

**DEEP-SEA FISHERY IN THE COLOMBIAN CARIBBEAN SEA: MANAGEMENT  
AND CONSERVATION STRATEGIES FOR AN ECOSYSTEM APPROACH TO  
FISHERIES**

**Doctoral Thesis**

**By**

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DEEP-SEA FISHERY IN THE COLOMBIAN CARIBBEAN SEA: MANAGEMENT AND CONSERVATION STRATEGIES FOR AN ECOSYSTEM APPROACH TO FISHERIES

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## Abstract

The aim of this research was to identify the potential of new deep-sea fisheries in the Colombian Caribbean Sea determining their biomass and spatial distribution in order to advice management and conservation strategies, based on ecosystem approach to fisheries management. First, I examine morphological characteristics of the shallow water pink shrimp *Farfantepenaeus notialis* to investigate stock differentiation, presenting biological data such as size at 50% sexual maturity. The data on *F. notialis* were obtained from samples collected from June to December 2004, on board of commercial fishing vessels and from a time series of historic landings of catch and effort data. I did not find morphometric variability between the studied regions, which indicates the existence of a single population of *F. notialis* from a morphometric point of view. This study provides the first complete view, to date, of the stock structure and fishery dynamics of the pink shrimp *F. notialis* in the Colombian Caribbean Sea. This fishery is a typical case in which high exploitation, combined with non-existent fisheries management, have resulted in the significant depletion of stock. In response to this, I investigate possible new fishing areas, exploring the poorly understood deep sea habitats in the Colombian Caribbean Sea, to determine the potential for a viable deep-sea crustacean fishery. The sampling area extended from 100 m the isobaths to 600 m depth. I found high abundances of the giant red shrimp (*Aristaeomorpha foliacea*), the royal red shrimp (*Pleoticus robustus*), the pink speckled deep-sea shrimp (*Penaeopsis serrata*) and the deep-sea lobster (*Metanephrops binghami*) obtained in two experimental trawl surveys carried out in November and December 2009, all of which are important commercially. The highest biomass of these deep-sea crustaceans species were found mainly in the northern zone of the Colombian

Caribbean Sea, where the local oceanography is modulated by high productive seasonal upwelling. However, further scientific assessment is necessary to determine population life cycle parameters of these deep-sea crustaceans and associated biodiversity before initiating a new commercial fishery. Studies of deep-sea biodiversity are necessary in order to understand the degree of stability and vulnerability of deep-sea environments and enable comparison of conditions before and after exploitation of the fishery. This will enable a better understanding of the ecosystem, to advise ecosystem-based conservation and fisheries management strategies. The aim of this last study was to identify deep-sea fish assemblages across a depth range of 200-550 m from the Colombian Caribbean Sea and their implications for an ecosystem approach to fisheries management. Classification (Cluster analysis) and ordination (non-parametric multidimensional scaling – NMDS) were performed to identify deep-sea fish assemblages. A total of 102 species (13 Chondrichthyes and 89 Teleosteans) and 58 families (9 Chondrichthyes and 49 Teleosteans) of deep-sea fish were sampled. This study reveals the existence of three deep-sea fish assemblages and demonstrates that depth plays an important role in ichthyofaunal differentiation. I conclude that, the management of the shallow shrimp fishery and the potential new deep-sea crustacean fishery should be based on an ecosystem approach that considers population dynamics and structure, the optimum allocation of catches and effort, protection of nursery and spawning areas, the development of monitoring strategies and the care of ecosystems.

Key words: Deep-sea crustacean, deep-sea fish assemblages, ecosystem approach to fisheries, Colombian Caribbean Sea.

## Zusammenfassung

Das Ziel dieser Studie ist es, das Potential neuer Tiefseefischereien in der kolumbianischen Karibik zu identifizieren und für Management- und Konservationsstrategien auf Ökosystembasis die Biomasse und die räumliche Verteilung der Ressource zu bestimmen. Im ersten Schritt untersuchten wir die morphologischen Eigenschaften der Flachwasserart *Farfantepenaeus notialis* (pink shrimp) unter Nutzung von biologischen Daten wie  $L_{50\%}$ , um die Differenzierung verschiedener Stocks zu ermitteln. Daten zu *F. notialis* stammen aus Proben, die von Juni bis Dezember 2004 an Bord von kommerziellen Fischereischiffen gesammelt wurden sowie aus einer Zeitserie der historischen Anlandungsmengen und Fischereiaufwand. Wir fanden keine morphologische Variabilität bei *F. notialis* in verschiedenen Regionen des Studiengebietes, was aus morphometrischer Sicht auf eine *F. notialis* Population hindeutet. Die Arbeit zum pink shrimp *F. notialis* in der kolumbianischen Karibik, die auf Morphometrie, Fischereidaten und biologische Daten zur Struktur des Stocks und Fischereidynamik basiert, ist die erste umfassende Studie zu dieser Art. Seine Fischerei ist ein typischer Fall in dem hohe Ausbeutung zusammen mit nicht existentem Fischereimanagement zu einer signifikanten Einbruch der Stockabundanz geführt haben. Als Antwort darauf untersuchten wir die bisher nur unzulänglich erforschten Tiefseehabitate der kolumbianischen Karibik auf mögliche neue Fischereigebiete, um das Potential einer nachhaltigen Fischerei auf Tiefseecrustaceen zu ermitteln. Das Untersuchungsgebiet von zwei wissenschaftlichen Schleppnetzsurveys im November und Dezember 2009 erstreckte sich zwischen den 100 m und 600 m Isobathen. Wir fanden hohe Abundanzen für die Tiefseecrustaceen *Aristaeomorpha foliacea* (giant red shrimp), *Pleoticus robustus* (royal red shrimp), *Penaeopsis serrata* (pink speckled deep-sea shrimp) und *Metanephrops binghami* (deep-sea lobster), die alle kommerziell wichtig sind. Die höchsten Biomassen wurden vor allem in der nördlichen Zone der kolumbianischen Karibik

gefunden, wo die lokalen ozeanographischen Bedingungen von hochproduktivem, saisonalem Auftrieb moduliert werden. Vor der Initiierung einer neuen kommerziellen Fischerei sind weitere wissenschaftliche Untersuchungen nötig, um Parameter zur Biologie der Populationen der Tiefseecrustaceen und assoziierter Fauna zu ermitteln. Tiefsee-Biodiversitätsstudien sind notwendig um die Stabilität und die Vulnerabilität von Tiefseeökosystemen zu verstehen und in der Lage zu sein den Vergleich ihres Zustand vor und nach fischereilicher Nutzung zu ermöglichen. Ein besseres Verständnis der Ökosysteme ermöglichen es, die ökosystembasierte Konservierung und das Fischereimanagement zu beraten. Das übergreifende Ziel dieser Arbeit war es, Tiefseefischgesellschaften der kolumbischen Karibik im Tiefenbereich von 200 bis 550 m und die daraus folgenden Konsequenzen für den ökosystemaren Managementansatz der Fischerei zu identifizieren. Dazu wurden Clusteranalysis und multivariaten Ordinationsverfahren (nicht-metrische multivariate Skalierung) durchgeführt. Insgesamt wurden 102 Tiefseearten (13 Chondrichthyes und 89 Teleostei) aus 58 Familien (9 Chondrichthyes und 49 Teleostei) gesammelt. Die vorliegende Arbeit zeigt die Existenz von drei Tiefseefischgesellschaften und verdeutlicht, dass die wichtige Rolle der Tiefe in der Differenzierung von ichtyofaunischen Gruppen. Aus den Resultaten unserer Studie schließen wir, dass das Management der Flachwassergarnelenfischerei und die mögliche Tiefseefischerei auf Crustaceen auf einem ökosystemaren Ansatz basieren sollte, der Populationsdynamik und –struktur, die optimale Kontingentierung von Fängen und Aufwand, Schutz von Aufwuchs- und Laichgebieten, gut entwickelte Überwachungsprogramme und den Zustand der Ökosysteme berücksichtigt.

Schlagworte: Tiefseecrustaceen, Tiefseefischgesellschaften, ökosystemarer Ansatz in der Fischerei, kolumbische Karibik

## Resumen

El objetivo de esta investigación fué identificar el potencial de nuevas pesquerías de profundidad en el Caribe colombiano determinando su biomasa y distribución espacial con el propósito de recomendar estrategias de manejo y conservación, basados en un enfoque ecosistémico para el manejo de las pesquerías. Primero, yo examiné las características morfológicas del camarón rosado de aguas someras *Farfantepenaeus notialis* para investigar diferenciación de stock, presentando datos biológicos tales como talla al 50% de madurez sexual. Los datos de *F. notialis* fueron obtenidos de muestras colectadas desde Junio hasta Diciembre de 2004, a bordo de embarcaciones de pesca comercial y a partir de una serie de tiempo de datos de desembarque históricos de captura y esfuerzo. Yo no encontré variabilidad morfométrica entre las regiones estudiadas, lo cual indica una sola población de *F. notialis* desde el punto de vista morfométrico. Este estudio suministra la primera visión completa, hasta la fecha, de la estructura del stock y dinámica de la pesquería del camarón Rosado *F. notialis*. Esta pesquería es un típico caso en la cual la alta explotación, combinada con el no existente manejo pesquero, resultó en el significativo agotamiento del stock de camarón. En respuesta a esto, yo investigué nuevas áreas de pesca, explorando los poco entendidos hábitats de profundidad en el Caribe colombiano. El área de muestreo se extendió desde la isóbata de 100 m hasta los 600 m de profundidad. Yo encontré abundancias altas del camarón rojo gigante (*Aristaeomorpha foliacea*), el camarón rojo real (*Pleoticus robustus*), el camarón rosado manchado (*Penaeopsis serrata*) y la langosta de profundidad (*Metanephrops binghami*) obtenidos en dos cruceros de arrastre experimental realizados en Noviembre y Diciembre de 2009, todos comercialmente importantes. Las biomásas altas de estas especies de crustaceos de profundidad se encontraron principalmente en la zona norte del Caribe colombiano, donde la oceanografía local es modulada por la surgencia estacional con alta productividad. Sin

embargo, se necesita más investigación para determinar los parámetros del ciclo de vida de éstos crustáceos y la biodiversidad asociada antes de empezar una nueva pesquería comercial. Estudios a cerca de la biodiversidad son necesarios con el fin de entender el grado de estabilidad y vulnerabilidad de los ambientes de profundidad y permitir un mejor entendimiento del ecosistema para recomendar estrategias de manejo de las pesquerías y conservación. El propósito de éste último estudio fue identificar ensamblajes de peces de profundidad a través del rango de 200 – 550 m en el Caribe colombiano y sus implicaciones para un enfoque ecosistémico para el manejo pesquero. Se realizaron análisis de clasificación (análisis clúster) y ordenación (NMDS) para identificar ensamblajes de peces de profundidad. Se muestrearon un total de 102 especies (13 Condríctios y 89 Teleósteos) y 58 (9 Condríctios y 49 Teleósteos). Este estudio revela la existencia de tres ensamblajes de peces de profundidad y demuestra que la profundidad juega un rol importante en la diferenciación ictiofaunal. Yo concluyo que, el manejo de las pesquerías de camarón de aguas someras y la potencial nueva pesquería de crustáceos de profundidad debe ser basada en un enfoque ecosistémico que considere la dinámica y estructura de las poblaciones, la asignación óptima de las capturas y esfuerzo, la protección de áreas de crianza y desove, el desarrollo de estrategias de monitoreo y el cuidado del ecosistema.

Palabras clave: Crustáceos de profundidad, ensamblajes de peces de profundidad, enfoque ecosistémico para el manejo pesquero, Caribe colombiano.

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## **1. General introduction**

Fisheries have always been important to humanity (Christensen, 2011) and are the source of a significant amount of food produced for human consumption (Hart and Pearson, 2011). However, fisheries are depleting marine resources and fisheries management has been globally ineffective (Daan et al., 2011). Declining fish stocks, combined with the indirect effects of fishing on the marine ecosystems, demonstrate that fisheries management in a great part of the world has failed to achieve sustainability (Worm et al., 2006; Worm et al., 2009; Hutchings et al., 2010; Longhurst, 2010). This failure is mainly the result of increasing catch rates in response to the intense social-political pressure to obtain bigger catches in the short term, despite limited knowledge of fisheries systems (Pauly et al., 2003), and disregarding the complexity of wider ecological interactions and possible impacts on fragile marine ecosystems (Longhurst, 2010). Intensive exploitation of the fishing resources over the past decades, mainly on the continental shelves, has led to the progressively declining catches and the collapse of many fish and crustacean stocks (Pauly et al., 2003). In response, new fishing areas in deeper and deeper waters are being developed, taking advantage of recent advances in capture technologies (Pauly et al., 2003). Nevertheless, deep-sea ecosystems and fisheries are especially vulnerable to over-exploitation due to the life-history characteristics of deep-sea species, including extreme longevity, slow growth rate, late maturity and low fecundity (Morato et al., 2006; Follesa et al., 2011). Therefore, exploitation of these new fisheries should be in line with the current state of the resource, which requires a detailed knowledge of the life history of the target species, their ecology and bio-economic potential, as well as of the associated biodiversity

in tropical marine ecosystems (FAO, 2003; Munro, 2011). In the Colombian Caribbean Sea most of the coastal fisheries are currently being exploited at or above maximum sustainable level (Paramo et al., 2009). Furthermore, tropical fisheries are exceedingly complex multi-species systems, which intensively exploit a wide range of species and sizes, leading to generalized over-exploitation of fisheries resources (García, 1989; Munro, 2011). Therefore, the future development of the fishing sector in Colombia will depend on the identification of new resources with potential for sustainable exploitation. These considerations highlight the need for ecosystem approach to fisheries (EAF) based on knowledge of characteristics of the deep sea habitats and the organisms in the Colombian Caribbean Sea. EAF seeks to balance diverse societal objectives, by taking account of knowledge about biotic, abiotic and human components of ecosystems and their interactions and applying an integrated approach to fisheries within ecologically meaningful boundaries (Garcia et al., 2003; Bianchi, 2008).

Research aimed at exploration and stock assessment of fishing resources in the Colombian Caribbean Sea has been very intermittent and largely limited to initiatives carried out by international entities in association with national institutes. The first studies to assess fishing resources took place at the end of the 1960s (Ben Tuvia and Rios, 1969). One decade later JICA and INDERENA (JICA, 1981) carried out a second more complete exploration, which identified promising abundances of commercial sized shrimps (12.7 kg/h) and fishes (15.3 kg/h) between 200 and 800 m depth. A series of fisheries surveys were carried out in 1988 to search for demersal resources in the framework of the project PNUD/FAO/GLO/82/001; these estimated the biomass of snappers (Lutjanidae) to be 3400 t (Anon, 1989) and found high abundances of shrimps between 300 and 500 m. From the

1990s onwards, fisheries research focused exclusively on the assessment of demersal fish stocks (Quintero, 1992; Manjarrés et al., 1995, 1996; Paramo et al., 2009), confirming the importance of snappers as a fisheries resource. None of these studies adopted multidisciplinary approach towards quantifying the biological potential (biomass) and ecological aspects (associate biodiversity) of fisheries resources in a spatial context. Nor did they orient their evaluations towards the development of fisheries management strategies consistent with an ecosystem approach to fisheries.

Penaeids shrimps of shallow water constitute the most important fisheries resource in the Colombian Caribbean Sea, generating large amounts of direct and indirect employment and foreign currency through exports, due to their high value on international markets. There is little biological information available on this shallow water shrimp fishery and no stock assessment has been carried out to determine the abundance and spatial distribution of the species. Such an assessment would be required in order to establish artisanal and industrial fishing zones and solve current conflicts between stakeholders in accordance with the code of conduct for responsible fisheries (FAO, 1995). In the Colombian Caribbean Sea, the shallow water shrimp fishery targets *Farfantepenaeus notialis* (Pérez Farfante, 1967), *Farfantepenaeus brasiliensis* (Latreille, 1817), *Farfantepenaeus subtilis* (Pérez Farfante, 1967) and *Litopenaeus schmitii* (Burkenroad, 1936) with *F. notialis* constituting ~70% of the total shrimp catch. This is a typical case of a collapsed-uncontrolled fishery that has gone through different stages of development from growth, fully-exploited, over-exploited, to collapse and probably a recovery stage, having as resulted a significant depletion of shrimp stock (Paramo and Saint-Paul, 2010). Therefore, in the Colombian Caribbean Sea, additional fisheries management measures to those used traditionally are necessary in order

to protect fisheries resources and to improve the fishing production. These measures should be based on an ecosystem approach to fisheries, including the establishment of marine protected areas, which have recently emerged as a tool for marine conservation and fisheries management (Paramo et al., 2009). Most shrimps are benthic organisms, occupying a variety of bottoms such as sandy, muddy, rocky or a mixture of these. Commercial species are exploited in shallow waters at depths above 100 m (Carpenter, 2002). The principal commercial species in the Colombian Caribbean Sea is *Farfantepenaeus notialis* (Table 1), and, at present there is no deep-sea crustacean fishery in the Colombian Caribbean Sea. However, in FAO Fishing Area 31 (Caribbean Sea) (Fig. 1), there is a deep-sea shrimp fishery targeting the commercial species *Aristaeomorpha foliacea* and *Pleoticus robustus* at depths greater than 200 m (Carpenter, 2002). In addition, the Caribbean lobster *Metanephrops binghami* (Boone, 1927) is reported to have potential for economic exploitation in Venezuelan waters (Gómez et al. 2000; Gómez et al. 2005) (Fig.1, Table 1).

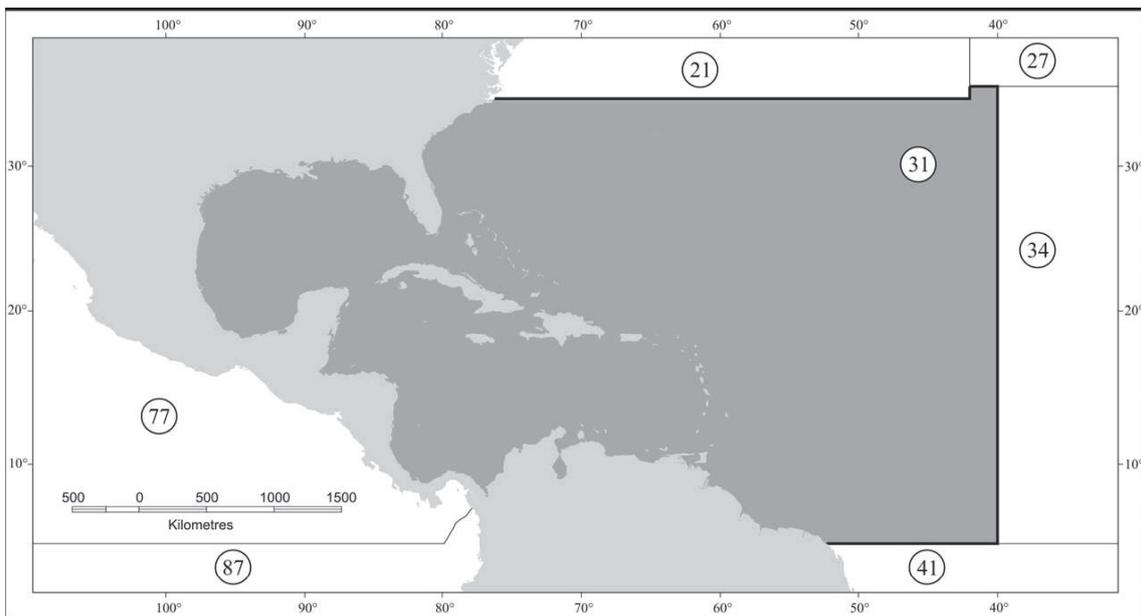


Figure 1. FAO Fishing Area 31 of the Western Central Atlantic Ocean (Carpenter, 2002).

Table 1. Taxonomic information on crustaceans of commercial importance in the Colombian Caribbean Sea.

<p>Class: Malacostraca  Order: Decapoda  Suborder: Dendrobranchiata  Family: Penaeidae  Species: <i>Farfantepenaeus notialis</i> (Pérez Farfante, 1967)  Common name: Southern pink shrimp</p>	 <p>FishBase Consortium FAO, 2008</p>
<p>Class: Malacostraca  Order: Decapoda  Suborder: Dendrobranchiata  Family: Aristeidae  Species: <i>Aristaeomorpha foliacea</i> (Risso, 1827)  Common name: Giant red shrimp</p>	
<p>Class: Malacostraca  Order: Decapoda  Suborder: Dendrobranchiata  Family: Solenoceridae  Species: <i>Pleoticus robustus</i> (Smith, 1885)  Common name: Royal red shrimp</p>	
<p>Class: Malacostraca  Order: Decapoda  Suborder: Dendrobranchiata  Family: Penaeidae  Species: <i>Penaeopsis serrata</i> (Bate, 1881)  Common name: Pink speckled shrimp</p>	 <p>Picture used with permission of Perry and Larsen © 2004 (www.gsmfc.org)</p>
<p>Class: Malacostraca  Order: Decapoda  Suborder: Pleocyemata  Family: Nephropidae  Species: <i>Metanephrops binghami</i> (Boone, 1927)  Common name: Caribbean lobster</p>	

**The southern pink shrimp (*F. notialis*)** is found in the Caribbean Sea from Quintana Roo Mexico to Río de Janeiro Brazil, and on the west coast of Africa, from Mauritania to Angola (Carpenter, 2002). This species inhabits shelf areas from the coastline to depths of about 100 m, the largest concentrations are found between 3 and 50 m, on bottom mud or sandy mud and sandy patches among rocks (Carpenter, 2002). The shrimp fishery in the Colombian Caribbean represents the most important source of economic activity in the continental shelf, generating significant employment and revenue (Paramo and Saint-Paul, 2010).

**The giant red shrimp (*A. foliacea*)** has a wide geographical distribution encompassing the Mediterranean Sea, the eastern and western Atlantic, the Indian Ocean and the western Pacific from Japan to Australia, New Zealand and the Fiji Islands (Tavares, 2002). *A. foliacea* is found in deep waters from 250 to 1300 m over bottom mud and is actively fished because of its high commercial value (Tavares, 2002). Recent exploration of deep waters off the Yucatan Peninsula in Mexico showed that *A. foliacea* represents a potential fisheries resource (Gracia et al., 2010). Today, *A. foliacea* constitutes a valuable deep shrimp fishery off the south-eastern and southern sectors of the Brazilian coast (Pezzuto et al., 2006; Dallagnolo et al., 2009), and is a commercially important shrimp in the deep waters of the Mediterranean Sea (D'Onghia et al., 1998; Figueiredo et al., 2001; Papaconstantinou and Kaporis, 2003; Politou et al., 2004; Mouffok et al., 2008).

