	MI				X	X	X				X	X	
*Novaculichthys taeniourus**	MI			X		X		X	X	X	X		
Thalassoma lucasanum	PL	X	X	X	X	X	X	X	X	X	X	X	X
T. grammaticum	MI											X	
*Iniistius pavo**	MI			X									
LABRISOMIDAE													
Malacoctenus ebisui	MI						X	X	X	X	X		
Malacoctenus margaritae	MI										X		
LUTJANIDAE													
Hoplopagrus guentherii	C												X

Family/Species	**TG**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Lutjanus argentiventris	C			X	X	X	X	X	X	X	X	X	
L. colorado	C								X				
L. guttatus	C	X					X						
L. inermis	C				X	X	X				X		
L. jordani	C					X							
L. novemfasciatus	C					X	X						
L. viridis	C												X
MALACANTHIDAE													
*Malacanthus brevirostris**	C			X	X				X				
MONACANTHIDAE													
*Aluterus scriptus***	O									X			
MUGILIDAE													
Mugil hospes	PL						X						
MULLIDAE													
Mulloidichthys dentatus	C			X	X	X	X				X		
MURAENIDAE													
*Echidna nebulosa**	C					X		X	X	X	X	X	
Enchelycore octaviana	C								X				
*Gymnomuraena zebra**	C							X		X			
Gymnothorax castaneus	C			X	X		X		X	X	X	X	X
*Gymnothorax flavimarginatus**	C											X	
Muraena lentiginosa	C			X	X			X	X	X		X	
NARCIDINIDAE													
Diplobatis ommata	MI								X				
OPISTOGNATHIDAE													
Opistognathus panamensis	PL								X				
OPHICHTHIDAE													
Myrichthys tigrinus	MI			X								X	
OSTRACIIDAE													
*Ostracion meleagris**	SI					X				X			
POMACANTHIDAE													
Holocanthus passer	O		X	X	X	X	X	X	X	X	X	X	X
Pomacanthus zonipectus	O			X	X	X	X				X		
POMACENTRIDAE													
Abudefduf concolor	O						X						
A. troschelii	O				X	X	X	X		X	X	X	X
Chromis atrilobata	PL	X	X	X	X	X	X	X	X	X	X	X	X
Microspathodon bairdii	TH						X	X					
M. dorsalis	TH					X	X	X		X	X		
Stegastes acapulcoensis	TH			X		X	X	X		X	X	X	X
S. flavilatus	TH	X	X	X	X	X	X	X	X	X	X	X	X
RHINOBATIDAE													
Zapteryx exasperata	MI			X									
SCARIDAE													
Scarus compressus	RH						X		X			X	
*S. ghobban**	RH	X	X	X	X	X	X	X	X	X	X	X	X

Family/Species	**TG**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
S. perrico	RH					X	X		X				X
*S. rubroviolaceus**	RH	X	X	X	X	X	X	X	X	X	X	X	X
SCIAENIDAE													
Pareques viola	C				X								
SCORPAENIDAE													
Scorpaena plumieri mystes	C	X	X	X			X	X		X	X		
SERRANIDAE													
Alphestes immaculatus	C								X				
Dermatolepis dermatolepis	C							X		X			
Epinephelus labriformis	C			X	X	X	X	X	X	X	X	X	
Cephalopholis panamensis	C			X	X	X	X	X	X	X	X	X	
Mycteroperca xenarcha	C				X								
Paranthias colonus	PL	X	X	X	X			X	X	X	X		
Serranus psittacinus	C	X	X	X	X	X	X	X	X	X	X	X	X
Pseudogramma thaumasium	C								X				
Rypticus bicolor	C			X	X			X	X	X	X		
R. nigripinnis	C								X				
SYNGNATHIDAE													
*Doryrhamphus excisus**	C					X			X	X	X		X
SYNODONTIDAE													
Synodus lacertinus	C						X			X			
Synodus sechurae	C	X		X		X			X				
TETRAODONTIDAE													
*Arothron hispidus**	O	X	X	X	X				X		X		X
*Arothron meleagris**	O	X	X		X	X	X	X	X	X	X	X	X
Canthigaster punctatissima	O	X	X	X	X	X	X	X	X	X	X	X	X
TRIPTERYGIIDAE													
Axoclinus lucillae	MI							X	X		X		
Lepidonectes clarkhubbsi	MI						X						
UROLOPHIDAE													
Urobatis halleri	MI			X					X				
ZANCLIDAE													
*Zanclus cornutus**	SI					X				X	X		X

Table 6 Numbers of reef fish species found in different geographical regions in the Tropical Eastern Pacific (TEP); relative coral or rocky character of reef habitats considered in the surveys: *low, **medium, *** important

Location	**Species number**	**Coral reef**	**Rocky reef**	**Reference**
Galapagos Islands, Ecuador	175	*	***	Edgard et al. 2004
Bahía Honda, Panama	126	**	***	This study
Clipperton Island, North Pacific Ocean.	115	**	***	Allen and Robertson 1997
Gulf of Papagayo, Costa Rica	78	*	**	Dominici-Arosemena et al. 2005
Gulf of California, Mexico	74	-	***	Aburto-Oropeza and Balart 2001
Gorgona Island, Colombia	71	**	*	Zapata and Morales 1997
Manuel Antonio, Costa Rica	39	-	***	Phillips and Perez-Cruet 1984

Acknowledgments

This research was sponsored by the Smithsonian Tropical Research Institute (STRI), the German Academic Exchange Service (DAAD) and the Bahía Honda project-Liquid Jungle lab (LJL) research station, and was performed in cooperation with the Centre for Marine Tropical Ecology (ZMT) and The Project Aware Foundation (PADI). We thank Ross Robertson for his advice at STRI and Mr. Jean Pigozzy for giving us the opportunity to conduct this research at Liquid Jungle Lab. Guilherme Vasconcellos, Irving Bethancourt, and Nina Kriegish helped on field and data management. We also thank Carlos L. Ferreira, Sergio Floeter, Suzanne Lao, Tom Nicolai, Denise Pope, Fernando Zapata, Luis D'Croz, Carlos Jiménez, Jorge Cortés, Hector Guzmán, Carlos Guevara, Marc Kochzius, Ghislain Rompré, Werner Ekau, Marc Taylor, Sebastian Ferse, Coralie D'lima, Paul Zachos, Ismael Núñez-Riboni, Friedemann Keyl and Juan Maté for advice offered. Additionally we thank Jaime Andrés Cabrera, María Patricia Castantes (LJL), Christa Müller, Silke Meyerholz, Andreas Hanning, Kai Bergmann, Stefanie Bröhl, Dieter Peterke, Petra Käpnick (ZMT), Harry Barnes, Xenia Saavedra, Adriana Bilgray, Marissa Batista, Ernesto Peña, Edgardo Ochoa, Reynaldo Tapia, Alejandro Arze and Mercedes Denis (STRI), for logistic and administrative support. Map and profile figures were drawn by Marco Luque Parigi.

References

Allen GA, Robertson DR (1997) An annotated checklist of the fishes of Clipperton Atoll, tropical eastern Pacific. Rev Biol Trop 45: 813-843

Almany GR (2004a) Priority effects in coral reef fish communities of the Great Barrier Reef. Ecology 85: 2872-2880

Almany GR (2004b) Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. Oecologia 141: 105-113

Arburto-Oropeza O, Balart E (2001) Community structure of reef fish in several habitats of a rocky reef in the Gulf of California. Mar Ecol 22: 283–305

Bay LK, Jones GP, McCormick MI (2001) Habitat selection and aggression as determinants of spatial segregation among damselfish on a coral reef. Coral Reefs 20: 289-298

Bellwood DR (1998) What are reef fishes? Comment on the report by D.R. Robertson: Do coral reef fish faunas have a distinctive taxonomic structure? (Coral Reefs 17:179–186) Coral Reefs 17: 187–189

Bellwood DR, Hughes TP (2001) Regional-scale assembly rules and biodiversity of coral reefs. Science 292: 1532-1534

Bellwood DR, Wainwright PC (2001) Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. Coral Reefs 20: 139-150

Bellwood D R, Wainwright PC, Fulton CJ, Hoey A (2002) Assembly rules and functional groups at global biogeographical scales. Funct Ecol 16: 557–562

Bellwood DR,Wainwright P C (2002) The history and biogeography of fishes on coral reefs. In: Sale PF (ed) Coral Reef Fishes. Dynamics and diversity in a complex ecosystem. Academic Press, San Diego, pp 5-32

Bermingham E, McCafferty S, Martin A (1997) Fish biogeography and molecular clocks: perspectives from the Panamanian Isthmus. In: Kocher T, Stepien C (eds) Molecular Systematics of Fishes. Academic Press, New York, pp 113-126

Beukers-Stewart BD, Jones GP (2004) The influence of prey abundance on the feeding ecology of two piscivorous species of coral reef fish. J Exp Mar Biol Ecol 299: 155-184

Bradbury RH, Young PC (1981) The effects of a major forcing function, wave energy, on a coral reef ecosystem. Mar Ecol Prog Ser 5: 229-241

Briggs JC (1995) Global Biogeography. Developments in Paleontology and Stratigraphy, 14.

Elsevier, Amsterdam

Cardiel JM, Castroviejo S, Velayos M (1997) Parque Nacional de Coiba: El Medio Físico. In: Castroviejo S (ed) Flora y fauna del Parque Nacional de Coiba (Panamá) Agencia Española de Cooperación Internacional-RJB Madrid, pp 75-106

Caribbean Coastal Marine Productivity (CARICOMP) (2001) Methods Manual Levels 1 and 2. Manual of methods for mapping and monitoring of physical and biological parameters in the coastal zone of the Caribbean. University of the West Indies Mona, Kingston Jamaica and Florida Institute of Oceanography

Cortés J (1990) The coral reefs of Golfo Dulce, Costa Rica: distribution and community structure. Atoll Res Bull 344: 1-36

Cortés J (1993) Comparison between Caribbean and eastern Pacific coral reefs. Rev Biol Trop 41 (suppl 1): 10-21

Cortés J (1997) Biology and Geology of Eastern Pacific Reefs. Coral Reefs 16 (suppl): S39-S46

D'Croz L, Mate JL (2004) Experimental responses to elevated water temperature in genotypes of the reef coral *Pocillopora damicornis* from upwelling and non-upwelling environments in Panama. Coral Reefs 23: 473-483

D'Croz L, Robertson DR (1997) Coastal ocanographic conditions affecting coral reefs on both sides of the Isthmus of Panama. Proc 8th Int Coral Reef Symp Vol 2:2053-2058

Dominici-Arosemena A, Wolff M (2005) Reef fish community structure in Bocas del Toro (Caribbean, Panama) along spatial scales and gradients in habitat complexity Caribb J Sci 41: 613-637

Dominici-Arosemena A, Brugnoli-Olivera E, Cortés-Nuñez J, Molina-Ureña H, Quesada-Alpizar, M (2005) Community Structure of Eastern Pacific Reef fishes (Gulf of Papagayo, Costa Rica). Rev. Tecnociencia, FCNET, Univ. Panamá 7 : 19-41

Edgar GJ, Banks S, Fariña JM, Calvopiña M, Martínez C (2004) Regional biogeography of shallow reef fish and macro-invertebrate communities in the Galapagos archipelago. J Biogeogr 31:1107-1124

English S, Wilkinson C, Baker V (1994) Survey manual for tropical marine resources. Australian Institute of Marine Science, Townsville

Ferreira CEL,Floeter SR, Gasparini JL, Ferreira BP, Joyeux JC (2004) Trophic structure patterns of brazilan reef fishes: a latitudinal comparison. J Biogeogr 31:1-13

Ferreira CEL,Gonçalves JEA, Coutinho R (2001) Community structure of fishes and habitat complexity in a tropical rocky shore. Environ Biol Fish 61: 353-369

Floeter SR, Gasparini JL (2000) The southwestern Atlantic reef fish fauna: composition and zoogeographic patterns. J Fish Biol 56: 1099-1114

Floeter SR, Ferreira CEL, Dominici-Arosemena A, Zalmon I (2004) Latitudinal gradients in Atlantic reef fish communities: trophic structure and spatial use patterns. J Fish Biol 64: 1-20

Fulton CJ, Bellwood DR (2002) Ontogenetic habitat use in labrid fishes: an ecomorphological perspective. Mar Ecol Prog Ser 236: 255-262

Fulton CJ, Bellwood DR,Wainwright PC (2005) Wave energy and swimming performance shape coral reef fish assemblages. Proc Roy Soc London B 272: 827-832

García-Chartron JA, Pérez-Ruzafa A (2001) Spatial pattern and the habitat structure of a Mediterranean rocky reef fish local assemblage. Mar Biol 138: 917–934

Genin A, Jaffe J, Reef R, Richter C, Franks P (2005) Swimming against the flow: a mechanism of zooplankton aggregation 308: 860-862

Glynn PW, Maté JL (1997) Field guide to the Pacific coral reefs of Panamá. Proc of 8th Int Coral Reef Symp Vol 1: 145–66

Harmelin-Vivien M (2002) Energetics and fish diversity on coral reefs. In: Sale PF (ed) Coral Reef Fishes: Dynamics and diversity in a complex ecosystem. Academic Press, San Diego, pp 265-274

Hastings PA, Robertson DR (2001) Systematics of tropical eastern Pacific fishes. Rev Biol Trop 49 (suppl 1): 209

Khalaf MA, Kochzius M (2002) Changes in trophic community structure of shore fishes at an industrial site in the Gulf of Aqaba. Mar Ecol Prog Ser 239: 287–299

Kwiecinski B, Chial ZB (1983) Algunos aspectos de la oceanografía del Golfo de Chiriquí, su comparación con el Golfo de Panamá. Rev Biol Trop 31: 323-325

Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef fish communities. Mar Biol 49: 317-323

McKenna J (1997) Influence of Physical Disturbance on the Structure of Coral Reef Fish Assemblages in the Dry Tortugas. Caribb J Sci 33: 82–97

Mora C, Robertson DR (2005) Factors shaping the range size frequency distribution of fishes in the Tropical Eastern Pacific. J Biogeogr 32:277-286

Mora C, Chittaro PM, Sale PF, Kritzer JP, Ludsin SA (2003) Patterns and processes in reef fish diversity. Nature 421:933-936.

NOOA/NOS (2005) Water Level Tidal Predictions. Tidal Station Locations and Ranges. http://140.90.121.76/tides05/tab2wc1a.html#121

Palumbi SR (1997) Molecular biogeography of the Pacific. Coral Reefs 16:S47-S52

Paulay G (1996) Dynamic clams: changes in the bivalve fauna of Pacific islands as a result of sea level fluctuations. Am Malacol Bull 12: 45-57

Phillips PC, Perez-Cruet M J. (1984) A comparative survey of reef fishes in Caribbean and Pacific Costa Rica. Rev Biol Trop 32: 95-102.

Pielou EC (1975) Ecological diversity. John Wiley and Sons, New Cork

Prahl H, Guhl F, Grogl M (1979) Gorgona. Futura. Bogotá. 279 p

Quesada-Alpízar M, Morales-Ramírez A (2004) Comportamiento de las masas de agua en el Golfo Dulce durante un periodo El Niño (1997-1998). Rev Biol Trop 52: 95-103

Roberts MR, Ormond RFG (1987) Habitat complexity and coral reef diversity and abundance on Red Sea fringing reefs. Mar Ecol Prog Ser 41: 1–8

Robertson DR (1998) Do coral-reef fish faunas have a distinctive taxonomic structure? Coral Reefs 17: 1–8

Robertson DR, Allen GR (2002) Shore fishes of the tropical eastern Pacific: an information system. Smithsonian Tropical Research Institute. Balboa, Panamá

Robertson DR, Grove JS, McCosker JE (2004) Tropical transpacific shore fishes. Pac Sci 58: 507-565

Rogers CS, Garrison G, Grober R, Hillis ZM, Franke MA (1994) Coral reef monitoring manual for the Caribbean and Western Atlantic. Southern Regional Office National Park Service. The Nature Conservancy WWF

Sluka RD, Miller MW (2001) Herbivorous fish assemblages and herbivory pressure on Laamu Atoll, Republic of Maldives. Coral Reefs 20: 255-262

Springer VG, Williams JT (1994) The Indo-West Pacific blenniid fish genus *Istiblennius* reappraised: a revision of *Istiblennius*, *Blenniella*, and *Paralticus*, new genus. Smithson Contrib Zool 565:1-193

Ter Braak CJF, Verdonschot PFM (1995) Canonical correspondance analisys and related multivariate methods in aquatic ecology. Aquat Sci 57: 255–289

Thresher RE (1983) Environmental correlates of the distribution of planktivorous fishes in the One Tree Reef Lagoon. Mar Ecol Prog Ser 10: 137-145

Vega AJ, Villareal N (2003) Peces asociados a arrecifes y manglares en el Parque Nacional Coiba. Rev. Tecnociencia, FCNET, Univ. Panamá 5 (1): 65-74

Veron JEN (1995) Corals in space and time. Cornell University Press, Ithaca

Wilson MEJ Rosen BR (1998) Implications of the paucity of corals in the Paleogene of SE Asia: plate tectonics or Centre of Origin?, In: Hall R, Holloway JD(eds) Biogeography and Geological Evolution of SE Asia. Backhuys Publishers, Leiden, The Netherlands, pp165-195

Wolff M, Alarcón E (1993) Structure of a scallop *Argopecten purpuratus* (Lamarck, 1819) dominated subtidal macro-invertebrate assemblage in Northern Chile. J Shellfish Res 12: 295-304

Wolff M, Hartmann H, Koch V (1996) A pilot trophic model for Golfo Dulce, a fjord-like tropical embayment, Costa Rica. Rev Biol Trop 44(suppl 3): 215-231

Zapata FA, Morales A (1997) Spatial and temporal patterns of fish diversity in a coral reef at Gorgona Island, Colombia. Proc 8th Int Coral Reef Symp 1: 1029–1034

Zar JH (1996) Biostatistical analysis, 3rd ed. Prentice Hall, Upper Saddle River

6.5 Publication III

COMPARING REEF FISH COMMUNITY STRUCTURE BETWEEN THE PACIFIC AND THE CARIBBEAN SIDE OF THE ISTHMUS OF PANAMA

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Manuscript summited to Coral Reef

Comparing reef fish community structure between the Pacific and the Caribbean side of the Isthmus of Panama.

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Abstract

This paper presents the results of a comparative study of reef fish communities on either side of the Western Isthmus of Panama (IOP). 288 visual censuses were carried out in each region. 128 fish species of 38 families were found in the Caribbean and 126 species of 44 families in the Pacific. The numbers of families and species do not differ markedly but the number of species recorded per sampling area was higher in the Pacific. Reef fishes depend on recruitment success, which is related to local oceanography and the connectivity and diversity of habitats, rather than to coral cover and diversity. Herbivores predominate in the Caribbean; planktivores and piscivores in the Pacific. Most reef fish reach larger sizes in Pacific. In both regions, the highest number of species is found in exposed rocky zones with high substrate diversity and complexity; followed by massive coral reefs. Individuals are smaller on low-complexity substrates in the Caribbean and in coral branches and holes in the Pacific, which provide refuge areas from predation and strong water movements. Better swimmers occur typically in exposed zones in Caribbean and have a wide spatial distribution in Pacific. Geminate species show strong habitat plasticity on both sides of the IOP, but retain similar habitat preferences in terms of morphology and depth regardless of the taxonomy of the benthic fauna and flora.

Keywords: Central America, reef fish, trophic groups, evolution of fish communities

Introduction

Geological changes in lower Mesoamerica: effect on corals and fish communities.

At present, the distance separating the Tropical Western Atlantic (Caribbean, TWA) from the Tropical Eastern Pacific (TEP) in the Lower Mesoamerica region is as little as 50 km (Leschine 1981). However, this separation has resulted in very different oceanographic settings and associated coral reef-dwelling communities (Bellwood and Wainwright 2002). Prior to 3.5 million years BP, the eastern side of the Isthmus of Panama (IOP) was part of a much wider ocean with abyssal-bathyal depths, while the western side consisted of interconnected small seas in a shallow basin that, after closure, was elevated to form the Talamanca mountain range (Coates et al. 2005). The IOP started to emerge in the late Miocene, about 7 million years ago (Coates and Obando 1996). At that time, the coral fauna in the shallow seas on the western side of the American continent was similar to that of the present-day TWA, as were the environmental conditions (Cortés 1997; O'Dea and Jackson 2002). During the closure of the IOP, the westward flowing warm equatorial current was blocked and deflected to the north, giving rise to the present-day Atlantic Ocean, a closed ocean basin with relatively stable currents. On the other side, extreme changes started to occur in the TEP, which fell under the influence of variable, but generally colder currents flowing towards the Equator from both North and South America, with cooling during periods of intense upwelling and warming during El Niño events (D'Croz and Robertson 1997). These highly variable oceanographic conditions led to a massive extinction of the previous coral fauna in the TEP. Present day corals in this region have strong affinities with those found in the Central Pacific (Cortés 1997). They occur sparsely in conditions inadequate for growth, with a discontinuous distribution and low coral diversity. Most of the present day TEP coral reefs thus started to develop in the Late Holocene following the closure of the IOP (Glynn and Maté 1997).

Palaentological data and phylogenetic research suggests that, following a massive extinction of the fish fauna due to the reduction of coral reef habitats during the glacial maximum, fish from the central Pacific colonized the region of the TWA prior to the formation of the IOP (Bellwood and Wainwright 2002). Thus, much of the fish fauna of the TWA is of Central Pacific origin and has subsequently evolved into the present-day fish assemblages (Rocha et al. 2005). The direct impact of the Isthmus has been of significance even down to species level (Bellwood and Wainwright 2002). There are more similarities between the fish fauna of the South-eastern Pacific (which includes the IOP) and that of the TWA than between the North-eastern and South-eastern Pacific (Lessios et al. 1995). Reef fish have evolved and survived in the TEP until the present and it seems that most of the characteristic reef fish families have survived despite the disappearance of their formerly dominant coral reef habitats.

Why compare reef fish community structure on both sides of the IOP?

In both the Caribbean and Pacific, the areas adjacent to the IOP contain more archipelago and island habitats than other Panamanian coastal waters. While coral-rich areas (in the TWA) have already received some attention, coral-poor regions such as the TEP (Robertson 1998) have not yet been extensively considered. Prior to this study no information was available for comparative study of the taxonomical-ecological structure (*e.g.* number of species among families or diversity patterns) in the IOP region. It is often stated that the TWA is more diverse than the whole TEP but this seems more of an assumption than a statement based on clear evidence. Information is not only needed for the identification of present-day assemblages and for the description of their evolution, but also in order to understand the interplay between the habitat characteristics of the fish communities (trophic groups, fish densities, and size classes) and the environmental variables operating on both sides of the IOP.

Objectives and research approach

Our aim is to present, for the first time, a trans-isthmian descriptive study of fish communities at both sides of the IOP and to understand how they are organized and how they have evolved since the formation of the Panamanian land bridge.

We can expect to find that fish assemblages in the two regions display major distinguishing taxonomic and functional characteristics. Recent geological changes, leading to a process of coral reef conversion into a rocky environment, may explain the changes that have occurred in reef fish assemblages (Bellwood 1996, 1998; Robertson 1998). The specific questions addressed in this study are: 1) Does the taxonomical structure of the fish fauna in the two regions differ significantly? 2) Has the existence of coral reefs been a crucial factor in the evolutionary diversification of reef fishes following the closure of the IOP and do we therefore find a higher species richness in the coral-rich TWA region? 3) Has there been a strong differentiation in the functional characteristics (trophic groups, fish densities, size class structure) of the fish communities in the two regions? 4) Are site-specific characteristics of the fish fauna, such as total fish abundance, richness and diversity, associated with particular physical characteristics of the habitat (e.g. substrate diversity, complexity)? 5) Are the present-day habitat associations of geminate species similar to the habitat preferences of the common ancestor species?

Materials and Methods

Study area and sampling

The recently elevated Talamanca mountain range separates the coastal waters on either side of the IOP. In TEP, the Gulf of Chiriquí, an area not influenced by coastal upwelling (Kwiecinski and Chial 1983; Cardiel et al. 1997), contains the largest inshore coral reef close to Coiba Island (D'Croz and Robertson 1997; Glynn and Maté 1997). In TWA, the Bocas del Toro, a lagunar-sedimentary system with ancient sediments overlaying the middle Miocene basaltic arc (Coates et al. 2005), consists of a network of islands and numerous sheltered shallow coral reefs, seagrass beds and mangrove forest in sheltered zones. Here the influence of rivers is large and tidal variation only small (Clifton et al. 1997; Guzmán and Guevara 1998). The two regions are affected by contrasting water circulation patterns, with those of the TEP being more variable, and characterized by a higher tidal variation (around 4 meters), more cold water intrusion and stronger currents. Sampling was carried out in Bocas del Toro from April to September 2002 and in the Gulf of Chiriquí (Bahia Honda) from February to July 2003 (Fig. 1).

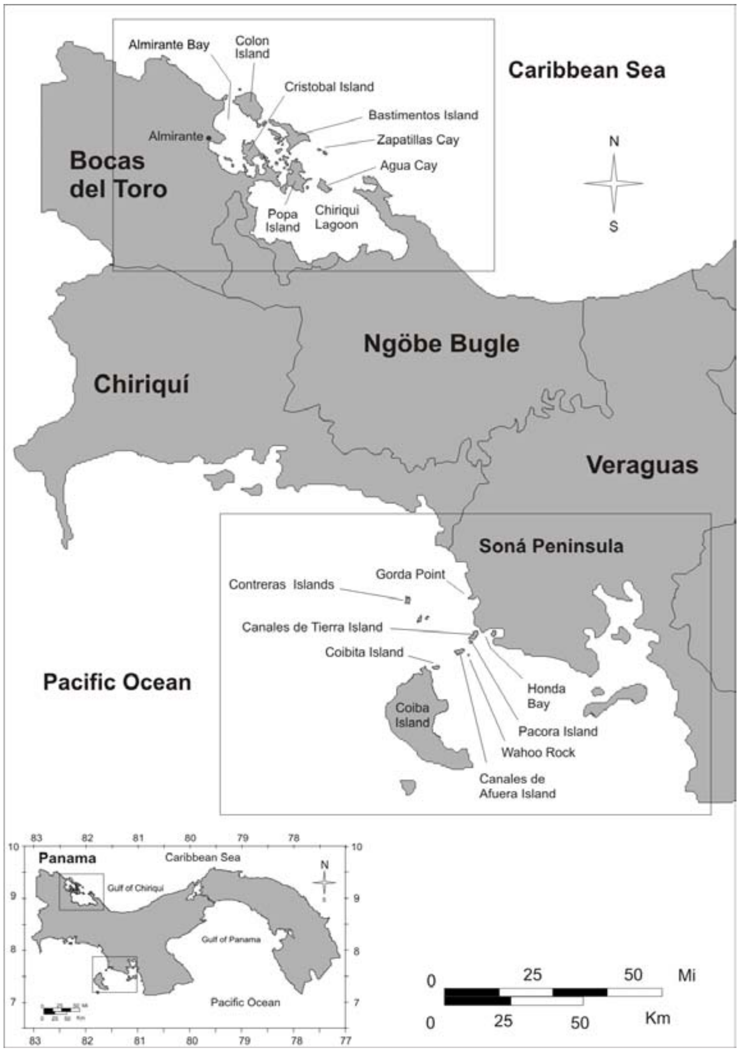

Fig. 1. Sampling areas, Tropical Western Atlantic (Bocas del Toro); Tropical Eastern Pacific (Gulf of Chiriquí). Site details are given in Dominici-Arosemena and Wolff (2005) and Dominici-Arosemena and Wolff (2006).