**The royal red deep shrimp (*P. robustus*)** inhabits continental slopes from 180 to 730 m depth, and is most abundant at depths between 250 and 475 m over mud, sand, muddy sand, or white calcareous mud. This species is only captured in high abundances off the

coast of northeastern Florida, near the Dry Tortugas islands, in the Mississippi delta and also off the coast of Venezuela (Tavares, 2002). However, recent exploration of deep waters off the Yucatan Peninsula in Mexico showed that *P. robustus* represents a potential fisheries resource in this area (Gracia et al., 2010).

**The pink speckled shrimp (*P. serrata*)** is of potential commercial importance in the western and eastern Atlantic (Holthuis, 1980). The species of genus *Penaeopsis* are benthic, occurring in the upper part of the continental and insular slopes of tropical and subtropical regions (Pérez-Farfante, 1980). *P. serrata* is distributed in the eastern Atlantic off north-west Africa (Morocco, Río de Oro), the western Atlantic in North Carolina (USA) to Surinam, the Bahamas Islands, the Gulf of Mexico, the Caribbean Sea (Holthuis, 1980; Pérez-Farfante, 1980) and in the Mediterranean Sea off Alborón Island and in the Sardinian Channel (Mura et al., 2002).

**The Caribbean lobster (*M. binghami*)** is distributed from the Bahamas and southern Florida to French Guiana including the Gulf of Mexico and the Caribbean Sea (Holthuis, 1991; Tavares, 2002). Crustaceans of the genus *Metanephrops* are an important economic resource (Holthuis, 1991; Chan, 1998; Chan et al., 2009) in some tropical and subtropical regions. Three deep-water crustaceans of the species *Metanephrops* are exploited commercially on the continental slopes of north-west Australia: *M. boschmai* (Holthuis, 1964), *M. andamanicus* (Wood-Mason, 1891) and *M. australiensis* (Bruce, 1966) (Ward and Davis, 1987; Wassenberg and Hill, 1989). New Zealand has developed a deep water lobster fishery, targeting scampi (*M. challenger* Balss, 1914) (Smith, 1999). An economically important commercial fishery exists in Taiwan and East China Sea for *M.*

*thomsoni* (Bate, 1888), *M. japonicus* (Tapparone-Canefri, 1873) and *M. formosanus* (Chan and Yu, 1987; Choi et al., 2008). *M. binghami* has potential for an economic exploitation in waters of Venezuela (Gómez et al., 2000; Gómez et al., 2005).

### **1.1. Hypothesis**

Whether there is deep-sea fishing resources and they are spatially structured.

Whether there are discrete deep-sea fish assemblages related to depth in the Colombian Caribbean Sea.

### **1.2. General objective**

The objective of this research was to identify the potential of new deep-sea fisheries determining their biomass and spatial distribution in order to advice management and conservation strategies, based on an ecosystem approach to fisheries.

### **1.3. Specific objectives**

To identify the stock structure and fishery dynamics of the shallow water pink shrimp *Farfantepenaeus notialis*.

To determine the spatial distribution patterns of biomass of deep-sea crustaceans of commercial importance.

To identify deep-sea fish assemblages and their implications for an ecosystem approach to fisheries management.

#### **1.4. Contribution of publications**

The different publications will respond to questions of interest to the Colombian fishing sector: Which resources can we exploit?; Where can we fish them?; How is the biodiversity associated and how can we achieve a sustainable fishery under an ecosystem approach to fisheries management?. To attain these goals, fisheries science traditionally makes use of two sources of information: I) dependent data from fishery (i.e. catch and effort of commercial fishing) and II) independent data from fishery (i.e. direct surveys of stock assessment). While the first one requires a great quantity of data taken in time series, the second doesn't require prior information and can, in a short period of time, diagnose the potential of a fishing resource and the associated biodiversity (Hilborn and Walters, 1992; Quinn and Deriso, 1999; Jennings et al., 2006; King, 2007). Normally, direct stock assessment uses geo-referenced information of population aggregations to estimate abundance and spatial distribution (Rivoirard et al., 2000).

The article in the second chapter describes the morphological characteristics of shallow water pink shrimp (*Farfantepenaeus notialis*). It investigates stock differentiation, based on biological data such as size at 50% sexual maturity. With this work we provide the first complete view, to date, based on morphometric, historical landings and biological data, of the stock structure and fishery dynamics of pink shrimp *F. notialis*, in the Colombian

Caribbean Sea. The shallow water shrimp fishery in the Colombian Caribbean is a typical case in which high exploitation, combined with non-existent fisheries management, have resulted in the significant depletion of stock. The articles in chapters 3, 4 and 5 explore the potential of the deep-sea giant red shrimp (*Aristaeomorpha foliacea*), the royal red shrimp (*Pleoticus robustus*) (Chapter 3), the pink speckled deep-sea shrimp (*Penaeopsis serrata*) (Chapter 4) and the deep-sea lobster (*Metanephrops binghami*) (Chapter 5) as new fishing resources. Due to the substantial marketability of these deep-sea crustaceans species, not only on the local level but also in numerous international markets, these deep-sea crustaceans represent a potential new economic resource in the Colombian Caribbean Sea. However, these papers recommend that further scientific assessment is necessary to determine population life cycle parameters of deep-sea crustaceans and associated biodiversity before initiating a new commercial fishery. The article in chapter 6 represents the first attempt to identify deep-sea fish assemblages across a depth range of 200-550 m from the Colombian Caribbean Sea and their implications for an ecosystem approach to fisheries management. The management of shallow shrimp fishery and potential new deep-sea crustacean fishery should be based on an ecosystem approach to fisheries, which considers population dynamics and structure, the optimum allocation of catches and effort, protection of nursery and spawning areas, the development of monitoring strategies and the care of ecosystems. This approach will allow an appropriate level of biodiversity and the habitat quality to be maintained, while achieving sustainable fisheries.

Publications:

Paramo, J., U. Saint-Paul. 2010. Morphological differentiation of southern pink shrimp *Farfantepenaeus notialis* in Colombian Caribbean Sea. *Aquatic Living Resources*. 23(1): 95-101. (Chapter 2).

Paramo, J., U. Saint-Paul. 2011. Deep-sea shrimps *Aristaeomorpha foliacea* and *Pleoticus robustus* (Crustacea: Penaeoidea) in the Colombian Caribbean Sea as a new potential fishing resource. *Journal of the Marine Biological Association of the United Kingdom*. DOI:10.1017/S0025315411001202. (Chapter 3).

Paramo, J., U. Saint-Paul. 2011. Spatial structure of the pink speckled deep-water shrimp (*Penaeopsis serrata*, Bate 1881) in the Colombian Caribbean Sea. *Crustaceana*. Accepted. (Chapter 4).

Paramo, J., U. Saint-Paul. 2011. Spatial structure of deep sea lobster (*Metanephrops binghami*) in the Colombian Caribbean Sea. *Helgoland Marine Research*. DOI 10.1007/s10152-011-0243-6. (Chapter 5).

Paramo, J., M. Wolff., U. Saint-Paul. 2011. Deep-sea fish assemblages in the Colombian Caribbean Sea: implications for an ecosystem approach to fisheries management. MS submitted to *Fisheries Research*. (Chapter 6).

## 1.5. Study area

The spatial scale of this research is from Punta Gallinas in the Guajira region ( $71^{\circ}14'$ ) to off Uraba gulf ( $76^{\circ}53'$ ). The data on shallow water pink shrimp (*F. notialis*) were obtained from samples collected from June to December 2004, on board of commercial fishing vessels and from a time series of historic landings of catch and effort data. Data on deep-sea crustaceans and fishes were taken in two experimental trawl surveys carried out in November and December 2009. The sampling area extended from 100 m isobath to 600 m depth. In the north Colombian Caribbean, the continental shelf is very narrow, with the 200 m isobath at a distance of only 10 nautical miles (nmi) from the coast. Moving south-west, the shelf widens to a maximum of 25 nmi off Riohacha and then narrows again and almost disappears off the Tayrona National Park (TNP) (Fig. 2). In front of Ciénaga Grande de Santa Marta (CGSM) the continental shelf is up to 12 nmi wide, while near Cartagena it is once again very narrow. It attains its maximum width (60 nmi) in the Gulf of Morrosquillo, before narrowing again towards the Gulf of Urabá. The Colombian Caribbean is under the influence of the north–south displacement of the Inter Tropical Convergence Zone (ITCZ). When the ITCZ is towards the south (dry season), a high-pressure system brings strong and constant westward trade winds. During this period, the Caribbean current is displaced towards the west. When this current nears the Panama coast, it is deflected southward and then eastward. In this way, a counter-current is formed. When the ITCZ is towards the north (rainy season), the trade winds relax and their direction becomes variable due to the influence of a low-pressure system. This condition promotes the extension of the counter-current along a northeast axis. In this way, counter-current forcing is seasonally dependent (Andrade et al., 2003). During the dry seasons (major summer: August–September; minor

summer: December–January), the northern zone is affected by the Caribbean current and the upwelling of deep waters. The upwelling is strongest at La Guajira Peninsula, and its effects are felt as far as waters near the TNP (Andrade et al., 2003). By contrast, during the rainy seasons (major winter: September–November; minor winter: May–June), the counter-current reaches as far as La Vela Cape (LVC) in La Guajira Peninsula (Bula-Meyer, 1990). The main upwelling coastal ecosystems in temperate zones are characterized by strong seasonal or permanent trade winds, a vertical current structure, and a persistent wind-induced offshore drift of surface waters (Brink, 1983). These ecosystems present high rates of primary productivity (Roy, 1998; Mackenzie, 2000), and they usually support large populations of pelagic fish (Cury and Roy, 1989; Pauly and Christensen, 1995; Paramo et al., 2003). In tropical environments conditions are quite different. Generally, two monsoon or trade wind seasons replace the four seasons of temperate zones, differentiated by wind patterns, rainfall, and currents. In addition, the concentration of dissolved nutrients is lower, except in upwelling zones (Johanes, 1978).

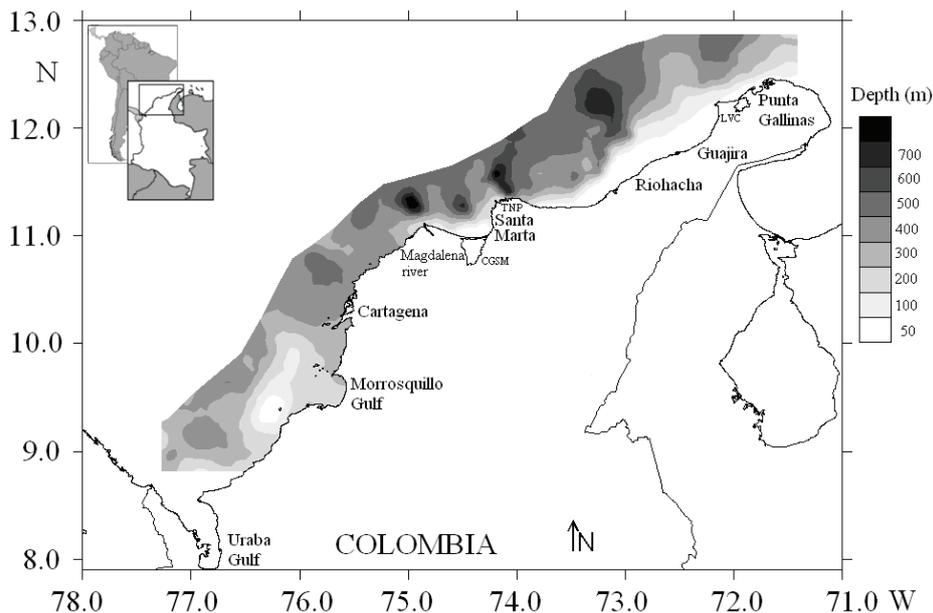


Figure 2. Study area in the Colombian Caribbean Sea.

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## 2. Morphological differentiation of southern pink shrimp

### *Farfantepenaeus notialis* in Colombian Caribbean Sea

*Aquatic Living Resources*. 2010. 23(1): 95-101.

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#### **Abstract.**

*Farfantepenaeus notialis* (Crustacea: Decapoda) constitutes about 70% of the total shrimp catch in the Colombian Caribbean. In this study we examine morphological characteristics of *F. notialis* to investigate stock differentiation, provide biological data such as size at 50% sexual maturity and discuss the importance of this information to fisheries management. The study was conducted in the Colombian Caribbean Sea from June to December of 2004 in four locations: the Uraba gulf (U), Morrosquillo gulf (M), Amansaguapos (AG), and La Vela cape (VC). Individual shrimp were measured according to ten body segments and sex determined. We used Discriminant Function Analysis (DFA)

of size-adjusted data to generate two-dimensional plots of the morphometric indices to test for geographic variation in morphometry by mean of canonical dimensions. The length-frequency distributions showed statistically significant differences between the measurements of both sexes, males were smaller than female in all measures. Size at 50% maturity ( $l_{50\%}$ ) in females was 30.56 mm CL. The DFA of morphological differences between individuals (female/male) show strong overlapping and no clear separation between regions. We did not find morphometric variability between regions, which indicates a single population of *F. notialis* from the morphometric point of view.

Key words: shrimp; morphometric; differentiation; stock; Colombia.

## **Introduction**

Penaeid shrimps inhabit tropical and subtropical shallow waters on the continental shelf (May-Kú et al. 2006), and constitute an important resource for fisheries near to the equatorial region (King 2007; Guillett 2008). The one to two year life cycle of a typical penaeid species is complex (Dall et al. 1990), involving the spawning of adults off the sea and larvae migration into the nursery regions which include coastal lagoons, mangroves, and estuaries (García and Le Reste 1987). The nursery regions provide food (Lee 1999; Loneragan and Bunn 1999) and refuge against predators (Minello and Zimmerman 1991). The migration comprises an estuarine phase when the post-larvae populations enter the mouths of the rivers, remain until the juvenile stage and then migrate toward the sea as sub-adults, and is a period characterized by quick growth and continuous migration (Dall et al. 1990). The pink shrimp *Farfantepenaeus notialis* (Pérez Farfante, 1967) is found in the Caribbean Sea from Quintana Roo Mexico to Río de Janeiro Brazil, and the west coast of

Africa, from Mauritania to Angola (Carpenter 2002). The shrimp fishery in the Colombian Caribbean provides the most important source of economic activity in the continental shelf, significant employment and revenue is generated. The target species of this fishery are *Farfantepenaeus notialis* (Pérez Farfante 1967), *Farfantepenaeus brasiliensis*, (Latreille 1817), *Farfantepenaeus subtilis* (Pérez Farfante 1967) and *Litopenaeus schmittii* (Burkenroad 1936), with *Farfantepenaeus notialis* constituting ~70% of the total shrimp catch. The landings for the shrimp fishery in this region can be described as a typical unmanaged fishery (Hilborn and Walters 1992; King 2007). The development of this commercial shrimp fishery may be described in stages (Hilborn and Walters 1992; Jennings et al. 2001; King 2007) (Fig. 1). Commercial exploitation of shrimp starts in the beginning of the 1970s, growth stage, fishing effort (days of fishing) was less active but the catch (landings in tons) larger, thus the CPUE was significantly higher. As fishing effort increased in the beginning of the 80's during the fully exploited stage, catches fluctuated and the CPUE showed a small decrease. An over-exploited stage was reached about the mid '80s when fishing effort and catch rate increased and during the first five years of the '90s when CPUE, fishing effort and catch fluctuated. In 1990 fishing effort fell drastically, but was again increased in 1991 and the CPUE fell. In the collapse stage, catch rates fell drastically, but fishing stabilized by the end of 90s and the CPUE decreased drastically. In the beginning of 2000 the fishing decreased as commercial fishers left the fishery activity, catches rates were significantly lower and the CPUE showed a small increase. Despite the importance of the shrimp fishery in the Colombian Caribbean, there is a lack of necessary information on the population dynamics in this region. For example in order to design sustainable management strategies (Cadrin et al. 2004), fishery managers in Colombia need to know whether they are dealing with single or multiple populations of *F. notialis*. In fact,

stock identification is a prerequisite for the correct application of stock assessment and population dynamics models, which assume that the group of individuals has homogeneous vital rates and closed life cycle (Hilborn and Walters 1992; Quinn and Deriso 1999; Jennings et al. 2001; Cadrin et al. 2004; King 2007). In this study we examine the morphological variability of pink shrimp *F. notialis* with regard to stock differentiation and provide biological data such as size at 50% sexual maturity which is vital to efficient fishery management.

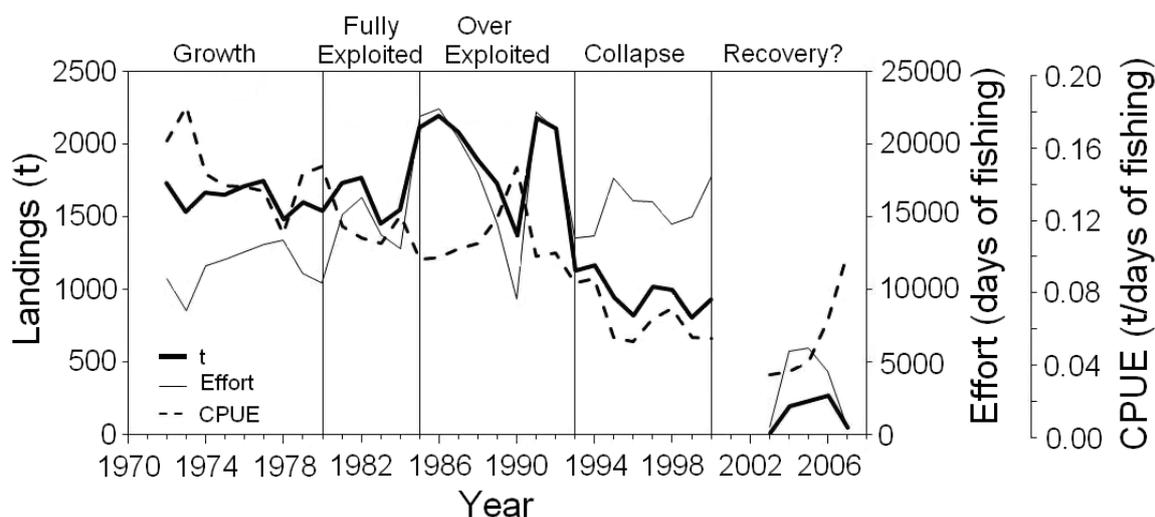


Figure 1. Development of shrimp fishery in Colombian Caribbean in stages (source: INDERENA, INPA and INCODER Colombian fisheries management institutes).

## Materials and methods

The morphometric study of pink shrimp (*F. notialis*) was conducted in the Colombian Caribbean Sea (Fig. 2) from June to December of 2004 in four sample locations: Uraba gulf (U), Morrosquillo gulf (M), Amansaguapos (AG) and La Vela cape (VC).

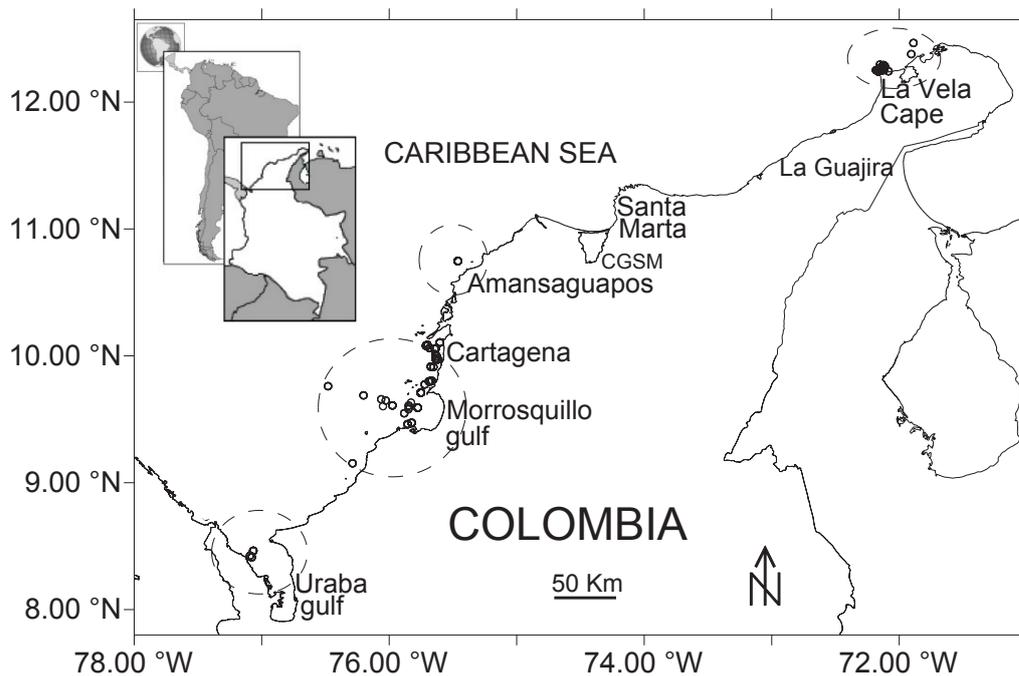


Figure 2. Locations in Colombian Caribbean Sea where pink shrimp (*F. notialis*) samples were obtained: Uraba gulf (U), Morrosquillo gulf (M), Amansaguapos (AG) and La Vela cape (VC).

The pink shrimp were measured using ten segments of the body to the nearest 0.1 mm, total wet weight (W) to the nearest 0.01 g and sexes were determined (Fig. 3): total length (TL), body length (BL), rostrum length (RL), first abdominal segment length (FSL), carapace length (CL), diagonal carapace length (DCL), first abdominal segment height (FSH), antennal spine width (ASW), hepatic spine width (HSW) and first abdominal segment width (FSW) (Tzeng et al. 2001; Tzeng and Yeh 2002).

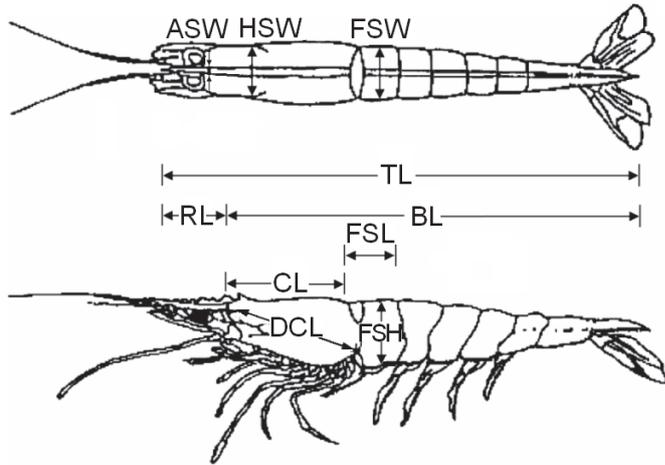


Figure 3. Diagram of a pink shrimp showing the body segments measured (Tzeng et al 2001).

Five macroscopic maturity stages were determined visually: I) Immature, translucent ovaries, II) In development, opaque ovaries, III) Almost mature, ovaries yellow orange color, IV) Mature, very enlarged ovaries olive color sometimes brown, and V) Spawning, empty ovaries. For estimation of the maturity at length we considered stages I and II as immature and stages III, IV and V as mature. Size at sexual maturity ( $L_{50\%}$ ) was modeled by fitting the logistic function of a mature specimen proportion with 1 mm of size interval of CL. The curve was fitted by applying the maximum likelihood and uncertainty by Monte Carlo resampling (Manly 2006) to obtain the estimated parameters and the confidence intervals (C.I.) (Roa et al. 1999; Quiroz et al. 2007).

$$P(l) = \frac{1}{1 + \exp(a + b * CL)}$$

Where  $P(l)$  is the mature female proportion,  $a$  and  $b$  are the parameters estimated by resampling and  $CL$  the carapace length. The size at 50% maturity is  $CL_{50\%} = -a/b$  (King 2007). The ANOVA One-Way was used to establish significant differences among sex

(female and male) of each measurement, once the normality and homogeneity variance assumption were verified with the log-transformed data. We used the Student's t-test for differences between means of CL by region for both females and males (Gotelli and Ellison 2004; Manly 2004). Measurements of the body were standardized using BL, which normalizes the individuals to the overall mean standard length to correct for correlation with body size (Tudela 1999; Salini et al. 2004; Pinheiro et al. 2005; Kristoffersen and Magoulas 2008). The measurement was adjusted by the following allometric equation  $\hat{Y} = aX^b$ , such that the standardized value of this variable of an individual of size  $X_i$  is give by,

$$M_c = M_x \left[ \frac{\overline{BL}}{BL_i} \right]^b$$

where  $\overline{BL}$  is the overall mean body length,  $b$  is the slope, within areas, on logarithms of  $M_x$  and  $BL$ . This standardization normalizes the individuals in a sample to a single, arbitrary size, common to all samples, and maintains the individual variation (Tudela 1999). Morphometric characteristics were analyzed using multivariate analysis. Principal components analysis (PCA) of log-transformed data was performed to explore patterns of variation among female and male and stages of maturity in female. PCA was used on the correlation matrix of analyzed parameters. Stepwise linear discriminant function analysis (DFA) of size-adjusted data was used to generate two-dimensional plots of the morphometric indices to test for geographic variation in morphometry by mean of canonical dimensions.

## Results

A total of 1094 specimens of *F. notialis* were measured between June and December of 2004: 44 individuals from Uraba gulf (28 female, 16 male), Morrosquillo gulf 385 individuals (159 female, 226 male), Amansaguapos 160 individuals (97 female, 63 male) and La Vela cape 505 individuals (283 female, 222 male). The length-frequency distributions for each morphometric measurement are illustrated separately for each sex (Fig. 4). Statistically significant differences (ANOVA test) between the measurements of both sexes were found (Fig. 4), revealing sexual dimorphism ( $P = 0.00$ ) in all morphometric characters, the males were smaller than females in all measurements.

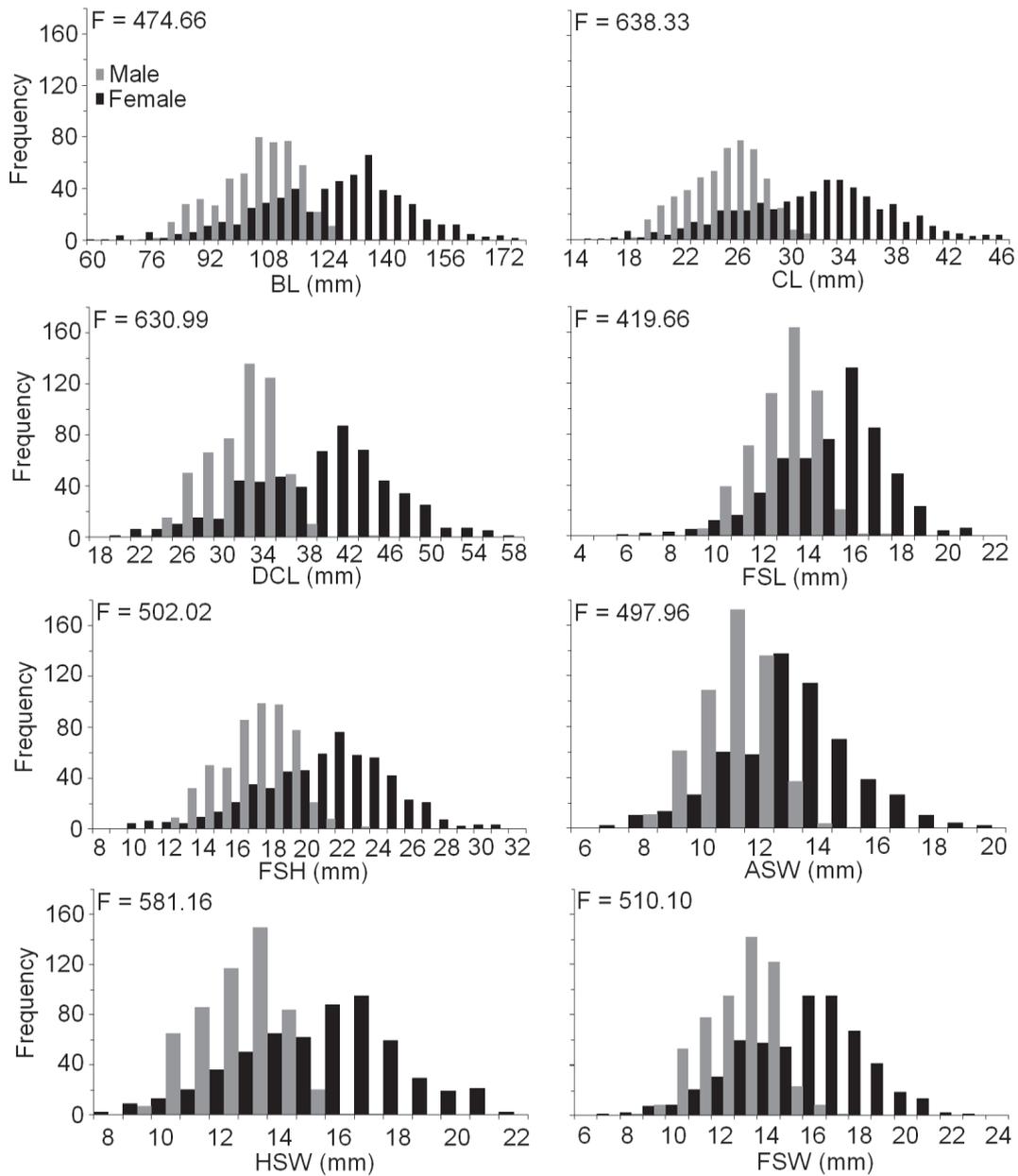


Figure 4. Histogram of the morphometric body parts measured (mm) by sex for *F. notialis*. One way ANOVA test (F value and p value = 0.00) for differences between the two sexes for each measurement.

The CL showed an increase in size with a decrease of latitude (Fig. 5), the larger individuals were found mainly in the south of the study area (Uraba gulf, Morrosquillo gulf and Amansaguapos) and otherwise smaller individuals were located more towards the north of the Colombian Caribbean (La Vela Cape in La Guajira region). The CL of females differs significantly among Uraba gulf, Amansaguapos and La Vela Cape regions, Morrosquillo gulf with Amansaguapos and La Vela Cape, but does not differ significantly for Uraba gulf with Morrosquillo gulf and Amansaguapos with La Vela Cape (Table 1). For males, just does not differ significantly among Uraba gulf and Morrosquillo gulf regions (Table 1).

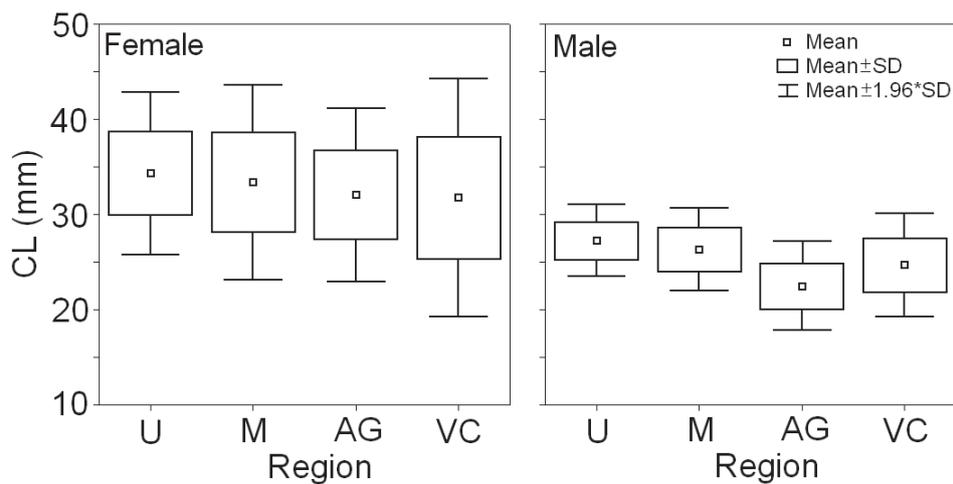


Figure 5. Box plot of the CL discriminated by regions for female and male of *F. notialis*.

U= Uraba gulf (n = 44), M= Morrosquillo gulf (n = 385), AG= Amansaguapos (n = 160), VC= La Vela Cape (n = 505).

Table 1. Student's t-test for differences between means of CL by region according to sex for *F. notialis*. \*  $P \leq 0.001$ ; \*\* $0.01 < P \leq 0.05$ . U= Uraba gulf, M= Morrosquillo gulf, AG= Amansaguapos, VC= La Vela Cape.

Group	CL Female	CL Male
U - M	0.384	0.106
U - AG	0.024**	0.000*
U - VC	0.039**	0.000*
M - AG	0.038**	0.000*
M - VC	0.006**	0.000*
AG -VC	0.673	0.000*

A total of 570 females were analyzed to determine different maturity stages, were 42.98%, corresponds to immature and the mature to 57.02% of the total. The size at 50% maturity ( $l_{50\%}$ ) in females (Fig. 6) was 30.56 mm CL (95% C.I. lower = 29.47, C.I. upper = 32.60), the parameters  $a = 11.56$  (C.I. lower = 8.82, C.I. upper = 12.75) and  $b = -0.38$  (C.I. lower = -0.43, C.I. upper = -0.27).

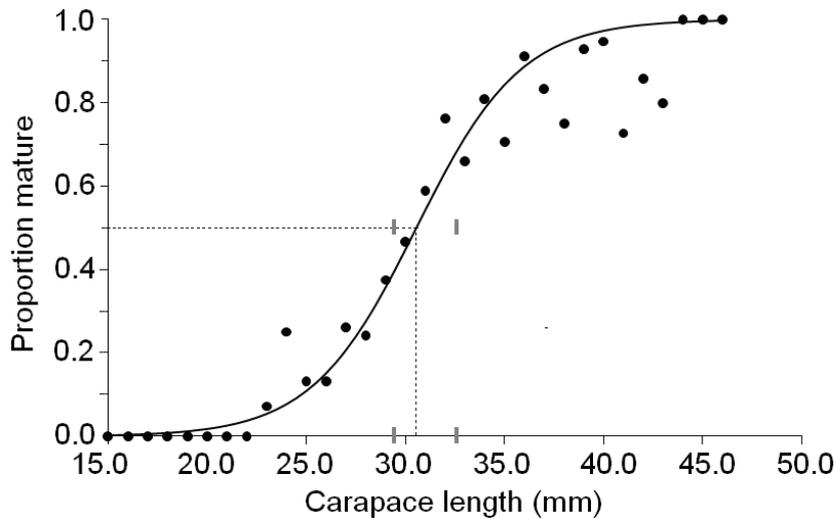


Figure 6. Size at 50% sexual maturity for females of *F. notialis*, Carapace length (CL) = 30.56 mm; Total length (TL) = 136.68 mm; Tail length (TaL) = 88.18 mm.

Principal components analysis (PCA) on the morphometric indices of *F. notialis* for female and male indicate that the first two components explain 94.3% of total variance and shows strong sexual dimorphism, which suggest to make the analysis separated by sex (Fig. 7 left). PCA for *F. notialis* females illustrates variability in stages of maturity and depicts differences in levels of maturity by morphometric measurements (Fig. 7 right). We extracted the first two components which explained 77.9% of total variance. The plot shows that all maturity groups are similar, which means that there is no difference between maturity stages. This analysis demonstrates that maturity stages of females did not confound the morphometric differentiation in *F. notialis*.

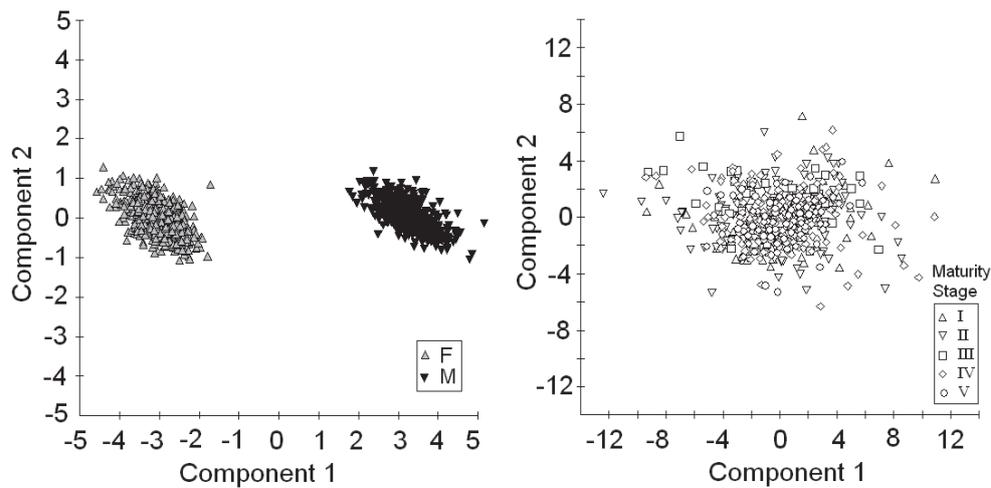


Figure 7. Factor loadings plot of PCA on the morphometric indices of *F. notialis*, grouped for patterns of variation according to female and male (left) and stages of maturity for females (right).

The DFA of morphological differences between the male and female individuals shows a strong overlapping and no clear separation between the regions (Fig. 8): Uraba gulf (U), Morrosquillo gulf (M), Amansaguapos (AG) and la Vela cape (VC). The first two canonical functions carry the analysis through the 97.0% and 94.5% for female and male, respectively (Table 2). The Wilk's lambda for female indicate that variable ASW contributes most to discriminate between different stocks, followed by FSL and CL (Table 3). The Wilk's lambda for male show that TL is the variable that allows to discriminate between different stock, followed by BL and ASW (Table 3). The means of canonical variables in female and male (Table 4) shows that the first two discriminant functions not discriminates between regions, because the canonical mean are not different between the other groups.

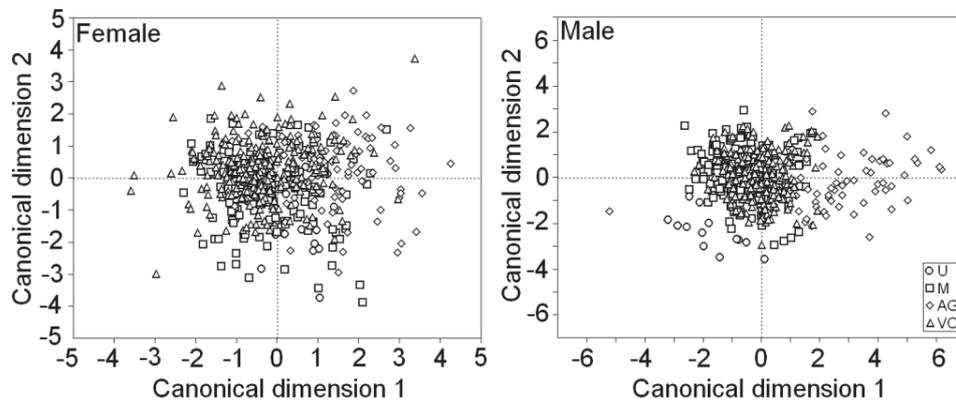


Figure 8. Canonical discriminant functions 1 and 2 on the morphometric indices of *F. notialis*, grouped according to localities for female and male. U= Uraba gulf, M= Morrosquillo gulf, AG= Amansaguapos, VC= La Vela Cape.

Table 2. Summary of the first two canonical discriminant functions of the morphometric indices for female and male.

Sex	Function	Eigenvalue	Cumulative percent	Canonical correlation	Wilk's lambda	Chi squared	df	P
Female	1	0.406	73.806	0.537	0.621	266.989	27	0.000
	2	0.127	97.000	0.336	0.872	76.360	16	0.000
Male	1	1.211	84.718	0.740	0.368	520.028	24	0.000
	2	0.140	94.503	0.350	0.813	107.415	14	0.000

Table 3. Summary of the stepwise discriminant function analysis for morphometric characters in female and male.

Female				Male			
Step no.	Variable entered	Wilk's lambda	P-level	Step no.	Variable entered	Wilk's lambda	P-level
1	ASW	0.706	0.000	1	FSL	0.407	0.000
2	FSL	0.687	0.000	2	FSW	0.380	0.001
3	FSH	0.642	0.000	3	ASW	0.412	0.000
4	HSW	0.628	0.099	4	HSW	0.390	0.000
5	FSW	0.634	0.007	5	DCL	0.380	0.001
6	DCL	0.629	0.050	6	FSH	0.385	0.000
7	CL	0.645	0.000	7	TL	0.583	0.000
-	-	-	-	8	BL	0.581	0.000

Table 4. Means of canonical variables for female and male. U= Uraba gulf, M= Morrosquillo gulf, AG= Amansaguapos, VC= La Vela Cape.

Group	Female		Male	
	Dimension 1	Dimension 2	Dimension 1	Dimension 2
U	0.313	-1.052	-1.349	-0.149
M	-0.199	-0.360	-0.667	0.267
AG	1.354	0.184	2.827	0.197
VC	-0.383	0.243	-0.026	-0.317

## Discussion

Knowledge of stock structures of a species is very important for effective and successful management of a fishery as well as to be able to implement rebuilding programs in collapsed fisheries (Begg et al. 1999; King 2007). A stock is considered to be a group of individuals with unique phenotypic attributes, but sexual dimorphism, timing of sampling, allometric growth, and the state of maturity may confound the morphological relationships (Tzeng et al. 2001). The samples analyzed in this study showed different stages of maturity for females. However, in this case the maturity does not seem to have affected the patterns of similarity between the samples in the PCA analysis. The analysis demonstrates that the morphometric indices are not affected by the particular stage of maturity of the female. Regional environmental factors (i.e. upwelling) tend to influence the phenotypic characteristics (Swain and Foote 1999; Begg and Waldman 1999; Kristoffersen and Magoulas 2008). Different regions show different sizes, the northern shrimps of *F. notialis* are smaller than from the south, and this characteristic is possibly influenced by the increase of temperature southward of the study area. This occurrence of a North-South gradient of sizes could be a strong indication that there may be a single stock, the smaller shrimps coming from the north. However, the Colombian Caribbean Sea has several

mangroves areas, which could be serve as nursery habitats for *F. notialis* (i.e. Ciénaga Grande de Santa Marta, Morrosquillo gulf, and Uraba gulf). At this point it is not possible to distinguish between these two alternatives and is necessary further research about currents, larval dispersion and spawning areas for *F. notialis*. Thus, the morphometric similarity of individuals of *F. notialis* along the Colombian Caribbean Sea seems to indicate that environmental conditions did not induce different morphologies in individuals of different localities. Morphometric data of *F. notialis* showed a great homogeneity between different geographical regions, indicating the existence of a single population along the Colombian Caribbean Sea from the morphometric point of view. With this work we provide the first complete view, to this date, of the pink shrimp *F. notialis* stock structure and fishery dynamics, based on morphometric, historic landings and biologic data in the Colombian Caribbean Sea. The identification and knowledge of shrimp stock must be based on more than a single methodology and should comprise other stock identification approaches such as life-history (rate growth, recruitment, etc) and genetic analysis (Begg and Waldman 1999; Cadrin 2000; Robainas-Barcia et al. 2005; Robainas-Barcia et al. 2008). The shrimp fishery in the Colombian Caribbean is a typical case in which high exploitation, combined with non-existent fisheries management, have resulted in the significant depletion of shrimp stock. It has been seriously negatively impacted by overfishing, where spawning stock could have been reduced to a level in which the number of recruits produced is insufficient to maintain the population. Additionally, due to the possible low levels of spawning stock, reproduction and survival is reduced (Allee effect) by the inability to find mates, to resist predators or to withstand environmental fluctuations (King 2007). However, because the short life cycle, the shrimp fishery when is an overfishing stage, can be quickly recovered (Guillet, 2008). Finally, to aid in the recovery

of this shrimp fishery, the task to be carried out in the near future is a direct stock assessment and fishing management should be directed towards maintain fishing effort until spawning populations show signs of full recovery.

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### **3. Deep-sea shrimps *Aristaeomorpha foliacea* and *Pleoticus robustus* (Crustacea: Penaeoidea) in the Colombian Caribbean Sea as a new potential fishing resource**

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#### **Abstract**

In the Colombian Caribbean Sea a shallow water commercial shrimp fishery has been developed, targeting mainly *Farfantepenaeus notialis*. Yet, similarly so many fisheries around the world, the exploitation of this shrimp is not regulated, and a significant depletion has resulted. This study investigates new fishing areas, exploring the poorly understood deep sea habitats in the Colombian Caribbean Sea, to determine the potential for a viable deep shrimp fishery, studying their abundance and spatial distribution. We found high abundances for giant red shrimp (*Aristaeomorpha foliacea*) and royal red

shrimp (*Pleoticus robustus*), both important commercially. The higher biomass of these two deep shrimp species were found mainly in the northern zone of the Colombian Caribbean Sea, where the local oceanography is modulated by the seasonal upwelling with high productivity. The size structure following depth strata showed that *A. foliacea* increase of size with the depth and the contrary for *P. robustus*. The majority of adult individuals in these two deep shrimp species reflect the non-fished populations in the study area. However, more scientific assessment is necessary to determine life cycle population parameters of deep-sea shrimps and associated biodiversity before initiating a new commercial shrimp fishery.