Physical parameters

We measured temperature with a portable thermometer (°C), salinity with a refractometer and visibility by the measured distance (in meters) between an acrylic plate from one diver to another, Depth was measured with a diving gauge.

In each region, 12 zones were selected and four benthic transects of 30 m length were set up parallel to the shore, yielding a total of 48 benthic transects/region. Different habitats were selected on coral or rocky reefs. Substrate coverage and complexity was determined using a link-chain methodology (Rogers et al. 1994; CARICOMP 2001) and substrate diversity was determined using Simpson's diversity index (Ferreira et al. 2001). The detailed methods applied in both regions are fully described in Dominici-Arosemena and Wolff (2005, 2006).

Habitat structure

We used a standardized habitat classification (Table 1) as the basis for our comparative analysis:

Deep rocky zones: Complex substrate in deeper areas (13 m, TWA; 15-20 m, TEP), with calcareous, turf and encrusting algae and strong currents.

Deep walls: Steep basaltic rocky walls to a depth of approximately 15-20 m, found in the TEP with encrusting algae, erect sponges and other sessile invertebrates.

Massive coral zones: Living and dead massive corals of different genera. These diverse zones consist of macro-algae, sponges, sessile invertebrates, sand and crevices.

Non-massive corals - shallow zones: Foliaceous, fire or branching corals and an absence of rocks.

Rubble zones: Adjacent to patches of the branching corals with a mixture of dead pieces of coral and sand.

Shallow rocky zones: Diverse benthic fauna and flora, covered by encrusting red algae. Encrusting and erect sponges in TWA and pocilloporid branching corals in TEP. Strong waves and currents.

Turf algae - dead non-massive coral zones: Only in TWA, approximately 12 m depth. Dead branching coral skeletons and turf algae.

Table 1. Environmental and habitat variables in both sides of Western Panama, numbers in parenthesis indicates standard deviation of determined average value.

Type of region	Close lagunar system in sheltered zones and current-wave exposed zones, low tidal variation, variable types of habitats mostly coral reef. Stable environmental conditions, low seasonal variation	Open system, wide tidal variation, strong currents, and variable types of habitats mostly rocky reef.
Temperature (^{0}C)	28.3 (1.1)	28.3 (1.9)
Salinity (PSU)	32.1 (2.2)	33.2 (1.6)
Visibility (m)	9.1 (3.0)	11.7 (4.6)
Deep (m)	5.5 (2.4)	7.2 (4.9)
Complexity index	1.6 (0.2)	2.0 (0.41)
Substrate diversity (Simpsom index)	0.38 (0.12)	0.24 (0.08)
Dead Massive coral (DMC, %)	6.79 (12.18)	0.05 (0.38)
Sand (%)	16.13 (22.30)	9.02 (9.00)
Calcareous algae (CA,%)	2.06 (4.67)	6.51 (10.56)
Turf Algae (TA, %)	4.34 (13.90)	25.78 (12.33)
Dead non-massive corals (DNMC, %)	13.79 (15.14)	0.22 (0.71)
Fleshy algae (FA, %)	3.0 (7.80)	7.68 (16.27)
Encrusting algae (EA, %)	0.45 (1.77)	19.26 (14.53)
Encrusting corals (EC, %)	1.5 (2.72)	0.27 (0.72)
Encrusting sponges (ENS, %)	2.72 (6.06)	0.58 (0.89)
Erect sponges (ERS, %)	1.18 (1.85)	0.11 (0.34)
Non-massive corals (NMC, %)	29.68 (30.10)	18.00 (25.5)
Rubble (RUB, %)	7.43 (15.60)	7.07 (10.96)
Massive corals (MC, %)	4.68 (8.85)	4.43 (9.86)
Other encrusting invertebrates (OEI, %)	0.54 (1.89)	0.26 (0.81)
Other sessile invertebrates (OSI, %)	3.40 (6.69)	0.01 (0.05)

Estimate of fish species and abundance

Each site was assessed using underwater visual surveys with scuba diving equipment (English et al. 1994). The same fixed benthic transects (30 x 5 m) used for the study of the benthos were used for the fish censuses. Monthly censuses were undertaken at all transects (six censuses per transect). Thus, a total of 288 visual censuses per region were undertaken of a total of 96 benthic transects, 48 in reach region. Two to three observers swam along the transects, recording all fish encountered within 2.5 m on both sides and 5 m above. The standard length (SL) was estimated to the nearest centimetre with a PVC ruler. Abundance (individuals/150 m^2), Shannon-Wiener diversity (H'/150 m^2), and species richness estimates (S/150 m^2) were calculated based on relative abundance/sampling area (Pielou 1975).

Trophic groups

Fish species were classified into trophic groups following Ferreira et al. (2004) as carnivores; mobile-invertebrate feeders; omnivores; piscivores; planktivores; roving herbivores; sessile-invertebrate feeders; and territorial herbivores.

Data analysis

The number of species per family, and the pooled fish abundance for each region were presented in a rank-order to visualize species dominance and to compare calculations of species richness, diversity and evenness in fish communities at the different sites (Log series model, see Wolff and Alarcón 1993). Graphical representations were used to show the distribution of size classes of trophic groups and families and the number of individuals per sampling area. For the present paper, data from both study areas (Dominici-Arosemena and Wolff 2005, 2006) were summarized as a basis for a general analysis. The association between some geminate species and habitat was examined using Canonical Correspondence Analysis (CCA, Ter Braak and Verdonschot 1995). The following species were selected for analysis according to frequency, abundance and phylogenetic relationship: Labridae: *Halichoeres bivittatus* -TWA vs. *H. dispilus*, *H. nicholsi*, *H. notospilus*-TEP (Barber and Bellwood 2005) Pomacentridade: *Chromis multilineata*-TWA vs. *Chromis atrilobata*-TEP (Bermingham et al. 1997), *Stegastes adustus*-TWA vs. *S. flavilatus*-TEP, *Stegastes planifrons*-TWA vs. *S. acapulcoensis*-TEP (Wellington and Robertson 2001) Chaetodontidae:

Chaetodon striatus-TWA vs. *C. humeralis*-TEP (Bermingham et al. 1997), Pomacanthidae: *Pomacanthus arcuatus*-TWA vs. *Pomacanthus zonipectus* (Bellwood et al. 2004). *Serranus Baldwini*, *S. Tigrinus*-TWA vs. *S. psittacinus*-TEP (Kochzius and Dominici-Arosemena, unpublished)

Results

Physical characteristics of study sites:

Salinity, Temperature, visibility:

Temperature values are similar in both regions with a higher variation in the TEP. Salinity is higher in the TEP, with higher variation in the TWA Visibility is higher but more variable in the TEP (>11 meters) compared to the TWA (9 meters) (Table 1).

Depth:

Rocky reefs in the TEP occur at depths of aproximately 20 meters). Reef habitats in the TWA are mostly restricted to shallower areas (aproximately 13 meters).

Habitat complexity:

Habitat complexity is relatively higher in the TEP.

General substrate characteristics of surveyed habitats:

The coverage of live corals and their dead skeletons is higher in the TWA. Rocky substrate is ubiquitous in the TEP, as is coral reef frame in the TWA. Branching and massive coral reef habitats are always found in areas sheltered from waves. Encrusting red algae and macro algae are more widespread in TEP and predominate in exposed zones in the TWA. Sponges are more widespread in most habitats in the TWA along with encrusting and sessile invertebrates.

Substrate diversity:

The Simpson's diversity index is closer to zero in the TEP, with the highest substrate diversity found on shallow rocky reefs. It is closer to one (monotony) in the TWA, where there is a strong dominance by certain species of corals.

Global Patterns of fish communities on both sides of the IOP

Taxonomic structure:

Number of families and species: The total number of families does not differ markedly and 62.75% of the IOP families occur in both regions. 13.73 % of families are restricted to the TWA and 23.52% to the TEP. The number of genera is higher in the TEP. Ten endemic genera occur in the TWA and eight in the TEP. Forty-two genera are found in both regions. Very similar numbers of species are found among the majority of diverse families in both regions. However,in the TEP, species numbers tend do be higher among acanthurids, carangids, gerreids and muraenids, while the the TWA presents higher numbers of species of chaetodontids, haemulids, holocentrids, labrids and serranids (Figure 2, Table 2).

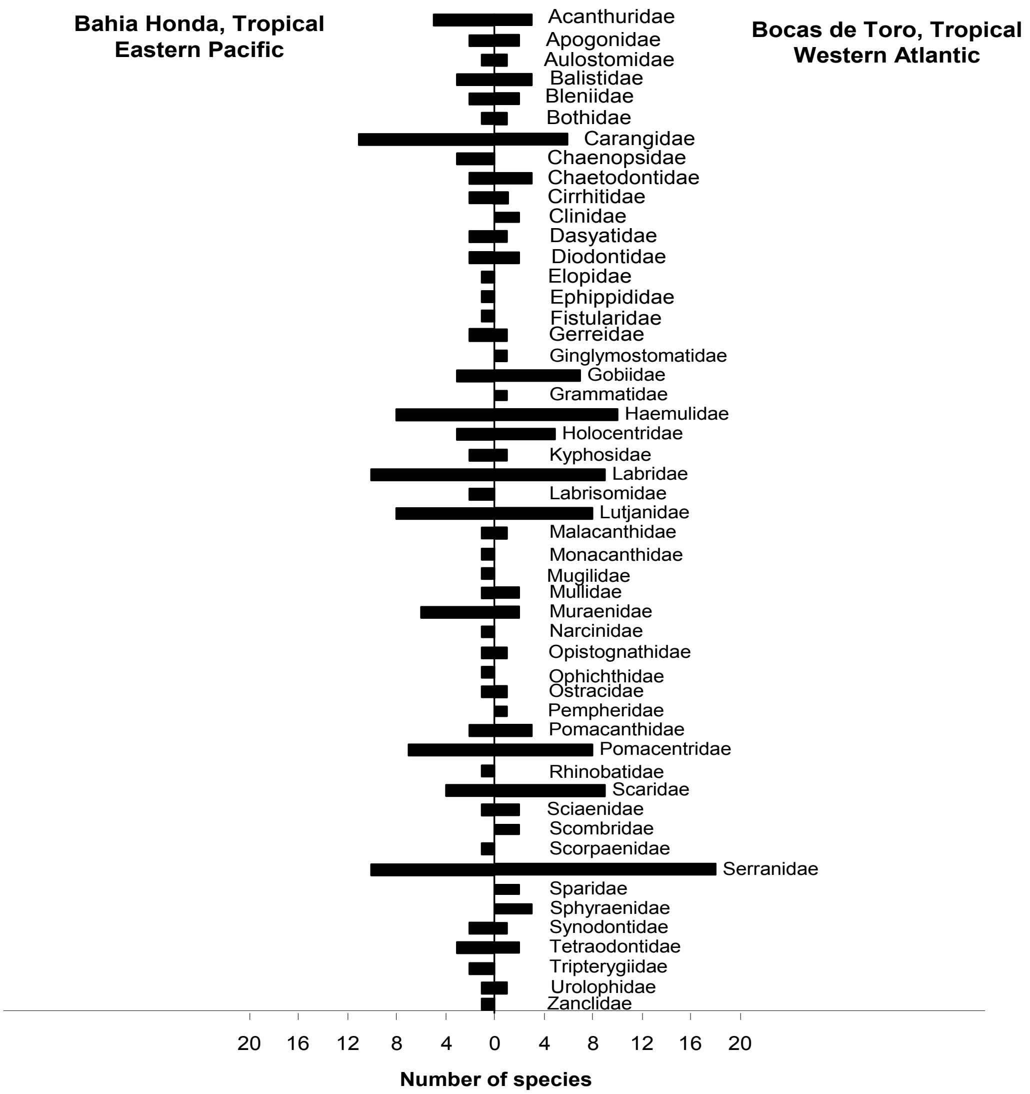

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Fig 2. Number of species within families on both sides of the Isthmus of Panama.

Table 2. Comparative taxonomy in both sides of the Lower Mesoamerican region

	TWA (Bocas del Toro)	**TEP (Gulf of Chiriqui)**
Total number of families	38	44
Shared families TWA and TEP	32	32
Families founded only in TWA or TEP	6	12
Abundant Reef fish families	Gobiidae, Pomacentridae (*Stegastes* sp), Scaridae, Serranidae (*S. tortugarum*), Labridae, Haemulidae, Chaetodontidae, Acanthuridae	Labridae, Pomacentridae (*Chromis* sp), Haemulidae, Apogonidae, Cirrhitidae, Chaenopsidae, Carangidae, Tetraodontidae
Most diverse families (sp numbers)	Serranidae (18), Haemulidae (10), Labridae (9), Scaridae (9), Lutjanidae (8), Pomacentridae (8), Gobiidae (7), Carangidae (6)	Carangidae (11), Labridae (10), Serranidae (10), Haemulidae (8), Lutjanidae (8) Pomacentridae (7), Muraenidae (6), Acanthuridae (5)
Total number of genera	72	86
Shared genera TWA and TEP	42	42
Endemic genera founded TWA or TEP	10	8
Total species numbers	128	126
Shared species BDT and BH	2	2
Circumtropical species	6	8
Recent-Indo-Pacific species	0	24

<u>*Diversity parameters, species richness and abundance*</u>:

Fish diversity:

The species richness per area is nine times higher in the TEP. In the TWA the dominant species are herbivores and planktivores, while the TEP is dominated by planktivores, carnivores and mobile invertebrate feeders . Abundance (position of the line with respect to the y-axis) and species richness (intersection with the x-axis) are higher in the TEP, where complex rocky substratesaccount for a greater proportion of total substrates (Figure 3).

<u>*Family distribution, size spectra and fish abundance within trophic groups*</u>:

<u>Planktivores</u>**:** Small individuals (0-5 cm and 5-10 cm) of the families pomacentridae and labridae are more abundant in the TEP, while in the TWA small sized (<5) gobids and serranids are the most abundant planktivores (Figure 4a).

<u>Carnivores</u>: The TEP presents a great abundance of haemulids over several size classes, with smaller numbers of serranids, and small (5-10 cm) cirrhitids. In the TWA, this group is represented only by small individuals (5-10 cm) of the family serranidae (Figure 4a).

<u>Omnivores</u>: In the TEP, omnivores are represented by gobids, tetraodontids, pomacanthids and pomacentrids . In the TWA there are just a few small sized gobids (Figure 4a).

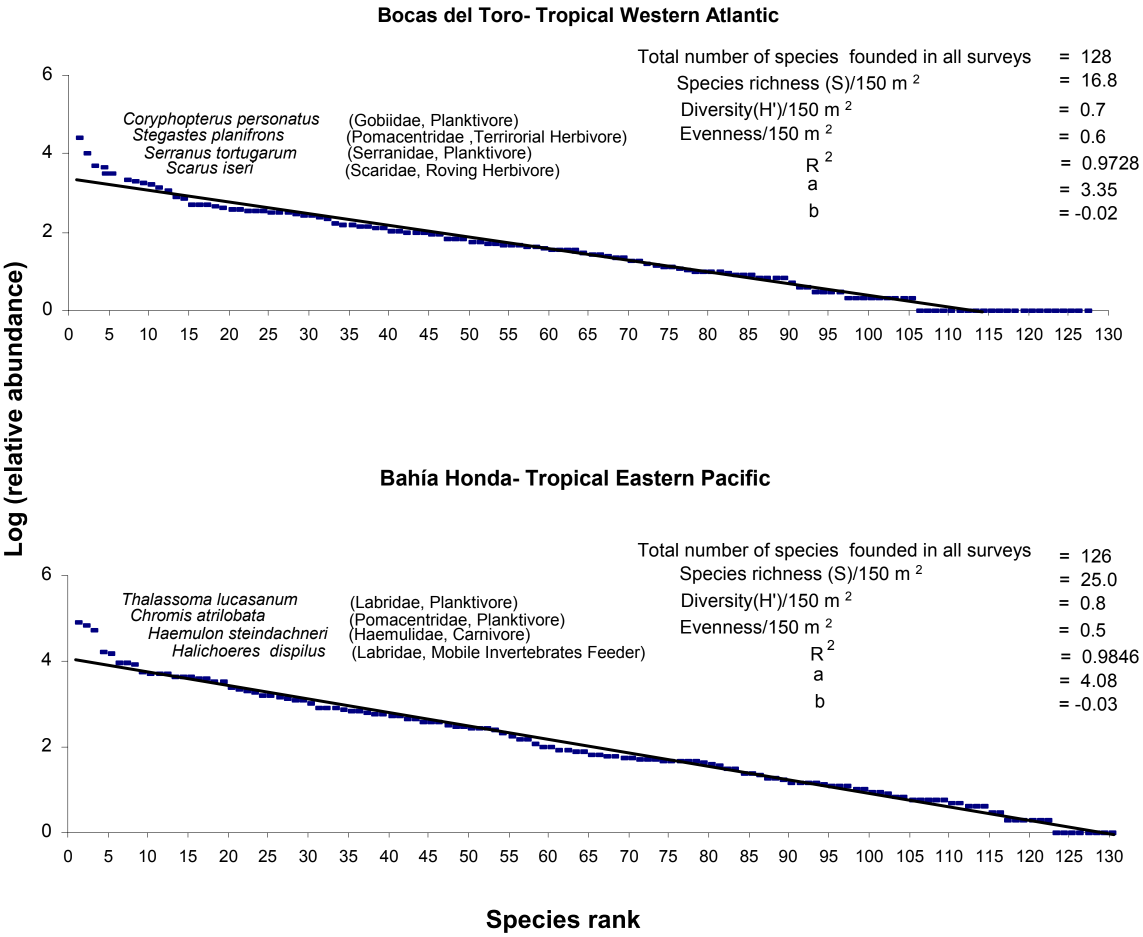


Fig 3. Log-series abundance-rank lots for reef fish communities on both sides of the Isthmus of Panama, most dominant species are listed. The least abundance species was set =1, abundance of remains species was computed accordingly. This results are based on average data on 150 m^2

<u>Mobile invertebrate feeders</u>: This group is present in smaller numbers than planktivores and carnivores. It is represented in the TEP by labrids of small size classes (0-5cm and 5-10 cm), and small chaenopsids (0-5cm). In the TWA, small labrids (5-10 cm) are also present but in lower numbers. as well as haemulids of small size classes (Figure 4a).

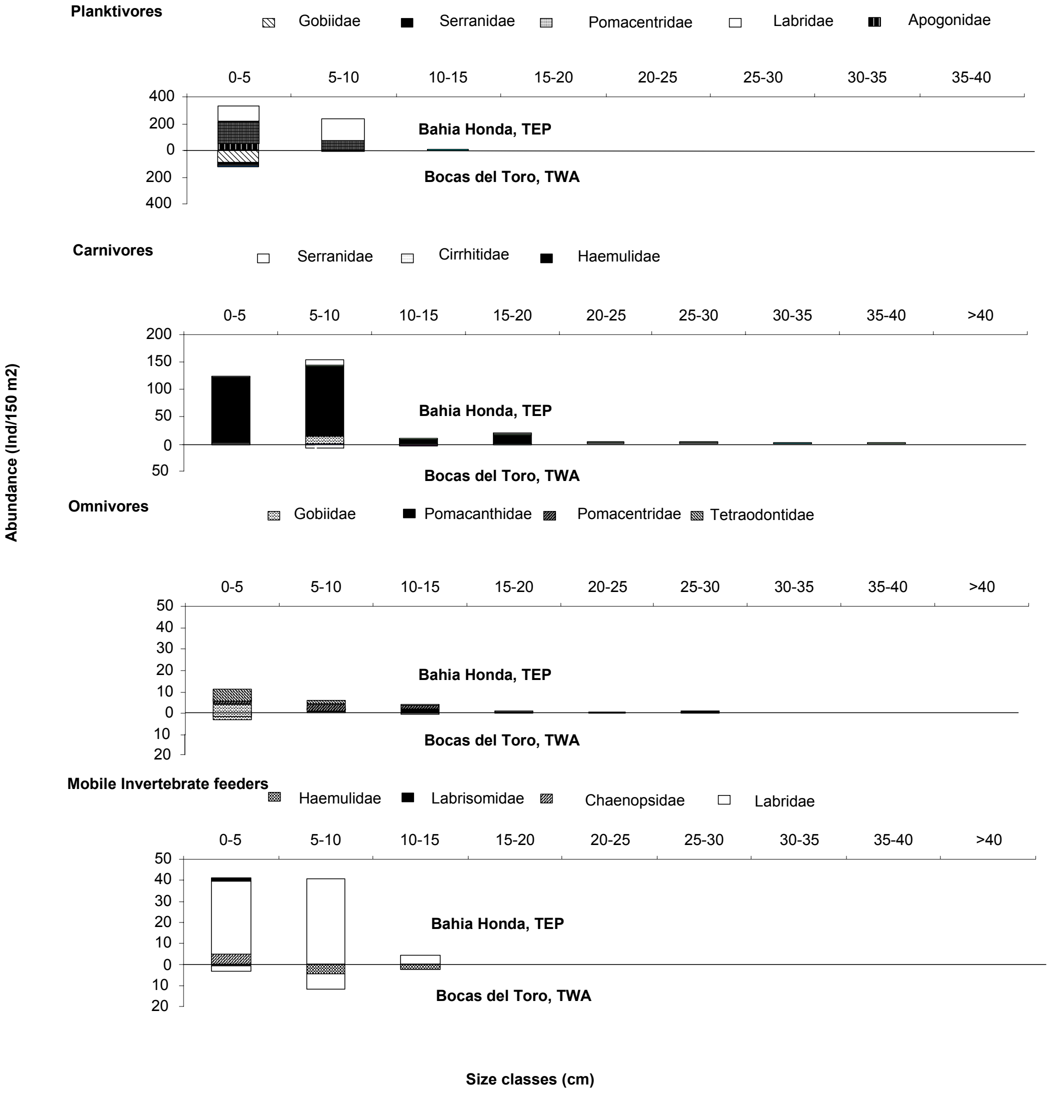


Fig 4a. Size classes and abundance of trophic groups/ families on both sides of the Isthmus of Panama.

Territorial herbivores: This group is less abundant in the TEP than in the TWA. In both regions it is represented by pomacentrids, with higher numbers of small individuals in the TWA (Figure 4b).

Roving herbivores: Similar assemblages of this group were encountered in both regions. Scarids are the most abundant group and there a few acanthurids were found in both regions. Densities within size classes were similar, but somewhat smaller individuals (recruits and post recruits) were found in higher abundance in the TEP (Figure 4b).

<u>Sessile invertebrate feeders</u>: This group is present in relatively low numbers, but in greater abundance in the TEP (small gobids, 0-5 cm, balistids,10 to 25 cm, few chaetodontids and zanclids). In the TWA only relatively small (5-10 cm) chaetodontids were found (Figure 4b).

<u>Piscivores:</u> This group is represented in the TEP by small bleniids that feed on fish scales (< 10 cm, *Plagiotremus azaleus*) and an abundance of carangids of a wide range of size classes, and amongin some cases reaching sizes > 40 cm. In the TWA, this group is underrepresented (Figure 4b).

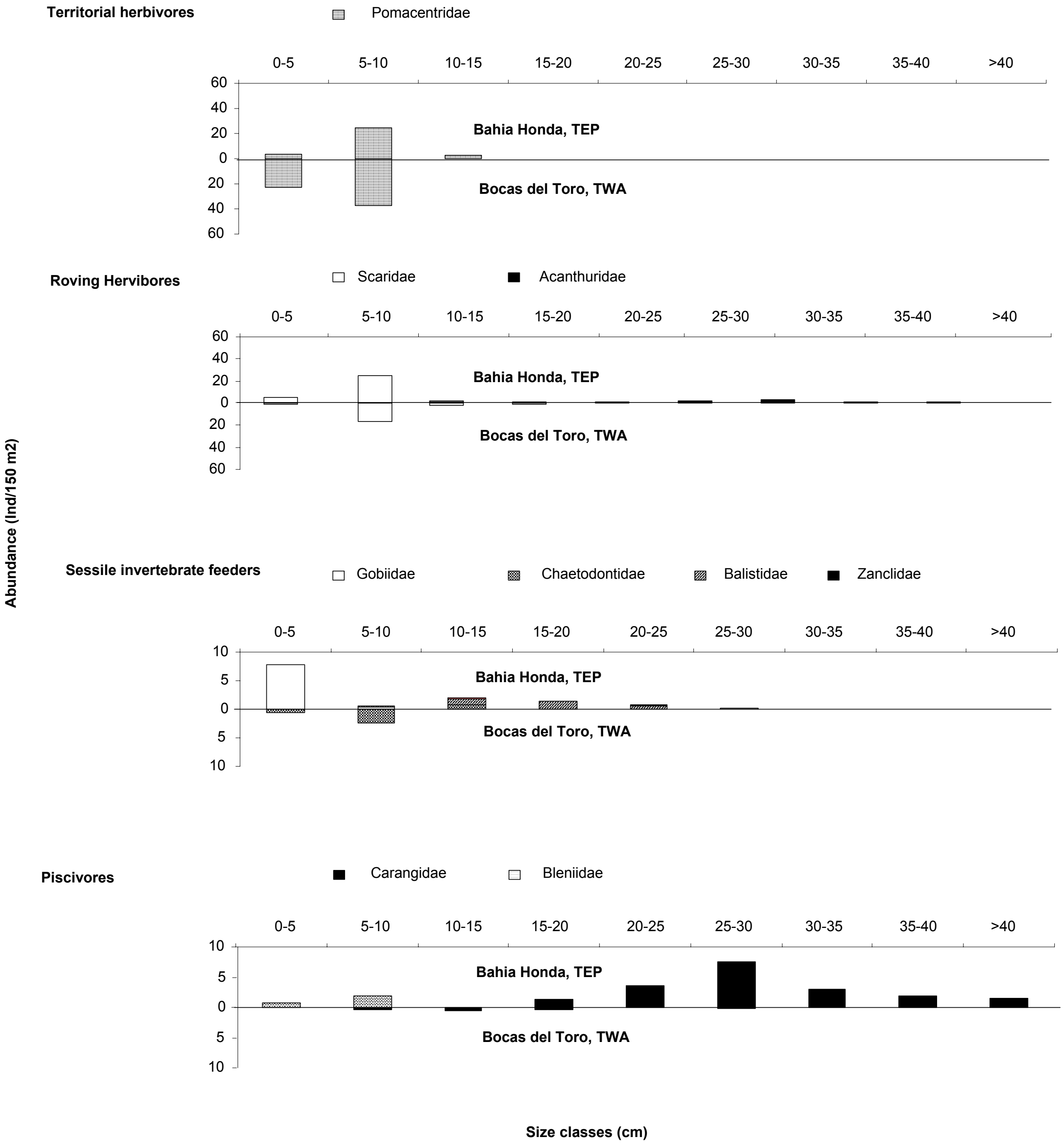


Fig 4b. (Cont.) Size classes and abundance of trophic groups/ families in both sides of the Isthmus of Panama.