Keywords: Colombian Caribbean Sea, spatial distribution, deep shrimps, *Penaeoidea*, *A. foliacea*, *P. robustus*.

## **Introduction**

Most tropical shrimps around the world are fully exploited and particularly when fisheries management is inefficient or lacking, serious socio-economic problems have resulted (Guillet, 2008). The failure in fisheries management has mainly originated under the pressure of the increased catch rate, a response to intense social-political pressure to obtain bigger catches in the short term and the intrinsic uncertainty of fisheries (Pauly et al., 2002; Pauly et al., 2003). Therefore, fisheries management requires a delicate balance between extraction and conservation of biodiversity and the ecosystem structure and function (Pikitch et al., 2004; Bianchi, 2008; Stokstad, 2009; Zhou et al., 2010), yet fisheries management must also consider food sources, income and livelihoods (Bianchi, 2008). Successful fisheries management also requires that the authorities incentivize conservation

and strong management strategies (Beddington et al., 2007; Worm et al., 2009), based on the characteristics of the habitats and its organisms (Pitcher et al., 2007). In the Colombian Caribbean Sea the shallow water shrimp fishery targets *Farfantepenaeus notialis* (Pérez Farfante, 1967), *Farfantepenaeus brasiliensis* (Latreille, 1817), *Farfantepenaeus subtilis* (Pérez Farfante, 1967) and *Litopenaeus schmitii* (Burkenroad, 1936) with *F. notialis* constituting ~70% of the total shrimp catch. This is a typical case of a collapsed-uncontrolled fishery with different development stages such as growth, fully-exploited, over-exploited, collapse and probably a recovery stage, having as resulted a significant depletion of shrimp stock (Paramo and Saint-Paul, 2010). In this sense, due to failure of traditional fisheries management measures, there is a necessity of additional fisheries management measures to those used traditionally that contribute to protect the fishing resources and to improve the fishing production, such as the identification of marine protected areas (MPAs) that have emerged as a tool for marine conservation and fisheries management (Worm et al., 2006; Fraser et al., 2009; Paramo et al., 2009). Therefore, the future development of the fishing sector should focus on the search for new resources that are economically attractive, yet at the same time exploitation should not put at risk sustainability. At the moment, there is not developed deep-sea fishery in the Colombian Caribbean Sea. The giant red shrimp *Aristaeomorpha foliacea* (Risso 1827) found in the deep waters of the Mediterranean Sea is a commercially important shrimp (D'Onghia et al., 1998; Figueiredo et al., 2001; Papaconstantinou and Kapiris, 2003; Politou et al., 2004; Mouffok et al., 2008). This species has a wide geographical distribution from the Mediterranean Sea and the eastern Atlantic, the western Atlantic, the Indian Ocean and the western Pacific from Japan to Australia, New Zealand and the Fiji Islands (Tavares, 2002). *A. foliacea* is found in deep waters from 250 to 1300 m over bottom mud and is actively

fished because of its high commercial value (Tavares, 2002). Gracia et al. (2010) recently explored deep waters off the Yucatan Peninsula in Mexico and showed that *A. foliacea* and *Pleoticus robustus* represent a potential fishing resource. Nowadays, *A. foliacea* constitute a valuable deep shrimp fishery off the south-eastern and southern sectors of the Brazilian coast (Dallagnolo et al., 2009). The royal red deep shrimp (*P. robustus*) inhabits continental slopes from 180 to 730 m depth, but larger abundances are found at depths between 250 and 475 m over mud, sand, muddy sand, or white calcareous mud. This species is only captured in high abundances off the coast of north-eastern Florida, near the Dry Tortugas islands, in the Mississippi delta and also off the coast of Venezuela (Tavares, 2002). This study is the first attempt to explore new fishing grounds in poorly understood deep sea habitats of the Colombian Caribbean Sea, to determine the potential for a viable deep sea shrimp fishery studying the abundance and spatial distribution of the giant red shrimp (*Aristaeomorpha foliacea*, Risso 1827) and royal red shrimp (*Pleoticus robustus*, Smith 1885), both species with increasing commercial value.

## **Materials and methods**

### **Study area and sampling design**

The Colombian Caribbean Sea is characterized by northeast trade winds with surface currents flowing in west and south-west directions almost parallel to coast. These trade winds are responsible for upwelling in the north zone of the study area, which increase the productivity on the Guajira coast (Andrade et al., 2003; Paramo et al., 2003; Paramo et al., 2009). Two experimental trawl surveys were carried out in 2009, the first in November (south zone) and the second in December (north zone). Data were collected by trawling in

depths ranging between 200 and 550 m (100 m strata intervals) in the Colombian Caribbean Sea. The location of trawl was based on trawlable bottoms found by the commercial echosounder FURUNO FCV 1150 with a transducer at a frequency of 28 kHz, on a grid of 87 stations, with at least two hauls per 100 m depth stratum (Fig. 1). Samples were collected by the commercial shrimp trawler “Tee Claude” using a trawl with a cod-end mesh size of 44.5 mm from knot to knot. Data between Cartagena and Magdalena River were not collected due to the irregular depths. The haul duration was 30 minutes and the distance travelled by the net was estimated by means of a GPS Garmin MAP 76CSx. The shrimp catch from each haul was calculated into biomass ( $\text{kg km}^{-2}$ ). The swept area was estimated from the spread of the net (11.58 m) and the speed of the vessel (average 2.5 knots) (King, 2007).

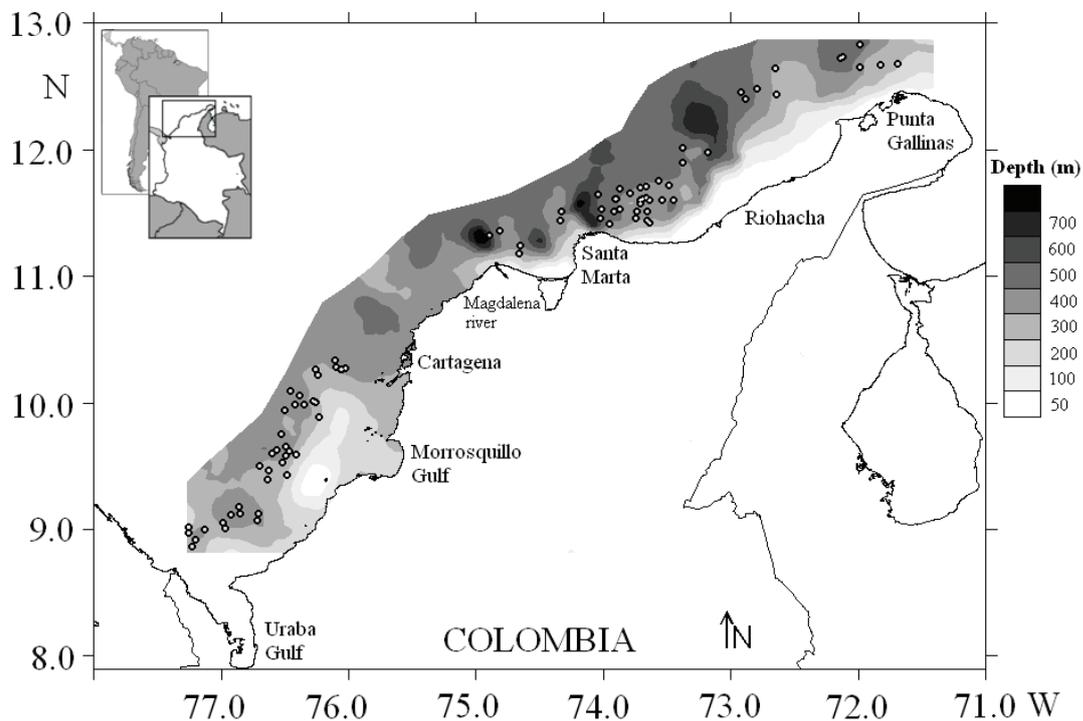


Figure 1. Study area in the Colombian Caribbean Sea. Circles indicate the sampled stations.

### **Size structure analysis**

Catches were identified at the species level. The total weight, sex and numbers of individuals per species from each station were recorded. All the specimens were weighed to the nearest 0.1 g and the cephalothorax length (CL) was measured to the nearest 0.1 mm using callipers from the posterior margin of the ocular indent to the posterior margin of CL. Size-frequency data of CL for female and male and for depth strata of *A. foliacea* and *P. robustus* were analyzed as a mixture of probability density functions (pdf), whose modes depend upon a combination of the distances between means, the magnitudes of the variances and the proportion of the individual numbers in each mode and the overall sample size, using the software MIX (Mixture Analysis) (MacDonald and Pitcher, 1979). The approach used was to minimize the chi-squared and to obtain a p-value in which the observed and estimated distributions were not significantly different (MacDonald and Pitcher, 1979). Differences in the frequency distributions among sex females or among depth-strata for both females and males were assessed using a non-parametric Kruskal-Wallis multi-sample test (Gotelli and Ellison, 2004). To determine which strata contributed to the observed significant differences, multiple comparisons using the Nemenyi and Dunn test were computed (Zar, 2009).

### **Spatial analysis**

Geostatistical analyses (Cressie, 1993; Petitgas, 1993) were used to describe the spatial structure of the deep shrimp distribution, as well as the mean density, biomass and its variance. The experimental variogram is defined as the variance of difference between values that are  $h$  units apart.

$$\hat{\gamma}(\mathbf{h}) = \frac{1}{2N(\mathbf{h})} \sum_{i=1}^{N(\mathbf{h})} z(x_i) - z(x_i + \mathbf{h})^2$$

where  $\hat{\gamma}(\mathbf{h})$  is semivariance,  $\mathbf{h}$  is a vector of distance and direction, and  $N(\mathbf{h})$  is the number of pairs of observations at distance  $h$  and given direction,  $z(x_i)$  is the shrimp density of *A. foliacea* for the  $i$ th data point. Since the *P. robustus* density was characterized by very many small and few large values, which can impact the variogram pattern and parameters (Paramo and Roa, 2003; Mello and Rose, 2005), we chose the robust (or stable) variogram estimator for this species (Cressie and Hawkins, 1980; Cressie, 1993).

$$2\hat{\gamma}(\mathbf{h}) = \frac{\left( \sum_{i=1}^{N(\mathbf{h})} |z(x_i) - z(x_i + \mathbf{h})|^{0.5} \right)^4}{\left( 0.457 + \frac{0.494}{|N(\mathbf{h})|} \right) N(\mathbf{h})^4}$$

In order to evaluate whether the spatial autocorrelations vary according to direction (anisotropic processes), experimental variograms were calculated for the raw data in four directions (0°, 45°, 90° and 135°). The spherical model of variogram was the most appropriate to explain the experimental variograms according to the weighted least-square minimization criterion (Cressie, 1993). Finally, ordinary point kriging was used to reproduce the stochastic processes across the region of interest, i.e. the mean density inside the spatial distribution area of these deep-sea shrimps (Isaaks and Srivastava, 1989). To estimate the variance of the mean shrimp density, the intrinsic geostatistical method was applied, in which the variance is dependent on the geometry in the area of spatial distribution, the sampling design, and the variogram structure (Petitgas and Prampart, 1995; Rivoirard et al., 2000). The spatial analysis were carried out in the R software (geoR library) (Ribeiro and Diggle, 2001).

## Results

### Size structure of deep-sea shrimps

Statistically significant differences for both species between sexes were found (Fig.2), revealing sexual dimorphism ( $p < 0.01$ ). Males were smaller than females in both species. The Kruskal-Wallis multisample test shows significant differences among depth strata for both females and males of *A. foliacea* and *P. robustus* ( $p < 0.01$ ). The size structure for *A. foliacea* females ranged between 18.5 and 63.1 mm CL (mean  $44.2 \pm 9.4$  mm) and for males between 23.5 and 59.1 mm CL (mean  $35.8 \pm 5.1$  mm). The entire frequency distribution of CL was characterized by 3 modes for the females of *A. foliacea* (Table 1). The first two modes of the total abundance represented 48% and the third 52% (mean 49.8 mm CL). In males of *A. foliacea*, one mode with 34.9 mm of CL was observed. The CL frequency distribution for *P. robustus* for females ranged between 21.2 and 62.8 mm CL (mean  $43.8 \pm 8.4$  mm) and for males between 24.3 and 54.8 mm (mean  $32.7 \pm 4.0$  mm). Furthermore, *P. robustus* showed three modes for females, the first mode represented 13% (size mean 28.0 mm CL) and the other two modes represented 68% (mean 42.3 mm CL) and 20% (mean 54.0 mm CL), respectively. The males of *P. robustus* showed one mode with 31.8 mm CL.

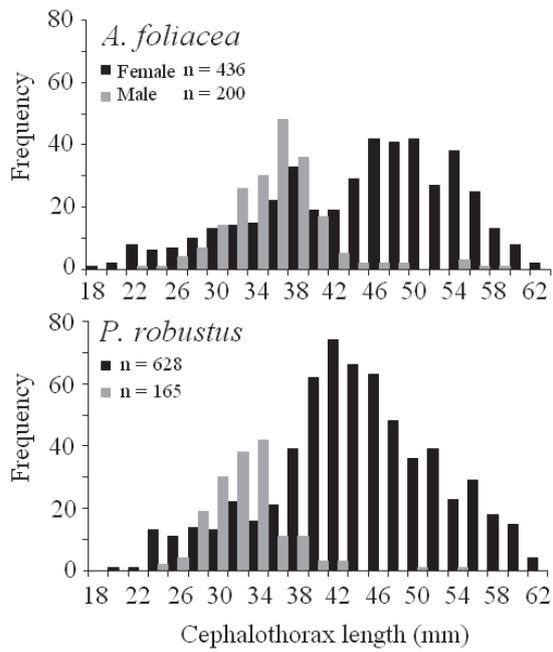


Figure 2. Size-frequency distributions of cephalothorax length (CL) for *Aristaeomorpha foliacea* and *Pleoticus robustus*.

Table 1. Frequency distribution parameters (proportions, means and standard deviations) for each mode of the histograms of CL of *Aristaeomorpha foliacea* and *Pleoticus robustus* by sex and strata.

Strata (m)	Species	Sex	Proportions			Means			Standard deviations			x <sup>2</sup>	p-value
			p1	p2	p3	μ1	μ2	μ3	σ1	σ2	σ3		
All	<i>A. foliacea</i>	F	0.02	0.46	0.52	21.33	36.70	49.84	0.99	7.38	4.73	19.06	0.211
All	<i>A. foliacea</i>	M	1.00	-	-	34.90	-	-	5.40	-	-	79.57	0.000
All	<i>P. robustus</i>	F	0.13	0.68	0.20	27.97	42.28	53.99	3.79	4.63	3.70	17.25	0.243
All	<i>P. robustus</i>	M	1.00	-	-	31.81	-	-	4.39	-	-	72.16	0.000
200-300	<i>A. foliacea</i>	F	0.18	0.67	0.15	22.39	35.22	47.57	1.93	4.88	2.83	6.4	0.696
300-400	<i>A. foliacea</i>	F	0.02	0.41	0.57	21.00	34.43	47.31	1.01	5.74	6.00	16.3	0.294
400-500	<i>A. foliacea</i>	F	0.10	0.90	-	33.09	48.94	-	5.80	5.07	-	12.2	0.594
>500	<i>A. foliacea</i>	F	0.18	0.82	-	44.11	54.18	-	4.26	2.92	-	10.1	0.183
200-300	<i>A. foliacea</i>	M	1.00	-	-	28.87	-	-	3.24	-	-	2.6	0.631
300-400	<i>A. foliacea</i>	M	1.00	-	-	34.34	-	-	4.29	-	-	22.4	0.033
400-500	<i>A. foliacea</i>	M	1.00	-	-	34.70	-	-	3.18	-	-	9.4	0.153
>500	<i>A. foliacea</i>	M	1.00	-	-	37.24	-	-	3.29	-	-	1.4	0.922
200-300	<i>P. robustus</i>	F	1.00	-	-	43.46	-	-	8.13	-	-	16.7	0.274
300-400	<i>P. robustus</i>	F	0.04	0.96	-	22.75	45.35	-	3.88	6.46	-	9.3	0.813
400-500	<i>P. robustus</i>	F	0.29	0.41	0.30	30.98	41.59	50.60	4.97	2.94	5.37	12.0	0.608
>500	<i>P. robustus</i>	F	0.14	0.73	0.13	26.55	43.18	57.63	2.78	3.95	2.14	18.1	0.079
200-300	<i>P. robustus</i>	M	-	-	-	-	-	-	-	-	-	-	-
300-400	<i>P. robustus</i>	M	1.00	-	-	33.71	-	-	3.82	-	-	9.1	0.104
400-500	<i>P. robustus</i>	M	1.00	-	-	31.51	-	-	4.52	-	-	76.9	0.000
>500	<i>P. robustus</i>	M	1.00	-	-	28.66	-	-	4.34	-	-	4.3	0.366

The size structure for female *A. foliacea* showed an increase in CL with depth, having a three modal trend for the 200-300 and 300-400 m strata and two modes for 400-500 and >500 m strata (Fig. 3; Table 1). The males of *A. foliacea* had a modal structure, also an increasing CL with depth. The means of CL of *A. foliacea* female differs significantly among strata, but means of males differ only in the first strata in comparison to the others (Table 2). Otherwise, the shrimp *P. robustus* showed a tendency to decreasing size with depth. The three modal dispositions for females in this species were found in the 300-400

and >500 m, the males showed a one-modal size structure in all strata (Table 1). The means of CL of the *P. robustus* females and males only show significant differences for the 300-400 vs 400-500 m depth strata (Table 2).

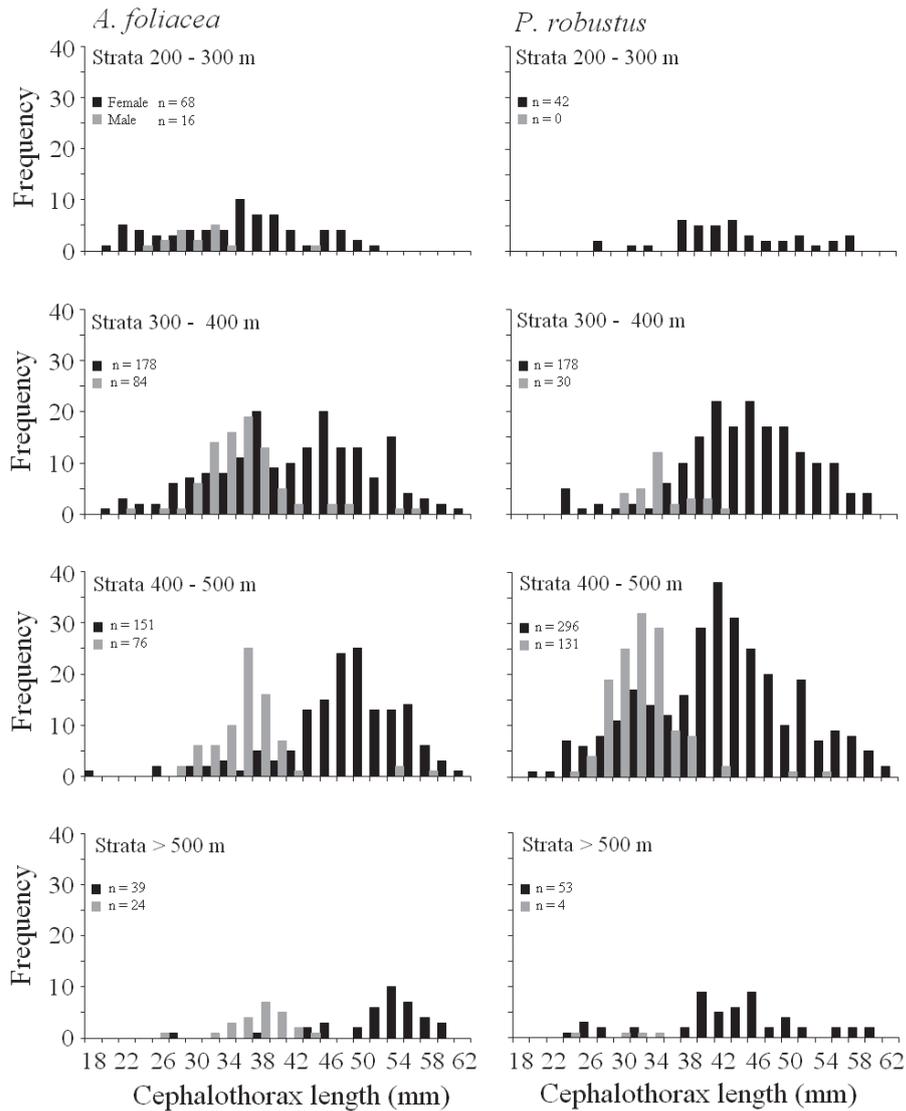


Figure 3. Size-frequency distribution of Cephalothorax length (CL) by sex and depth strata for *Aristaeomorpha foliacea* and *Pleoticus robustus*.

Table 2. Nemenyi and Dunn test for differences between means of cephalothorax length (CL) by strata for *Aristaeomorpha foliacea* and *Pleoticus robustus*. Strata: I (200 – 300 m), II (300 – 400 m), III (400 – 500 m), IV (> 500 m).

Strata	<i>A. foliacea</i>		<i>P. robustus</i>	
	Female	Male	Female	Male
I - II	0.000	0.000	0.717	-
I - III	0.000	0.000	0.214	-
I - IV	0.000	0.000	0.764	-
II - III	0.000	0.730	0.000	0.005
II - IV	0.000	0.268	0.169	0.022
III - IV	0.036	0.565	0.668	0.255

### Spatial analysis

The unidirectional variograms showed spatial similarity in their modelling of spatial characteristics for both species (Fig. 4a,b). In fact, the anisotropy ratio between the maximum and minimum value of spatial autocorrelation range in the unidirectional variograms was less than 2 (Table 3), which suggests the absence of anisotropy. Therefore, the spatial structure of deep sea shrimp biomass ( $\text{kg km}^{-2}$ ) was studied through an experimental isotropic variogram (Fig. 4c, d), to which a spherical model was fitted. The variograms showed a non-resolved structure for the sampling design that considered for *A. foliacea* 8.5% and for *P. robustus* 0.0% of total variance (nugget as percentage of sill) (Table 3). The autocorrelation range of the shrimp aggregation for *A. foliacea* was 24.7 km and for *P. robustus* 38.2 km (Table 3). For both shrimps the higher biomass values were distributed in well defined spatial patches in the northern zone of the Colombian Caribbean Sea (Fig. 5). The bulk of biomass for both species was distributed between Santa Marta and Riohacha. However, the patches of *P. robustus* were more abundant, with higher concentrations off Punta Gallinas. In the southern zone, this species revealed high

abundances between Cartagena and southwest off the Morrosquillo gulf. *P. robustus* presented higher values of mean density and biomass than *A. foliacea*, the precision was between 10.0 and 23.3%, respectively (Table 4).

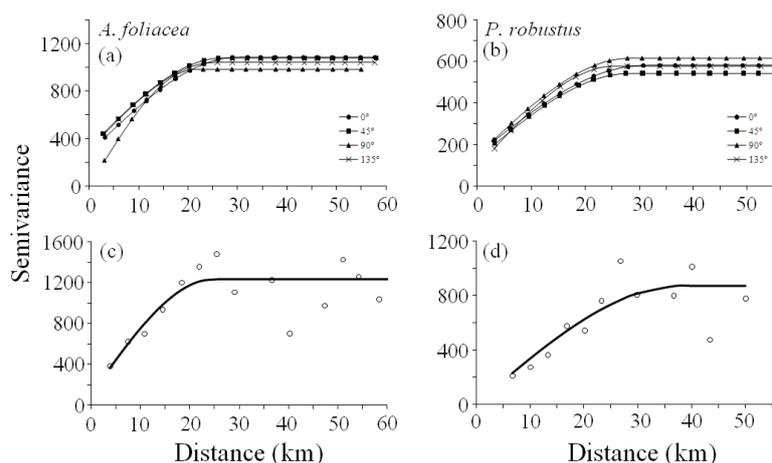


Figure 4. Directional experimental (a,b) and omnidirectional (c,d) variograms showing an isotropic process for abundance of *Aristaeomorpha foliacea* (a,c) and *Pleoticus robustus* (b,d) in Colombian Caribbean Sea.

Table 3. Analysis of anisotropy, a spherical variogram model fitted to the directional empirical variogram and omnidirectional spherical model of variogram for *Aristaeomorpha foliacea* and *Pleoticus robustus*.

Species	Parameter	0°	45°	90°	135°	Isotropic
<i>A. foliacea</i>	Nugget	281.0	319.9	0.0	311.9	104.5
	Nugget (%sill)	25.9	29.6	0.0	30.0	8.5
	Sill	803.1	759.1	985.5	729.5	1130.2
	Range	30.0	26.8	21.4	25.4	24.7
	Ratio	1.0	1.1	1.4	1.2	-
<i>P. robustus</i>	Nugget	155.9	134.8	148.7	89.3	0.0
	Nugget (%sill)	26.8	24.8	24.2	15.5	0.0
	Sill	424.8	408.0	465.9	486.5	868.5
	Range	30.9	28.1	28.3	25.3	38.2
	Ratio	1.0	1.1	1.1	1.2	-

Table 4. Assessment of biomass of deep shrimp species obtained by geostatistic in the Colombian Caribbean Sea.

Shrimp species	Estimated mean biomass ( $\text{kg km}^{-2}$ )	Estimated total biomass (kg)	Variance	Coefficient of Variation (CV %)
<i>A. foliacea</i>	16.3	457 947	14.3	23.3
<i>P. robustus</i>	34.6	1 037 106	12.1	10.0

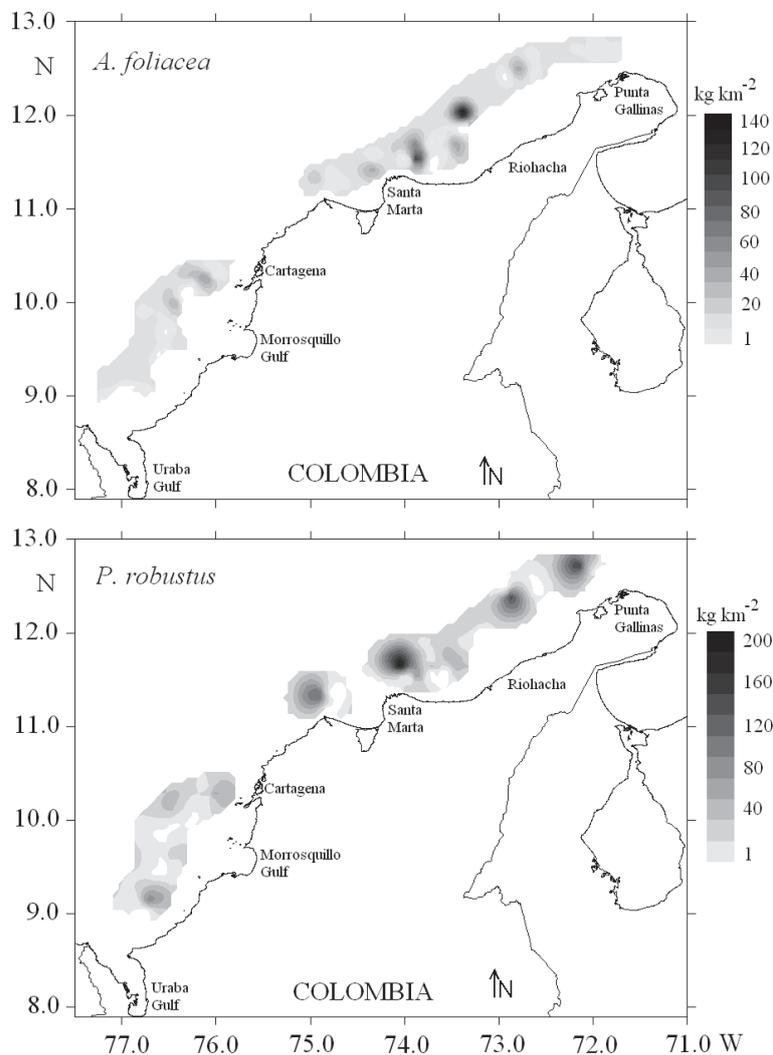


Figure 5. Spatial distribution of *Aristeomorpha foliacea* and *Pleoticus robustus* abundances ( $\text{kg km}^{-2}$ ) as the reproduction of a spatially stochastic process by kriging.

## Discussion

The deep-sea shrimps have a patchy distribution (D'Onghia et al., 1998; Belcari et al., 2003), which justifies the importance of using spatial statistical methods such as the geostatistic to address the spatial distribution structure and calculate the biomass more precisely (Paramo and Roa, 2003). Studying the spatial distribution of populations is of great importance for ecological studies, because in the nature most of marine organisms are not distributed at random, rather, they are forming patches, gradients or other types of spatial structures (Legendre and Legendre, 1998; Rivoirard et al., 2000; Paramo and Roa, 2003). Also, successful fisheries management in new fisheries require the knowledge of population abundance, the spatial distribution and size structure (Rivoirard et al., 2000), since failure to recognize spatial complexity of fisheries has resulted in stock collapses (Hilborn and Walters, 2003; Katsanevakis and Maravelias, 2009). The higher biomass of these two deep shrimp species were found mainly in the northern zone of the Colombian Caribbean Sea, where the local oceanography is modulated by the seasonal upwelling with high productivity (Paramo et al., 2003; Paramo et al., 2009). In the eastern Ionian Sea *A. foliacea* is associated with areas of significant upward nutrient transport, which may result in greater biological productivity (Politou et al., 2004).

Our results showed that in both species the number of females was higher than males. This characteristic was also found for *A. foliacea* in the Mediterranean Sea indicating segregation between sexes (D'Onghia et al., 1998; Papaconstantinou and Kapisris, 2003). The different modes showed for both species (3 modes for females and 1 for males), which

agree with the growth of *A. foliacea* in the Mediterranean Sea, in females is faster than males and the longevity of females (3-4 year classes) is higher than males (2 year classes) (Papaconstantinou and Kapiris, 2003). The mean size of *A. foliacea* (female 44.2 mm; male 35.8 mm CL) is similar to the same species found at an unexploited fishing ground in the Greek Ionian Sea in depths between 250 and 800 m (Papaconstantinou and Kapiris, 2003) and higher than size of maximum reproductive potential in females (37.11 mm CL) (D'Onghia et al., 1998). The pattern of increasing size with depth was also found throughout the Mediterranean basin (Politou et al., 2004), in the Greek Ionian Sea (Papaconstantinou and Kapiris, 2003), and in the Portuguese continental slope (Figueiredo et al., 2001). D'Onghia et al. (1998) found that the very small individuals of *A. foliacea* in the north-western Ionian Sea had a shallower distribution (upper 500 m). Additionally, during the winter-spring season the population rise out from deepest areas and migrate to the upper slope. Then, after the mating peak in summer, when spawning take place, the population is again displaced on the deeper grounds (D'Onghia et al., 1998). Therefore, the bathymetric gradient in size could be explained by reproductive aspects and spatial segregation of the different year classes. *P. robustus* showed a mean size (female 43.8 mm; male 32.7 mm CL), similar to what has been reported off the Yucatan Peninsula in Mexico (Gracia et al., 2010). Our study found that the majority of adult individuals in these two deep shrimp species reflect the non-fished populations in the study area. The *A. foliacea* biomass reported here was higher than the same species from the Balearic (0.76 kg km<sup>-2</sup>) and western Ionian Sea (1.00 kg km<sup>-2</sup>), but similar to that reported from the Eastern Ionian Sea (14.33 – 95.35 kg km<sup>-2</sup>) (Politou et al., 2004), which provides crucial support to the proposed development of a new fishery in the Colombian Caribbean Sea.

The non-overlapping of abundances in spatial distribution, suggest use of different niche areas. However, *A. foliacea* is found from 250 to 1300 m (Tavares, 2002) and higher concentrations were located between 500 and 600 m in the Greek Ionian Sea (Papaconstantinou and Kapiris, 2003), therefore, more research is need in deeper strata to delimit the spatial distribution of this species in the Colombian Caribbean Sea. Our results point to the necessity of more scientific biological research to aid in the understanding of the life cycle parameters of these deep water shrimps, including growth, recruitment, mortality, areas and seasons of spawning, nursery regions, and associated biodiversity, before beginning concrete steps to initiate a new commercial fishery. Management and conservation strategies, taking into account the ecosystem approach to fisheries management must be also considered. The substantial marketability of these deep-sea shrimp species, not only on the local level but also in numerous international markets (Belcari et al., 2003; Papaconstantinos and Kapiris, 2003), make these deep-sea shrimps a potential new economic resource in the Colombian Caribbean Sea.

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#### **4. Spatial structure of the pink speckled deep-sea shrimp *Penaeopsis serrata* (Bate, 1881) (Decapoda, Penaeidae) during November-December 2009 in the Colombian Caribbean Sea**

*Crustaceana*. 2011. InPress.

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#### **Abstract**

The objective of this work is to describe for the first time the patterns of spatial distribution of abundance of the pink speckled deep-sea shrimp *Penaeopsis serrata* (Bate, 1881) in the Colombian Caribbean Sea. Data were collected by trawling at depths between 100 and 550 m. Significant differences between sexes were found, revealing sexual dimorphism, males were smaller than females. The size structure for female showed an increase in association to depth. The higher biomass of *P. serrata* was found between 350 and 450 m, which suggest that this species prefers narrow depth strata. Due to vulnerability of deep-sea species and habitats, are necessary actions of protection, which limits to fishing in order to guarantee a sustainable management and conservation of fisheries.

## **Introduction**

Species of the family Penaeidae are the most valuable marine commercial shrimps in tropical and subtropical waters (Tavares, 2002; Guillet, 2008), which accounts for 95% of the total shrimp production from the western central Atlantic (Tavares, 2002). Deep-sea shrimps are commercially exploited around the world and *P. serrata* is of potential commercial importance in the western and eastern Atlantic (Holthuis, 1980). The species of the genus *Penaeopsis* are benthic, occur in the upper part of the continental and insular slopes, on sandy-muddy bottoms of tropical and subtropical regions (Pérez-Farfante, 1980). *P. serrata* is distributed in the eastern Atlantic off north-western Africa (Morocco), the western Atlantic in North Carolina (USA) to Surinam, Bahamas Islands, Gulf of Mexico, Caribbean Sea (Holthuis, 1980; Pérez-Farfante, 1980) and the Mediterranean Sea off Alboran Sea and the Sardinian Channel (Mura et al., 2002). As far we know, very little is known about the biology and distribution of *P. serrata*. The objective of this work is to describe for the first time the patterns of spatial distribution of abundance of the pink speckled deep-sea shrimp *P. serrata* in the Colombian Caribbean Sea.

## **Material and methods**

Data were collected by trawling in water depths between 100 and 550 m at 24 h intervals in the Colombian Caribbean Sea, during two experimental trawl surveys carried out the first one in November 2009 (south zone) and the second in December 2009 (north zone) (fig. 1). The sample period corresponds to the dry season when the high-pressure system forces strong and constant westward trade winds, and the northern zone is affected by the Caribbean current and the upwelling of deep waters (Paramo et al., 2003). Samples were

collected by the commercial shrimp trawler “Tee Claude” using a trawl with a cod-end diamond mesh size of 44.5 mm from knot to knot, on a grid of 87 stations, with at least two hauls inside of 100 m depth stratum. We were unable to collect data between Cartagena and the Magdalena River because of irregular depths. The location of trawl depended on the presence of trawlable bottoms using a commercial echosounder FURUNO FCV 1150 with a transducer at a frequency of 28 kHz. Haul duration was 30 minutes and the distance travelled by the net was estimated by means of a GPS Garmin MAP 76CSx. The swept area was estimated from the spread of the net (11.58 m) and the speed of the vessel (average 4.63 km/h) (Gunderson, 1993; King, 2007). The pink speckled deep-sea shrimp catch from each haul was calculated into CPUA (catch per unit area) ( $\text{kg}/\text{km}^2$ ).

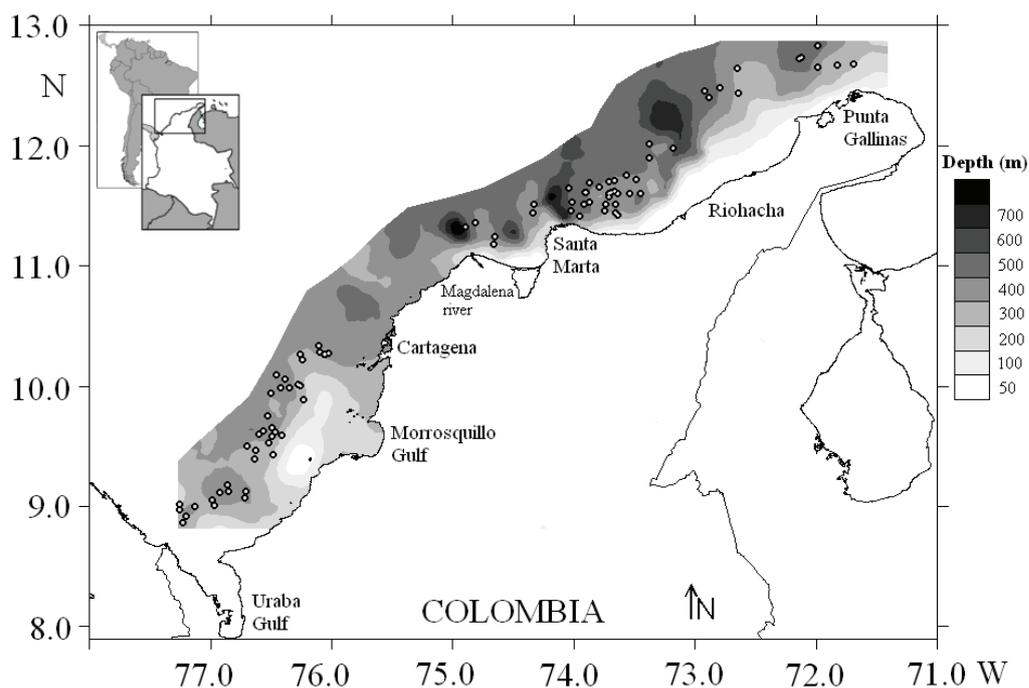


Figure 1. Study area in the Colombian Caribbean Sea. Circles indicate the sampled stations during November-December 2009.

The total weight, size, sex and numbers of individuals per species from each station were recorded. All the specimens were weighed to the nearest 0.1 g and the carapace length (CL) was measured to the nearest 0.1 mm using callipers from the posterior margin of the ocular indent to the posterior margin of CL. The frequency data of CL for female and male and for depth strata of *P. serrata* were analysed as a Gaussian mixture of probability density functions (pdf), whose modes depend upon a combination of the distances between means, the magnitudes of the variances and the proportion of the individual numbers in each mode and the overall sample size (MacDonald & Pitcher, 1979). The quasi-Newton algorithm was used to fit the frequency of data per individual to obtain the means (MacDonald & Pitcher, 1979). Differences in the frequency distributions among sex females or among depth-strata for both females and males were assessed using a non-parametric Kruskal-Wallis multi-sample test (Gotelli & Ellison, 2004). To determine which strata contributed to the observed significant differences, multiple comparisons using the Nemenyi and Dunn test were computed (Zar, 2009).

Geostatistical analyses (Cressie, 1993; Petitgas, 1993; Rivoirard et al., 2000) were used to describe the spatial structure of the pink speckled deep-sea shrimp distribution, as well as the mean density, biomass and its variance. The experimental variogram is defined as the variance of difference between values that are  $h$  units apart.

$$\hat{\gamma}(\mathbf{h}) = \frac{1}{2N(\mathbf{h})} \sum_{i=1}^{N(\mathbf{h})} z(x_i) - z(x_i + \mathbf{h})^2$$

where  $\hat{\gamma}(\mathbf{h})$  is semivariance,  $\mathbf{h}$  is a vector of distance and direction, and  $N(\mathbf{h})$  is the number of pairs of observations at distance  $h$  and given direction,  $z(x_i)$  is the density of P.serrata for the  $i$ th data point. In order to evaluate the anisotropic processes, experimental variograms were calculated for raw data in four directions (0°, 45°, 90° and 135°). The spherical

variogram model was the best in explaining the experimental variograms according to the weighted least-square minimization criterion (Cressie, 1993). Finally, ordinary point kriging was used to map the spatial distribution, estimate the variance of the mean density, and the biomass (Isaaks & Srivastava, 1990; Petitgas & Prampart, 1995; Rivoirard et al., 2000).

Generalized Additive Modelling (GAM) (Hastie & Tibshirani, 1990) was used to analyze the depth preferences in abundance of P. serrata. An additive model is an extension of linear models, but allows linear functions of predictors (depth) to be replaced by smoothing functions:

$$y = \alpha + \sum_{i=1}^n f_i(X_i) + \varepsilon$$

Where  $y$  is the response,  $X_i$  is the predictor,  $\alpha$  is a constant and  $\varepsilon$  is the error. The  $f_i$  is estimated using smoothers. We used spline (s) smoothing function with a Gaussian family and to evaluate the probability level of the nonlinear contribution of the nonparametric terms was made with the significance value (p) for judging goodness-of-fit.

## Results

The size of *Penaeopsis serrata* females ranged between 11.5 and 32.7 mm CL (mean 22.2 mm  $\pm$  3.8 standard deviation, SD) and for males between 12.2 and 27.6 mm CL (mean 19.0 mm  $\pm$  2.6 SD). Statistically significant differences between sexes were found (fig.2), revealing sexual dimorphism (p = 0.00), males were smaller than females. The entire frequency distribution of CL was characterized by 2 modes for female and 1 for male (table I). For females the first mode represented 70% (mean 19.6 mm CL) and the second one

30% of all females analysed (mean 24.2 mm CL). The males showed one mode with mean size of 18.0 mm CL (table I).

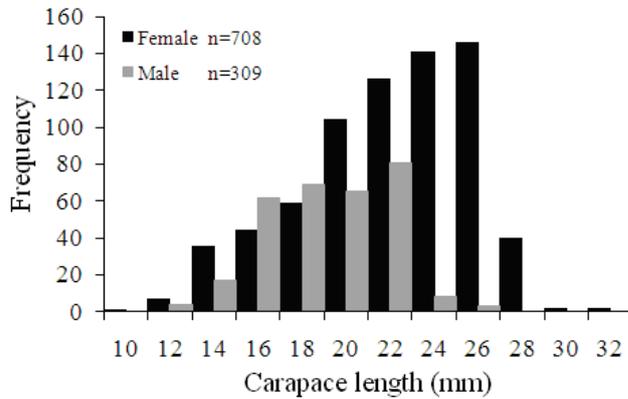


Figure 2. Length frequency distributions of *Penaeopsis serrata* of carapace length (CL).

Table I. Frequency distribution parameters (proportions, means and standard deviations (SD) for each mode of the histograms of CL of *Penaeopsis serrata* by sex and strata. Mean and standard deviations are from normal pdf.

Strata (m)	Sex	Proportions		Means		SD	
		$p1$	$p2$	$\mu1$	$\mu2$	$\sigma1$	$\sigma2$
All	F	0.7	0.3	19.6	24.2	3.7	1.5
All	M	1.0	-	18.0	-	2.7	-
100-200	F	1.0	-	18.2	-	3.6	-
200-300	F	0.7	0.3	14.7	21.8	2.4	4.2
300-400	F	0.8	0.2	20.0	24.7	3.4	0.9
400-500	F	1.0	-	22.6	-	2.4	-
>500	F	1.0	-	25.1	-	1.9	-
100-200	M	1.0	-	12.9	-	2.9	-
200-300	M	1.0	-	17.6	-	2.6	-
300-400	M	1.0	-	16.1	-	2.3	-
400-500	M	1.0	-	19.4	-	2.1	-
>500	M	-	-	-	-	-	-

The Kruskal-Wallis multisample test shows significant differences among depth strata for both females and males of *P. serrata* ( $p < 0.01$ ). The size structure for female *P. serrata* showed an increase in CL in association to depth, with an one modal trend for the 100-200 and two modes for 200-300 and 300-400 m strata (fig. 3; table I), and one mode for 400-500 and >500 m strata. The two modes of the females in the second and third strata seem to mix in the fourth strata (400-500 m). The males of *P. serrata* showed a one-modal size structure in all strata, also increasing CL with depth, but in the >500 m strata we did not found males. Nemenyi and Dunn test between means of CL by strata showed significant differences for females and males ( $p \leq 0.01$ ).