Local patterns: comparative results for Dominici-Arosemena and Wolff (2005 and 2006)

Ontogenic movements among surveyed habitats: Habitat complexity plays an important role for juveniles in the TEP region; while in the TWA juveniles tend to hide in rubble substrates. Adults of larger size classes tend to occupy complex habitats in both regions.

Habitat assemblages: Similar fish assemblages are found in both regions in shallow rocky reef zones, where planktivore labrids and acathurids predominate. Shallow branching corals follow a similar pattern, with haemulids and scarids present in these habitats. A deep rocky reef assemblages could be defined only in the TEP, and a rubble habitat assemblage was identified only in the TWA region. No assemblages could be defined for massive corals. .

Diversity parameters: Minimum species richness was found in low complexity habitats and maximum richness in shallow-complex rocky reef zones. The diversity index is relatively high for all rocky reef and massive coral reef zones but lower for the sand-rubble habitat in the TWA and on monospecific pocilloporid reefs in the TEP region.

Fish abundance (individuals/census): Abundance seems positively correlated with substrate complexity only in the TEP. Total fish abundance is positively correlated with sand and rubble substrates in the TWA.

Mobility groups: Category 1 fish, which include strong swimmers adapted to strong currents and wide tidal variations, and displaying vertical mobility within the water column predominate in all exposed zones in the TWA and have a homogeneous distribution in the TEP. Relative sedentary individuals (category 2) are found in rubble areas in the TWA, while in the TEP they were only found on massive coral reefs. Category 3, which includes site-attached individuals, is represented by markedly different assemblages in the two regions. There is a high number of territorial herbivores in the TWA, while attached chaenopsids, gobiids and chirrhitids are found in shallow wave-exposed rocky reef areas in the TEP.

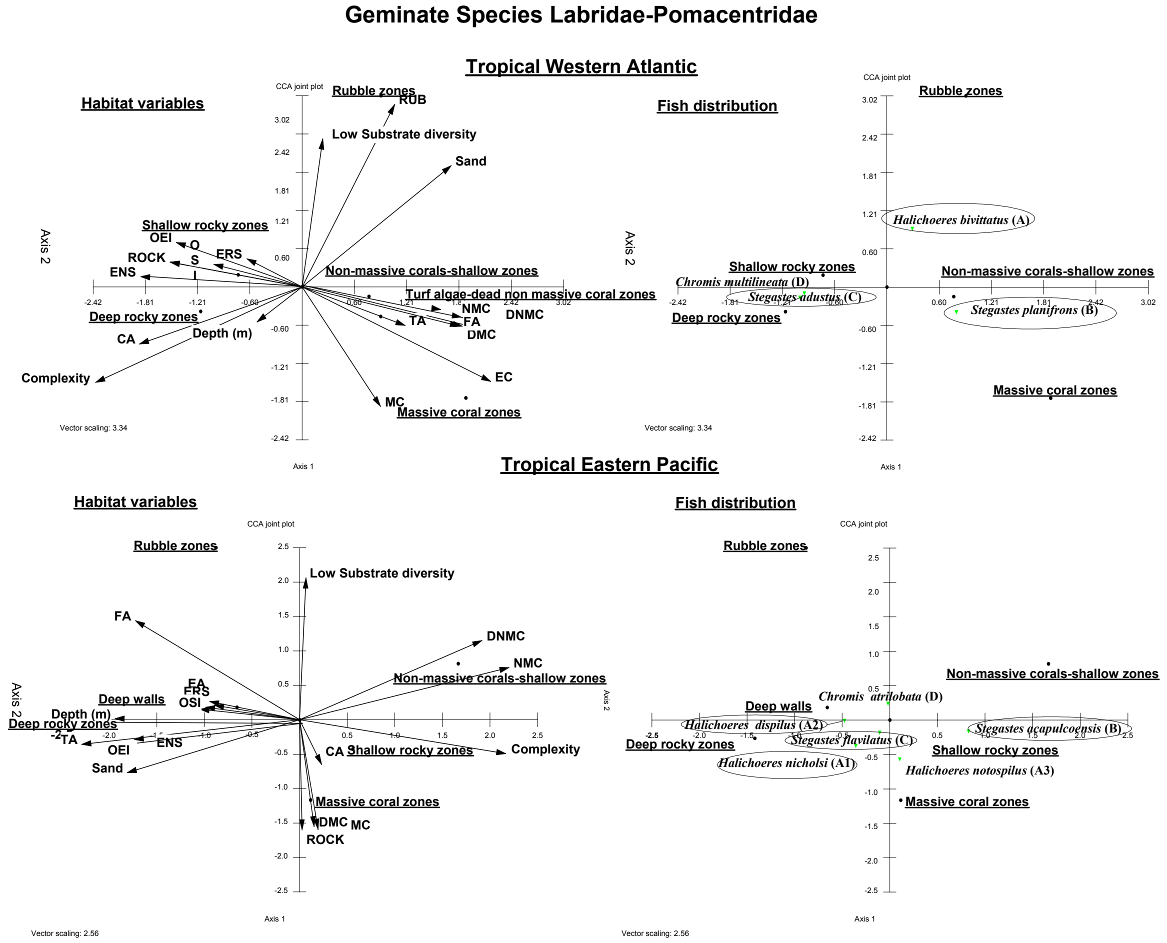
Species richness within trophic groups: Carnivores and mobile invertebrate feeders present the highest number of species. Similar numbers of omnivore species were found in both regions. Roving-territorial herbivores are more diverse in the TWA, while more species of piscivores and planktivores are found in the TEP.

Table 3. Comparison of fish communities in both sides of the Isthmus of Panama: TWA(Bocas del Toro, Dominici-Arosemena and Wolff 2005) and TEP (Gulf of Chiriqui, Dominici-Arosemena and Wolff 2006).

	TWA	**TEP**
Small fish sizes	Low complexity substrates (e.g. reef edges, sand-rubble, algae beds)	Shallow high complex substrates (e.g. Pocilloporid-rocky reefs)
Larger fish sizes	All complex zones	Complex deep zones
Increasing of species number among zones	More spatial, from sheltered to complex exposed zones	More vertical, from deep to shallow complex zones.
Rocky shallow assemblages	*Thalassoma* spp*, Chromis* sp, *Stegastes adustus*, acanthurids.	*Thalassoma* spp, Chaenopsids, gobids, haemulids, cirrhitids, acanthurids.
Branching coral shallow assemblage	Territorial pomacentrids, scarids, Haemulids, *Hypoplectrus* spp.	Haemulids, scarids *Thalassoma* spp , cirrhitids.
Deep-rock assemblages	Not defined, murky water below 11 m	Subdivisions in relation to depth to 30 m
Massive corals assemblages	Not strongly defined, relatively high species number, low densities.	Not strongly defined, relatively high species numbers, low densities
Sand rubble	Nursery habitat, defined assemblage high densities of demersal planktivores (e.g. *Serranus tortugarum*, *Coryphopterus personatus*)	Not defined assemblage, low fish abundance
Minimum average species richness	11, turf algae-dead corals	10, sand rubble
Maximum diversity index, habitat	0.9, all rocky zones, Massive corals	0.9, all rocky zones, Massive corals
Minimum diversity index, habitat	0.5, sand rubble	0.6, pocilloporid reefs
Fish abundance	High in low complexity substrates	High in high complexity substrates
Mobility: Category 1	In complex-exposed zones	In shallow exposed but also in oceanic deep zones
Mobility: Category 2	Between rubble and exposed zones, no massive corals	Massive coral zones, rubble and big crevices
Mobility: Category 3	Sheltered coral zones (territorial herbivores)	In exposed zones (dwelling chaenopsids, gobiid and cihrhitids)
Most diverse trophic groups (max species number/zone)	Carnivores (20), Mobile invertebrate feeders (15), Roving herbivores (12), Omnivores (10), Territorial herbivores (6), Planktivores (2)	Carnivores (26), Mobile invertebrate feeders (18), Planktivores (11), Omnivores (11), Piscivores (10), Roving herbivores (7)

Geminate species and their relationship with habitat characteristics in the IOP.

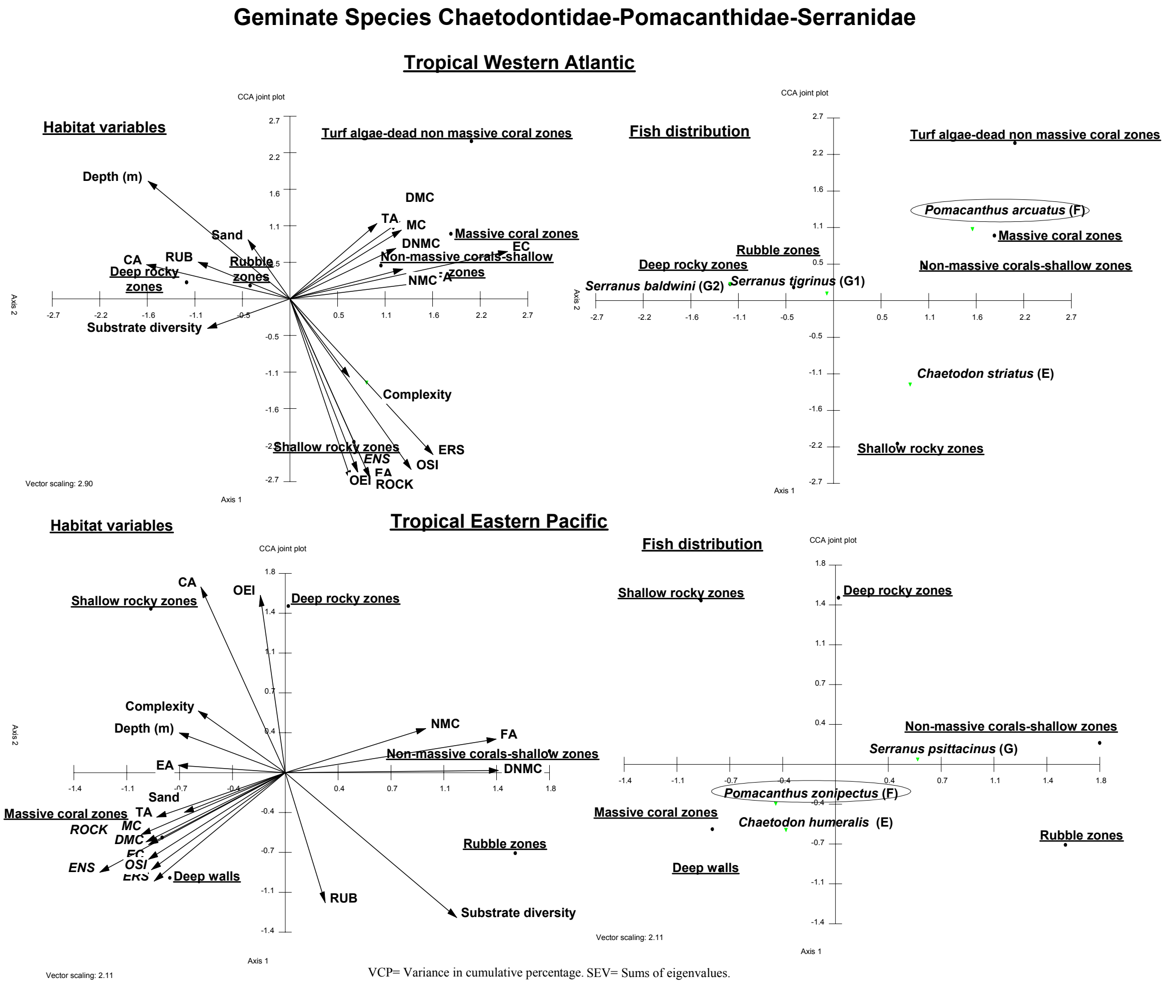
Most species of genus *Halichoeres* in both regions are associated with sandy and rocky environments, in both deep and shallow waters. In the TEP, *H. notospilus* is more associated with shallow rocky reefs and massive corals. *Stegastes planifrons* (TWA) and *S. acapulcoensis* (TEP) are both associated with branching corals in shallow wave-sheltered habitats. *Stegastes adustus* (TWA) and *S. flavilatus* (TEP) are associated with exposed areas on rocky shores. *Chromis multilineata* (TWA) is associated with exposed oceanic currents while *C. atrilobata* (TEP) does not show a clear association with any type of habitat (Figure 5a). *Chaetodon striatus* (TWA) is associated with complex, shallow, rocky areas; *C. humeralis* (TEP) is associated with massive corals and deep rocky walls. Both species are associated with sponges and encrusting invertebrates. *Pomacantus arcuatus* (TWA) and *P. zonipectus* (TEP) are mainly associated with massive coral reef habitats on both sides and the latter also shows an association with branching coral reefs. *Serranus balwini* and *S. tigrinus* (TWA) are associated with sand and rubble but their counterpart *S. psittacinus* (TEP) shows a preference for wave-sheltered, branching coral reefs (Figure 5b).



VCP= Variance in cumulative percentage. SEV= Sums of eigenvalues.

	Labridae - Pomacentridae TWA					Labridae - Pomacentridae T EP				
VCP	57.03	87.33	96.02	99.29	100	66.57	85.91	96.38	99.86	100
E	0.42	0.22	0.06	0.02	0.005	0.15	0.04	0.02	0.008	0

Fig 5a. Canonical Correspondance Analysis. Geminate species (Labridae-Pomacentridae) from both sides of the Isthmus of Panama, same letters indicates sister species, species on circle indicates similar habitat preferences for a respective sister species in both regions. Increasing numbers after letters indicate distance-separation among the respective clade on the Phylogenetic tree



VCP= Variance in cumulative percentage. SEV= Sums of eigenvalues.

	Chaetodontidae- Lutjanidae- Pomacanthidae - Serranidae TWA					Chaetodontidae- Lutjanidae-Pomacanthidae - Serranidae TEP				
VCP	46.11	77.28	97.95	100	-----	72.15	95.89	100	----	----
E	0.38	0.26	0.17	0.017	-----	0.25	0.08	0.01	----	----

Fig 5b (cont). Canonical Correspondence analysis. Geminate species (Chaetodontidae-Pomacanthidae-Serranidae) from both sides of the Isthmus of Panama, same letters indicates sister species, species on circles indicates similar habitat preferences for a respective sister species in both regions. Increasing numbers after letters indicates distance-separation among the respective clade on the Phylogenetic tree

Discussion

Habitat

The influence of major rivers affects salinity in the TWA-IOP region (Bocas del Toro), with implications for distribution of oceanic plankton and larvae, particularly in sheltered areas where water circulation is limited and salinity can drop as low as 20 PSU after heavy rain (D'Croz et al. 2005; Kaufmann and Thompson 2005). In the Gulf of Chiriqui (TEP), although riverine input can be significant during the rainy season (Kwiecinsky and Chial 1983), there are no marked reductions in salinity even in mouths of major rivers, probably due to the intensive mixing of salt and fresh waters by strong tides and currents (Seixas 2005). In this region, the influence of major rivers is comparatively low in areas where reef communities have developed (Glynn and Maté 1997). Currents in the Gulf of Chiriqui produce vertical and horizontal temperature gradients with cold-water intrusion from other regions at the TEP, particularly those characterized by coastal upwelling (Glynn and Maté 1997). For most reef fish a dynamic environment may have a positive influence on the larval survival, dispersion, distribution and settlement in different habitats in the TEP. Mean temperatures in the Gulf of Chiriqui seem to be higher than in other TEP regions (Kwiecinsky and Chial 1983; Quesada-Alpízar and Morales 2004; Dominici-Arosemena et al. 2005). Clear surface waters are typical in the TEP-IOP (close to 12 meters visibility). By contrast, TWA-IOP (Bocas del Toro) is a more closed lagunar system that retains sediments and these limit visibility, which further decreases during the rainy season due to intensive run-off from major rivers (D'Croz et al. 2005). Substrate complexity in the TEP is high due to the morphology of the sharp basaltic-volcanic rocks, which contain a large number of crevices. In shallow areas, the presence of pocilloporid corals further increases substrate complexity (Glynn and Maté 1997). TWA-IOP has a diverse but shallow coral reef component (Guzmán and Guevara 1998), with increased complexity in areas where fire corals in exposed areas (*Millepora* sp) and foliaceous corals in sheltered areas (*Agaricia* sp) are present. Complex corals over rocky shores are absent in the TWA. The substrate diversity index is relatively higher (closer to 0) in the TEP, where a variety of rocky substrates and benthic fauna and flora are encountered.

Global patterns: the taxonomical structure of reef fishes in the IOP

A larger number of famlies are found in the TEP. Of the total of 50 fish families found in the IOP 64% occur in both regions. The number of species of the most diverse taxa of reef fishes, following the consensus list drawn up by Bellwood (1996) does not differ significantly between both sides of the IOP (Robertson 1998). Both surveys yielded a total of 112 genera, of which 28 (25%) were only found in the TWA and 42 (37.5 %) only in the TEP. The number of genera is higher in the TEP. Of these, eight (7.14 %) are endemic, and 13 (11%) of Indo-Pacific origin (Robertson et al. 2004). Of the 24 species that have their centre of origin in the Indo-Pacific, eight are circumtropical. In the TEP, 25.3% of the species are not endemic to this region, suggesting their recent immigration (as drifting larvae) from the Indo-Pacific during and after the closure of the IOP (Robertson and Allen 2002; Edgar et al. 2004). Overall species richness in our Pacific study area, the Gulf of Chiriqui, is higher than in other TEP regions described in the literature. Only 40 to 56% of the species found in our area are also reported by studies of other areas in the TEP (Table 4). The lack of relatively stable environments and a wide range of habitats for shelter may account for the lower species diversity found at other sites in the TEP (Dominici-Arosemena and Wolff 2006). The Galapagos archipelago, which has a higher total species richness than the the IOP-TEP, is considered a separate province, characterised by the presence of species from subtropical regions of Peru and Chile (Edgar et al. 2004). There is a similar situation at Clipperton Island (Allen and Robertson 1997). In the coastal waters adjacent to IOP, the overall species richness of the TEP is similar to that of the TWA (Gamma diversity, Hunter 2002) despite the high species overlap and relatively high species/area ratio in the TEP (Dominici-Arosemena and Wolff 2005, 2006). Extrapolating from all habitats surveyed in each region, we found that the variation in diversity parameters per habitat (Alfa Diversity) is higher in the TEP. In the TWA, the closure of the IOP has affected local oceanographic patterns and the input of riverine fresh water to the fragmented habitat along the path of a southward current (an "eddy" in the opposite direction of the main Caribbean current, Clifton et al. 1997) have a small but rather constant influence, which reduces larval distribution and recruitment. Larval exchange between the Mesoamerican Caribbean and the insular Caribbean probably affects the density but not the composition of fish assemblages in the IOP-TWA. Thus, Bocas del Toro contains a relatively high number of species, considering that is close to the mainland and is subject to considerable fresh water input (Table 4). On the other side in the Gulf of Chiriqui (IOP-TEP), local patterns result in better conditions for larval survival, dispersion and settlement, with clear waters, variable currents and a continuous interconnected rocky habitat along the northern and the southern coasts (Mora and Robertson 2005). These conditions explain the relative diversity of communities found in this area compared to those found in similar habitats in the IOP-TWA (Beta diversity, Zapata and Morales 1997). Species richness in the IOP-TEP is lower than in the east Panamanian Caribbean (San Blas), a region that has less input from major rivers, a complex-diverse habitat and probably more larval input, with larvae being transported from other regions by the main Caribbean current (Clifton et al. 1997).Species richness in the IOP-TEP is also lower than around most islands in the TWA and is similar to other TWA regions including South Atlantic locations (Table 4). This study shows that fish considered characteristic of coral reefs are not restricted to coral reef regions and the distribution of reef fishes may depend on historical pattern of recruitment success and connectivity of habitats other than coral reefs. Non-reef areas may have acted as refuges for reef fish during periods of diminished growth or loss of shallow water corals in both regions (Bellwood 1997). These findings are somewhat unexpected considering that the TWA is dominated by coral reefs (~ 20.000 Km^2), while they are largely lacking in the whole TEP (~25 Km^2, Robertson 1998). In the latter region,most of the complex-rocky reef surveyed in our study harbours a higher fish species richness.

Table 4. Reef fish species numbers found among different geographical regions in the Tropical Eastern Pacific (TEP) and Tropical Western Atlantic (TWA). Relative coral or rocky reef habitat considered on each survey:*Low, **Medium, *** Important

	Location	Species numbers	Coral reefs	Rocky reef	Reference
TEP	Galapagos Islands, Ecuador	175	*	***	Edgard et al 2004
TEP	**Gulf of Chiriqui,Panama,**	**126**	**	***	**Dominici-Arosemena and Wolff 2006**
TEP	Clipperton Island	115	**	***	Allen and Robertson 1997
TEP	Gulf of Papagayo, Costa Rica	78	*	**	Dominici-Arosemena et al 2005
TEP	Gulf of California, Mexico	74	-	***	Aburto-Oropeza and Balart 2001
TEP	Gorgona Island, Colombia	71	**	*	Zapata and Morales 1997
TEP	Manuel Antonio, Costa Rica	39	-	***	Phillips and Perez-Cruet 1984
TWA	San Andrés, Colombia,	273	***	*	Mejía et al 1998;
TWA	San Blas, Panama	229	***	**	Check list by Clifton et al 1997.
TWA	Cayos Cochinos,Honduras	214	***	*	Clifton and Clifton, 1998;
TWA	Guadeloupe spp, French antillies	167	***	*	Bouchon-Navaro et al 2005.
TWA	Flower gardens Gulf of México	153	**	*	Pattengil et al; 1997
TWA	Martinique	150	***	*	Bouchon-Navaro et al 2005.
TWA	St Martin	135	***	*	Bouchon-Navaro et al 2005.
TWA	**Bocas del Toro, Panama**	**128**	***	**	**Dominici-Arosemena and Wolff 2005**
TWA	South-eastern of Dominican Republic	126	***	**	Schmitt et al 2002
TWA	Bequia, French Antilles	123	***	**	Bouchon-Navaro et al 2005
TWA	Saint-Barthélemy, French Antilles	114	***	**	Bouchon-Navaro et al 2005
TWA	Anguila	113	***	**	Bouchon-Navaro et al 2005
TWA	South-eastern Brazil,	91	**	***	Ferreira et al., 2001
TWA	St Pauls Rocks, Mid Atlantic ridge, Brazil	75	*	***	Feitoza et al 2003
TWA	Florida Keys, USA	74	**	**	McKenna, 1997
TWA	Puerto Rico	71	***	**	McGehee, 1994;
TWA	Cahuita, Costa Rica	49	**	-	Phillips and Perez-Cruet 1984

Global patterns-families, abundance, size classes and trophic groups

There are high densities of gobids, herbivorous pomacentrids, scarids and small serranids in the TWA, while labrids, planktivorous pomacentrids, haemulids and apogonids are dominant in the TEP. Territorial and roving herbivores account for less than 15% in all zones in the TEP, while they are abundant and have wide spatial distribution in the TWA (Ferreira et al. 1998; Ceccarelli et al. 2001). These differences in densities of herbivores on either side of the IOP are related to differences in temperature and nutrient concentrations. , Environmental instability (*e.g.* changes in temperature, upwelling, and surges as consequences of tidal variation) may have the effect of increasing primary productivity in the TEP, with important consequences for individuals higher up in the trophic chain (D'Croz and Robertson 1997). Recent research on the latitudinal variation in the Atlantic Ocean shows that the relative abundance of herbivores decreases towards higher latitudes due to physiological constrains related to changes in temperature. The assimilation of plants and other low-energetic food material is relatively easier and more efficient in warmer regions (Harmelin-Vivien 2002; Floeter et al. 2004). However, the latitudinal variation in a region such as the Atlantic Ocean, with stable currents and temperature patterns, will not necessarily be repeated in an unstable region such as the TEP: Our data suggest that some genera have adapted to feeding on high protein food in the TEP (*e.g.* zooplankton, mobile invertebrates, and other fishes), where we found wide variation in temperature values. Thus, planktivores account for as much as 80% in most surveyed zones in the TEP and are represented by a higher number of species than in the TWA; mobile invertebrate feeders, carnivores and piscivores also are more abundant and widely distributed in the TEP. Our study shows a significant difference between fish sizes of both sides of the IOP, confirming the results of other regional studies reported by Choat and Robertson (2002), who conclude that fish in the West Pacific achieve greater maximum ages-sizes than tropical Atlantic species and that Caribbean fishes are generally short lived and smaller. In general, there is a typical distribution of individuals among size classes, with most fish in small size classes. However, a relatively large number of specimens from the TEP belong to larger size classes. Systematic trends in life history parameters should be seen as a response to local gradients in environmental conditions. Most species may thus have certain plasticity in terms of life history traits and may therefore develop marked differences in their population dynamics if environmental conditions differ over long (geological) time periods, as is the case for the two sides of the IOP after the uplift of the land bridge. Probably, the periodically lower temperatures in the TEP strongly influenced longevity and maximum size of many species (Pauly 1998).

Other factors besides temperature may contribute to these differences among size classes within IOP fish families. If the physical habitat provides primarily small refuge areas, small fish species may be favoured. If predation is strong, a high growth rate and small adult size may be the population response of the prey fish species. Single-species population sizes and the number of populations of a community will finally be determined by the actual amount of food-energy available for maintenance, growth and storage and by how individuals share that resource (Jones and McCormick 2002). When food declines and/or fish densities increase to a point which the supply of food does not meet the demand, competition will affect the growth of individuals (Ma et al. 1998; Wootton 1998; Ali and Wootton 1999; Jones and McCormick 2002), negatively influencing the maturation and fecundity of inferior competitors, particularly when they are displaced into lower quality habitats (Jones and McCormick 2002). Dominant individuals may limit access to food by subordinates, especially if food is in short supply as in tropical coral reefs (Jones and McCormick 2002). In the TWA we observed a high density of territorial individuals that will displace or affect recruitment of other species. Predator density was also low (*e.g.* carnivores and piscivores) and primary production is considered to be relatively low as well. These and other conditions (variable salinity, high sedimentation, higher coral-benthic degradation, Guzmán and Guevara 1998; D'Croz et al. 2005) point to a lower quality of the habitat when compared to the TEP. Here the density of predators is higher, which results in fewer numbers of territorial herbivores, usually of a small size. Larger individuals may be able to access higher energy food sources, which seem to be more abundant in the TEP.

The "openness" of the habitat may also greatly affect the community structure: Open populations (with long-range larval transport under the influence of intermittent oceanographic currents, as in TEP-IOP) can beexpected to exhibit greater phenotypic plasticity in life history traits than more closed populations (as TWA-IOP, which is characterized by limited larval distribution, closed bays, and fresh water input). This is because the environment experienced by the immigrants is less predictable (Jones and McCormick 2002); thus populations tend to be more size structured (Ebenman and Persson 1988; Olson 1996).

Fish growth and life span are not only influenced by natural environmental conditions, but may also be influenced by fisheries activities. Fish populations of the Caribbean, are under intense pressure from fisheries and Bocas del Toro is no exception (Jackson et al. 2001; Dominici-Arosemena and Wolff 2005). It is likely that this region is more heavily impacted by fisheries than the Gulf of Chiriqui-TEP, which is relatively isolated (Dominici-Arosemena and Wolff 2006).

Local patterns: diversity, species richness and assemblages among habitats

In the TWA, the number of species increases towards exposed zones with high substrate diversity and densities of specialized feeders like herbivores increase in sheltered zones. In the TEP, patterns generally display taxonomical variation among habitats, rather than variations in abundance between trophic groups, since high protein feeders predominate throughout the region. The fish associations found in shallow complex rocky zones in the TEP are somewhat different to those in exposed coral reefs in the TWA. Groups of planktivores such chaenopsids are represented by numerous genera in the TEP, where they are found in holes and coral branches. (Munday 2002). Both regions contain *Thalassoma* sp*,* *Chromis* sp and acanthurids in shallow rocky exposed zones; while medium to high densities of haemulids and scarids are also found in shallow scleractinean branching coral zones on both sides of the IOP. In the TWA, no clear taxonomic assemblages were found in deeper zones; but in the TEP such assemblages could be distinguished, with subdivisions between groups of species in rocky zones that vary along a gradient of depth., Assemblages on massive corals in both regions are diverse compared to all other habitats surveyed, except for complex rocky zones,. In the TWA, small adults of the genera *Serranus* and *Coryphopterus* are typical inhabitants of sand-rubble areas. This is not particularly true for the TEP, where adaptations to these habitats may be prevented by periodic disruptions caused by variable oceanographical conditions (*e.g.* tides and currents).

We found positive correlations of species richness with hard substrates (usually massive corals and shallow rocky complex reefs), but not with branching corals (*Pocillopora* sp. in the Pacific or *Porites* sp. in the TWA, respectively). Corals are shown to be important in enhancing the physiographic structure of the substrate in many of the more complex massive coral reefs and shallow rocky zones. In the TWA and in the TEP, wave-exposed zones are physically more complex with high benthic diversity and the fish communities are correspondingly more diverse. Exposed zones are likely to contain more diverse and abundant food resources (*e.g.* oceanic plankton).

Local patterns: general fish size distribution and ontogenic movements

In the TWA rubble substrates may serve as nursery areas for juveniles, which can move easily between habitats. In the TEP, coral branches and holes in shallow areas may be an good place to avoid predation and may protect juveniles from unfavourable water movements (Fulton and Bellwood 2002).

Local patterns: mobility groups

According to Floeter et al. (2004), many of the species that were not associated with any particular habitat in the TEP are considered highly mobile (Category 1 *Chromis, Thalassoma*). In the TWA, these genera show well-marked distributions in exposed zones.

Here, site-attached species are typical of sheltered zones, while site-attached species dwell in rocks in the TEP. All these results are related to the marked difference in oceanography between the two regions.

The rise of the IOP and closely related species

In general, pairs of species found on opposite sides of the IOP are relatively similar in morphology and in coloration (Humann and Deloach. 1996; Robertson and Allen 2002) but ecological requirements may be associated with local environmental conditions. Trophic interactions are related to habitat plasticity. The physical barrier of the IOP resulted in reproductive separation and the independent evolution of populations of species present on both sides of the barrier. Many of these species may have shown parapatric speciation and particular habitat characteristics, such as depth, wave exposure, variation in currents, sources of food and predation may be important environmental variables affecting the organization of reef fish communities. In the case of labrids, in five Atlantic wrasses of the genera *Halichoeres,* strong genetic partition was observed among species in adjacent and ecologically distinct habitats, but high genetic connectivity was found between species in similar habitats separated by thousands of kilometres (Rocha 2003). We propose that similar habitat preferences may persist in widely separated regions among closely related species of this genera. *Halichoeres bivittatus*, considered a generalist species, prefers rubble-sandy habitats in the TWA (Rocha 2003): in TEP, *Halichoeres nicholsi* and *H. dispilus* prefer the same sandy-rubble "edge" habitats as their TWA counterpart. Geographic (allopatric) and parapatric speciation may have a strong effect on this group of species. We found that *H .notospilus* (separated in the IOP clade on the phylogenetic tree, sensu Barber and Bellwood 2005), has shifted from rubble sandy habitats to shallow rocky-exposed zones and parapatric speciation may have occurred during and after the closure of the IOP (Rocha 2003). *Stegastes planifrons* and *S. acapulcoensis* are described by Wellington and Robertson (2001) as sheltered habitat geminate species and we found that this group inhabits shallow scleractinean coral reefs on both sides of the IOP. This pattern of association is found regardless of the taxonomic or evolutionary origin of the associated corals but is closely related to similarities in morphology (branching, foliaceous) and location type, (areas protected from waves). We found that *Stegastes adustus* and *S. flavilatus* are geminate species inhabiting wave-exposed zones on both sides of the IOP (Wellington and Robertson 2001). For *Chromis*, the species *C. multilineata* predominates in exposed areas and is virtually absent in sheltered zones in the

TWA, while in the TEP *C. atrilobata* has a more homogeneous distribution across different habitats. This genus is associated with currents, thus the homogeneous distribution in the TEP may be related to more unstable and marked current-tide patterns in this region. *Chaetodon striatus* in the TWA is generally restricted to shallower zones where benthic invertebrates are predominant, while *C. humeralis* is common among massive corals but may reach deeper rocky zones. This may be due to the presence of the benthic invertebrates that these species feed on in deeper regions in the clearer waters of the IOP-TEP. The family *Pomacanthids,* is among the last to have been impacted by the rising of the IOP and the geminate species are associated with massive coral reefs in both regions. After the massive extinction of corals following the closure of the IOP, mangroves were the principal marine habitat available for shelter for these and other fish species (Knowlton and Weigt 1998). Following coral recolonization in the TEP, these species may have taken to massive corals, due to their structural similarity with this type of heterogeneous habitat. For the genus *Serranus*, in the TWA, where less predators are found, the rubble-sandy habitat is shared by the two closely related species *S. tigrinus* and *S. baldwini*, but their TEP counterpart *S. psittacinus* (Kochzius and Dominici-Arosemena, unpublished) is more closely associated with branching coral reefs, where shelter against predators is available.

We conclude that greater temperature differences (and often lower water temperatures) and greater nutrient concentrations may increase primary productivity and affect the trophic web in the TEP, resulting in the greater abundance of carnivorous fish and a tendency for maximum fish size to increase. In the TWA region, on the other hand, increased territoriality and low-quality habitats may result in smaller individuals feeding on low quality food (plant material). A diverse stratum (be it with or without corals) provides more niches and shelter, and thus increases species richness at any region. In addition, further habitat conditions such as depth, wave exposure, currents, type of substrate, feeding sources, territoriality and predation may explain the differentiated organization of formerly related reef fish communities on both sides of IOP.

ACKNOWLEDGMENTS

This research was sponsored by the Smithsonian Tropical Research Institute (STRI), the German Academic Exchange Service (DAAD) and the Bahia Honda project-Liquid Jungle lab (LJL) research station, with the cooperation of the Centre for Marine Tropical Ecology

(ZMT), The Project Aware Foundation (PADI) and the World Wildlife Fund (WWF-BMZ). We thank Ross Robertson for his advice at STRI and Mr. Jean Pigozzy for giving us the opportunity to conduct this research at Liquid Jungle Lab. Guilherme Vasconcellos, Irving Bethancourt and Juan Gabriel Domínguez helped on field and data management. Thanks to Carlos L. Ferreira, Fernando Zapata Luis Fernández de Córdoba, Christie Constantine, Friedemann Keyl, and Ghislain Rompré, for advice offered for this research. Additionally we thank Jaime Andrés Cabrera, María Patricia Castantes (LJL),, Petra Kaepnick, Andreas Hanning, Stefanie Bröhl, Dieter Peterke (ZMT), Harry Barnes, Georgina DeAlba, Xenia Saavedra, Adriana Bilgray, Marissa Batista, Ernesto Peña, Edgardo Ochoa, Reynaldo Tapia, Alejandro Arze and Mercedes Denis (STRI), for logistic and administrative support. Map and profile figures were drawn by Marco Luque Parigi.

References

Allen GA, Robertson DR (1997) An annotated checklist of the fishes of Clipperton Atoll, tropical eastern Pacific. Revista de Biología Tropical 45:813-843

Ali M, Wootton RJ (1999) Effect of variable food levels on reproductive performance of breeding female three-spined sticklebacks. Journal of Fish Biology 55:1040-1053

Arburto-Oropeza O, Balart E (2001) Community structure of reef fish in several habitats of a rocky reef in the Gulf of California. Marine Ecology 22:283-305

Barber PH, Bellwood DR (2005) Biodiversity hotspots: evolutionary origins of biodiversity in wrasses (*Halichoeres*: Labridae) in the Indo-Pacific and new world tropics. Molecular Phylogenetics and Evolution 35:235-253

Bellwood DR (1996) The Eocene fishes of Monte Bolca: the earliest coral reef fish assemblage. Coral Reefs 15:11-19

Bellwood DR (1997) Reef Fish biogeography: habitat associations, fossils and phylogenies. Proc 8th Int Coral Reef Symp 1:379-384

Bellwood DR (1998) What are reef fishes? Comment on the report by D.R. Robertson: Do coral reef fish faunas have a distinctive taxonomic structure? (Coral Reef 17:179–186). Coral Reef 17:187-189

Bellwood DR, Wainwright PC (2002) The history and biogeography of fishes on coral reefs. In: Sale PF (ed) Coral Reef Fishes. Dynamics and diversity in a complex ecosystem. Academic Press, San Diego, pp5-32

Bellwood DR, van Herwerden L, Konow N (2004) Evolution and biogeography of marine angelfishes (Pisces: Pomacanthidae). Mol Phylogenet Evol 33:140-155

Bermingham E, McCafferty S, Martin A (1997) Fish biogeography and molecular clocks: perspectives from the Panamanian Isthmus. In: Kocher T, Stepien C (eds) Molecular Systematics of Fishes. Academic Press, New York, pp113-126

Bouchon-Navaro Y, Bouchon C, Louis M, Legendre P (2005) Biogeographic patterns of coastal fish assemblages in the West Indies. Journal of Experimental Marine Biology and Ecology 315: 31-47

Cardiel JM, Castroviejo S, Velayos M (1997) Parque Nacional de Coiba: El Medio Físico. 11-31. In: Castroviejo S (ed) Flora y fauna del Parque Nacional de Coiba (Panamá). Panamá, pp75- 106

Caribbean Coastal Marine Productivity (CARICOMP) (2001) Methods Manual Levels 1 and 2. Manual of methods for mapping and monitoring of physical and biological parameters in the coastal zone of the Caribbean. University of the West Indies Mona, Kingston Jamaica and Florida Institute of Oceanography

Ceccarelli DM, Jones GP, McCook LJ (2001) Territorial damselfishes as determinants of the structure of benthic communities on coral reefs. Oceanogr Mar Biol Annu Rev 39:355–389

Choat JH, Robertson DR (2002) Age-based studies on coral reef fishes. In: Sale PF (ed) Coral Reef Fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego, pp57-80

Clifton KE, Clifton LM (1998) A survey of fishes from various coral reef habitats within the Cayos Cochinos Marine Reserve, Honduras. Rev Biol Trop 46:109–124

Clifton KE, Kim K, Wulff JL (1997) A field guide to the reefs of Caribbean Panamá with an emphasis on western San Blas. Proc 8th Int Coral Reef Symp1:167-184

Coates AG, Obando JA (1996) Geological evolution of the Central American Isthmus. In: Jackson JBC, Budd AF, Coates AG (eds) Evolution and Environment in Tropical America. University of Chicago Press, Chicago, pp21-56

Coates AG, Mcneill DF, Aubry MP, Berggren WA, Collins LS (2005) An introduction to the Geology of the Bocas del Toro Archipelago. Panama Caribbean Journal of Science 41:374-391

Cortés J (1997) Biology and Geology of Eastern Pacific Reefs. Coral Reefs 16 :39-46.

D'Croz L, Robertson DR (1997) Coastal ocanographic conditions affecting coral reefs on both sides of the Isthmus of Panama. Proc. 8th Int Coral Reef Symp 2:2053-2058

D'Croz L, Del Rosario JB, Góndolav P (2005) The effect of Fresh Water Runoff on the Distribution of Dissolved Inorganic Nutrients and Plankton in the Bocas del Toro Archipelago, Caribbean Panama. Caribbean Journal of Science 41:465-475

Dominici-Arosemena A, Wolff M (2005) Reef fish community structure in Bocas del Toro (Caribbean, Panamá) along spatial scales and gradients in habitat complexity. Caribbean Journal of Science 41:613-637

Dominici-Arosemena A, Brugnoli-Olivera E, Cortés-Nuñez J, Molina-Ureña H, Quesada-Alpizar M (2005) Community Structure of Eastern Pacific Reef fishes (Gulf of Papagayo, Costa Rica). Rev Tecnociencia, FCNET, Univ Panamá 7:19-41

Dominici-Arosemena, A, Wolff M (2006) Reef fish community structure in the Tropical Eastern Pacific (Panama): Living on a relatively stable rocky reef environment Helgoland Marine Research (in press)

Ebenman B, Persson L (1988) Size-structured populations: ecology and evolution. Springer, Berlin

Edgar GJ, Banks S, Fariña JM, Calvopiña M, Martínez C (2004) Regional biogeography of shallow reef fish and macro-invertebrate communities in the Galapagos archipelago. Journal of Biogeography 31:1107-1124

English S, Wilkinson C, Baker V (1994). Survey manual for tropical marine resources. Australian Institute of Marine Science, Townsville

Feitoza BM, Rocha LA, Luiz-Júnior OJ, Floeter SR, Gasparini JL (2003) Reef fishes of St. Paul's Rocks: new records and notes on biology and zoogeography. Aqua, Journal of Ichthyology and Aquatic Biology 7:61–82

Ferreira CEL, Peret AC, Coutinho R (1998) Seasonal grazing rates and food processing by tropical herbivorous fishes. J Fish Biol 53:222–235

Ferreira CEL, Gonçalves JEA, Coutinho R (2001) Community structure of fishes and habitat complexity in a tropical rocky shore. Env Biol Fish 61:353–369

Ferreira CEL, Floeter SR, Gasparini JL, Ferreira BP, Joyeux JC (2004) Trophic structure patterns of brazilan reef fishes: a latitudinal comparison. Journal of Biogeography 31:1–13

Floeter SR, Ferreira CEL, Dominici-Arosemena A, Zalmon I (2004) Latitudinal gradients in Atlantic reef fish communities: trophic structure and spatial use patterns. Journal of Fish Biology Vol 64:1-20

Fulton CJ, Bellwood DR (2002) Ontogenetic habitat use in labrid fishes: an ecomorphological perspective. Mar Ecol Prog Ser 236:255-262

Glynn PW, Maté JL (1997) Field guide to the Pacific coral reefs of Panamá. Proc 8th Int Coral Reef Symp 1:145–166

Guzmán HM, Guevara CA (1998) Arrecifes coralinos de Bocas del Toro, Panamá: II. Distribución,estructura, diversidad y estado de conservación de los arrecifes de las Islas Bastimentos, Solarte, Carenero y Colón. Rev Biol Trop 46:889–912

Harmelin-Vivien M (2002) Energetics and Fish Diversity on Coral Reefs. In: Sale P (ed) Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem. Academic Press, San Diego, pp265-274

Humann P, Deloach N (1996) Reef Fish Identification. New World Publications, Jacksonville

Hunter M (2002) Fundamentals of Conservation Biology (2nd Edition). Blackwell Science, Massachusetts

Jackson JBC, Budd A, Coates AG(1996) Evolution and Environment in Tropical America. Jeremy University of Chicago Press, Chicago

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629-638

Jones GP (1988) Experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of two coral reef fishes. J Exp Mar Biol Ecol 123:115-126

Jones GP (1997) Relationships between recruitment and postrecruitment processes in lagoonal populations of two coral reef fishes. J Exp Mar Biol Ecol 213:231–246

Jones GP, McCormick MI (2002) Numerical and energetic processes in the ecology of coral reef fishes. In: Sale P (ed) Coral reef fishes; dynamics and diversity in a complex ecosystem. Academic Press, San Diego, pp221–238

Kaufmann KW, Thompson RC (2005) Water temperature variation and the meteorological and hydrographic environment of Bocas del Toro. Panama Caribbean Journal of Science 41:392-413

Kwiecinski B, Chial ZB (1983) Algunos aspectos de la oceanografía del Golfo de Chiriquí, su comparación con el Golfo de Panamá. Rev Biol Trop 31:323-325

Knowlton N, Weigt LA (1998) New dates and new rates for divergence across the Isthmus of Panama. Proceedinos of the Royal Society: Biological Sciences 265:2257-2263

Leschine TM (1981) The Panamanian sea level canal. Oceanus 24:20-30

Lessios HA; Allen GR, Wellington GM, Bermingham E (1995) Genetic and morphological evidence that the Eastern Pacific damselfish *Abudefduf declivfrons* is distinct from *A. concolor* (Pomacentridae). Copeia:277-288

Ma Y, Kjesbu OS, Jørgensen T (1998) Effects of ration on the maturation and fecundity in captive Atlantic herring (*Clupea harengus*). Can J Fish Aquat Sci 55:900-908

McKenna J (1997) Influence of Physical Disturbance on the Structure of Coral Reef Fish Assemblages in the Dry Tortugas. Caribbean Journal of Science 33:82–97

Mejía LS, Garzón-Ferreira J, Acero A (1998) Peces registrados en los complejos arrecifales de los cayos Courtown, Albuquerque y los bancos Serrana y Roncador, Caribe occidental, Colombia. Bol Ecotrópica 32:25–41

McGehee A (1994) Correspondence between assemblages of coral reef fishes and gradients of water motion depth, and substrate size off Puerto Rico. Mar Ecol Prog Ser 105: 243–255

Mora C, Robertson DR (2005) Causes of latitudinal gradients in species richness: a test with fishes of the tropical eastern Pacific. Ecology 86:1771-1782

Munday PL (2002) Does habitat avaibility determine geographical-scale abundance of coral-dwelling fishes? Coral Reefs 21:105-116

O'Dea A, Jackson JBC(2002) Bryozoan growth mirrors contrasting seasonal regimes across the Isthmus of Panama. Palaeogeography, Palaeoclimatology, Palaeoecology 185:77-94

Olson MH (1996) Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. Ecology 77:179-190

Pattengill CV, Semmens BX and Gittings SR (1997) Reef fish trophic structure at the Flower Gardens and Stetson Bank, NW Gulf of Mexico. Proc. 8th Int. Coral Reef Sym. 1: 1023-1028

Pauly D (1998) Tropical fishes : patterns and propensities. J Fish Biol 53:1-17

Phillips PC, Perez-Cruet MJ (1984) A Comparative Survey of Reef Fishes in Caribbean and Pacific Costa Rica. Rev Biol Trop 32:95-102

Pielou EC (1975) Ecological diversity. John Wiley and Sons, New York

Quesada-Alpízar M, Morales-Ramírez A (2004) Comportamiento de las masas de agua en el Golfo Dulce durante un periodo El Niño (1997-1998). Rev Biol Trop 52:95-103

Robertson DR (1998) Do coral-reef fish faunas have a distinctive taxonomic structure? Coral Reefs 17:1–8

Robertson DR, Allen GR (2002) Shore fishes of the tropical eastern Pacific: an information system. Smithsonian Tropical Research Institute, Balboa

Robertson DR, Grove JS, McCosker, JE (2004) Tropical transpacific shore fishes. Pacific Science 584: 507-565

Rocha LA (2003) Patterns of distribution and processes of speciation in Brazilian reef fishes. J Biogeog 30:1161–1171

Rocha LA, Robertson DR, Roman J, Bowen BW (2005) Ecological speciation in tropical reef fishes. Proceedings of the Royal Society B 272:573-579

Rogers CS, Garrison G, Grober R, Hillis ZM, Franke MA (1994) Coral reef monitoring manual for the Caribbean and Western Atlantic. Southern Regional Office National Park Service. The Nature Conservancy WWF

Schmitt EF, Sluka RD, Sullivan-Sealey KM (2002) Evaluating the use of roving diver and transect surveys to assess the coral reef fish assemblage off southeastern Hispaniola. Coral Reef 21:216-223

Seixas CE (2005) Spatial variations of chlorophylls and carotenoids in the Gulf of Montijo, Panama. Rev Tecnociencia, FCNET, Univ Panamá Vol 7:113-115

Ter Braak CJF, Verdonschot PFM (1995) Canonical correspondance analysis and related multivariate methods in aquatic ecology. Aquat Sci 57:255–289

Wellington GM, Robertson DR (2001) Variation in larval life-history traits among reef fishes across the Isthmus of Panama. Marine Biology 138:11-22

Wolff M, Alarcón E (1993) Structure of a scallop *Argopecten purpuratus* (Lamarck, 1819) dominated subtidal macro-invertebrate assemblage in Northern Chile. Journal of Shellfish Research 12:295-304

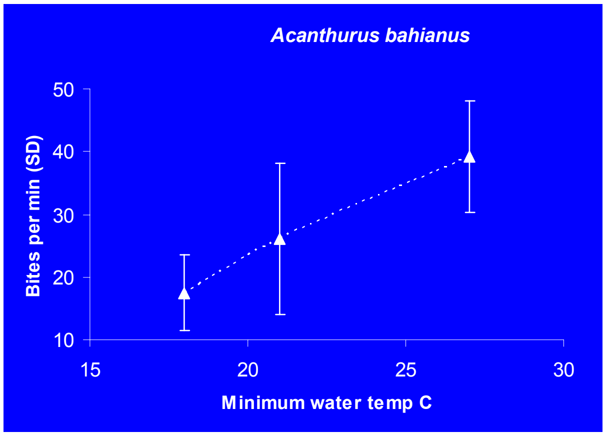
Wootton RJ (1998). Ecology of teleost fishes, 2nd edition. Kluwer Academic Publishers

Zapata FA, Morales A (1997) Spatial and temporal patterns of fish diversity in a coral reef at Gorgona Island, Colombia. Proc. 8th Int Coral Reef Symp 1:1029–1034

6.6 Publication IV

LATITUDINAL GRADIENTS IN ATLANTIC REEF FISH COMMUNITIES: TROPHIC STRUCTURE AND SPATIAL USE PATTERNS

Sergio Floeter, Carlos Eduardo Leite Ferreira, Arturo Dominici-Arosemena and Iliana Zalmon



Average feeding rate of the ocean surgeonfish *Acanthurus bahianus* (Ferreira et al 1998 b)

Journal of Fish Biology

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Journal of Fish Biology (2004) **64,** 1680–1699
doi:10.1111/j.1095-8649.2004.00428.x, available online at http://www.blackwell-synergy.com

Latitudinal gradients in Atlantic reef fish communities: trophic structure and spatial use patterns

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(Received 1 August 2003, Accepted 19 March 2004)

Trophic strategies and spatial use habits were investigated in reef fish communities. The results supported the hypothesis of differential use of food resources among tropical and higher latitude reef fishes, *i.e.* the number of species and relative abundance of fishes relying on relatively low-quality food significantly decreased from tropical to temperate latitudes. The species : genus ratio of low-quality food consumers increased toward the tropics, and was higher than the overall ratio considering all fishes in the assemblages. This supports the view that higher speciation rates occurred among this guild of fishes in warm waters. It was also demonstrated that density of herbivorous fishes (the dominant group relying on low-quality food resources) in the western Atlantic decreased from tropical to temperate latitudes. Spatial use and mobility varied with latitude and consequently reef type and complexity. Fishes with small-size home ranges predominated on tropical coral reefs.

Key words: community structure; herbivory; latitudinal gradient; macroecology; reef fishes.

INTRODUCTION

Fish diversity characteristically decreases from tropical to temperate latitudes (Ebeling & Hixon, 1991; Hobson, 1994; Briggs, 1995). In the Atlantic Ocean, the Caribbean is the centre of diversity, both in terms of fishes and corals (Briggs, 1995; Veron, 1995; Floeter & Gasparini, 2000). The extent to which fish trophic structure is modified between tropical coral reefs of the Caribbean and marginal rocky reefs of the Atlantic, however, remains unknown.

A functional categorization approach could be a useful tool for gathering broad-scale data on community structure, transcending taxonomic boundaries (Bellwood *et al.*, 2002). Thus, it is possible to infer general evolutionary trends based on ecologically relevant attributes such as feeding performance

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(*i.e.* functional morphology, physiology and biomechanics), mobility amplitude and resource-use patterns used by reef fishes. Trophic strategies, food availability and spatial use habits certainly play an important role in shaping patterns of abundance and habitat distribution in fishes (Harmelin-Vivien, 1989; Bellwood *et al.*, 2002; Wainwright & Bellwood, 2002).