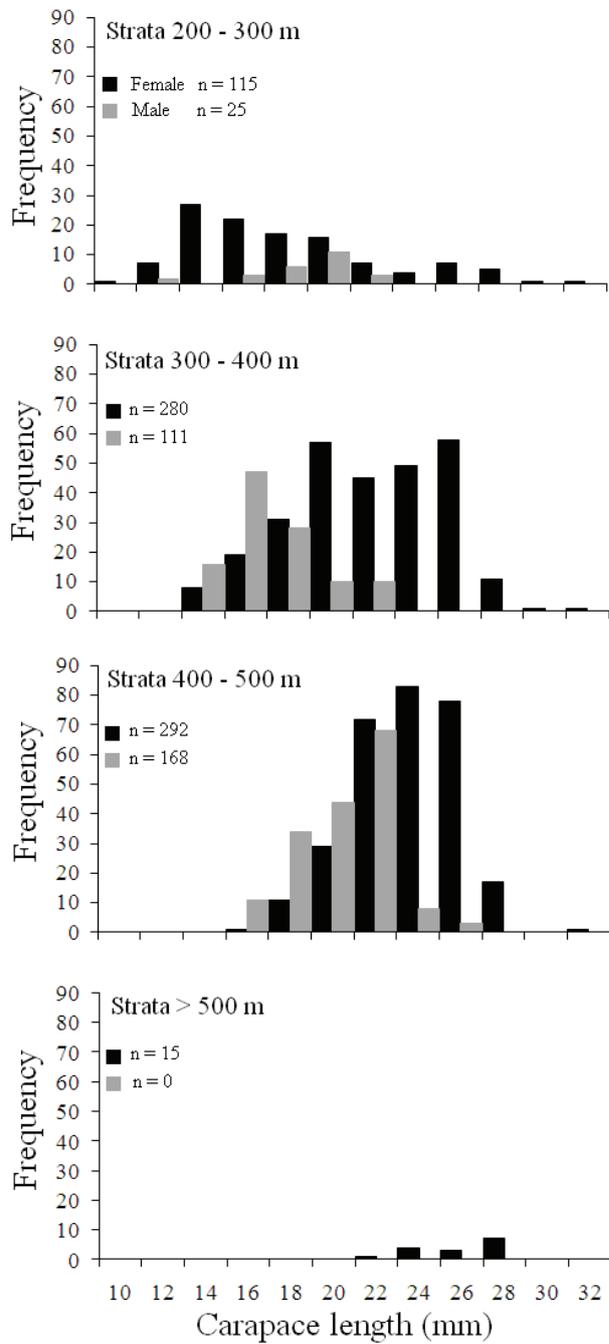


Figure 3. Length frequency distribution of carapace length (CL) by sex and strata for *Penaeopsis serrata*.

The unidirectional variograms showed similarities in their modelling of spatial characteristics for *P.serrata* (fig. 4a). This absence of geometric anisotropy can be demonstrated with the ratio between the maximum and minimum values of the spatial autocorrelation range in the unidirectional variograms, which was less than 2 (table II). Therefore, the spatial structure of the pink speckled deep-sea shrimp biomass ( $\text{kg}/\text{km}^2$ ) was studied using an experimental isotropic variogram (fig. 4b). The fitted spherical variogram showed a non-resolved structure for the sampling design that considered 10.6% of total variance (nugget as percentage of sill) (table II). The autocorrelation range of the pink speckled deep-sea shrimp was 198.0 km, i.e. the diameter of *P. serrata* aggregations of high-density patches (table II). The higher biomass values were distributed in one well defined spatial patch in the northern zone of the Colombian Caribbean Sea off Riohacha and Punta Gallinas (mean density =  $14.0 \text{ kg}/\text{km}^2$ ; biomass = 213 288 kg; CV = 25.4). In the southern zone, this species revealed high abundances between Cartagena and off the Morrosquillo gulf (mean density =  $11.0 \text{ kg}/\text{km}^2$ ; biomass = 110 018 kg; CV = 32.4) (fig. 5). The estimated mean density and biomass for the combined study area was  $12.7 \text{ kg}/\text{km}^2$  and 323 306 kg (CV=27.9).

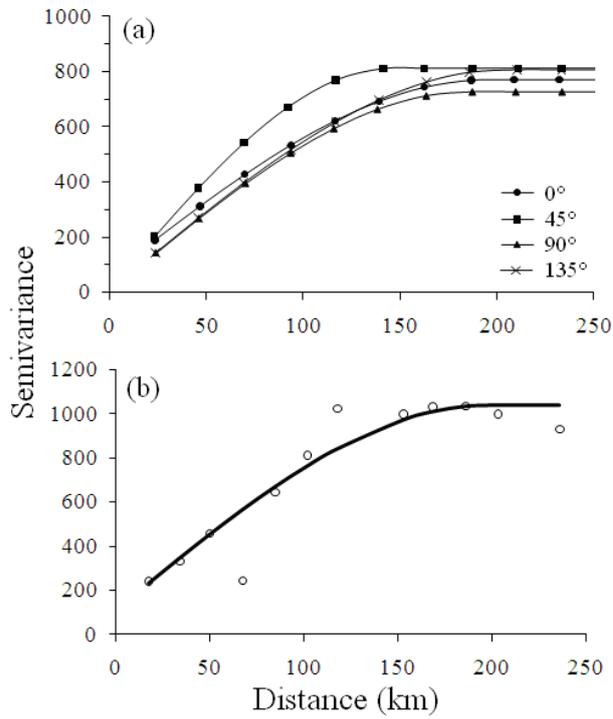


Figure 4. Directional experimental and omnidirectional variograms showing an isotropic process in abundance of *Penaeopsis serrata* in Colombian Caribbean Sea.

Table II. Analysis of anisotropy, spherical variogram model fitted to the directional empirical variogram and Omnidirectional spherical model of variogram for *Penaeopsis serrata*.

Parameter	0°	45°	90°	135°	Isotropic
Nugget	61.7	11.9	3.1	3.2	110.2
Nugget (%sill)	8.0	1.5	0.4	0.4	10.6
Sill	709.1	798.7	724.5	803.3	x927.5
Range (km)	194.4	144.8	185.0	204.2	198.0
Ratio	1.1	1.4	1.1	1.0	-

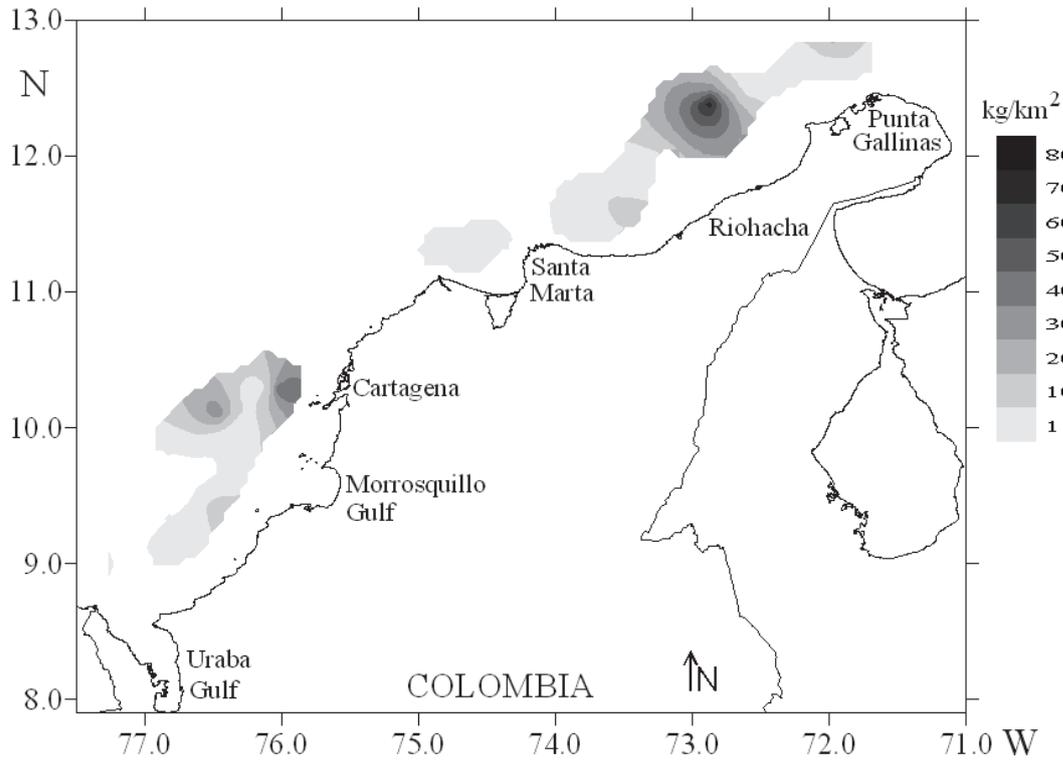


Figure 5. Spatial distribution of *Penaeopsis serrata* abundances (kg/km<sup>2</sup>) as the reproduction of a spatially stochastic process by kriging.

The nonlinear contribution of the nonparametric terms was significantly ( $p=0.00$ ) in explaining the variability of depth preferences in abundance of *P. serrata*. The relationship between the biomass of *P. serrata* and depth shows that higher biomass was found between 350 and 450 m (fig. 6).

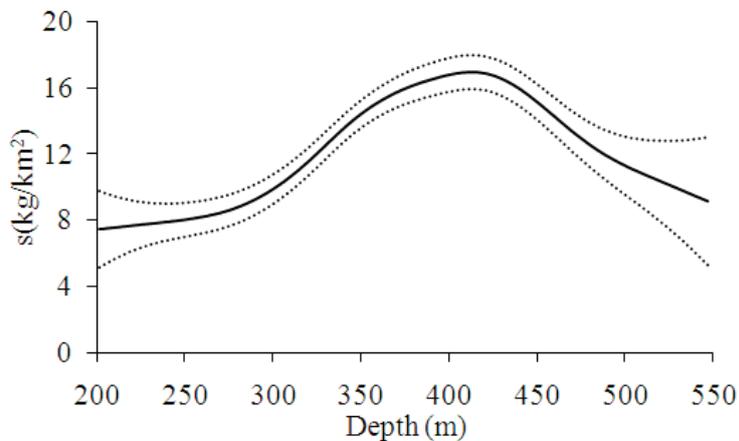


Figure 6. Modelling of functional relationship between biomass with depth preferences in catches.

## Discussion

Studying the spatial distribution of populations is of great importance for ecological studies, because in the nature most of marine organisms are not distributed at random, rather, they are forming patches, gradients or other types of spatial structures (Legendre & Fortin, 1989; Legendre, 1993; Legendre & Legendre, 1998; Rivoirard et al., 2000). Also, successful fisheries management require the knowledge of population abundance, the spatial distribution and size structure (Rivoirard et al., 2000), since failure to recognize spatial complexity of fisheries has resulted in stock collapses (Hilborn & Walters, 2003; Katsanevakis & Maravelias, 2009). Additionally, deep-sea shrimps may have a patchy distribution (D'Onghia et al., 1998; Maynou et al., 1998; Belcari et al., 2003), which justifies the importance of using spatial statistical methods such as the geostatistic to address the spatial distribution structure and calculate the biomass more precisely (Paramo & Roa, 2003). The higher biomass of *P. serrata* was found mainly in the northern zone of the Colombian Caribbean Sea, where the local oceanography is modulated by the seasonal

upwelling with high productivity (Paramo et al., 2003; Paramo et al., 2009). The Colombian Caribbean Sea is characterized by northeast trade winds with surface currents flowing in westerly and south-westerly directions almost parallel to the coast. These trade winds are responsible for upwelling in the northern zone of the study area, which increases the productivity along the Guajira coast (Andrade et al., 2003; Paramo et al., 2003; Paramo et al., 2009). In the eastern Ionian Sea, a similar deep-sea shrimp *Aristaeomorpha foliacea* (Risso, 1827) is associated with areas of significant upward nutrient transport, which may result in greater biological productivity (Politou et al., 2004). The abundance of *A. foliacea* tend to be higher at more than 600 m in the western Atlantic (Guéguen, 2000; Pezzuto et al., 2006) and eastern Atlantic (D'Onghia et al., 1998; Politou et al., 2004), but *P. serrata* is present in depths between 120 to 750 m with maximum concentrations occurring from 300 to 450 m (Holthuis, 1980; Pérez-Farfante, 1980). Indeed, we found this species in all depths strata, but higher biomass was found between 350 and 450 m, which suggest that *P. serrata* prefers narrow depth strata. The pattern of increasing size with depth was also found in other deep-sea shrimp *Aristaeomorpha foliacea* in the Colombian Caribbean Sea (Paramo & Saint-Paul, 2011), throughout the Mediterranean basin (Politou et al., 2004), in the Greek Ionian Sea (Papaconstantinou & Kapiris, 2003), and in the Portuguese continental slope (Figueiredo et al., 2001). The median carapace lengths of females of *Aristeus antennatus* (Risso, 1816) also showed a significant increasing trend with depth in the Italian areas of Mediterranean Sea (D'Onghia et al., 2005). The very small individuals of *A. foliacea* in the north-western Ionian Sea had a shallower distribution (upper 500 m) (D'Onghia et al., 1998). Additionally, during the winter-spring season the population rise out from deepest areas and migrate to the upper slope. Then, after the mating peak in summer, when spawning take place, the population is again displaced on the deeper

grounds (D'Onghia et al., 1998). Therefore, the bathymetric gradient in size of *P.serrata* could be explained by reproductive aspects and spatial segregation of the different year classes. The *P. serrata* biomass reported here was higher than similar deep-sea shrimp *A. foliacea* from the Balearic (0.76 kg/km<sup>2</sup>) and western Ionian Sea (1.00 kg/km<sup>2</sup>), but similar to that reported from the Eastern Ionian Sea (14.33 – 95.35 kg/km<sup>2</sup>) (Politou et al., 2004). Gracia et al. (2010) explored recently deep-sea shrimps off the Yucatan Peninsula in Mexico showing that *P. serrata* ranked second in number (26.8%) among others deep-sea shrimps. Nevertheless, according to our results, more scientific biological research is needed to understand the life cycle parameters of *P. serrata* such as growth, reproduction size, recruitment, mortality, areas and season of spawning, nursery areas and associate biodiversity. This research show results during November-December upwelling season (Paramo et al., 2003). Therefore, further studies must be carried out to look into the temporal seasonality to know how the spatial distribution of *P. serrata* changes as a response to the environmental changes and the interaction with other species. Therefore, quantitative analysis with other environmental variables (i.e. temperature, salinity, oxygen) apart from depth, need to be conducted. Also, the diel pattern could affect the catches of shrimps because the individuals can move horizontally or vertically (Tobar & Sàrda, 1992), which requires more investigation for *P. serrrata* in the study area. Additionally, due to vulnerability of deep-sea species and habitats, are necessary actions of protection, which limits to fishing in order to guarantee a sustainable management and conservation of fisheries (Roberts, 2002; Devine et al., 2006; Hart & Pearson, 2011), such as the identification of marine protected areas that have emerged as a tool for marine conservation and fisheries management following an ecosystem-based management (Worm et al., 2006; Fraser et al., 2009; Paramo et al., 2009; Jackson & Jacquet, 2011).

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## 5. Spatial structure of the Caribbean lobster (*Metanephrops binghami*) in the Colombian Caribbean Sea

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### Abstract

Crustaceans of the genus *Metanephrops* are of great commercial value in some tropical and subtropical regions. With the potential development of a new deep lobster fishery in the Colombian Caribbean Sea, the objective of this work is to describe for first time the patterns of spatial and bathymetric distribution, and diel migratory periodicity of the Caribbean lobster (*M. binghami*). Data were collected by trawling in depths between 200 and 550 m (100 m strata intervals) in the Colombian Caribbean Sea. Higher biomass and size of these crustaceans were found between 250 to 350 m, with a maximum at about 300 m. The study offers diel patterns of *M. binghami*, which suggests nocturnal activity and burrowing during daylight hours.

Keywords: Colombian Caribbean, deep sea Caribbean lobster, diel periodicity, abundance.

## Introduction

Species of the genus *Metanephrops* (Decapoda, Nephropidae) are dwellers of the outer continental shelf and continental slope (Tshudy et al. 2007) and are divided into four morphologic groups: *arafurensis*, *binghami*, *japonicus* and *thomsoni* (Tshudy et al. 2007; Chan et al. 2009). The *binghami* group is the only one distributed throughout the western Atlantic and is also known from southern high latitudes (Tshudy et al. 2007; Chan et al. 2009). This group contain only two species, the Caribbean lobster (*Metanephrops binghami* Boone 1927) and the Urugavian lobster (*Metanephrops rubellus* Moreira 1903). *M. binghami* is distributed from the Bahamas and southern Florida to French Guiana including the Gulf of Mexico and the Caribbean Sea (Holthuis 1991; Tavares 2002). Crustaceans of the genus *Metanephrops* are an important economic resource (Holthuis 1991; Chan 1998; Chan et al. 2009) in some tropical and subtropical regions. Three deep-sea crustaceans of the species *Metanephrops* are exploited commercially on the continental slopes of northwest Australia: *M. boschmai* (Holthuis 1964), *M. andamanicus* (Wood-Mason 1891) and *M. australiensis* (Bruce 1966) (Ward and Davis 1987; Wassenberg and Hill 1989). New Zealand has developed a deep sea lobster fishery, targeting scampi (*M. challenger* Balss 1914) (Smith 1999). An economically important commercial fishery exists in Taiwan and East China Sea for *M. thomsoni* (Bate 1888), *M. japonicus* (Tapparone Canefri 1873) and *M. formosanus* (Chan and Yu 1987; Choi et al. 2008). *M. binghami* has potential for an economic exploitation in waters of Venezuela (Gómez et al. 2000; Gómez et al. 2005). Due to the substantial potential new fishery in the Colombian Caribbean Sea, the objective of

this work is to describe for first time the patterns of spatial and bathymetric distribution of abundance and the diel periodicity of the Caribbean lobster (*M. binghami*).

## **Materials and Methods**

Samples were collected in the Colombian Caribbean Sea by trawling in water depths between 200 and 550 m (100 m depth strata sampled at 24 h intervals). Two experimental trawl surveys were carried out in November 2009 (south zone) and in December 2009 (north zone) (Fig. 1). The sample period corresponds to the dry season when the high-pressure system forces strong and constant westward trade winds and the northern zone is affected by the Caribbean current and the upwelling of deep waters (Paramo et al., 2003). Samples were collected by the commercial shrimp trawler “Tee Claude” using a trawl with a cod-end mesh size of 44.5 mm from knot to knot, on a grid of 87 stations, with at least two hauls per 100 m depth stratum. We were unable to collect samples between Cartagena and the Magdalena River because of irregular depths. Appropriate trawl locations were identified using a commercial echosounder FURUNO FCV 1150 with a transducer frequency of 28 kHz. The haul duration was 30 minutes and the distance travelled by the net was estimated by means of a GPS Garmin MAP 76CSx. The swept area was estimated from the spread of the net (11.58 m) and the speed of the vessel (average 2.5 knots) (Gunderson 1993; King 2007) and biomass of the Caribbean lobster was estimated in kg km<sup>-2</sup>.

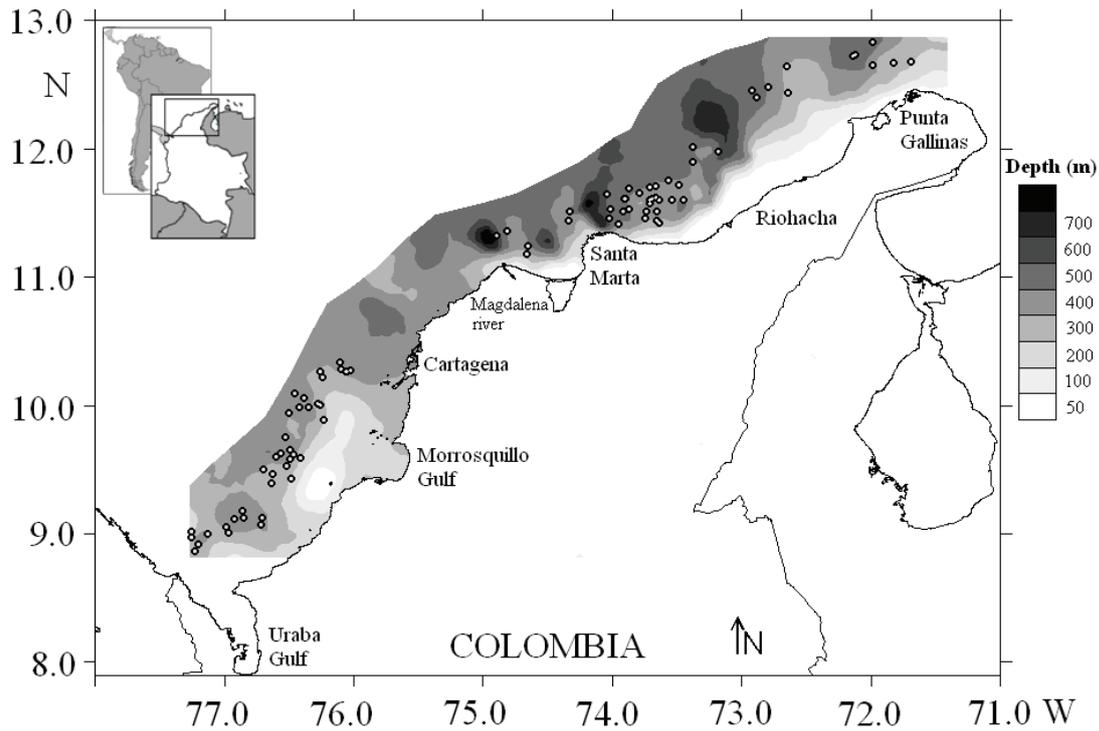


Figure 1. Study area in the Colombian Caribbean Sea. Circles indicate the sampled stations.

The total weight, sex and number of individuals per species from each station were recorded. All the specimens were weighed to the nearest 0.1 g and the carapace length (CL) was measured to the nearest 0.1 mm using callipers from the posterior edge of the eye socket to the middle hind margin of the carapace. The frequency data of CL by sex and by strata of depth of *Metanephrops binghami* were analyzed as a mixture of probability density functions (pdf), whose modes depend upon a combination of the distances between means, the magnitudes of the variances, the proportion of the individual numbers in each mode and the overall sample size. The quasi-Newton algorithm was used to fit the frequency of data per individual to obtain the means, using the software MIX (Mixture analysis). The statistical method used to fit the mixture distribution to the data is maximum-likelihood estimation for grouped data (MacDonald and Pitcher 1979). One way ANOVA

was used to test for significant differences between sexes of each measurement, once the assumptions of normality and homogeneity of variance were achieved following log-transformation of the data. We used the Student's t-test for differences between means of CL by depth strata for both females and males (Gotelli and Ellison 2004; Manly 2004). Ovary staging was based on the colour of the ovary (adapted from Mente et al., 2009): stage 1, white-immature; stage 2, opaque-in development; stage 3, yellow-maturing; stage 4, green-mature; stage 5, ovigerous female carrying eggs on its pleopods. For estimation of the maturity at length we considered stages I and II as immature and stages III, IV and V as mature. Size at sexual maturity ( $I_{50\%}$ ) was modelled by fitting the logistic function of a mature specimen proportion with 2 mm of size interval of CL. The curve was fitted by applying the maximum likelihood and uncertainty by Monte Carlo resampling (Manly 2006) to obtain the estimated parameters and the confidence intervals (C.I.) (Roa et al. 1999).

$$P(l) = \frac{1}{1 + \exp(a + b * CL)}$$

Where  $P(l)$  is the mature female proportion,  $a$  and  $b$  are the parameters estimated by resampling and  $CL$  the carapace length. The size at 50% maturity is  $CL_{50\%} = -a/b$  (King 2007).