Trophic strategies are an important functional attribute that could be distinct between tropical and temperate regions. For example, the relative diversity of herbivorous fishes is known to decrease drastically in colder waters (Horn, 1989; Choat, 1991; Ebeling & Hixon, 1991). In a recent review, Harmelin-Vivien (2002) hypothesized an evolutionary trend toward the better use of less energetic food resources among tropical reef fish communities (in contrast to temperate areas), based on qualitative comparisons between feeding behaviours and fish phylogeny and biogeography. She argued that the high diversity of fishes occurring on coral reefs is related to the sustained higher temperatures in the tropics over geological time, and to the more efficient use and transfer of energy permitted by long-term temperature stability. Planktivore, piscivore and motile invertebrate-feeding fishes that eat high protein and energy-rich food with high assimilation rates (Bowen *et al.*, 1995) form the most diverse trophic group worldwide (Randall, 1967; Harmelin-Vivien, 1989; Jones *et al.*, 1991; Ferreira *et al.*, 2004). Many reef fishes, however, exhibit morphological and physiological specialization to exploit comparatively low-quality resources like algae, seagrasses, detritus and sessile invertebrates (*e.g.* sponges, cnidarians and ascidians) and indeed sustain large populations in the tropics (Choat, 1991; Bruggemann, 1994; Dunlap & Pawlik, 1996; Hill, 1998). Although abundant and easy to locate, these resources are usually structural and chemically defended against grazing (Hay, 1991, 1997; Paul, 1992; Epifânio *et al.*, 1999; Burns & Ilan, 2003; Burns *et al.*, 2003) and their processing and assimilation present a major challenge to the digestive system (Horn, 1989; Choat, 1991; Meylan, 1991; Choat & Clements, 1998). Compared to carnivores, they have to ingest larger quantities of food to compensate for low nutritional value (Bruggemann *et al.*, 1994; Bowen *et al.*, 1995; Ferreira *et al.*, 1998*a*, *b*; Horn, 1998). For example, herbivorous fishes may eat many times their required energetic needs in order to gain enough nitrogen from seaweeds (Hay, 1991). Some parrotfishes (Scaridae) spend over 90% of the day foraging, taking thousands of bites per day (Carpenter, 1986; Hay, 1991; Bruggemann, 1994; Bruggemann *et al.*, 1994), and the same occurs with sponge-eating angelfishes (Pomacanthidae) (Dunlap & Pawlik, 1996). Corallivores, herbivores, detritivores and omnivores also tend to have longer intestines than do carnivores, whose diets are more nutritious (Goldschmid *et al.*, 1984; Horn, 1989, 1998; Elliott & Bellwood, 2003). An explanation for this pattern is that fishes relying on low-protein diets require longer guts, *i.e.* large surface area relative to volume, in order to process the large amount of poor-quality food needed (Horn, 1998).

Another functional aspect that could differentiate tropical fish assemblages from colder ones is the spatial use and mobility patterns of fishes. At tropical coral reefs, many species (mainly herbivores or sessile invertebrate feeders) have small-size home ranges or swim close to the coral matrix (Harmelin-Vivien, 1989). Some even defend their territory in a very aggressive way, like the herbivorous damselfishes (Pomacentridae) (Robertson, 1996; Ceccarelli *et al.*, 2001). Structural complexity has been correlated to reef fish space utilization (Luckhurst & Luckhurst, 1978) and abundance (Bell & Galzin, 1984; Friedlander & Parrish, 1998; S.R. Floeter, C.E.L. Ferreira & J.L. Gasparini unpubl. data) indicating that biogenic reefs could potentially sustain higher fish densities than non-reef-building peripheral areas, especially site-attached species. In true coral reefs, structural complexity is associated with coral growth form, especially those arborescent or branching forms in the shallower waters. On rocky shore systems, topographic complexity relies mostly on the presence or absence of holes (Ferreira *et al.*, 2001; S.R. Floeter, pers. obs.).

In contrast to previous publications (Harmelin-Vivien, 1989, 2002), the present work examined trophic strategies, spatial use and mobility patterns, based on quantitative (*i.e.* relative abundance and density) data collected along a broad latitudinal gradient in the Atlantic, as well as published data. Two specific questions were addressed: 1) is diversity and abundance of fishes that use relatively low-caloric food resources higher in the tropics than in subtropical or temperate regions? 2) Does fish spatial use (*i.e.* differential mobility and home-range patterns such as schooling behaviour and territoriality) vary according to latitude and reef type (*i.e.* coral *v.* rocky reefs)?

MATERIALS AND METHODS

DATASETS

Three datasets were used, the first one with relative abundance of reef fishes derived from replicated strip transects: underwater visual censuses (UVC) conducted in the Bocas del Toro, Panama (Caribbean), Guarapari Islands (south-east Brazil) and Arvoredo (south Brazil) (Table I). The sampling design included different habitats within each site, covering reefs of various depths, exposures and complexity profiles. Replicated point-count censuses from the Canaries (Bortone *et al.*, 1991; Falcon *et al.*, 1996; Hajagos & Van Tassell, 2001) were also included in the database. Assembling data from different sampling methods is always problematic for statistical purposes, however, in a recent method re-evaluation, Samoilys & Carlos (2000) did not find significant differences between transect and point-count visual censuses for many taxa.

In order to verify if the results obtained from the four sites could be generalized for their entire regions, a second database was compiled from the literature, with the addition of seven more sites: Florida Keys, 24°39′ N (Bohnsack & Bannerot, 1986); Cayos Cochinos, Honduras, 15°56′ N (Clifton & Clifton, 1998); Manuel Luiz Reefs, north-east Brazil, 0°52′ S (Rocha & Rosa, 2001); Tamandaré, north-east Brazil, 8°45′ S (B.P. Ferreira, unpubl. data); Abrolhos Reefs, north-east Brazil, 17°30′ S (C.E.L. Ferreira, unpubl. data); Arraial do Cabo, south-east Brazil, 23°S (C.E.L. Ferreira, unpubl. data); south-east Mediterranean, Spain, 37°38′ N (García-Charton & Pérez-Ruzafa, 2001); southern Italy, 35°35′ N (Mazzoldi & Girolamo, 1997). Original densities were converted in relative abundances in order to standardize data collected through different methodologies.

A third database was assembled to examine if actual densities support conclusions obtained from relative abundance data. This approach was based on densities derived from 20×2 m (40 m^2) standardized transects conducted in four localities in the western Atlantic (Panama, Abrolhos Reefs, Guarapari Islands and Arvoredo). Censuses were performed on all locations, and included juveniles of all species. Selected similar sheltered and shallow reefs (<10 m) were chosen on each location, because this is the preferred habitat for ‘herbivorous’ species. Herbivores (including detritivores, Wilson *et al.*, 2003) were analysed in detail due to their important role in the organization of shallow marine benthic communities, and to the knowledge accumulated about this guild in the last decades (Horn, 1989; Choat, 1991; Hixon, 1997; Choat & Clements, 2002; Wilson *et al.*, 2003).

TABLE I. Site characteristics and number of reef fish species richness (bold) with respective relative abundance (percentage of species number in parenthesis) in each diet category (food quality = nutritional value) and their mobility. Fish data were derived from visual census. Category definitions are the same as in Figs 1 and 5. Data from south-eastern Spain were added for comparison

	Bocas (Caribbean)	Guarapari Island (south-east Brazil)	Arvoredo (South Brazil)	Canaries[1] (Macaronesia)	South-east Spain[2] (Mediterranean)
Latitude	9°N	20°S	27°30′ S	28°N	37°N
SWT range (° C)	27–33	19–24	17–24	16–24	14–24
Coral richness (species)*	54[3]	14[4]	1[4]	0	0
Coral cover (%)	21·4[3]	4·6[5]	~0	0	0
Number of census	125	166	85	57	140
Fish diversity					
Number of fish species	97	81	62	61	45
Number of fish genera	52	53	44	48	30
Species : genera ratio	1·9	1·5	1·4	1·3	1·5
Trophic strategies					
High-quality	**63** (64·9)	**56** (69·1)	**39** (61·5)	**40** (65·6)	**33** (73·3)
Intermediate	**5** (5·2)	**4** (4·9)	**4** (7·7)	**16** (26·2)	**11** (24·4)
Low-quality	**29** (29·9)	**21** (25·9)	**18** (30·8)	**5** (8·2)	**1** (2·2)
Species : genera ratio[6]	2·4	1·9	1·6	1·0	1·0
Spatial use and mobility					
Category 1	**29** (29·9)	**24** (29·6)	**22** (34·6)	**29** (47·5)	**22** (51·2)
Category 2	**48** (49·5)	**38** (46·9)	**26** (42·3)	**17** (27·9)	**18** (41·9)
Category 3	**20** (20·6)	**19** (23·5)	**14** (23·1)	**15** (24·6)	**3** (7·0)

*, Reef-building scleractinian + millepores; [1], Fálcon *et al.* (1996), Bortone *et al.* (1991); [2], García-Charton & Pérez-Ruzafa (2001); [3], Guzmán & Guevara (1998); [4], Floeter *et al.* (2001); [5], W. Krohling & S.R. Floeter (unpubl. data); [6], only fishes utilizing low-quality diets.; SWT, sea surface temperature.

TROPHIC STRATEGIES

In all databases every genus was classified according to its diet (*i.e.* trophic guild and associated food quality) and spatial use and mobility (Table II). They were divided in three classes based on food quality: (1) high-quality, fishes that feed on highly energetic (with high protein content) and easily digestible food, *e.g.* zooplankton (Norrbin & Bamstedt, 1984), mobile invertebrates and fishes (Brey *et al.*, 1988; Bowen *et al.*, 1995); (2) low-quality, fishes that eat relatively low-energy content resources, generally with lower assimilation rates and indigestible components, *e.g.* high ash content (Meylan, 1991; Montgomery & Targett, 1992; Bowen *et al.*, 1995). Among this food are algae, seagrasses and detritus (all relatively protein-poor), and sessile invertebrates (*e.g.* cnidarians, hidrozoans and sponges, usually with high percentage of inorganic components in tissues). These resources generally contain structural (*e.g.* calcium carbonate) and chemical defences against grazing such as secondary metabolites (Paul, 1992; Pawlik, 1993; Pawlik *et al.*, 1995; Hay, 1997; Burns & Ilan, 2003; Burns *et al.*, 2003). Although various authors have recently demonstrated that the nutritional value of sponges and gorgonians (Chanas & Pawlik, 1995; O' Neal & Pawlik, 2002), detritus (Wilson, 2002; Wilson *et al.*, 2003) and endolithic algae (Bruggeman, 1994) are higher than previously thought, these resources have to be consumed in large amounts and the costs of their processing and assimilation are high (Horn, 1989; Choat, 1991; Meylan, 1991; Bowen *et al.*, 1995; Choat & Clements, 1998); (3) intermediate-quality, fishes that forage both on algae and some protein-rich animal food, *i.e.* omnivores (Montgomery & Targett, 1992). The problem of grouping reef fishes in broad diet categories has been widely discussed in recent reviews (Jones *et al.*, 1991). Fish feeding plasticity makes categorization into independent trophic groups difficult. In this study, however, every genus was assigned to one of three food quality categories associated with eight major trophic guilds (Table II) in order to search for general patterns. Dominant food items were determined from direct behavioural observations, stomach content analysis as well as the available literature (Randall, 1967; Froese & Pauly, 2003; pers. obs.).

Fishes have evolved a wide variety of ways to obtain their food and meet their energy and nutritional requirements (Horn, 1998). Overall diet quality is a function of the relationship between food composition and digestive physiology. The three proposed categories based on 'food quality' do not imply that a better general nutrition is obtained by any of the categories. Feeding strategies maximizing ingestion rates or presenting specialized digestion (*e.g.* microbial fermentation) are also successful ones. Indeed, the highest growth rates reported for freshwater fishes occur in herbivorous and detritivorous species (Bowen *et al.*, 1995; Choat & Clements, 1998).

SPATIAL USE AND MOBILITY

Each species was also assigned to one of three categories based on mobility patterns and home-range sizes: category 1, species with high mobility, generally associated with schooling behaviour in the water column (*i.e.* mid-water carnivores and planktivores) or demersal species with wide horizontal displacements (*e.g.* roving herbivores, sparids and mullids); category 2, demersal relatively sedentary species that live in close association with the reef substratum, including serranids, haemulids, labrids and chaetodontids; category 3, site-attached species with very small home ranges, many of them presenting territorial behaviour (*e.g.* damselfishes, labrisomids and gobies).

STATISTICAL ANALYSES

MANOVA (repeated measures) were used to test for differences among locations concerning mean relative abundances of food quality groups and spatial use and mobility categories. One-way ANOVA were performed to analyse total fish densities and densities of herbivores (Zar, 1999). Appropriate transformations ($\log_{10}$, square root or arc-sin) were applied when necessary in order to stabilize the variances when necessary (Underwood, 1997). Additional Student–Newman–Keuls (SNK) multiple comparisons

TABLE II. Food quality, mobility and trophic classification of reef fish genera in the four studied sites. Families are arranged according to Nelson (1994)

Family	Genus	Trophic guild	Food quality	Mobility	Family	Genus	Trophic guild	Food quality	Mobility
Ogcocephalidae	*Ogcocephalus*	C	H	3		*Spondyliosoma**	O	I	1
Synodontidae	*Synodus*	P	H	3	Scianidae	*Odontoscion*	C	H	2
Holocentridae	*Holocentrus*	MI	H	2		*Pareques*	MI	H	2
	Myripristis	PL	H	2		*Sciaena**	C	H	2
	Sargocentrum	MI	H	2		*Umbrina*	MI	H	2
Aulostomidae	*Aulostomus*	P	H	2	Mullidae	*Mulloidichthys*	MI	H	1
Scorpaenidae	*Scorpaena*	C	H	3		*Mullus*	MI	H	1
Centropomidae	*Centropomus*	C	H	1		*Pseudupeneus*	MI	H	1
Serranidae	*Alphestes*	C	H	2	Chaetodontidae	*Chaetodon*	SI	L	2
	Cephalopholis	C	H	2	Pomacanthidae	*Holacanthus*	SI	L	2
	Dermatolepis	C	H	2		*Pomacanthus*	O	L	2
	Diplectrum	C	H	2	Kyphosidae	*Kyphosus*	RH	L	1
	Epinephelus	C	H	2	Cirrhitidae	*Amblycirrhitus*	MI	H	3
	Hypoplectrus	C	H	2	Pomacentridae	*Abudefduf*	O	I	1
	Mycteroperca	P	H	2		*Chromis*	PL	H	1
	Paranthias	PL	H	1		*Microspathodon*	TH/D	L	3
	Rypticus	C	H	2		*Stegastes*	TH/D	L	3
	Serranus	MI	H	3	Labridae	*Bodianus*	MI	H	2
	S. tortugarum	PL	H	2		*Centrolabrus**	MI	H	2
Grammatidae	*Gramma*	MI/PL	H	3		*Clepticus*	PL	H	1
Priacanthidae	*Heteropriacanthus*	MI	H	2		*Coris**	MI	H	2
	Priacanthus	C	H	2		*Doratonotus*	MI	H	2
Carangidae	*Carangoides*	P	H	1		*Halichoeres*	MI	H	2
	Caranx	P	H	1		*Thalassoma*	PL	H	1
	Decapterus	P	H	1		*Xyrichthys*	MI	H	3
	Elagatis	P	H	1	Scaridae	*Cryptotomus*	RH	L	1
	Pseudocaranx	PL	H	1		*Scarus*	RH/D	L	1

TABLE II. Continued

Family	Genus	Trophic guild	Food quality	Mobility	Family	Genus	Trophic guild	Food quality	Mobility
	Seriola	P	H	1		*Sparisoma*	RHD	L	1
	Trachinotus	MI	H	1	Labrisomidae	*Labrisomus*	C	H	3
Lutjanidae	*Lutjanus*	C	H	2		*Malacoctenus*	MI	H	3
	Ocyurus	C	H	1	Blenniidae	*Ophioblennius*	TH/D	L	3
Haemulidae	*Anisotremus*	MI	H	2		*Parablennius*	O	I	3
	Haemulon	MI	H	2	Chaenopsidae	*Emblemariopsis*	MI	H	3
	Orthopristis	MI	H	2	Tripterygiidae	*Enneanectes*	MI	H	3
	*Parapristipoma**	MI	H	2		*Tripterygion**	MI	H	3
	Pomadasys	MI	H	2	Gobiidae	*Coryphopterus*	PL	H	3
Sparidae	*Archosargus*	O	I	1		*Elacatinus*	MI	H	3
	Boops	O	I	1		*Gobius**	MI	H	3
	Calamus	MI	H	1		*Vanneaugobius**	O	I	3
	*Dentex**	C	H	1	Acanthuridae	*Acanthurus*	RH/D	L	1
	Diplodus	O	I	1	Bothidae	*Bothus*	C	H	3
	*Lithognathus**	MI	H	1	Balistidae	*Balistes*	MI	I	1
	*Oblada**	O	I	1	Monacanthidae	*Aluterus*	O	L	1
	*Pagellus**	O	I	1		*Cantherhines*	O	I	1
	Pagrus	C	I	1		*Stephanolepis*	O	I	1
	*Sarpa**	RH	L	1	Ostraciidae	*Acanthostracion*	O	I	1
	*Sparus**	O	I	1	Tetraodontidae	*Canthigaster*	SI	L	2

C, carnivore; P, piscivore; MI, mobile invertebrate feeder; SI, sessile invertebrate feeder; PL, planktivore; O, omnivore; RH, roving herbivore; TH, territorial herbivore; D, detritivore; H, high-quality food; I, intermediate; L, low; 1, high mobility; 2, relatively sedentary; 3, site attached. *, not present in the western Atlantic.

of means test were performed as a *post hoc* test (Zar, 1999). When transformations did not produce homogeneous variances, ANOVA was used nevertheless because of its robustness, following Underwood's (1997) recommendation. A setting of $\alpha = 0{\cdot}01$ was used to compensate for the increased likelihood of Type I error (Underwood, 1997). A multivariate canonical correspondence analysis (CCA) was conducted to explore the generality of large-scale trends in food resource use among 11 sites in the Atlantic, *i.e.* the second database (ter Braak & Verdonschot, 1995). The *t*-test was employed for comparing the average feeding rate of the ocean surgeonfish *Acanthurus bahianus* Castelnau in Panama and south-eastern Brazil.

RESULTS

UTILIZATION OF FOOD RESOURCES

Fish species using food resources of high nutritional value were dominant in all sites, both in terms of diversity and relative abundance, ranging from 62 to 73% of the total number species and 52 to 65% of counted fishes (Table I and Fig. 1). The number of species and relative abundance of fishes relying on low-energy food significantly decreased towards higher latitudes (Fig. 1 and Table I). The species : genus ratio of this fish guild decreased toward colder waters (2·4 in Bocas, 1·9 in Guarapari, 1·6 in Arvoredo and 1·0 in the Canaries) and it was higher than the overall ratio considering all fishes in the western Atlantic assemblages (Table I). On the other hand, fishes that fed on intermediate-quality resources (*i.e.* algae, detritus and also animal protein) were highly abundant at colder peripheral sites (Arvoredo and Canaries) and their proportional importance diminished in warmer locations (Fig. 1). Their species richness also increased with latitude (Table I), and the omnivorous sparids were the main speciose family in this guild.

A sharp decrease in the importance of fishes depending on low-caloric food could be observed in relation to the minimum water temperature of locations. A ratio of mean relative abundance of fishes that feed on high-quality resources divided by mean relative abundance of fishes using intermediate or low-quality diets revealed a consistent trend (Fig. 2).

A CCA analysis performed with data from 11 sites along the Atlantic (Fig. 3) showed the same trends observed in the four detailed studied sites (Fig. 1), confirming that a consistent regional generalization could be drawn. Trophic strategies accounted for 45·6% of the variance in the weighted averages. Tropical sites were all clustered following the trend of better use of low-quality resources (intraset correlations between diet and site scores = 0·819). On the right side of the diagram, high-quality (−0·939) and intermediate diets (0·319) affected the marginal eastern Atlantic and the Mediterranean sites. A balance of intermediate (*i.e.* omnivore) and low-quality category influenced high latitude rocky reefs on the Brazilian coast.

DENSITY OF HERBIVORES AND DETRITIVORES

Standardized visual censuses in four sheltered and shallow localities in the western Atlantic provided comparable data on densities of reef fishes along an extensive latitudinal gradient. Total density of fishes was similar in all tropical

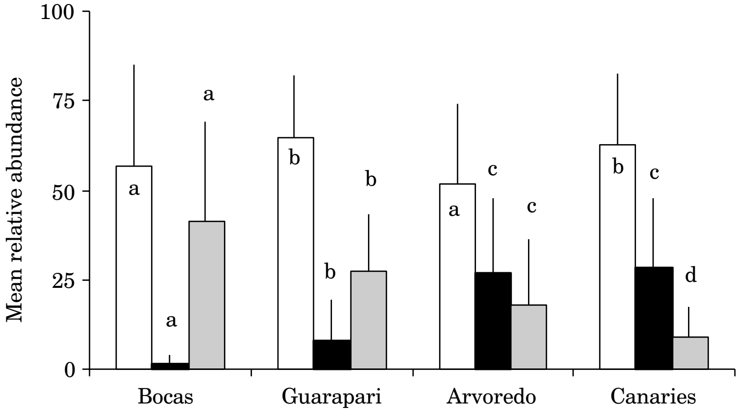

FIG. 1. Mean + S.D. relative abundance of food quality categories: high-quality (☐) (fishes that feed on high protein and energy content food, which are highly digestible, *e.g.* macro-plankton, mobile invertebrates and fishes), low-quality (▨) (fishes that eat relatively low-energy content resources, with indigestible components such as algae, seagrasses, detritus, sponges and cnidarians and intermediate-quality (■) (fishes that forage both on algae and protein-rich animal food, *i.e.* omnivores). MANOVA showed that all categories varied significantly between locations ($P < 0{\cdot}001$); different lower case letters indicate significantly different (Student–Newman–Keuls test, $P < 0{\cdot}01$) values and those with the same lower case letter are not significantly different ($P > 0{\cdot}01$).

sites: Bocas del Toro, Panama, Abrolhos, north-east Brazil and Guarapari, south-east Brazil (175–200 fishes 100 m^{-2}) and only half of it was found on Arvoredo (92 fishes 100 m^{-2}) in the southern Brazil (Fig. 4). Total density and relative proportion of herbivores follow a clear significant latitudinal trend (158 fishes 100 m^{-2} constituting 79% of fishes counted in Bocas del Toro, Panama,

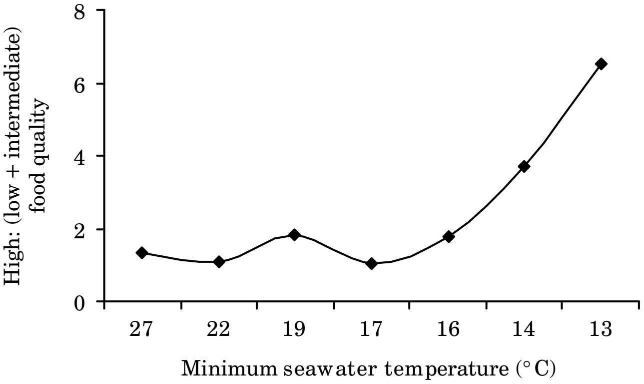

FIG. 2. High-quality: (intermediate + low) quality food ratio in relation to minimum water temperature. Data from relative abundances derived from visual censuses: Bocas del Toro, Panama, 9°N; Abrolhos Reefs, north-east Brazil, 17°30′ S (C.E.L. Ferreira unpubl. data); Guarapari Islands, south-east Brazil 20°S; Arvoredo, 27°30′ S; Canaries, Macaronesia, 28°N (Fálcon *et al.*, 1996; Bortone *et al.*, 1991; Hajagos & Van Tassell, 2001); south-east Mediterranean, Spain, 37°38′ N (García-Charton & Pérez-Ruzafa, 2001); Santa Catalina Island, California, U.S.A. 33°30′ N (Hobson & Chess, 2001).

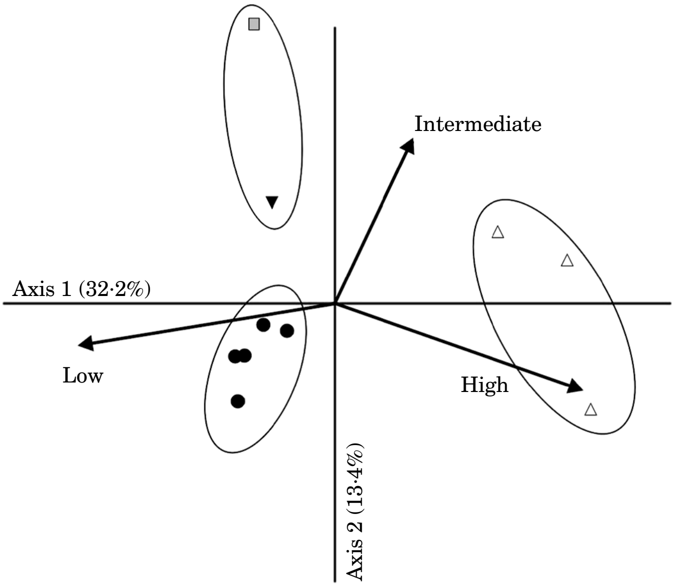

FIG. 3. Canonical correspondence analysis ordination diagram with reef sites and diet categories (➔) (see Fig. 1). The sites were: tropical (●) [Florida Keys, 24°39′ N (Bohnsack & Bannerot, 1986); Cayos Cochinos, Honduras, 15°56′ N (Clifton & Clifton, 1998); Bocas del Toro, Panama, 9°N; Manuel Luiz Reefs, north-east Brazil, 0°52′ S (Rocha & Rosa, 2001); Tamandaré, north-east Brazil, 8°45′ S (B.P. Ferreira unpubl. data); Abrolhos Reefs, north-east Brazil, 17°30′ S (C.E.L. Ferreira unpubl. data); Guarapari Islands, south-east Brazil 20°S], south-east (▼) and southern Brazil (■) [Arraial do Cabo, south-east Brazil, 23°S (C.E.L. Ferreira unpubl. data); Arvoredo, southern Brazil 27°30′ S] and north-east Atlantic (△) [Canaries, Macaronesia, 28°N (Fálcon *et al.*, 1996; Bortone *et al.*, 1991; Hajagos & Van Tassell, 2001); south-east Mediterranean, Spain, 37°38′ N (García-Charton & Pérez-Ruzafa, 2001); southern Italy, 35°35′ N (Mazzoldi & Girolamo, 1997)].