Geostatistical analyses (Cressie 1993; Petitgas 1993; Rivoirard et al. 2000) were used to describe the spatial structure of the Caribbean lobster distribution. The experimental variogram is defined as the variance of difference between values that are  $h$  units apart.

$$\hat{\gamma}(\mathbf{h}) = \frac{1}{2N(\mathbf{h})} \sum_{i=1}^{N(\mathbf{h})} z(x_i) - z(x_i + \mathbf{h})^2$$

where  $\hat{\gamma}(\mathbf{h})$  is semivariance,  $\mathbf{h}$  is a vector of distance and direction, and  $N(\mathbf{h})$  is the number of pairs of observations at distance  $h$  and given direction,  $z(x_i)$  is the density of *M. binghami* for the  $i$ th data point. In order to evaluate the anisotropic processes, experimental directional variograms were calculated for raw data (0°, 45°, 90° and 135°). Finally, ordinary point kriging was used to map the spatial distribution, to estimate the mean density, the variance of the mean density and the biomass (Isaaks and Srivastava 1989; Petitgas and Prampart 1995; Rivoirard et al. 2000).

Generalized Additive Modelling (GAM) (Hastie and Tibshirani 1990) was used to analyze the depth preferences and diel periodicity in abundance of *M. Binghami*. An additive model is an extension of linear models, but allows linear functions of predictors (depth and hour) to be replaced by smoothing functions (Agenbag et al. 2003):

$$y = \alpha + \sum_{i=1}^n f_i(X_i) + \varepsilon$$

Where  $y$  is the response,  $X_i$  is the predictor,  $\alpha$  is a constant and  $\varepsilon$  is the error. The  $f_i$  is estimated using smoothers. We used spline (s) smoothing with a Gaussian family to estimate the non parametric functions. The probability level of the nonlinear contribution of the nonparametric terms was made with the significance value (p) for judging goodness-of-fit (Burnham and Anderson 2002).

## Results

The size of *M. binghami* females ranged between 15.5 and 55.3 mm CL (mean 33.6 mm,  $\pm 7.2$ ) and for males between 17.0 and 56.3 mm CL (mean 34.8 mm,  $\pm 8.9$ ). Statistically significant differences between the sexes were not found (Fig.2), revealing size

homogeneity for both sexes ( $p = 0.12$ ). The entire length frequency distribution of *M. binghami* CL was characterized by two modes for female and three for male (Table 1). For females the first mode represented 20% (mean  $22.3 \pm 4.4$  mm CL) and the second one the 80% (mean  $35.9 \pm 4.3$  mm CL). For males three modes were observed, the first (mean  $20.8 \pm 2.2$  mm CL) and third ( $45.9 \pm 1.4$  mm CL) with 20% and the second represented 80% (mean  $34.2 \pm 7.2$  mm CL).

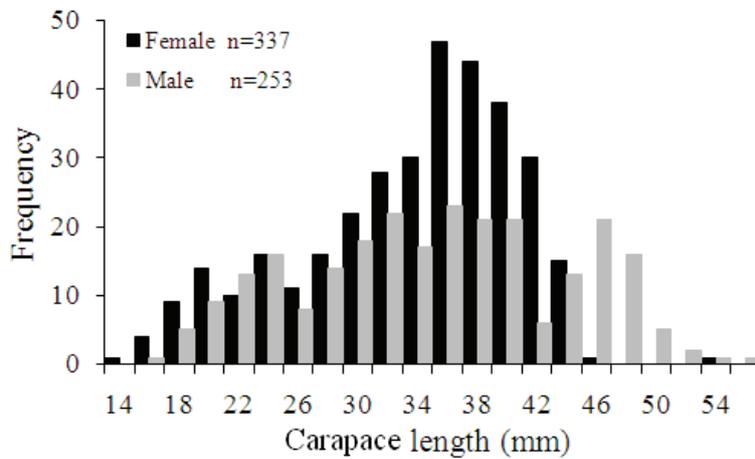


Figure 2. Length frequency distributions of *Metanephrops binghami* of cephalotorax length (CL).

Table 1. Frequency distribution parameters (proportions of participation, means and standard deviations) for each mode of the histograms of CL of *M. binghami* by sex and strata. Mean and standard deviations are from normal pdf.

Strata (m)	Sex	Proportions			Means			Standard deviations		
		$p1$	$p2$	$p3$	$\mu1$	$\mu2$	$\mu3$	$\sigma1$	$\sigma2$	$\sigma3$
All	F	0.2	0.8	-	22.3	35.9	-	4.4	4.3	-
All	M	0.1	0.8	0.1	20.8	34.2	45.9	2.2	7.2	1.4
200-300	F	0.2	0.8	-	20.2	35.6	-	4.0	3.9	-
300-400	F	0.6	0.4	-	28.1	38.0	-	6.3	3.1	-
200-300	M	0.2	0.6	0.2	20.9	33.0	46.3	3.2	4.8	2.0
300-400	M	1.0	-	-	33.9	-	-	8.5	-	-

The size structure for the female *M. binghami* showed a small increase in CL associated to depth, with a two modal trend for all depth strata (Fig. 3; Table 1). The male *M. binghami* had three-modal for the 200-300 m strata and one-modal structure for the 300-400 m strata, also an increasing CL with depth. The three modes of the males in the second strata seem to mix in the third strata. The largest numbers were found in the 200-300 and 300-400 m strata (Table 1). Low numbers of individuals caught in the strata 100-200 and 400-500 m prevented their inclusion in the test for significant differences of CL by depth strata. However, the mean CL of female and male of *M. binghami* did not differ significantly between 200-300 and 300-400 m strata ( $p = 0.58$ ).

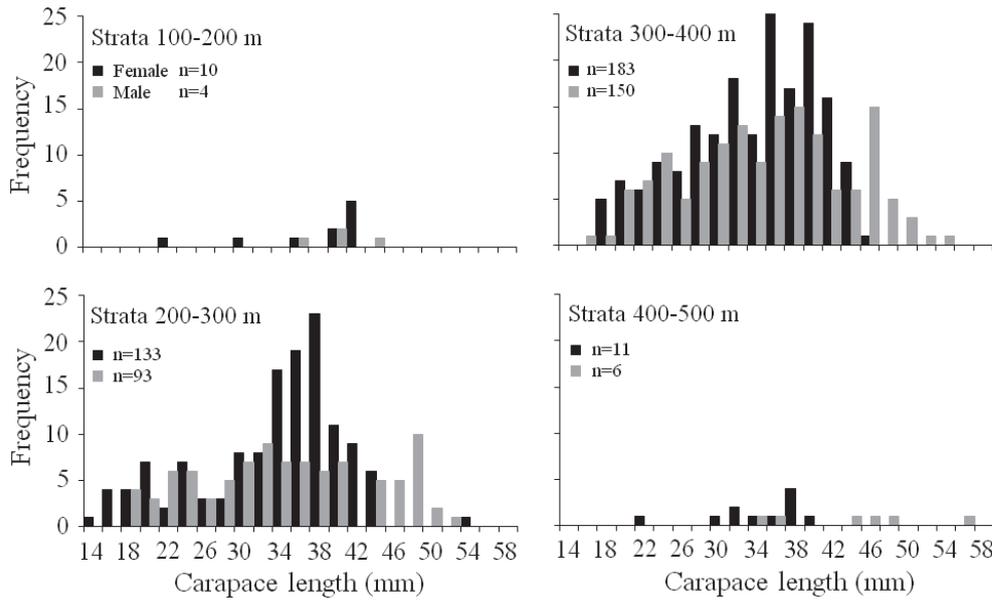


Figure 3. Length frequency distribution of carapace length (CL) by sex and depth strata for *M. binghami*.

Of the 336 females analyzed to determine different maturity stages, 31.25% were immature and 68.75% mature. The size at 50% maturity ( $l_{50\%}$ ) in females (Fig. 4) was 30.55 mm CL (95% C.I. lower = 30.53, C.I. upper = 30.58), the parameters  $a = 16.35$  (C.I. lower = 16.34, C.I. upper = 16.50) and  $b = -0.54$  (C.I. lower = -0.54, C.I. upper = -0.54).

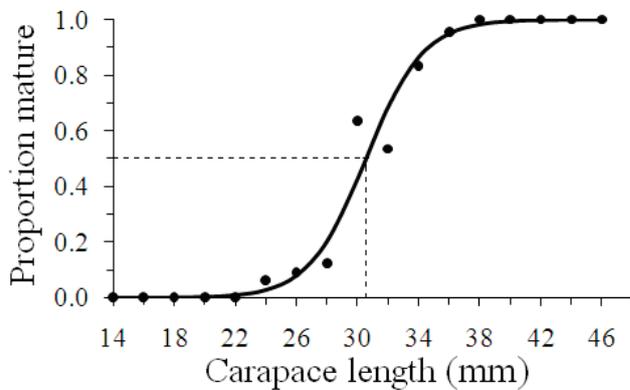


Figure 4. Size at 50% sexual maturity for females of *M. binghami*.

The unidirectional variograms showed similarities in their modelling of spatial characteristics for *M. binghami* (Fig. 5a). This absence of geometric anisotropy can be demonstrated with the ratio between the maximum and minimum values of the spatial autocorrelation range in the unidirectional variograms, which was less than 2 (Table 2). This means that the spatial structure of *M. binghami* aggregation has the same size in all directions of spatial autocorrelation. Therefore, the spatial structure of Caribbean lobster biomass ( $\text{kg km}^{-2}$ ) was studied using an experimental isotropic variogram (Fig. 5b). The fitted spherical variograms showed a non-resolved structure for the sampling design that considered 0.0% of total variance (nugget as percentage of sill) (Table 2). The autocorrelation range of the Caribbean lobster was 25.7 km, i.e. the diameter of *M. binghami* aggregation of high-density patches (Table 2). The higher biomass values were distributed in two well-defined spatial patches in the northern zone of the Colombian Caribbean Sea. The bulk of the biomass was distributed between Riohacha and off Punta Gallinas (mean density =  $30.96 \text{ kg km}^{-2}$ ; biomass = 445 945 kg; CV = 13.48). In the southern zone, this species revealed high abundances between Cartagena and off the Morrosquillo gulf (mean density =  $20.40 \text{ kg km}^{-2}$ ; biomass = 234 840 kg; CV = 20.46) (Fig. 6). The estimated mean density and biomass for the combined study area was  $26.40 \text{ kg km}^{-2}$  and 684785 kg (CV=15.81), respectively.

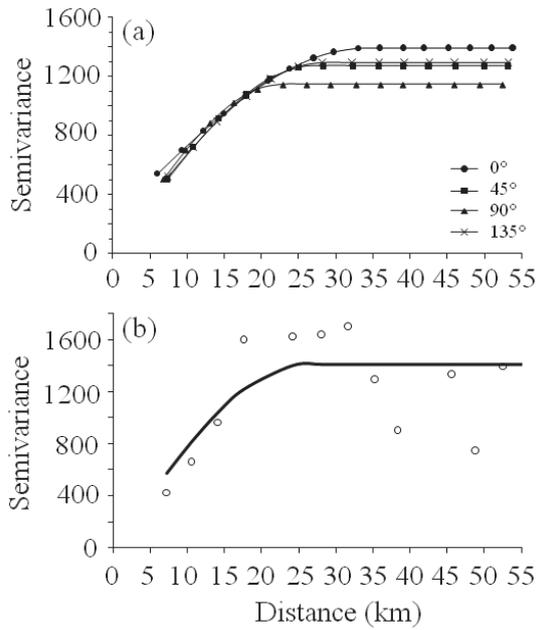


Figure 5. Directional experimental (a) and omnidirectional (b) variograms showing an isotropic process in abundance of *Metanephrops binghami* in Colombian Caribbean Sea.

Table 2. Analysis of anisotropy, spherical variogram model fitted to the directional empirical variogram and Omnidirectional spherical model of variogram for *Metanephrops binghami*.

Parameter	0°	45°	90°	135°	Isotropic
Nugget	239.2	0.0	0.0	39.4	0.0
Nugget (% sill)	17.1	0.0	0.0	3.0	0.0
Sill	1156.3	1271.3	1146.0	1257.6	1410.9
Range	34.0	27.0	22.6	28.5	25.7
Ratio	1.0	1.3	1.5	1.2	-

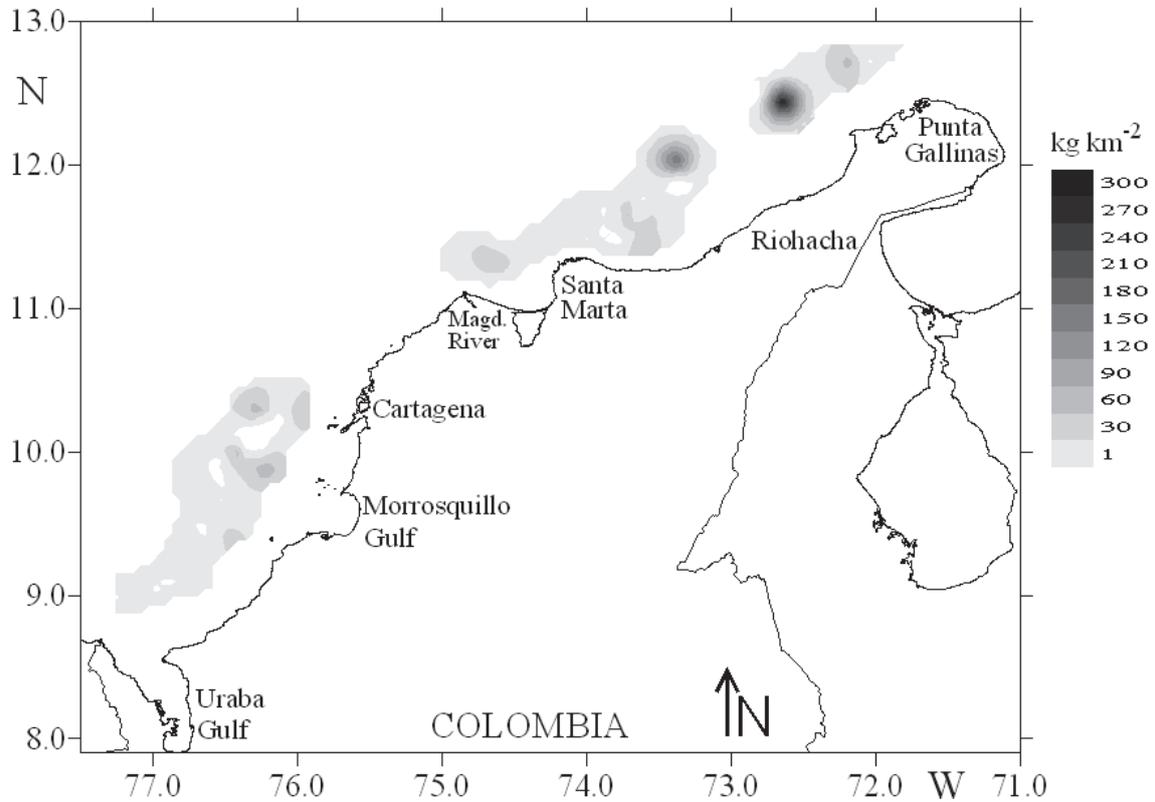


Figure 6. Spatial distribution of *Metanephrops binghami* abundances ( $\text{kg km}^{-2}$ ) as the reproduction of a spatially stochastic process by kriging.

The nonlinear contribution of the nonparametric terms was significant ( $p=0.00$ ) in explaining the variability of depth preferences and diel periodicity in abundance of *M. binghami*. The relationship between the biomass of *M. binghami* and depth ( $R^2 = 0.41$ ) shows that this species was distributed between 110 and 440 m, but higher biomass was found between 250 and 350 m (Fig. 7). *M. binghami* showed a marked diel pattern in the catches ( $R^2 = 0.28$ ), with high values of biomass found in the nocturne trawls, increasing after 18:00 with highest values from 0:00 to 4:00 and lowest values during daylight hours.

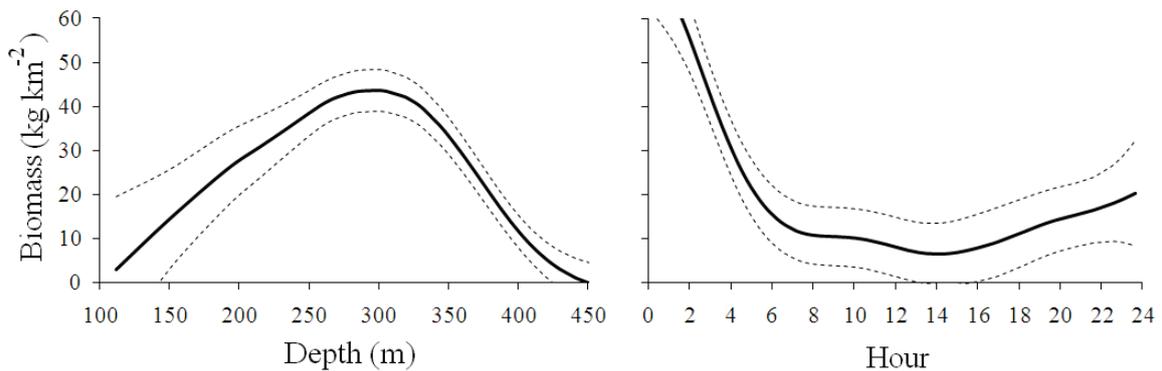


Figure 7. Modelling of functional relationships between biomass with depth preferences and diel periodicity in catches.

## Discussion

The Colombian Caribbean Sea is influenced by the northeast trade winds, causing the surface currents flowing in west and south-west directions almost parallel to the coast. These trade winds are responsible of upwelling in the northern zone of the study area, which increases the productivity in the Guajira coast (Andrade et al. 2003; Paramo et al. 2003; Paramo et al. 2009). In fact, the highest biomass of *M. binghami* was found in the northern zone of the Colombian Caribbean Sea, where the local oceanography is modulated by the seasonal upwelling with high productivity (Paramo et al. 2003; Paramo et al. 2009). Studying the spatial distribution of populations is of great importance for ecological studies, because in the nature most of marine organisms are not distributed at random, rather, they are forming patches, gradients or other types of spatial structures (Rivoirard et al. 2000; Legendre and Fortin 1989; Legendre 1993; Legendre and Legendre 1998; Paramo and Roa 2003). Also, successful fisheries management in new fisheries require the knowledge of population abundance, the spatial distribution and size structure (Rivoirard et al., 2000), since failure to recognize spatial complexity of fisheries has resulted in stock

collapses (Hilborn and Walters 2003; Katsanevakis and Maravelias 2009). Additionally, deep-sea crustaceans have a patchy distribution (D'Onghia et al. 1998; Maynou et al. 1998; Belcari et al. 2003), which justifies the importance of using geostatistics methods to address the spatial distribution structure and calculate the biomass more precisely (Paramo and Roa 2003). *M. binghami* is found between 230 and 700 m, although is most abundant between 300 and 500 m in the sand and mud bottoms (Tavares 2002); however, our results show higher biomass and size are found between 250 to 350 m, with a maximum at about 300 m, which suggests that this species prefers a narrow depth strata. The biomass obtained in this study (26.40 kg km<sup>-2</sup>) was higher than similar Nephropidae species (*Nephrops norvegicus*) on the Catalan Sea (18.87 kg km<sup>-2</sup>) (Maynou et al. 1998), which gives support to the proposed development of a new fishery in the Colombian Caribbean Sea. The higher biomass of *M. binghami* in the Colombian Caribbean Sea by depth strata is according to high aggregations of *M. boschmai* (250-350 m) in Australian waters, but *M. andamanicus* (350-400 m) and *M. australiensis* (430-470 m) were more deeper (Ward and Davis 1987). However, the Norway lobster (*N. norvegicus*) is distributed between 200 to 500 m (Maynou et al., 1998; Abelló et al. 2002), but the highest yields take place at the 500 m stratum (Fonseca et al. 2007). The size of *M. binghami* in this study is similar to other *Nephropidae* species (*Nephrops norvegicus*) caught in Portuguese waters, ranging from 18 to 59 mm CL (Fonseca et al. 2007) and in the Catalan Sea (Spain, northwest Mediterranean), ranging from 12 to 58 mm CL (Maynou et al. 1998), but smaller than reported of *Nephrops andamicus* in South Africa, ranging from 47 to 55 mm CL (Berry 1969). Moreover, the fecundity for females of *M. binghami* in Venezuela range between 102 and 781 eggs (mean 326) in the size range of 29-52 mm CL (Gómez et al. 2000; Gómez et al. 2005), which agree with our results (30.55 mm CL for females) in the Colombian Caribbean Sea. The

great proportions of large-sized individuals of *M. binghami* in our study reflect the unexploited populations in the study area.

Lobsters are described as nocturnal (Golet et al. 2006), remaining in shelters during daylight hours, which allows for protection from predators, and emerging from their burrows in the evening. Indeed, it is known that species of genus *Metanephrops* live in burrows (Tavares 2002). Ward and Davis (1987) showed that deep water benthic crustaceans have a marked diel periodicity with higher abundances of *Metanephrops australiensis* in nocturnal catches. The Norway lobster (*Nephrops norvegicus*) shows diel activity patterns at dawn and dusk when it leaves the burrows; the catches were higher at these times and were conversely sparse during the day (Trenkel et al. 2008). Aguzzi and Bahamon (2009) describe this behavioural rhythm as endobenthic, in which burrowers and buries shows phases of emergence from the substrate and retraction in it. The animals rest when light increases and feed at darkness (Aguzzi and Company 2010). These patterns of diel periodicity agree with our results for *M. binghami* which also showed a nocturnal behaviour most likely for feeding and a burying behaviour during daylight, as the largest catches were taken during nocturnal trawls. This study is the first to provide evidence of diel patterns for *M. binghami*. Therefore, fishers can adapt their fishing strategy to the diel behaviour of this specie. Holthuis (1991) reported on the big size and potential commercial importance of the species *Metanephros*. Nevertheless, according to our results, more scientific biological research is needed to understand the life cycle parameters of *M. binghami* such as growth, reproduction size, recruitment, mortality, areas and season of spawning, nursery areas and associate biodiversity before the initiation of a new commercial fishery. This information will aid in developing appropriate strategies to

initiate, manage and sustain a new commercial fishery, while taking into account protection and conservation of the existing ecosystem.