99 and 57% on Abrolhos Reefs, north-east Brazil, 41 and 23% on Guarapari Island, south-east Brazil, and 19 and 21% on Arvoredo Archipelago in the south).

MOBILITY AND HOME-RANGE PATTERNS

Regarding the amplitude of fish spatial use and mobility, the category 1 (high mobility generally associated with schooling behaviour) is proportionally more diverse in the Canaries (Table 1) where it also achieves significantly higher relative abundance (Fig. 5). Schooling sparids and the omnivorous pomacentrid genus *Abudefduf* are abundant in the marginal sites. On the Canarian Archipelago, the planktivorous *Thalassoma* and *Chromis* are also very abundant. Relatively sedentary species (category 2) are a diverse group in tropical sites (Table I), and are highly abundant in the Brazilian sites (Fig. 5). This is because of the high relative abundance of haemulids, holocentrids and the labrid genus *Halichoeres* on Guarapari Islands, and serranids (primarily *Mycteroperca*) and the puffers (*Sphoeroides*) on Arvoredo. Site-attached species (category 3) are the dominant group in the Caribbean in terms of abundance (66·5% of the counted fishes; Fig. 5). Gobiids and territorial damselfishes are mainly responsible for

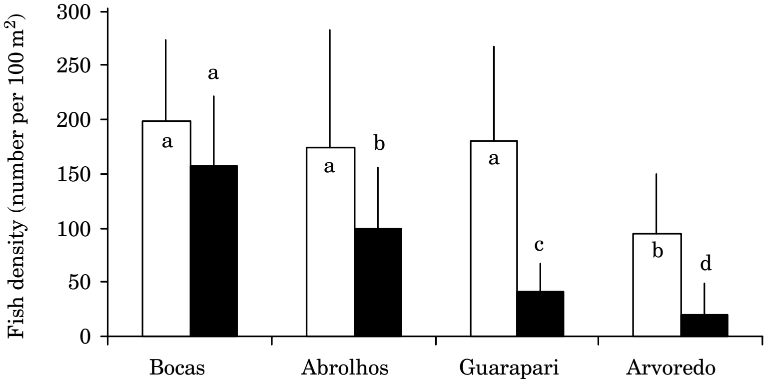

FIG. 4. Mean + S.E. total fish densities (☐) and herbivores only (■) at four sites in a latitudinal gradient along the western Atlantic. Data were derived from 20 × 2 m transects (visual censuses) in selected shallow (<10 m deep) sheltered habitats at: Bocas del Toro, Punta Hospital, 9°N ($n = 60$); Abrolhos, Timbebas reefs, 17°30′ S ($n = 56$); Guarapari Island, 20°S ($n = 84$); Arvoredo, 27°30′ S ($n = 85$). ANOVA showed that all categories varied significantly between locations ($P < 0{\cdot}001$); different lowercase letters indicate significantly different (Student–Newman–Keuls test, $P < 0{\cdot}01$) values and those with the same lower case letter are not significantly different ($P > 0{\cdot}01$).

these figures. On the Brazilian coast, site-attached species account for 15–30% decreasing to just 1·3% in the Canaries. Many fishes in category 3 are small and cryptic and are often underestimated by UVC (Willis, 2001). Their diversity and abundance are probably higher than indicated in Fig. 5, especially on tropical reefs.

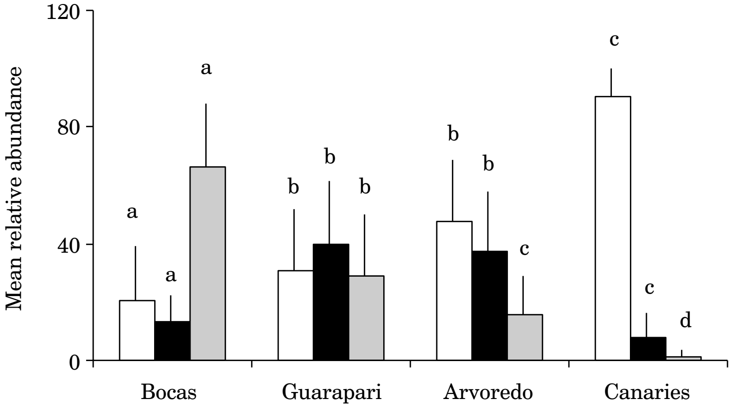

FIG. 5. Mean + S.D. relative abundances of categories of spatial use (mobility and home-range size): category 1, (☐) (species with high mobility, generally associated with schooling behaviour in the water column or demersal species with wide horizontal displacements); category 2 (■) (demersal relatively sedentary species that live in close association with the reef substratum, including serranids, haemulids, labrids and chaetodontids); category 3 (▨) (site-attached species with very small home-ranges, many of them presenting territorial behaviour). MANOVA showed that all categories varied significantly between locations ($P < 0{\cdot}001$); different lower case letters indicate significantly different (Student–Newman–Keuls test, $P < 0{\cdot}01$) values and those with the same letter were not significantly different ($P > 0{\cdot}01$).

DISCUSSION

Species richness declines from Bocas del Toro to the Canaries conforming to the general trend of decreasing fish diversity from tropical to temperate latitudes (Hobson, 1994; Briggs, 1995). These trends could be related to: (1) differential extinction rates suffered in peripheral areas due to sea-level and temperature changes over geological time (Briggs, 1966, 1995; Vermeij & Rosenberg, 1993), (2) differences in recent speciation rates, decreasing from tropical to temperate sites, as indicated by the species per genus ratios found (Table I), and (3) habitat availability (and heterogeneity) and resource diversity and temporal persistence (tropical *v*. temperate reefs; Holbrook *et al*., 1990).

IS THERE A TREND TOWARD THE USE OF LOW-ENERGY FOOD RESOURCES AMONG TROPICAL REEF FISHES?

Harmelin-Vivien (2002) presented qualitative data of herbivorous fish species and their significant correlation with latitude (increasing richness towards the equator), and also showed that the percentage of algae in the diet of blenniid and gobiid fish species on coral reefs was higher than in warm-temperate waters. In the present study, it was unequivocally demonstrated that although planktivores, piscivores and carnivores preying on motile invertebrates dominated in all sites, the relative abundance of fishes that fed on algae, organic detritus and sessile invertebrates decreased from tropical to temperate latitudes. These differences are probably not related to differences in the abundance of food resources between latitudes, because algae, seagrasses and sessile invertebrates (except for reef-building corals) are also abundant and available (although seasonal for some algae species) for feeding in temperate zones (Holbrook *et al*., 1990; Fasola *et al*., 1997; Pawlik, 1998; Harmelin-Vivien, 2002; Pihl & Wennhage, 2002). Differences, however, could be driven by algae productivity (Russ, 2003) and rate of detritus decomposition (higher on tropical reefs; Cebrian, 2002).

The species : genus ratio of low-quality food consumers increased towards the tropics, and was higher than the overall ratio considering all fishes in the assemblages. This supports the view that higher speciation rates occurred among this guild of fishes in warm waters. Indeed, low-quality feeders contain the morphologically derived taxa, indicating a relationship between radiation and the energetic value of the food (Table II; Bruggemann, 1994; Harmelin-Vivien, 2002). The higher diversity and abundance of low-quality feeders (*i.e.* herbivores and sessile invertebrate feeders) in lower latitudes compared to marginal areas could be viewed as a reflection of a progressive adaptation to the use low-energy food sources (Harmelin-Vivien, 2002).

Although herbivory, spongivory and corallivory by fishes is known to affect distribution and abundance of benthic organisms (Lewis, 1985; Horn, 1989; Hixon, 1997; Hill, 1998; Pawlik, 1998), these feeding strategies are a relatively recent evolutionary phenomenon (Wood, 1999; Bellwood & Wainwright, 2002; Bellwood, 2003). Herbivores and sessile invertebrate browsers are found in the most derived families (Table II), and within these families extended adaptations to use poor-quality resources are found in the morphologically most derived genera (Motta, 1989; Bellwood, 1994; Harmelin-Vivien, 2002). Cooper & Vitt

(2002) found the same trend in lizards. The 'Cenozoic marine grazing revolution' appears to mark a major shift in the ecological structure of coral reefs due to changes in the nature of fish-based predation. During this transition, fish faunas went from primarily carnivorous in the Mesozoic to a large variety of grazers or browsers in the Cenozoic (Wood, 1999; Bellwood & Wainwright, 2002; Bellwood, 2003).

In colder peripheral sites, such as the southern Brazilian coast, the Canaries or the Mediterranean, fishes that feed on intermediate-quality food (*e.g.* omnivorous sparids) have higher abundance and diversity, compared to warmer sites. It seems that these fishes could exploit low-nutritional resources only if they are associated with substantial portions of highly digestible animal protein. So, they could fulfil their metabolic needs to live in harsh colder environments. Bowen *et al.* (1995) interpreted omnivory as a compromise strategy in which protein from scarce animal prey is complemented by energy from abundant primary foods. At Santa Catalina, California, U.S.A. two nominally herbivores, *Girella nigricans* (Ayres) and *Medialuna californiensis* (Steindachner), differ from most tropical herbivores in consuming a relatively large number of invertebrates on a seasonal basis (Holbrook *et al.*, 1990; Hobson & Chess, 2001). In winter, when preferred algae are scarce and when fermentative digestion processes could be less efficient, it seems necessary to increase feeding on animal protein. In North Carolina, U.S.A., a similar behaviour was observed (M. Hay, pers. comm.) with omnivorous fishes shifting diets with changes in temperature. When it was warm, they consumed more seaweed. As temperature dropped they consumed more animal material, and eventually refused to eat any seaweed once temperatures were <17° C.

'HERBIVOROUS' FISHES: A TROPICAL PHENOMENON?

The density (and relative proportion) of herbivores and detritivores censused in similar habitats, with standardized procedures, significantly decreases toward higher latitudes. Meekan & Choat (1997) when comparing the Caribbean and the Great Barrier Reef to New Zealand reefs also found the same pattern. Within the herbivores, some differences were obvious. Fishes that have an important part of their diet constituted by detritus and calcified material (scarids and acanthurids) achieve higher densities in warmer sites (Bruggemann, 1994; Ferreira *et al.*, 2004). Conversely, kyphosids and some sparisomatines that feed on macroalgae increase their relative abundance at higher latitudes on the Brazilian coast (Ferreira *et al.*, 2004). On the Great Barrier Reef, scarids on the southern limit of their range consume more macroscopic algae compared to those on lower latitudes (J.H. Choat, pers. comm.). The domination of exclusive selective macroalgae feeders, which use a special digestion by hind gut fermentation and symbionts ('true herbivores'; Choat & Clements, 2002) such as kyphosids, odacids, aplodactylids and stichaeids) is also found in New Zealand temperate rocky reefs (Jones, 1988; Meekan & Choat, 1997; Choat & Clements, 1998; Mountfort *et al.*, 2002). Other counter-examples, however, complicate the situation (*e.g.* the browsing acanthurid *Acanthurus coeruleus* Bloch & Schneider are only found in the tropical Atlantic, and macroalgae eating siganids are more diverse and abundant at lower latitudes in the Pacific).

Herbivory pressure seems to be lower in higher latitudes not only due to lower density of herbivores, but because feeding rates (bites per unit time) are generally lower too (Choat & Clements, 1993), which is probably a reflection of lowered metabolism in colder water. For example, parrotfishes of the genus *Sparisoma* have average biting rates during the daytime (1100–1600 hours) of 30–35 bites per 5 min in south-east Brazil (Ferreira *et al.*, 1998*b*) and Azores (J.P. Barreiros, pers. comm.), and of 55–65 bites per 5 min in Panama (C.E.L. Ferreira & S.R. Floeter, unpubl. data). Also, the roving acanthurid *Acanthurus bahianus* Castelnau have an average grazing rate of 88 ± 30 bites per 5 min (mean ± S.D.) in south-east Brazil, where water temperature usually falls to 18–19° C (Ferreira *et al.*, 1998*b*), and more than the double (196 ± 43 bites per 5 min) in the tropical Bocas del Toro, Panama (*t*-test, d.f. = 121, $P < 0{\cdot}0001$). This pattern seems to indicate that below a critical temperature, nutrient assimilation may fall below metabolic requirements, thus physiological constraints associated with size and an ectothermic metabolism could be excluding many 'herbivorous' fishes from temperate and higher latitudes (Gaines & Lubchenco, 1982; Horn, 1989). Further studies should also consider if productivity and algae and detritus chemical composition are linked with the herbivorous fish abundance patterns found.

It is worth noting that the capacity to 'make a living' from plant material has been found for a long time in terrestrial vertebrate populations, probably since the Permian (Sues & Reisz, 1998). In fishes there is clearly a much later 'time-horizon' in the appearance of herbivory (Bellwood & Wainwright, 2002). Although some fishes occupying cold water habitats (down to 45°S) are herbivores, feeding exclusively on macroscopic algae and maintaining rates of fermentative digestion in a similar way to terrestrial endotherms (Mountfort *et al.*, 2002), the great majority of marine fish 'herbivores' have tropical affinities and are rare in temperate environments in the Atlantic. These fishes find their optimal environmental factors in the tropics (Choat, 1991; Bruggemann, 1994; Ferreira *et al.*, 2004). It is thus clear that the real trophic status of herbivorous fishes in the Atlantic requires further detailed studies (Choat & Clements, 2002).

DO FISH SPATIAL USE AND MOBILITY VARY WITH LATITUDE AND REEF TYPE?

Differential mobility and home range patterns (*e.g.* schooling behaviour and territoriality) are expected to occur if: 1) distinct foraging strategies are used to access unpredictable and spaced resources (*e.g.* plankton) and 2) there is variation in reef type and complexity (*e.g.* coral and rocky). Horizontal and vertical fish distribution in space is not uniform across the reef complex. Its heterogeneity operates at two scales, the geomorphological reef zones (macrohabitat), and the specific fish habitats (microhabitat). Bellwood *et al.* (2002) found highly congruent patterns of habitat use (sheltered *v.* exposed) of labrids, in terms of functional characteristics at global biogeographical scales.

On high-latitude reefs, fishes presenting high mobility or wide horizontal displacements (category 1) are proportionally more diverse and achieve significantly higher abundances. These fishes generally exhibit schooling behaviour, which is the privileged foraging tactic used by fishes that have to roam over large areas to find patchy or randomly distributed food (*e.g.* plankton and small clupeids). High-latitude environments are generally affected by seasonal temperature changes and unpredictable upwelling processes (Ebeling & Hixon, 1991; Sala & Boudouresque, 1997; Pihl & Wennhage, 2002). High mobility fishes, usually in large schools, are less reliant on the reef substratum for protection, and seem to respond more readily to environmental fluctuations, *i.e.* they are better able to move among reefs and vertically in the water column in response to the availability of resources or to satisfy their environmental preferences, such as optimal temperature. Among fishes that thrive well in these marginal reefs are the omnivorous schooling sparids (*Diplodus*), the sargent major (*Abudefduf*), and the planktivorous *Chromis*.

In a highly complex substratum, species sheltering in reef crevices or holes or in near-reef sand or rubble are expected. Structural complexity or bottom relief has been positively correlated to reef fish abundance in coral reefs (Bell & Galzin, 1984; Friedlander & Parrish, 1998), tropical and subtropical rocky shores (Aburto-Oropeza & Balart, 2001; Ferreira *et al.*, 2001; S.R. Floeter, unpubl. data), and temperate reefs (García-Charton & Pérez-Ruzafa, 1998). On tropical reefs, relatively sedentary taxa (category 2) such as the labrid genus *Halichoeres*, haemulids, chaetodontids and serranids form the most diverse group detected by UVC. In terms of abundance, fishes with small-size home ranges (category 3) predominate on coral reefs (67% of the counted fishes in Bocas del Toro, Panama). Similar values are found on coral reefs worldwide (72% at Tulear, Madagascar; 61% at Moorea, French Polynesia; Harmelin-Vivien, 1989). Substratum complexity promoted by coral growth (especially branching forms) seems to provide adequate microhabitats for small territorial fishes such as pomacentrids and gobies. On many tropical reefs, territorial damselfishes are extremely abundant, and the areas they defend can occupy >70–80% of the surface of some reef habitats (Robertson & Lassig, 1980; Ferreira *et al.*, 1998*a*; Ceccarelli *et al.*, 2001). The higher diversity and abundance of type 3 species can also be also linked to their diets. Most of them defend algae or feed on detritus which is more available in the tropics. In other words, home range size and 'food security' are probably linked and confounding factors.

In summary, the data support the situation proposed by Harmelin-Vivien (2002) that trophic structure of tropical fish communities contrast with those from temperate regions in terms of more efficient use of relatively low-quality food resources. In relation to the spatial use and mobility, relatively sedentary species form the most diverse group on tropical reefs, although fishes with small-size home ranges dominate in terms of abundance. Not all patterns found in the Atlantic, however, are likely to be general at the global-scale because of the different evolutionary histories and diversity profiles among ocean basins (Van Alstyne *et al.*, 2001; Bellwood & Wainwright, 2002). For example, a significant decrease in the proportion of species and densities of herbivorous fishes from tropical to temperate waters is observed worldwide (Horn, 1989; Meekan & Choat, 1997; S.R. Floeter and C.E.L. Ferreira, unpubl. data), but in terms of relative biomass, temperate New Zealand is an exception with herbivores presenting similar values as tropical locations (Jones, 1988). Thus, further comparative studies between the Atlantic and the Indo-Pacific regions regarding functional characteristics of species (*e.g.* spatial use, mobility and resource-use patterns) are needed.

We thank J.L. Gasparini, O.J. Luiz-Júnior, W. Krohling, M. Hostin, J.P. Barreiros, J.G. Domínguez, I. Bethancourt, A. Castillo, W. Pomare, L.C. Gerhardinger, A.G.V. Floeter, IEAPM and D.R. Roberston (STRI) for invaluable help in the field and logistical support. M. Kulbicki, J.H. Choat, M. Harmelin-Vivien, J.P. Barreiros, B.P. Ferreira, M. Hay, J.-C. Joyeux, M.S.G. Floeter, M. Wolff, O. Ocaña, R. Stevens, D. Vázquez, A. Moles and J. Pawlik for exchanging ideas, unpublished records and provision of literature. Smithsonian Tropical Research Institute (STV grant), Padi Aware Foundation, Fundação O Boticário de Proteção à Natureza, WWF, UENF, and the Center for Tropical Marine Ecology (ZMT) for essential funding. This work was partly conducted at the National Center for Ecological Analysis and Synthesis, Santa Barbara, CA, U.S.A. where S.R.F. is a postdoctoral associate.

References

Aburto-Oropeza, O. & Ballart, E. F. (2001). Community structure of reef fish in several habitats of a rocky reef in the Gulf of California. *PSZN Marine Ecology* **22,** 283–305.

Bell, J. D. & Galzin, R. (1984). Influence of live coral cover on coral-reef fish communities. *Marine Ecology Progress Series* **15,** 265–274.

Bellwood, D. R. (1994). A phylogenetic study of the parrotfishes family *Scaridae* (Pisces: Labroidei), with a revision of genera. *Records of the Australian Museum, Supplement* **20,** 1–86.

Bellwood, D. R. (2003). Origins and escalation of herbivory in fishes: a functional perspective. *Paleobiology* **29,** 71–83.

Bellwood, D. R. & Wainwright, P. C. (2002). The history and biogeography of fishes on coral reefs. In *Coral Reef Fishes*: *Dynamics and Diversity in a Complex Ecosystem* (Sale, P. F., ed.), pp. 5–32. San Diego, CA: Academic Press.

Bellwood, D. R., Wainwright, P. C., Fulton, C. J. & Hoey, A. (2002). Assembly rules and functional groups at global biogeographical scales. *Functional Ecology* **16,** 557–562.

Bohnsack, J. A. & Bannerot, S. P. (1986). A stationary visual technique for quantitatively assessing community structure of coral reef fishes. *NOAA Techical Report NMFS* **41,** 1–11.

Bortone, S. A., Van Tassell, J., Brito, A., Falcón, J. M. & Bundrick, C. M. (1991). A visual assessment of the inshore fishes and fishery resources off El Hierro, Canary Islands: a baseline survey. *Scientia Marina* **55,** 529–541.

Bowen, S. H., Lutz, E. V. & Ahlgren, M. O. (1995). Dietary protein as determinants of food quality: trophic strategies compared. *Ecology* **76,** 899–907.

ter Braak, C. J. F. & Verdonschot, P. F. M. (1995). Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences* **57,** 255–289.

Brey, T., Rumohr, H. & Ankar, S. (1988). Energy content of macrobenthic invertebrates: general conversion factors from weight to energy. *Journal of Experimental Marine Biology and Ecology* **117,** 271–278.

Briggs, J. C. (1966). Oceanic islands, endemism and marine paleotemperatures. *Systematic Zoology* **15,** 1153–163.

Briggs, J. C. (1995). *Global Biogeography. Developments in Paleontology and Stratigraphy*. Amsterdam: Elsevier.

Bruggemann, J. H. (1994). Parrotfish grazing on coral reefs: a trophic novelty. PhD Thesis, University of Groningen, Netherlands.

Bruggemann, J. H., Begeman, J., Bosna, E. M., Verbug, P. & Breeman, A. M. (1994). Foraging by the stoplight parrotfish *Sparisoma viride*. II. Intake and assimilation of food, protein, and energy. *Marine Ecology Progress Series* **112,** 57–71.

Burns, E. & Ilan, M. (2003). Comparison of anti-predatory defenses of Red Sea and Caribbean sponges. II. Physical defence. *Marine Ecology Progress Series* **252,** 115–123.

Burns, E., Ifrach, I., Carmeli, S., Pawlik, J. R. & Ilan, M. (2003). Comparison of anti-predatory defenses of Red Sea and Caribbean sponges. II. Chemical defence. *Marine Ecology Progress Series* **252,** 105–114.

Carpenter, R. C. (1986). Partitioning herbivory and its effects on coral reef algal communities. *Ecological Monographs* **56,** 345–363.

Cebrian, J. (2002). Variability and control of carbon consumption, export, and accumulation in marine communities. *Limnology and Oceanography* **47,** 11–22.

Ceccarelli, D. M., Jones, G. P. & McCook, L. J. (2001). Territorial damselfishes as determinants of the structure of benthic communities on coral reefs. *Oceanography and Marine Biology Annual Review* **39,** 355–389.

Chanas, B. & Pawlik, J. R. (1995). Defenses of Caribbean sponges against predatory reef fish. II. Spicules, tissue toughness, and nutritional quality. *Marine Ecology Progress Series* **127,** 195–211.

Choat, J. H. (1991). The biology of herbivorous fishes on coral reefs. In *The Ecology of Fishes on Coral Reefs* (Sale, P. F., ed.), pp. 120–155. San Diego, CA: Academic Press.

Choat, J. H. & Clements, K. D. (1993). Daily feeding rates in herbivorous labroid fishes. *Marine Biology* **117,** 205–211.

Choat, J. H. & Clements, K. D. (1998). Vertebrate herbivores in marine and terrestrial environments: a nutritional ecology perspective. *Annual Review of Ecology and Systematics* **29,** 375–403.

Choat, J. H. & Clements, K. D. (2002). The trophic status of herbivorous fishes on coral reefs 1: dietary analyses. *Marine Biology* **140,** 613–623.

Clifton, K. E. & Clifton, L. M. (1998). A survey of fishes from various coral reef habitats within the Cayos Cochinos Marine Reserve, Honduras. *Revista de Biologia Tropical* **46,** 109–124.

Cooper, W. E. & Vitt, L. J. (2002). Distribution, extent, and evolution of plant consumption by lizards. *Journal of Zoology, London* **257,** 487–517.

Dunlap, M. & Pawlik, J. R. (1996). Video-monitored predation by Caribbean reef fishes on an array of mangrove and reef sponges. *Marine Biology* **126,** 117–123.

Ebeling, A. W. & Hixon, M. A. (1991). Tropical and temperate reef fishes: comparison of community structure. In *The Ecology of Fishes on Coral Reefs* (Sale, P. F., ed.), pp. 509–563. San Diego, CA: Academic Press.

Elliott, J. P. & Bellwood, D. R. (2003). Alimentary tract morphology and diet in three coral reef fish families. *Journal of Fish Biology* **63,** 1598–1609. doi: 10.1046/j.1095-8649.2003.00272.x.

Epifânio, R. A., Martins, D. L., Gabriel, R. & Villaça, R. C. (1999). Chemical defenses against fish predation in three Brazilian octocorals: 11ß,12ß-Epoxypukalide as a feeding deterrent in *Phyllogorgia dilatata. Journal of Chemical Ecology* **10,** 2255–2265.

Falcón, J. M., Bortone, S. A., Brito, A. & Bundrick, C. M. (1996). Structure of and relationships within and between the littoral, rock-substrate fish communities off four islands in the Canarian Archipelago. *Marine Biology* **125,** 215–231.

Fasola, M., Canova, L., Foschi, F., Novelli, O. & Bressan, M. (1997). Resource use by a Mediterranean rocky slope fish assemblage. *PSZN Marine Ecology* **18,** 51–66.

Ferreira, C. E. L., Gonçalves, J. E. A., Coutinho, R. & Peret, A. C. (1998*a*). Herbivory by the dusky damselfish *Stegastes fuscus* (Cuvier, 1830) in a tropical rocky shore: effects on the benthic community. *Journal of Experimental Marine Biology and Ecology* **229,** 241–264.

Ferreira, C. E. L., Peret, A. C. & Coutinho, R. (1998*b*). Seasonal grazing rates and food processing by tropical herbivorous fishes. *Journal of Fish Biology* **53,** 222–235.

Ferreira, C. E. L., Gonçalves, J. E. A. & Coutinho, R. (2001). Community structure of fishes and habitat complexity in a tropical rocky shore. *Environmental Biology of Fishes* **61,** 353–369.

Ferreira, C. E. L., Floeter, S. R., Gasparini, J. L., Ferreira, B. P. & Joyeux, J. C. (2004). Trophic structure patterns of Brazilian reef fishes: a latitudinal comparison. *Journal of Biogeography* **31** (in press).

Floeter, S. R. & Gasparini, J. L. (2000). The southwestern Atlantic reef fish fauna: composition and zoogeographic patterns. *Journal of Fish Biology* **56,** 1099–1114.

Floeter, S. R., Guimarães, R. Z. P., Rocha, L. A., Ferreira, C. E. L., Rangel, C. A. & Gasparini, J. L. (2001). Geographic variation in reef-fish assemblages along the Brazilian coast. *Global Ecology and Biogeography* **10,** 423–431.

Friedlander, A. M. & Parrish, J. D. (1998). Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology* **224,** 1–30.

Gaines, S. D. & Lubchenco, J. (1982). A unified approach to marine plant–herbivore interactions. II. Biogeography. *Annual Review of Ecology and Systematics* **13,** 111–138.

García-Charton, J. A. & Pérez-Ruzafa, A. (1998). Correlation between habitat structure and a rocky reef fish assemblage in the southwest Mediterranean. *PSZN Marine Ecology* **19,** 111–128.

García-Charton, J. A. & Pérez-Ruzafa, A. (2001). Spatial pattern and the habitat structure of a Mediterranean rocky reef fish local assemblage. *Marine Biology* **138,** 917–934.

Goldschmid, A., Kotrschal, K. & Wirtz, P. (1984). Food and gut length of 14 Adriatic Blenniid fish (Blenniidae; Percomorpha; Teleostei). *Zoologischer Anzeiger, Jena* **213,** 145–150.

Guzmán, H. M. & Guevara, C. A. (1998). Arrecifes coralinos de Bocas del Toro, Panamá. II. Distribuión, estructura y estado de conservación de los arrecifes de las Islas Bastimentos, Solarte, Carenero y Colón. *Revista de Biologia Tropical* **46,** 889–912.

Hajagos, J. G. & Van Tassel, J. L. (2001). A visual survey of the inshore fish communities of Gran Canaria (Canary Islands). *Arquipélago – Life and Marine Sciences* **18,** 97–106.

Harmelin-Vivien, M. L. (1989). Reef fish community structure: an Indo-Pacific comparison. In *Ecological Studies* (Harmelin-Vivien, M. L. & Bourlière, F., eds), pp. 21–60. New York: Springer-Verlag.

Harmelin-Vivien, M. L. (2002). Energetics and fish diversity on coral reefs. In *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem* (Sale, P. F., ed.), pp. 265–274. San Diego, CA: Academic Press.

Hay, M. E. (1991). Fish–seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey. In *The Ecology of Fishes on Coral Reefs* (Sale, P. F., ed.), pp. 96–119. San Diego, CA: Academic Press.

Hay, M. E. (1997). The ecology and evolution of seaweed–herbivore interactions on coral reefs. *Coral Reefs* **16,** 67–76.

Hill, M. S. (1998). Spongivory on Caribbean reefs releases corals from competition with sponges. *Oecologia* **117,** 143–150.

Hixon, M. A. (1997). Effects of reef fishes on corals and algae. In *Life and Death of Coral Reefs* (Birkeland, C., ed.), pp. 536. New York: Chapman & Hall.

Hobson, E. S. (1994). Ecological relations in the evolution of acanthopterygian fishes in warm–temperate communities of the northern Pacific. *Environmental Biology of Fishes* **17,** 201–226.

Hobson, E. S. & Chess, J. R. (2001). Influence of trophic relations on form and behavior among fishes and benthic invertebrates in some California marine communities. *Environmental Biology of Fishes* **60,** 411–457.

Holbook, S. L., Schimitt, R. S. & Ambrose, R. F. (1990). Biogenic habitat structure and characteristics of temperate reef fish assemblages. *Australian Journal of Ecology* **15,** 489–503.

Horn, M. H. (1989). Biology of marine herbivorous fishes. *Oceanography and Marine Biology Annual Review* **27,** 167–272.

Horn, M. H. (1998). Feeding and digestion. In *The Physiology of Fishes* (Evans, D. H., ed.), pp. 41–60. New York: CRC Press.

Jones, G. P. (1988). Ecology of rocky reef fish on New Zealand: a review. *Marine and Freshwater Research* **22,** 445–462.

Jones, G. P., Ferrell, D. J. & Sale, P. F. (1991). Fish predation and its impact on the invertebrates of coral reefs and adjacent sediments. In *The Ecology of Fishes on Coral Reefs* (Sale, P. F., ed.), pp. 156–179. San Diego, CA: Academic Press.

Lewis, S. M. (1985). Herbivory on coral reefs: algal susceptibility to herbivorous fishes. *Oecologia* **65,** 370–375.

Luckhurst, B. E. & Luckhurst, K. (1978). Diurnal space utilization in coral reef fish communities. *Marine Biology* **49,** 325–332.

Mazzoldi, C. & Girolamo, M. (1997). Littoral fish community of the island Lampedusa (Italy): a visual census approach. *Italian Journal of Zoology* **65,** 275–280.

Meekan, M. G. & Choat, J. H. (1997). Latitudinal variation in abundance of herbivorous fishes. *Marine Biology* **128,** 373–383.

Meylan, A. (1991). Nutritional characteristics of sponges in the diet of the hawksbill turtle, *Eretmochelys imbricata*. In *New Perspectives in Sponge Biology* (Rützler, K., ed.), pp. 472–477. Washington, DC: Smithsonian Institution Press.

Montgomery, J. L. M. & Targett, T. E. (1992). The nutritional role of seagrass in the diet of the omnivorous pinfish *Lagodon rhomboides* (L.). *Journal of Experimental Marine Biology and Ecology* **158,** 37–57.

Motta, P. J. (1989). Dentition patterns among Pacific and western Atlantic butterflyfishes (Perciformes, Chaetodontidae): relationship to feeding ecology and evolutionary history. *Environmental Biology of Fishes* **25,** 159–170.

Mountfort, D. O., Campbell, J. & Clements, K. D. (2002). Hindgut fermentation in three species of marine herbivorous fish. *Applied and Environmental Microbiology* **2002,** 1374–1380.

Nelson, J. S. (1994). *Fishes of the World*. 3rd edn. New York: John Wiley & Sons, Inc.

Norrbin, F. & Bamstedt, U. (1984). Energy contents in benthic and planktonic invertebrates of Kosterfjorden, Sweden. A comparison of energetic strategies in marine organism groups. *Ophelia* **23,** 47–64.

O' Neal, W. & Pawlik, J. (2002). A reappraisal of the chemical and physical defenses of Caribbean gorgonian corals against predatory fishes. *Marine Ecology Progress Series* **240,** 117–126.

Paul, V. J. (1992). Chemical defenses of benthic marine invertebrates. In *Ecological Roles of Marine Natural Products* (Paul, V. J., ed.), pp. 164–188. Ithaca, NY: Comstock.

Pawlik, J. R. (1993). Marine invertebrate chemical defenses. *Chemical Reviews* **93,** 1911–1922.

Pawlik, J. R. (1998). Coral reef sponges: do predatory fishes affect their distribution? *Limnology and Oceanography* **43,** 1396–1399.

Pawlik, J. R., Chanas, B., Toonen, R. J. & Fenical, W. (1995). Defenses of Caribbean sponges against predatory reef fish. I. Chemical deterrency. *Marine Ecology Progress Series* **127,** 183–194.

Pihl, L. & Wennhage, H. (2002). Structure and diversity of fish assemblages on rocky and soft bottom shores on the Swedish West Coast. *Journal of Fish Biology* **61** (Suppl. A), 148–166. doi: 10.1006/jfbi.2002.2074.

Randall, J. E. (1967). Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography* **5,** 665–847.

Robertson, D. R. (1996). Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. *Ecology* **77,** 885–899.

Robertson, D. R. & Lassig, B. (1980). Spatial distribution patterns and coexistence of a group of territorial damselfishes from the Great Barrier Reef. *Bulletin of Marine Sciences* **30,** 187–203.

Rocha, L. A. & Rosa, I. L. (2001). Baseline assessment of reef fish assemblages of Parcel Manuel Luiz Marine State Park, Maranhão, north-east Brazil. *Journal of Fish Biology* **58,** 985–998. doi: 10.1006/jfbi.2000.1504.

Russ, G. R. (2003). Grazer biomass correlates more strongly with production than with biomass of algal turfs on a coral reef. *Coral Reefs* **22,** 63–67.

Sala, E. & Boudouresque, C. F. (1997). The role of fishes in the organization of a Mediterranean sublittoral community. I: Algal communities. *Journal of Experimental Marine Biology and Ecology* **212,** 25–44.

Samoilys, M. A. & Carlos, G. (2000). Determining methods of underwater visual census for estimating the abundances of coral reef fishes. *Environmental Biology of Fishes* **57,** 289–304.

Sues, H. D. & Reisz, R. R. (1998). Origins and early evolution of herbivory in tetrapods. *Trends in Ecology & Evolution* **13,** 141–145.

Underwood, A. J. (1997). *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge: Cambridge University Press.

Van Alstyne, K. L., Dethier, M. N. & Duggins, D. O. (2001). Spatial patterns in macroalgal chemical defenses. In *Marine Chemical Ecology* (McClintock, J. B. & Baker, W. J., eds), pp. 301–324. New York: CRC Press.

Vermeij, G. J. & Rosenberg, G. (1993). Giving and receiving – the tropical Atlantic as donor and recipient for invading species. *American Malacological Bulletin* **10,** 181–194.

Veron, J. E. (1995). *Corals in Space and Time: Biogeography and Evolution of the Scleractinia*. New York: Cornell University Press.

Wainwright, P. C. & Bellwood, D. R. (2002). Ecomorphology of feeding in coral reef fishes. In *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem* (Sale, P. F., ed.), pp. 33–55. San Diego, CA: Academic Press.

Willis, T. J. (2001). Visual census methods underestimate density and diversity of cryptic reef fishes. *Journal of Fish Biology* **59,** 1408–1411. doi: 10.1006/jfbi.2001.1721.

Wilson, S. K. (2002). Nutritional value of detritus and algae in blenny territories on the Great Barrier Reef. *Journal of Experimental Marine Biology and Ecology* **271,** 155–169.

Wilson, S. K., Bellwood, D. R., Choat, J. H. & Furnas, M. J. (2003). Detritus in the epilithic algal matrix and its use by coral reef fishes. *Oceanography and Marine Biology: an Annual Review* **41,** 279–309.

Wood, R. (1999). *Reef Evolution*. Oxford: Oxford University Press.

Zar, J. H. (1999). *Biostatistical Analysis*. New Jersey: Prentice Hall.

Electronic Reference

Froese, R. & Pauly, D. (Eds) (2003). *FishBase*. Available at: www.fishbase.org.

7 Synopsis

7.1 *General taxonomic structure*

The taxonomical structure of reef fishes around IOP shows marked patterns at local and regional scales. At a local scale, in TWA there is a decrease in the number of species per area in sheltered zones. Weak habitat connectivity (marked patchiness), stable currents and small tidal ranges in the lagoon system in TWA restrict most of the species to exposed areas with higher benthic diversity. In the TEP, the number of species per area also increases from low to high substrate diversity and is higher than in any similar habitat in the TWA. These results suggest that rates of larval dispersal and recruitment are higher over a wide range of habitats in TEP, which is more interconnected by rocky shore habitats and affected by intrusive currents than TWA (**Publication I, Publication II, Publication III**). On the global scale, the taxonomic composition in term of the number of families and species of reef fishes is similar in the two geographical regions (Robertson 1998). Unlike Indo-Pacific fish assemblages, fishes in New World have been affected in recent geological time by the separation caused by the recent closure of IOP, which has given rise to the particular oceanographic characteristics of the zone. (**Publication III**). This is reflected in the high degree of plasticity shown by these reef fishes, which are present in any area with high substrate diversity, with or without coral reefs (**Publication II**). Reef fish diversity is dependent on many factors and is not significantly lower on the TEP side of the IOP due to lower coral cover in this region, as is often presumed in the literature referring to this question (**Publication I**, **Publication II** and **Publication III**).

7.2 *Abundance of trophic groups and size classes among reef fish families*

The abundance of trophic groups, their size classes and representative genera on both sides of IOP is strongly differentiated: Gobiidae (*Coryphopterus*), Pomacentridae (*Stegastes* sp), Scaridae (*Scarus*) and Serranidae (*S. tortugarum*) predominate in TWA. Here a marked spatial distribution was found, with territorial herbivores increasing in abundance in sheltered zones while mobile invertebrate feeders and planktivores were more common in exposed zones. Overall, herbivores in the TWA account for approximately 77% of the total relative abundance, while piscivores were relatively underrepresented. Carnivores were present in low densities but showed higher species richness compared with other trophic groups (**Publication I; Publication IV**). In the TEP, Labridae (*Thalassoma*), Pomacentridae (*Chromis* sp), Haemulidae (*Haemulon*), and Apogonidae (*Apogon*) are the most abundant genera. These are all fishes that feed on high protein food sources: plankton feeders account for more that 50% and up to 80% of total relative abundance in most zones and mobile invertebrate feeders were also abundant. Piscivores were also more abundant in comparison with TWA (**Publication II; Publication III**). This contrasts with the very low densities of groups that feed on low quality food material found in the TEP: herbivores accounted for less than 10% of the total, while sessile invertebrate feeders were even sparser in all zones surveyed. For both regions, the number of species within most trophic groups increased in shallow rocky and massive coral zones. The Harmelin-Vivien theory of a differential use of low quality food material in warmer waters is supported by results obtained for the TWA (**Publication I and Publication IV**). The patterns found in the TEP suggest that under certain conditions this theory is applicable not only to changes observed along latitudinal gradients but also at local scales in response to differences in water temperature caused by variations in the intensity of upwelling. More research is thus required to test this theory in marginal regions where changes in temperature may not be so strongly related to latitudinal variation (**Publication I**; **Publication II; Publication III; Publication IV**). The marked variation in temperature can also have an influence on the size range of most reef fish families, and this may help explain why TEP exhibits fish size patterns that are more characteristic of temperate regions (**Publication III**; Pauly 1998). Results indicate marked differences between TEP and TWA in the maximum sizes of fishes within all families; fish being generally larger in TEP. This can be explained by the fact that food with a high protein content is easier to digest in colder waters, which means that probably all trophic groups in TEP will show preferences for this type of food, even territorial herbivores, which may include invertebrates living on gardened algae as a secondary source of food (Robertson 1984). Consumption of food with high energy content in a productive region will increase the fat deposition and may influence the growth and maximum size attained by most reef fish (**Publication III** and **Publication IV**). In addition to these environmental parameters, it is suggested that an inverse relation exists between predation pressure and the densities of territorial fishes, which would explain the relative scarcity of this group in TEP. It is further suggested that there is an inverse relation between territoriality and size classes, since dominant territorial fish limit the food available to growing subordinate fishes in the TWA. (**Publication III and Publication IV**).

7.3 *Mobility groups*

The multivariate analysis (CCA) and ANOVA analysis applied to data on mobility classification shows that in the TWA better swimmers predominate in zones influenced by oceanic currents, while site-attached species (mostly territorial herbivores) are predominant in sheltered zones (**Publication I**). In the TEP, the situation is very different from what might be expected in what is geographically a *tropical* region: Better swimmers are slightly less common in zones close to the mainland but overall they represent the most abundant mobility category and are widely distributed among most zones (**Publication II**). The TEP shows similarities to temperate regions in the Atlantic, characterized by the predominance of fishes that present high mobility or wide horizontal displacements to find randomly distributed food such as plankton (e.g. *Thalassoma* and *Chromis).* This pattern is characteristic of regions with seasonal temperature changes and unpredictable upwelling processes, where fishes less associated with reef substrata are able to respond more readily to environmental fluctuations (**Publication II** and **Publication IV**)**.** In the TEP**,** Chaenopsids and cirrhitids (site attached Category 3) were found in exposed zones but territorial herbivores, which also belong to this category, are present in comparatively low numbers. As would be expected in view of their weaker swimming adaptations, numbers of relatively sedentary individuals (Category 2) decrease in shallow, wave-exposed zones. (**Publication II**). The presence of homogeneously distributed currents and tides is suggested as a factor that helps explain why this is a region dominated by better swimmers that can feed on oceanic plankton, alongside the high productivity that is characteristic of the TEP (**Publication I** and **Publication II,** D'Croz and Robertson 1997**)**. This result confirms that, despite their evolutionary affinity, fish assemblages in the TEP are different from the TWA and that their characteristics are strongly related to local oceanography. Changes in temperature and other environmental variables have affected the organization of fish assemblages in a relatively short period following the most recent geological changes **(Publication III**).

7.4 *Relationship between habitat structure and fish diversity parameters*

In both regions, correlation analysis shows that reef fish species richness and diversity are less strongly related to live coral coverage and more so to substrate diversity and complexity. Diversity of substrate is in general positively correlated to strength of currents, but this is not a rule since a diverse benthic component is also characteristic of massive coral reefs found where currents are weak. Fish species richness is greater there than in all other habitats, with the exception of complex rocky shores (**Publication I** and **Publication II**). Comparative Statistical analysis of study zones in each region shows significant differences in fish species richness horizontally and vertically between reefs of different types and complexity (e.g. coral and rocky reefs), being higher in complex and heterogeneous zones. The degree of variation found is not uniform at any of these scales and itself varies across the reef complex (**Publication II** and **Publication IV**). In any geographical region a highly complex substrate will serve as shelter for many species in crevices and holes, which may be a source of different types of food for specialized feeders (**Publication II** and **Publication IV**). These results suggest that diverse fish communities develop in areas of topographic complexity, which in turn is inextricably related to substrate diversity. This factor is more important than the influence of geological changes or the wider oceanographic conditions in a region.

7.5 *Relationship between fish abundance vs. habitat structure.*

In contrast to the similar relationships between fish diversity and habitat structure observed in the two regions, the relationship between fish abundance and habitat structure is markedly different on both sides of IOP, where small recruits are the principal component of overall fish abundance: In the TWA, small recruits and small-sized adults (serranids) were found in high numbers in low complexity-edge habitats such as rubble, while large predators were present in relative low numbers (**Publication I**). Recruits of many species are exceedingly selective as to habitat (Ohman et al 1998), particularly where predation pressure is high - and densities of piscivores are higher in TEP (Steele 1999; **Publication II**). Habitat structure and predation can affect the magnitude of recruitment in space and over time, particularly in the case of species that exhibit strong habitat preferences at the time of settlement onto the reef. Thus, the highest recruitment rates were observed in the most complex zones in TEP (**Publication II**; Tolimieri 1998; Srinivasan et al 1999; Schmitt and Holbrook 1999; Syms and Jones 2000). In TWA, small sized adults (e.g. *Serranus tortugarum*) and juveniles of other species may, under low predation, be able to recruit and live in low complexity habitats such as rubble, while reef frames are heavily populated by territorial herbivores (which have low densities in TEP) that displace small recruits (**Publication III**).

7.6 *Are the study regions in IOP representative for these patterns ?*

For tropical reef fishes, some regions can exhibit characteristics similar to those of other regions in terms of taxonomical composition, but local habitat characteristics and oceanography affect distribution, densities and interactions and thus the general ecology of fish assemblages (**Publication I** and **Publication II**).

For example, in the isolated Bocas del Toro region(TWA), the taxonomical composition of fish assemblages is relatively similar to other regions. However, fish densities are affected by limitations on recruitment caused by partial and/or intermittent barriers such as rives and the lack of habitat connectivity - even tough this lack of demographic exchange may not affect genetic connectivity with the other Caribbean populations (Choat 2006). The distribution of mobility groups is strongly affected by local geography, currents, and other local parameters in a region. This variation between exposed and sheltered zones is not necessarily found in the whole Caribbean region (**Publication I**), even though, at global scale, it exhibits a similar pattern of high densities of herbivores as the rest of the tropical Atlantic regions (**Publication IV**). The Gulf of Chiriqui (TEP) may not be representative of the rest of the region in terms of taxonomic composition (total number of species), since its more stable environment, wide range of habitats and complex geography all permit the development of a relatively highly diverse community. Thus, this region is suggested as a refuge or center of origin for the whole TEP, which is markedly affected by strong seasonality due to coastal upwelling. On the other hand, in term of species abundance and the presence of trophic and mobility groups, the gulf seem to be more representative of the region as a whole, since the abundance of planktivores and carnivores (protein feeders) and fishes that display a wide horizontal displacement is due to strong currents and the wide tidal variation, which are regional characteristics (**Publication II**).

Habitat connectivity will have an influence on the global composition of fish assemblages regardless of location in the tropics. Any region may have similar assemblages if habitat characteristics and oceanography are similar, regardless of geographical distance as long as they are located within the tropical range.

This work suggest that there may not be representative fish assemblages but representative patterns that all reef fish reef communities (even in high latitudes) follow. One such pattern is the positive correlation found between a complex (irregular) substrate with a heterogeneous benthic component on the one hand, and fish species richness on the other. If this is a universal pattern, habitat complexity and substrate diversity should be inextricably interlinked. As an example at a global scale, the Indo-Pacific is characterized by thousands of species of complex corals and other benthic organisms; this region contains the highest diversity of fish on the planet.

7.7 *Geminate species, relationship with habitat and effect of IOP*

The results obtained from the application of a multivariate analysis (CCA, **Publication III**) on geminate species vs. habitat components suggest that some species may exhibit a shift in habitat preference, particularly related to the appearance of “new habitats” in the TEP region (e.g. pocilloporid reefs, *sensu* Cortes1997). Closely-related sister taxa share similar ecological traits, while more distantly related species from the same clade-group on a phylogenetic tree occupy ecological habitats which are proportionally more distinct. If–Sympatric (not geographically isolated) speciation occurred, then the evolution of sister species that come from a common origin species from TWA may have started to diverge, accentuating ecological differences between them. This means that differences due to resource availability (e.g. habitat use) may have contributed to speciation both during and after the closure of IOP (**Publication III;** Taylor and Hellberg 2005). Results obtained by this research strongly suggest that a coral reef dwelling habit may not have been a fundamental factor in the origins of the fish lineages but may rather have played an instrumental role in the diversification of these lineages, especially during periods when TWA was a shallow basin connected to what is at present the TEP (Bellwood and Wainwright 2002). A specific analysis of some representative geminate species from selected families shows that geminate species of labrids of the genus *Halichoeres,* prefer edge habitats in both regions - except for one species, which has probably adapted recently to shallow rocky-pocilloporid reefs (Rocha 2003; **Publication III**). Nevertheless, this group has basal divisions that incorporate temperate and deep-water lineages, as well as species adapted to soft sediment habitats (Rocha 2003). Reef fish may show marked plasticity, but some habitats may still be preferred; and in this case their distribution will depend on local conditions. A good example comes from the results obtained for pomacentrids, as in the case of *Stegastes:* related species from shallow regions continue to find similar sources of food and protection on shallow wave-sheltered reefs, while species already adapted to exposed regions continue to use resources found in that environment and exhibit morphological adaptations for swimming in areas of strong currents. Both geminate species of *Chromis* spp are associated with oceanic currents and feed on zooplankton and their distribution in each region shows a similar relation to oceanographic patterns of currents and tides. With regard to chaetodontids, the plasticity of this group is confirmed by comparing geminate species on both sides of IOP: one show a preference for coral zones in TWA, but a shift to deeper rocky zones with high benthic diversity is observed in the closely related species in TEP. This group also appears to have non-reef origins and the basal taxa originate from deep water rocky substrates**,** feeding on benthic invertebrates (Pyle and Chave 1994). On the other hand, pomacanthids on both sides of IOP show a preference for coral reef habitats that are comparable in terms of morphology and substrate diversity (e.g. massive corals). Many species, even those which are able to live in other habitats, will continue to prefer corals reefs habitats with diverse substrates and shelter availability, particularly groups that feed on sponges and tunicates which common on this type of coral reefs (Aburto-Oropeza et al 2000; **Publication I**; **Publication II** and **Publication III**). For small serranids, which may feed on a variety of mobile invertebrates in different habitats, a wider distribution from reef to edge habitats is expected in TWA but in the presence of large predators a branching coral-complex habitat is used for protection in TEP (**Publication III**).

8 General conclusion

The results presented in this thesis demonstrate the extent to which local patterns of fish assemblages are dependent on regional factors, which in turn are shaped by historical and biogeographical events. Both sides of IOP have been characterized by a history of decline and loss of species and present conditions in both oceans are the result of these changes, caused particularly by the rise of the geographical barrier. Reef fishes defy simple definition, since coral reefs may have acquired lineages of existing non-reef fauna, acting as sanctuary for the maintenance of diversity without having played a specific role in the origin of this diversity; or they may have provided the physical environment where fish lineages arose, playing a critical role in both the origin and maintenance of extant reef fish taxa. In the specific case of IOP, the plasticity of reef fish is demonstrated by their recent shift from corals to rocky reef environments, still on highly diverse benthic substrates, following the rise of the geographical barrier. On the other hand, fish assemblages are relatively resilient in the face of change, as shown by the similarities in familial composition and relative species richness of families in the two regions. Regardless of the taxonomical structure, reef fish assemblages in IOP appear to be a collection of lucky survivors, while their diversity depends on the presence of complex and diverse substrates. The distribution of fish trophic groups may be related to latitudinal gradients, with increasing numbers of herbivores and low quality food feeders in tropical-warmer regions; however, similar patterns in temperate regions may also be found at a local scale, within areas of the same latitude, where these are influenced by coastal upwellings. Parameters such as temperature, which are particularly influenced by local upwelling, can also affect growth parameters, which seem to be consistent within taxa over geographic, temperature and other environmental gradients, with fish size generally increasing in relatively colder regions, such as TEP. Geminate species in some cases follow similar patterns of habitat preferences or in other cases exhibit shifts in habitat preferences and their distribution is dependent on particular characteristics and interrelationships in the region. Their plasticity reflects the ability of reef fishes to survive in non-coral habitats, and suggests that they even may have started to diversify on coral reef before to the closure of IOP**.** Reef fishes are a complex group comprising numerous lineages with distinctive life-history features, restricted to shallow depths and subjected to major episodes of habitat disturbance, including sea level and temperature fluctuations over geological short time periods (Choat 2006).

9 Recommendations

Even though this thesis contains much new information, more data and surveys from different regions, particularly in the TEP, are necessary to understand the extent to which ecosystem function is shaped by species richness and regional history, and to determine at what point declining species richness begins to compromise ecosystem function. Further questions, which remain to be answered are: to what extent are the results discussed by this thesis fully dependent on the biogeographical location of the study sites, or are peripheral regions on both sides of IOP more vulnerable to human and natural impacts than others which lie closer to high-diversity areas?

In general, not only destructive human practices, but also applied ecosystem conservation methods fail to take into account the fact that reef fish assemblages are not uniform. Differences in reef fish assemblages are the product of both historical and ecological factors, and their consequences for management of reef resources are far reaching. In many cases, the need for site-specific conservation measures is overlooked because over-generalized methods are used to determine ecosystem health. Examples of the latter include the use of coral cover instead of substrate diversity and complexity to determine reef health; and the use of members of the family Chaetodontidae, as indicators of coral presence and ecosystem health. This family is normally considered to consist of "coral feeders" but showed extreme plasticity of habitat preferences in this study, and it is thus a mistake to use this family as an indicator of reef health in the new world oceans. Another frequent problem is the lack of attention paid to the oceanography and geography of the region being studied. In particular relatively closed regions may be characterized by self-recruitment and thus show less capacity for recuperation by larval dispersal from other regions following losses caused by human impacts. Coral reefs and rocky reefs, along with most other coastal ecosystems, are endangered by human practices not only at a local but also at a global scale. As discussed in this thesis, reef fish assemblages may follow assembly rules, but these assembly rules may not apply directly to functional groups, which can be strongly variable depending on variations on temperature and currents that are related also to atmospherics changes. An extensive database is urgently required, particularly in the TEP, to determine future impacts of global warming on the trophic structure and growth patterns in fish communities. If global warming can affect the trophic structure, due to the impacts of increasing sea temperatures on the oceanography and patterns of upwelling and currents in the TEP, a gradual slide into crisis by marine ecosystems of this region is to be expected. This will affect the balance of the ecosystem, decreasing the numbers of predators and increasing those of herbivores. Ocean productivity will also be affected and this will impact directly on human populations that depend on fisheries. A project that permits the standardization of data and surveying procedures, based on a comparison of trophic structure and covering reefs in subtropical regions such as Northern Peru and Southern Mexico, as well as other tropical regions in the TEP, is required not only to test theories of differential food use and physiological constrains put forward in this work, but also as an urgently needed database to track long-term changes in fish trophic structures in response to global warming.

10 References

Almany GR (2004a) Priority effects in coral reef fish communities of the Great Barrier Reef. Ecology 85(10): 2872-2880.

Almany GR (2004b) Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. Oecologia 141 (1): 105-113.

Aburto-Oropeza, O., E. Sala & C. Sanchez-Ortiz. 2000. Feeding behavior, habitat use, and abundance of the angelfish *Holacanthus passer* (Pomacanthidae) in the southern Sea of Cortez. Environmental Biology of Fishes 57: 435-442

Arburto-Oropeza O, Balart E 2001 Community structure of reef fish in several habitats of a rocky reef in the Gulf of California. Marine Ecology 22(4): 283–305

Barber, PH & Bellwood, D.R 2005 Biodiversity hotspots: evolutionary origins of biodiversity in wrasses (*Halichoeres*: Labridae) in the Indo-Pacific and new world tropics. *Molecular* Phylogenetics and Evolution 35: 235–253

Bell J. D.& Galzin R. 1984. Influence of live coral on coral reef communities Mar. Ecol. Prog. Ser 15: 265-274.

Bellwood DR 1998 What are reef fishes? Comment on the report by D.R. Robertson: Do coral reef fish faunas have a distinctive taxonomic structure? (Coral Reef. 17:179–186) Coral Reef 17: 187–189.

Bellwood, D. R. and Wainwright, P. C. 2002. The history and biogeography of fishes on coral reefs. pp. 5-32. In: Coral Reef Fishes. Dynamics and diversity in a complex ecosystem (P.F. Sale, ed.), Academic Press, San Diego.

Bellwood D R, Wainwright PC, Fulton CJ, Hoey A. 2002. Assembly rules and functional groups at global biogeographical scales. Functional Ecol 16: 557–562.

Bermingham, E., S. McCafferty and A. Martin. 1997. Fish biogeography and molecular clocks: perspectives from the Panamanian Isthmus. Pp. 113-126 in Kocher T. and C. Stepien (eds.), Molecular Systematics of Fishes. Academic Press, NY, USA.

Beukers, J. J., and G. P. Jones. 1997. Habitat complexity modifies the impact of piscivores on a coral reef fish population. Oecologia 114: 50-69.

Blum, S.D., 1989. Biogeography of the Chaetodontidae: an analysis of allopatry among closely related species.. Environ. Biol. Fish. 25(1-3):9-31.

Bouchon- Navarro Y. & Bouchon C. 1989. Correlations between chaetodontid fishes and coral communities of the Gulf of Aqaba (Red Sea) Environ. Biol. Fish. 25: 47-60.

Budd, A.F. 2000. Diversity and extinction in the Cenozoic history of Caribbean reefs (Invited review). Coral Reefs 19: 25-35.

Carpenter K.E.; Miclat, R.I; Albadejo & V.D. Corpuz V.T. 1981. The influence of substratum structure on the local abundance and diversity of Philippine reef fishes. Proc. 4th Int. Coral Reef Symp. 2: 495-502.

Choat J.H., Robertson D.R. 2002 Age-based studies on coral reef fishes. pp 57-80. In: Sale P.F., ed. Coral Reef Fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego.

Choat J.H. 2006 Phylogeography and reef fishes: bringing ecology back into the argument Journal of Biogeography 33: 967-968

Clifton K. E. 1995 Asynchronous food availability on neighboring Caribbean coral reefs determines seasonal patterns of growth and reproduction for herviborous parrotfish *Scarus iserti*. Mar. Ecol. Prog. Ser.116:39-46

Clifton K.E. ; Kim K. & Wulff J. L.1996. Guía de campo para los arrecifes del Caribe de Panamá con énfasis en el sector occidental de San Blas. 8vo Simp. Int. Arrecifes de Coral. 27pp.

Coates,A.G.,and J.A.Obando. 1996 Geological evolution of the Central American Isthmus in Jackson, J.B.C., A.F. Budd,and A.G. Coates (eds.), Evolution and Environment in Tropical America: University of Chicago Press.

Coles S.L. & Tarr A.B. 1990. Reef fish assemblages in the estern Arabian Gulf: a geographically isolated population in an extreme environment. Bull. Mar. Sci. 47: 696-720.

Cortés J. 1997. Biology and geology of eastern pacific coral reef. Proc. 8th Int. Coral Reef Symp 57-64.

Craig MT, Hastings PA, Pondella DJ 2004 Speciation in the Central American Seaway: the importance of taxon sampling in the identification of trans-isthmian geminate pairs. Journal of Biogeography, **31**, 1085–1091.

D′Croz L. 1988 Survey of marine pollution in the Bay of Panamá. UNEP Regional Seas and Studies 97: 115-123.

D′Croz L, DelRosario JB, Gómez JA 1991. Upwelling and phytoplankton in the Bay of Panamá. Rev. Biol. Trop 39:233-241.

D'Croz, L. and D.R. Robertson. 1997. Coastal ocanographic conditions affecting coral reefs on both sides of the Isthmus of Panama. Proc. 8th Int. Coral Reef Symp. 2:2053-2058

Dominici-Arosemena A; Brugnoli-Olivera E; Cortés-Nuñez J.; Molina-Ureña H and M. Quesada-Alpizar. 2005. Community Structure of Eastern Pacific Reef fishes (Gulf of Papagayo, Costa Rica). Rev. Tecnociencia, FCNET, Univ. Panamá. Vol.7 (2):19-41.

Emery A. R. 1978. Comparative ecology and functional osteology of fourteen species of damselfish (Pisces: Pomacentridae) ay Alligator Reef, Florida Keys. Bull. Mar. Sci. 23: 649-770.

Ehrlich P.R. 1975. The population biology of coral reef fishes Ann. Rev. Ecol. Syst 6: 211-247.

Fulton, C.J. and D.R. Bellwood 2002. Ontogenetic habitat use in labrid fishes: an ecomorphological perspective. Mar. Ecol. Prog. Ser. 236: 255-262.

Fulton CJ, Bellwood DR,Wainwright PC (2005) Wave energy and swimming performance shape coral reef fish assemblages. Proc of the Royal Society London Ser B. 272: 827-832.

Gladfelter W.B. & Gladfelter E. H. 1978. Fish community structure as a function of habitat structure on West Indian patch reefs. Rev.Biol.Trop 26: 65-84

Gladfelter W. B; Odgen J.C &. Gladfelter E. H 1980. Similarity and diversity among coral reef fish communities: A comparison between Tropical Western Atlantic (Virgin Island) and tropical central Pacific (Marshall Islands) patch reefs. Ecology 6: 1156-1168.

Glynn P.W. & Maté J. L 1996. Guía de campo para los arrecifes de coral del Pacífico de Panamá. 8vo Simp. Int. Arrecifes de Coral. 36pp

Goldman B. & Talbot F.H. 1976. Aspects of the ecology of coral reef fishes. In: O. A., Endean, R. (Eds) Biology and Geology of coral reef Vol3 Biology Part 2. Academic Press New York. 125-154.

Gosline W.A. 1965. Vertical zonation of inshore fishes in the upper water layers of The Hawaiian Island. Ecology 46: 823-831.

Green D. G., Bradbury R.H & Reichel R.E. 1987. Patterns of predictability in coral reef community structure. Coral Reefs 6: 27-34.

Harmelin-Vivien M.L 1977. Ecological distribution of fishes on the outer slope of Tulear reef (Madagascar) Mar. Biol. 37: 329-340.

Harmelin-Vivien, M.L. 1989. Reef fish community structure: an Indo-Pacific comparison. In: Harmelin-Vivien, M.L. and Bourlière, F. (Eds), *Vertebrates in complex tropical systems*. Springer-Verlag, New York.

Harmelin-Vivien, M. 2002. Energetics and Fish Diversity on Coral Reefs. Pp. 269 in P. Sale, ed. *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*. San Diego, CA: Academic Press.

Jones R. S. 1968. Ecological relationships in Hawaiian and Johnston Island Acanthuridae (surgeonfishes). Micronesica 4: 309-361.

Jones G. P. 1988. Experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of two coral reefs fishes. J. Exp. Mar. Biol. Ecol. 123: 115-126.

Keller, G., Zenker, C.E., and Stone, S.M., 1989. Late Neogene history of the Pacific-Caribbean gateway. J. South Am. Earth Sci: 2:73-108.

Levin P. S. 1991. Effects of microhabitat on recruitment variation in a Gulf of Maine reef fish. Mar. Ecol. Prog. Ser 75: 183-189.

Luckhurst, B. E., Luckhurst K 1978a Diurnal space utilization in coral reef fish communities. Mar. Biol. 49: 325-332.

Luckhurst B. E., Luckhurst K 1978b. Analysis of the influence of substrate variables on coral reef fish communities. Mar. Biol. 49: 317-323

McCormick M. I. 1994. Comparison of field methods for measuring surface topography and their associations with a tropical reefs fish assemblage. Mar. Ecol. Prog. Ser 112: 87-96.

McGehee A. 1994. Correspondence between assemblages of coral reef fishes and gradients of water motion depth, and substrate size off Puerto Rico. Mar. Ecol. Prog. Ser Vol. 105: 243-255.

McMannus J. W., Miclat, R. I., Palaganas, V.P 1981. Coral and fish community structure of Sombrero Island, Batangas, Philippines. Proc. 4th int. coral Reef Symp 2: 271-280.

McManus, J.W. 1985.Marine speciation, tectonics, and sea-level changes in southeast Asia. Proceedings of the 5th International Coral Reef Congress, Tahiti. 4:133-138.

Myers R.F. 1991. Micronesian reef fishes (2nd edn) Coral Graphics, Guam.

O'Dea, A and J.B.C. Jackson**.** 2002. Bryozoan growth mirrors contrasting seasonal regimes across the Isthmus of Panama. Palaeogeography, Palaeoclimatology, Palaeoecology 185: 77-94.

Ohman, M.C., P.L. Munday, G.P. Jones and M.J. Caley 1998. Settlement strategies and distribution patterns of coral-reef fishes. Journal of Experimental Marine Biology and Ecology, *225:* 219-238.

Pandian, T.J. and E. Vivekanandan. 1985. Energetics of Feeding and Digestion, in Fish Energetics: New Perspectives, P. Tytler and P. Calow, eds. The Johns Hopkins University Press, Baltimore, Maryland.

Pauly, D. 1998. Tropical fishes : patterns and propensities. J. Fish Biol. 53 (A) :1-17.

Pérez-España H. & Abitia-Cárdenas 1996 Description of the digestive tract and feeding habits of the king angelfish and the Cortes angelfish. J. Fish. Biol. 48:807-817.

Pyle, R.L. & E.H. Chave. 1994. First record of the chaetodontid genus *Prognathodes* from the Hawaiian Islands. Pacific Science 48(1):90-93.

Roberts C. M & Ormond R.F.G. 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. Mar. Ecol.Prog. Ser 41: 1-8.

Robertson, D. R. 1984. Cohabitation of competing territorial damselfishes on a Caribbean coral reef. Ecology 65:1121-1135.

Robertson, D. R. 1998. Do coral-reef fish faunas have a distinctive taxonomic structure? Coral Reefs. Vol 17: 1-8.

Rocha, L.A. 2003. Patterns of distribution and processes of speciation in Brazilian reef fishes.J. Biogeog. 30:1161–1171.

Rosa R.S. & Moura R.L. 1997. Visual assesment of reef fish community structure in the Atol Das Rocas Biologtical reserve, off Northeastern Brazil. Proc 8th In the. Coral. Reef. Sym 1 :983-986.

Rubio E. 1986 Notas sobre la ictiofauna de la Isla Gorgona, Pacífico colombiano Boletin Ecotropica 13: 86-112

Rosenblatt R.H 1967. The zoogeographic relationships of the marine shorefish fauna of Tropical America. Stud. Trop. Oceanogr. 5: 579-592.

Russ G. 1984. Distribution and abundance of herbivorous grazing fishes in The central Great Barrier Reef. I. Levels of variability across the entire continental shelf. Mar. Ecol. Prog. Ser. 20: 23-34.

Russ G 1984. Distribution and abundance of herbivorous grazing fishes in The central Great Barrier Reef. II Patterns of zonation of mid-shelf and outershelf reefs. Mar. Ecol. Prog. Ser. 20: 35-44

Schlosser I.J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. Ecol. Monogr. 52: 395-414.

Schmitt, R.J. and S.J. Holbrook. 1999. Settlement and recruitment of three damselfish species: larval delivery and competition for shelter space. Oecologia 118:76-86.

Shulman M.J. 1983. Species richness and community predictability in coral reef fish faunas. Ecology 64 (5): 1308-1311.

Steele M A 1999 Effects of shelter and predators on ref. fishes. J. Exp. Mar. Biol. Ecol. 233: 65-79

Springer V.G. 1982. Pacific plate biogeography, with special reference to shore fishes Smith. Contrib. Zool. 367: 1-181.

Springer V.G. 1988 The Indo-Pacific blenniid fish genus *Ecsenius*. Smithson. Contrib. Zool. 465: 1-134.

Springer VG, Williams JT 1994. The Indo-West Pacific blenniid fish genus *Istiblennius* reappraised: a revision of *Istiblennius*, *Blenniella*, and *Paralticus*, new genus. Smithson Contrib Zool 565:193 p.

Srinivasan, M., Jones, G.P. and Caley, M.J. 1999. Experimental evaluation of the roles of habitat selection and interspecific competition in determining patterns of host use by two anemonefishes. Mar. Ecol. Prog. Ser. 186, 283-292.

Smith, A. G.; Hurley, A. M.; Briden, J. C. 1981. Phanerozoic Paleocontinental World Maps. Cambridge: Cambridge University Press, 1–102.

Syms, C., and G. P. Jones. 2000. Disturbance, habitat structure, and the dynamics of a coral reef fish community. Ecology 81:2714-2729.

Talbot F.H. & Goldman B. 1972. A preliminary report on the diversity and feeding relationships of the reef fishes of One Tree Island, Great Barrier Reef system. Proc. 1st int. coral Reef Symp. 1: 425-440.

Taylor, M. S. and M. E. Hellberg. 2005. Marine radiations at small geographic scales: speciation in neotropical reef gobies (*Elacatinus*). Evolution 59: 374-385.

Thresher R. E. 1991. Geographic variability in the ecology of coral reef fishes: evidence, evolution, and possible implications. In: Sale PF (Ed) The ecology of fishes on coral reef. Academic Press, New York, pp 401-436.

Todd A., Jackson, J BC., Johnson, K G., Fortunato, H. M., Heitz, A N, Alvarez F., MA. and Jung, P. 2002. The ecology of extinction: molluscan feeding and faunal turnover in the Caribbean Neogene. Proceedings of the Royal Society (London) B. 269(1491): 571-578.

Tringali, M. D., T. M. Bert, S. Seyoum, E. Bermingham, and D. Bartolacci. 1999. Molecular phylogenetics and ecological diversification of the transisthmian fish genus *Centropomus* (Perciformes: Centropomidae). Molecular Phylogenetics and Evolution. 13: 193-207.]

Veron J.E.N 1995. Corals in space and time. Cornell University Press, Ithaca

White B.N. 1986 The isthmian link, antitropicality and American biogeography: distributional history of the Atherinopsinae (Pisces: Atherinidae). Systematic Zoology, 35, 176–194.

Williams D. McB 1982. Patterns in the distribution of fish communities across the central Great Barrier Reef. Coral Reefs 1: 35-43

Zapata F.A. & Morales A. 1997. Spatial and temporal patterns of fish diversity in a coral reef at Gorgona Island, Colombia. Proc. 8th Int. Coral Reef Sym. Panama 1: 1029-1034.

11 Acknowledgements

I would like to thank Dr. Matthias Wolff for his advice, contribution, and support for this work. Throughout, he has been a great example of a distinguished scientist. From him, I have acquired an initiative for research and I have learned to better focus my ideas. He has exhibited an unending willingness to offer his support at anytime regarding any situation. From him, I will always have a role model.

I would also like to thank Dr. D.R. Ross Robertson for his advice and for giving me the opportunity to work with him at the STRI. Thanks to him for keeping a door open to get in to this amazing world of reef fish and for the support he gave me at anytime, and with anything that I needed, to conduct all of the extensive fieldwork in Panama.

I would like to thank Marc Kochzius, for been my second referee of this thesis and all hes advice, Carlos Eduardo Leite Ferreira, Sergio Floeter, Luis D'Croz, Jaime Mendo Aguilar, Harilaos Lessios, Neal Smith, David Bellwood, Jorge Cortés, Hector Guzmán, Suzanne Lao, Juan Antonio Gómez, Janzel Villalaz, Ricaute Pacheco, Carlos Jimenez, Carlos Gamboa, Alvaro Morales, Ernesto Brugnoli, Christie Constantine, Joel Whitney, David Kline, Nélida Gómez, Andrew Kern, Ghislain Rompé, Angel Vega, Carmen Schloeder, Greta Earle, Gustavo Concheiro, Luis Fernandez de Córdoba, Marco Luque, Martina Keller, Ronald Meyer, Lukas Scharer, Gustavo Castellanos, Sacha Lozano, Camilo Mora, Fernando Zapata and Carlos Guevara. It is their feedback that gave me the chance to exchange many ideas and information to conduct this research.

Thanks to Dr Wilhelm Hagen and Uwe Krumme for being member of my committee for the defense of this thesis.

Thanks to Guilherme Vasconcellos, Irving Betancourt and Juan Gabriel Domínguez for their great efforts in the field. With the greatest motivation, professionalism, and courage, they spent many amazing, yet long, exhausting, and difficult hours underwater observing the fish and compiling many numbers to be included in the database.

Thanks to Denise Pope for her support to organize all of the ideas for the research on my first proposal, and also for the motivation she gave me to continue with my studies.

I would like to thank to Dr Venugopalan Ittekkot, Dr. Ulrich St Paul and all of the ZMT family for letting me be part of this team. Particularly, I will always remember Ms Christa Müller, for all of her support and help.

Thanks to everyone from the ZMT who either directly or indirectly collaborated with logistics and ideas to finish this work: Dr Ursel Selent, Petra Käpnick, Sabine Kadler, Stefanie Bröhl, Silke Meyerholz, Joseph Agrrey Finn, Iris Freytag, Andreas Kunzmann, Susanne Eickhoff, Marion Glaser, Wolfgang Ludwig, Dieter Peterke, Claudio Richter, Andreas Echterhoff, Jolanta Burba, Kai Bergmann, Werner Ekau, Annika Weseloh, Christian Brandt and Ivette Nuckel.

Special thanks to Ursula Mendoza, Jorn Gieseler & Uta, Gaby Boheme, Ruben Lara, Carlos Jiménez, Jenny Leal Flores, Marcelo Protazio, Tilman Alpermann, Friedemann Kyel, Christiane Hueerkamp, Ana Rosa Araujo, Moriah Menezes, Uta Berger, Paula Cilene, Milena Arias-Schreiber, Andrew Halliday, Ricardo & Ramón Chero, Gonzalo Olivares, Esther Borell, Sebastian Ferse, Leyla Knittweis, Gesche Krause, Hilly Ann Roa-Quiaoit, Mohammad Alkhatib, Hoang Lai, Ole Morisse, Coralie D'lima, Bettina Schmitt, Tommaso Giarrizzo, Marc Taylor, Marie Badjeck, Matthias Birkicht, Julian Oxmann, Fernando Porto, Marcelo Cohen, Cyril Piou, Martha Fontalvo, Simon Geist, Julia Bush, Janne Timm, Tawfiq Froukh, Britta Grote, Ruth (Peru), Cornelia Roder,Vincent Vedel, Sönke, Soledad Luna for their friendship and comradeship.

I want to thank also, all friends and colleagues from the administration from the Smithsonian Tropical Research Institute (STRI). I am grateful that the doors of STRI were not only open during my fieldwork, but also anytime when I went back to Panama. I appreciate the collaboration from Maria Leone, Marissa Batista, Mercedes Denis, Osmila Sanchez Galan, Georgina de Alba, Orelis Arosemena, Marcela Paz, Adriana Bilgray, Ernesto Peña, Edgardo Ochoa, Rachel Collin, Gabriel Jácome, María Luz Calderón, Plinio Góndola and Reinaldo Tapia.

For the support of the complex logistics, thanks to Edgardo Ochoa, Reynaldo Tapia, Xenia Saavedra, and Alejandro Arze.

For the support and motivation for me to continue with my PHD studies while working in the STRI office of Education, thanks to Argelis Ruíz, Lidia Valencia, Adriana Sautu, Dayra Navarro, Renier Vargas and the docent team at the Marine Exhibition Center at Culebra.

Many thanks to Jaime Andrés Cabrera, María Patricia Castantes, Doña Luz and the many nice Colombian workers for supporting us during our stay in the Liquid Jungle Lab Station. Although we were living in an isolated place with many limitations, including a station under construction, we had the opportunity to live with a nice family during our eight month stay.

Quiero dedicar esta tesis a mi familia, pasamos por difíciles situaciones y por eso, ahora estamos mas unidos, a mi madre Berta Arosemena de Dominici por todo su apoyo para que yo pueda seguir adelante siempre y a mi padre Félix Dominici-Mayer ("El Corso"), por todo su coraje y por estar vivo! A todos mis hermanos (as), ustedes son un ejemplo de esfuerzo, nobleza, sinceridad y empeño. A mi primo Briant Dominici y su esposa Carmen Reyes. A todos mis viejos amigos (as), los de siempre, los de los viejos tiempos de el puente en Panamá, y mis amigos (as) en Costa Rica: los de las noches de música, los viajes, las comidas, los que quieren un mundo mejor, gracias por siempre estar allí en las buenas y las malas.

Gracias Ana Luisa, por tus consejos, tu visita, tu música y apoyo en tiempos buenos y tiempos difíciles!

Während meines Studiums in Deutschland hatte ich die Gelegenheit, sehr nette Freunde außerhalb meines akademischen Lebens zu treffen. Sie haben mir eine gute Zeit und viel Hilfe gegeben. Dank an Tom Nicolai, Paul Zachos, Mostapha "Mfa" Benazzi, Birger Stein (S.I.S.) dafür, dass sie mir die Chance gegeben haben, zu erkennen, wie sehr der Ozean und die Musik mit meinem Leben verbunden sind.

An das Optimystika-Team und Freunde (Stephan "Bische", Jeena, Torben, Juli, Hendrick, Andre, Petra, Olli, Annette, Malte, Nicole, Tarkan, Fabian, Tim, Nina, Masha und Timo) für die gute Zeit und all die Träume, die wir geteilt haben.

Alex Vogt, Ismael Nuñez-Riboni, Anna Akimova & Britta, Nikko Kosmatopoulos, Mustafa Kutlu, Holger Dick, Ursula Werner, Kyriakos Vamvakopoulos, Ralf Mertins, Jochen Nowaczyk, Wiebke Ehmann, Marc Hohle, Micaela Klaisse & Cristoph, "Guido Bosch, Alexander Lang, Daniel Alselm & Schwarzwald friends" Kuno Von Wattenwyl, Frauke Buismann, Catherine Fürsich, Nils Behrens, Steve Robert ("Roberto") Benjamin Arnold, Olaf Clausing und Lenart Seehausen will ich für die Freundschaft danken.

Dank an Markus Saxinger, Christian Jacob, Fritz Bauch, Ricardo ("El Brasilero"), Mema und Freunde (Karawane) sowie Santiago Gonzales, Cornelius Hertz und Detlef Quintern (Sud-Nord) für die Freundschaft und die Möglichkeit, bei ihnen mitzuwirken. Danke für all die Anstrengungen, die ihr unternehmt, um die die Welt zu einem besseren Ort zu machen, an dem Menschen in Frieden leben können. Mit gleichen Chancen für alle, einer geschützten Umwelt und ohne Diskriminierung.

This research was sponsored by the World Wildlife Fund (BMZ, Mesoamerican Biological corridor fellowship) for the fieldwork stage in Bocas del Toro. I want to thank Jorge Ventocilla for his support on the application and Oscar Brenes for his support during this fellowship.

This research was also with cooperation of the Centre for Marine Tropical Ecology in the University of Bremen (ZMT), The German Academic Exchange Service (DAAD), where I would like to thank Blanca de Olmos, Elke Massa, and Veronica Metje for all their collaboration during my short-term fellowships.

This thesis was sponsored by the Smithsonian Tropical Research Institute (STRI) as a Panamanian Research Fellowship supporting me with logistics and funds during the fieldwork in Panama and afterwards. The Bahía Honda Liquid Jungle lab (LJL) research station supported this research with logistics, materials, and a place to stay during my fieldwork in Bahia Honda, Tropical Eastern Pacific in Panama. The Project Aware Foundation (PADI) collaborates with partial funding for photographic material. The Panamanian National Institute for the Formation and Approach of Human Resources (IFARHU) contributed with a student loan for doctoral studies.