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## **6. Deep-sea fish assemblages in the Colombian Caribbean Sea: implications for an ecosystem approach to fisheries management**

Submitted to *Fisheries Research*

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### **Abstract**

Studies of the species composition, relative abundance and biomass of deep-sea assemblages are needed to create a knowledge base for the assessment of the resource potential and to advise ecosystem-based conservation and fisheries management strategies. This study attempts to create an initial knowledge base of the system by assessing the deep-sea fish assemblages of Colombian Caribbean Sea across a depth range of 200-550 m and their implications for an ecosystem approach to fisheries management. A total of 102 species (13 Chondrichthyes and 89 Teleosteans) and 58 families (9 Chondrichthyes and 49

Teleosteans) of deep-sea fish were sampled. This study reveals the existence of three deep-sea fish assemblages and demonstrates that depth plays an important role in ichthyofaunal group differentiation. Most species of the shallower assemblage exhibited a narrow depth range, while species of middle depth assemblage showed the widest depth range. From the point of view of conservation and fisheries management strategies, we need to know the status of deep-sea fish assemblages more fully to initiate a new deep-sea fishery in the Colombian Caribbean Sea. Conservation and protection of the habitats is therefore fundamental to develop a rational and sustainable management of the deep-sea fishery resources of the Colombian Caribbean Sea.

Key words: Deep-sea fish, assemblage, management, Colombia.

## **1. Introduction**

Fish are important marine resources for humans, moreover, knowledge of fish assemblages contributes to improved understanding of coastal biodiversity and ecosystem functioning (Bussotti and Guidetti, 2009). Deep-sea ecosystems and their fish resources are especially vulnerable to over-exploitation due to the life-history characteristics of deep-sea species that include extreme longevity, slow growth rate, late maturity and low fecundity (Morato et al., 2006; Follesa et al., 2011). Therefore, stock depletion is more rapid and recovery will be much slower than for species in shallow waters (Roberts, 2002). When this kind of fishery begins, initial yields tend to be high, but a drastic decline soon follows (Koslow et al., 2000). Due to the great vulnerability of deep-sea species and habitats, protective measures are needed to limit fishing, based on a precautionary approach (Roberts, 2002; Devine et al., 2006; Hart and Pearson, 2011): Such measures may include the creation of marine protected areas as a tool for marine conservation and a fisheries management that

follow an ecosystem approach to fisheries (EAF) (Worm et al., 2006; Fraser et al., 2009; Paramo et al., 2009; Jackson and Jacquet, 2011). Deep-sea assessments of biodiversity are necessary to understand the degree of stability and vulnerability of deep-sea environments (Merrett and Haedrich, 1997). Since fishing activities can be expected to cause profound changes in these ecosystems, assessments before and after fishing take place are essential to provide information on impacts, these needs to be done via a structured investigation (Atkinson et al., 2011). Thus, studies of the deep-sea ecosystem are needed in advance to assess the risks that fisheries could cause significant ecological impacts (Powell et al., 2003). Information on deep-sea fish assemblages is particularly scarce in the Colombian Caribbean Sea, where a deep-sea fishery has not yet been developed, and the environment can be considered as still pristine. There are no comprehensive studies of the deep-fish assemblages in the Colombian Caribbean Sea. A preliminary description of fishes dwelling between 200 and 800 m of depth (Polanco et al., 2010) found that the dominant order of fishes on the continental shelf (20-150 m), in term of number of species, is Perciformes, followed by Pleuronectiformes; on the continental slope (200-800 m) the dominant order is also Perciformes, followed by Anguilliformes.

The future of fisheries lies in a better management and utilization of fisheries resources (Jacquet, 2011) that takes account of knowledge about the impact of trawling on the marine ecosystems (Allsopp et al., 2009). Indeed, a sustainable increase in world fish production may be achievable, not by increasing effort, but by fishing less (Christensen, 2011) and thereby allowing populations to recover to healthy (and at the same time economically viable) stock sizes. The ecosystem approach to fisheries (EAF) seeks to balance diverse societal objectives. It takes account of knowledge about biological, environmental and human components of the fisheries system and their interactions and adopts an integrated

approach to fisheries within ecologically meaningful boundaries (Bianchi, 2008). By doing so, EAF attempts to avoid the degradation of ecosystems by minimizing the risk of irreversible change and at the same time seeks to obtain and maintain long-term socioeconomic benefits (Pikitch et al., 2004). Previous studies have identified the potential for a new deep-crustacean fishery in the Colombian Caribbean Sea (Paramo and Saint-Paul, 2011a,b). This study attempts to create an initial knowledge base of the system by assessing the deep-sea fish assemblages of Colombian Caribbean Sea across a depth range of 200-550 m and their implications for an ecosystem approach to fisheries management.

## **2. Materials and methods**

### *2.1. Study area and sampling design*

Two experimental trawl surveys were carried out in 2009, the first in November (southern zone) and the second in December (northern zone). Data were collected by trawling in depths ranging from 200 to 550 m (100 m strata intervals) in the Colombian Caribbean Sea. Trawling locations were on trawlable bottoms found by the commercial echosounder FURUNO FCV 1150 with a transducer at a frequency of 28 kHz, on a grid of 87 stations, with at least two hauls per 100 m depth stratum (Fig. 1). Samples were collected by the commercial shrimp trawler “Tee Claude” using a trawl with a cod-end mesh size of 44.5 mm from knot to knot. No trawling was done between Cartagena and Magdalena River due to the irregular depth profile in this zone. The haul duration was 30 minutes and the distance travelled by the net was estimated by means of a GPS Garmin MAP 76CSx. The deep-sea fish catch from each haul was analysed for total abundance ( $N/km^2$ ) and biomass ( $kg/km^2$ ). The swept area was estimated from the spread of the net (11.58 m) and the speed of the vessel (average 2.5 knots) (Gunderson, 1993; King, 2007).

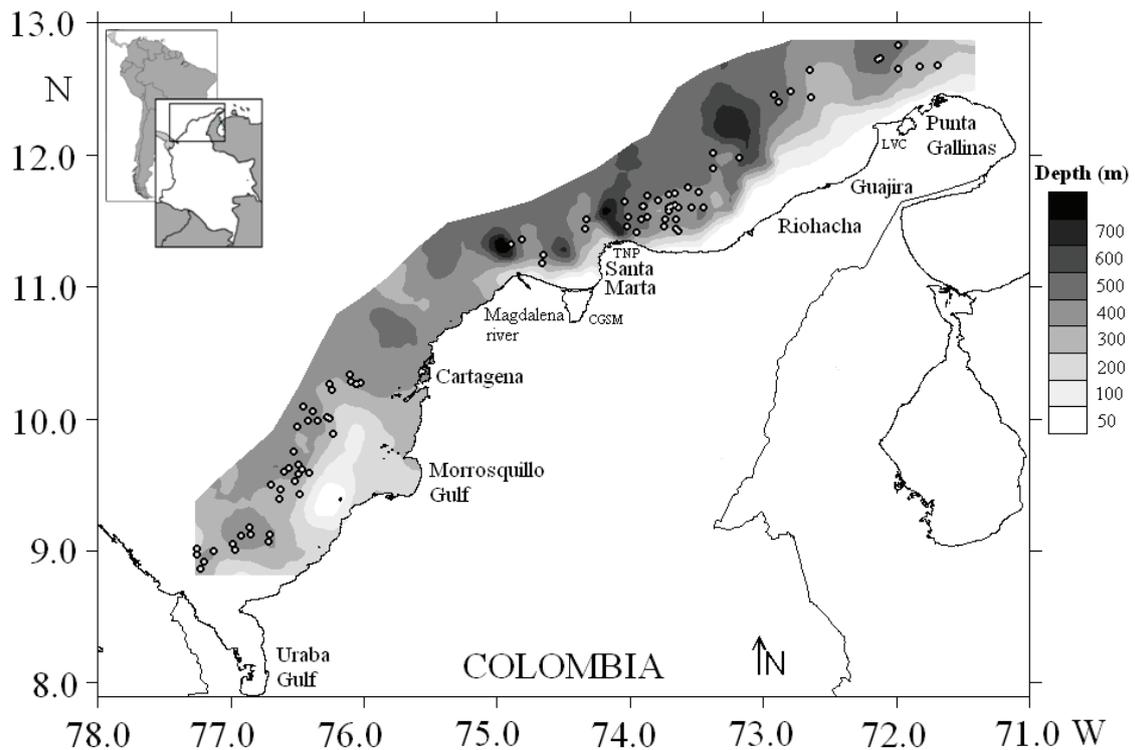


Figure 1. Study area in the Colombian Caribbean Sea. Circles indicate the sampled stations.

## 2.2. Statistical analysis

For each deep-sea fish species, numbers and individual weights were registered at each station. Abundance and biomass were then standardised to one km<sup>2</sup> of sample area. Changes with depth in the abundance (N/km<sup>2</sup>), biomass (kg/km<sup>2</sup>), species richness (d), total species (S), and diversity (H') and Pielou's evenness indexes were evaluated using Generalized Additive Models (GAM) (Hastie and Tibshirani, 1990). The analysis was exploratory only with the aim of describing the bathymetric distribution of the abovementioned ecological indexes. An additive model is an extension of a linear model, but allows linear functions of predictors (depth) to be replaced by smoothing functions (Agenbag et al., 2003), as follows:

$$y = \alpha + \sum_{i=1}^n f_i(X_i) + \varepsilon$$

where  $y$  is the response,  $X_i$  is the predictor,  $\alpha$  is a constant and  $\varepsilon$  is the error term. The function  $f_i$  is estimated using smoothers. We used spline (s) smoothing with a Gaussian family to estimate the non parametric functions and to evaluate the probability level of the nonlinear contribution of the nonparametric terms (Burnham and Anderson, 2002).

Cluster analysis using the Bray-Curtis index was applied to calculate and visualize similarities between the taxonomic compositions at each station in terms of the abundance ( $N/km^2$ ) of main assemblages. For the analysis, only those deep-fish species that represented more than 3% of total catch were considered (Magnussen, 2002). Further, species with pelagic habits were excluded from the multivariate analysis. Data were log-transformed ( $\log X+1$ ) to reduce the influence of the most abundant species. The characteristics of the deep-sea fish assemblage were analyzed using multivariate analysis. We used Non-metric Multidimensional Scaling (NMDS) ordination to generate two-dimensional plots of the assemblages based on the species composition at each sampling site. NMDS is robust in representing the high dimensional data as indicated by the stress values (Gotelli and Ellison, 2004; Manly, 2004). Analysis of similarity (ANOSIM) (Clarke, 1993) was carried out to test the degree and significance of differences between assemblages in the NMDS plot. ANOSIM output is a test statistic (R) that is equal to 1 if there are differences between assemblages and 0 if there are no differences between assemblages. Then, we calculated the percentage contribution of each species to the average similarity within the assemblage in which it occurred. This data was used to analyze dissimilarities between species composition of assemblages by means of the

Similarity Percentages (SIMPER) procedure (Gotelli and Ellison, 2004). The average abundance, biomass, species richness, total species, Shannon-Wiener diversity and Pielou's evenness indexes were determined for all stations and the main assemblages resulting from the classification and ordination. Differences in ecological indexes between assemblages were evaluated using Kruskal-Wallis non-parametric test (Gotelli and Ellison, 2004). To determine which assemblage contributed to the observed significant differences of ecological indexes, multiple comparisons using the Nemenyi and Dunn test were carried out (Zar, 2009).

### 3. Results

One hundred and two species (13 Chondrichthyes and 89 Teleost) and fifty eight families (9 Chondrichthyan and 49 Teleostean) of deep-sea fish were caught during the two surveys carried out in November (south zone) and December (north zone) 2009 (Table 1). *Coelorinchus caelorhincus* (96.30%), *Bembrops anatiostris* (75.93%), *Cyttopsis rosea* (75.93%), *Steindachneria argentea* (70.37%), *Hymenocephalus gracilis* (68.52%), *Chaunax suttkusi* (68.52%), *Poecilopsetta beanii* (68.52%), *Zenion hololepis* (57.41%), *Dibranchius atlanticus* (55.56%), *Neobythites gilli* (55.56%), *Argentina striata* (55.56%), *Chlorophthalmus agassizi* (53.70%) and *Hoplostethus occidentalis* (53.70%) were the dominant teleost species, with over 50% of frequency of occurrence (%F). Chondrichthyes species with high %F (>20%) were *Etmopterus perryi* (38.89%), *Galeus cadenati* (27.78%) and *Anacanthobatis americanus* (22.22%) (Table 1).

Table 1. Frequency of occurrence (%F), abundance (%A), biomass (%B) and depth range (m) of species collected in the Colombian Caribbean Sea. Habitat = Demersal: D; Bathydemersal: BD; Benthopelagic: BeP; Bathypelagic: BaP; Reef associated: RA.

	Species	Habitat	%F	%A	%B	Depth range (m)
Chondrichthyes Family						
Anacanthobatidae	<i>Anacanthobatis americanus</i> (Bigelow and Schroeder, 1962)	BD	22.22	0.22	0.61	268-530
Anacanthobatidae	<i>Anacanthobatis longirostris</i> (Bigelow and Schroeder, 1962)	BD	1.85	0.03	0.04	501
Centrophoridae	<i>Centrophorus granulosus</i> (Bloch and Schneider, 1801)	BD	1.85	0.01	0.09	328
Chimaeridae	<i>Hydrolagus alberti</i> (Bigelow and Schroeder, 1951)	BD	12.96	0.14	0.35	328-530
Etmopteridae	<i>Etmopterus perryi</i> (Springer and Burgess, 1985)	BaP	38.89	1.07	1.04	230-530
Rajidae	<i>Cruriraja rugosa</i> (Bigelow and Schroeder, 1958)	BD	11.11	0.13	0.82	286-502
Rajidae	<i>Dactylobatus clarkii</i> (Bigelow and Schroeder, 1958)	BD	1.85	0.01	0.23	421
Rajidae	<i>Gurgesiella atlantica</i> (Bigelow and Schroeder, 1962)	BD	16.67	0.24	0.63	392-480
Scyliorhinidae	<i>Galeus cadenati</i> (Springer, 1966)	BD	27.78	0.19	0.49	262-421
Scyliorhinidae	<i>Scyliorhinus boa</i> (Goode and Bean, 1896)	BD	7.41	0.05	0.35	262-530
Squalidae	<i>Squalus cubensis</i> (Howell Rivero, 1936)	D	12.96	0.16	0.40	246-388
Squatinae	<i>Squatina dumeril</i> (Lesueur, 1818)	D	7.41	0.04	0.79	262-326
Rhinochimaeridae	<i>Neoharriotta carri</i> (Bullis and Carpenter, 1966)	BD	5.56	0.02	0.10	328-420
Teleosteans Family						
Acropomatidae	<i>Neoscombrops atlanticus</i> (Mochizuki and Sano, 1984)	-	11.11	0.16	0.53	246-535
Acropomatidae	<i>Synagrops bellus</i> (Goode and Bean, 1896)	BD	3.70	0.25	0.30	350-421
Acropomatidae	<i>Synagrops trispinosus</i> (Mochizuki and Sano, 1984)	BD	7.41	0.60	0.39	262-387
Argentinidae	<i>Argentina striata</i> (Goode and Bean, 1896)	BaP	55.56	1.19	0.51	230-443
Argentinidae	<i>Glossanodon pygmaeus</i> (Cohen, 1958)	BaP	1.85	0.04	0.00	371
Ateleopodidae	<i>Ijimaia antillarum</i> (Howell Rivero, 1935)	D	37.04	0.48	1.52	320-502
Bathyclupeidae	<i>Bathyclupea argentea</i> (Goode and Bean, 1896)	BaP	37.04	1.44	2.85	306-535
Bothidae	<i>Chascanopsetta lugubris</i> (Alcock, 1894)	BD	3.70	0.01	0.00	400-450
Bothidae	<i>Trichopsetta caribbaea</i> (Anderson and Gutherz, 1967)	D	3.70	0.09	0.02	246-387
Bythitidae	<i>Diplacanthopoma brachysoma</i> (Günther, 1887)	BD	16.67	0.15	0.08	328-530
Callionymidae	<i>Foetorepus agassizii</i> (Goode and Bean, 1888)	BD	7.41	0.02	0.01	262-306
Caproidae	<i>Antigonia capros</i> (Lowe, 1843)	D	22.22	0.64	0.53	230-371
Caproidae	<i>Antigonia combatia</i> (Berry and Rathjen, 1959)	BD	20.37	2.46	1.03	230-350
Chaunacidae	<i>Chaunax suttkusi</i> (Caruso, 1989)	BD	68.52	2.31	2.47	230-535
Chlorophthalmidae	<i>Chlorophthalmus agassizi</i> (Bonaparte, 1840)	BD	53.70	2.04	0.75	247-501
Chlorophthalmidae	<i>Chlorophthalmus brasiliensis</i> (Mead, 1958)	BD	50.00	1.45	1.22	262-535
Congridae	<i>Bathycongrus bullisi</i> (Smith and Kanazawa, 1977)	BD	9.26	0.07	0.27	304-440
Congridae	<i>Xenomystax bidentatus</i> (Reid, 1940)	D	35.19	0.75	0.86	246-530
Cynoglossidae	<i>Symphurus caribbeanus</i> (Munroe, 1991)	D	1.85	0.01	0.01	320
Cynoglossidae	<i>Symphurus pelicanus</i> (Ginsburg, 1951)	D	1.85	0.01	0.00	530
Diretmidae	<i>Diretmus argenteus</i> (Johnson, 1864)	BaP	9.26	0.08	0.03	356-430
Epigonidae	<i>Epigonus occidentalis</i> (Goode and Bean, 1896)	BD	37.04	2.00	3.58	262-530
Epigonidae	<i>Epigonus pandionis</i> (Goode and Bean, 1881)	BD	35.19	1.16	2.03	262-443
Gempylidae	<i>Neoepinnula americana</i> (Grey, 1953)	BeP	27.78	0.42	1.27	246-426
Gempylidae	<i>Promethichthys prometheus</i> (Cuvier, 1832)	BeP	5.56	0.03	0.21	328-502
Gempylidae	<i>Ruvettus pretiosus</i> (Cocco, 1833)	BeP	1.85	0.01	0.13	480
Gonostomatidae	<i>Gonostoma elongatum</i> (Günther, 1878)	BaP	42.59	0.95	0.40	230-502
Grammicolepididae	<i>Grammicolepis brachiusculus</i> (Poey, 1873)	BaP	38.89	1.26	0.74	286-443
Grammicolepididae	<i>Xenolepidichthys dalgleishi</i> (Gilchrist, 1922)	BeP	1.85	0.01	0.00	430
Halosauridae	<i>Halosaurus ovenii</i> (Johnson, 1864)	BD	1.85	0.02	0.00	430
Lophiidae	<i>Lophiodes monodi</i> (Le Danois, 1971)	BD	22.22	0.12	2.32	230-430
Lutjanidae	<i>Pristipomoides aquilonaris</i> (Goode and Bean, 1896)	D	1.85	0.04	0.07	262
Macrouridae	<i>Coelorinchus caelorhincus</i> (Risso, 1810)	BeP	96.30	20.21	16.71	230-535
Macrouridae	<i>Coryphaenoides armatus</i> (Hector, 1875)	BD	5.56	0.26	0.23	413-501
Macrouridae	<i>Hymenocephalus billsamorum</i> (Iwamoto, 1990)	BD	18.52	1.14	2.15	396-530
Macrouridae	<i>Hymenocephalus gracilis</i> (Gilbert and Hubbs, 1920)	BaP	68.52	1.34	2.72	284-530

Table 1. Continued.

	Species	Habitat	%F	%A	%B	Depth range (m)
Teleosteans Family						
Macrouridae	<i>Hymenocephalus italicus</i> (Giglioli, 1884)	BeP	27.78	0.98	0.22	328-530
Macrouridae	<i>Malacocephalus laevis</i> (Lowe, 1843)	BD	1.85	0.01	0.09	535
Macrouridae	<i>Malacocephalus occidentalis</i> (Goode and Bean, 1885)	BD	22.22	3.01	2.04	328-530
Macrouridae	<i>Malacocephalus okamurai</i> (Iwamoto and Arai, 1987)	BD	1.85	0.01	0.02	502
Merlucciidae	<i>Merluccius albidus</i> (Mitchill, 1818)	BD	33.33	0.30	2.40	246-535
Macrouridae	<i>Nezumia atlantica</i> (Parr, 1946)	BD	1.85	0.01	0.00	328
Merlucciidae	<i>Steindachneria argentea</i> (Goode and Bean, 1896)	BD	70.37	4.46	9.38	230-502
Moridae	<i>Gadella imberbis</i> (Vaillant, 1888)	BeP	27.78	0.37	0.31	262-530
Moridae	<i>Laemonema barbatulum</i> (Goode and Bean, 1883)	BeP	31.48	1.92	2.66	230-530
Muraenidae	<i>Gymnothorax conspersus</i> (Poey, 1867)	BD	3.70	0.03	0.40	262-286
Myctophidae	<i>Diaphus splendidus</i> (Brauer, 1904)	BaP	12.96	0.12	0.03	306-535
Neosopelidae	<i>Neosopelus microchir</i> (Matsubara, 1943)	BaP	20.37	1.14	0.67	403-535
Ogcocephalidae	<i>Dibranchius atlanticus</i> (Peters, 1876)	BD	55.56	1.49	0.63	230-430
Ogcocephalidae	<i>Halieutichthys aculeatus</i> (Mitchill, 1818)	RA	7.41	0.10	0.04	246-430
Ogcocephalidae	<i>Ogcocephalus nasutus</i> (Cuvier, 1829)	RA	3.70	0.75	0.08	247-262
Ophidiidae	<i>Lepophidium marmoratum</i> (Goode and Bean, 1885)	BD	5.56	0.03	0.03	262-326
Ophidiidae	<i>Lepophidium stauraphor</i> (Robins, 1959)	BD	44.44	0.61	0.85	230-535
Ophidiidae	<i>Neobythites gilli</i> (Goode and Bean, 1885)	BeP	55.56	2.26	0.74	230-454
Paralichthyidae	<i>Ancylosetta cycloidea</i> (Tyler, 1959)	D	5.56	0.05	0.08	262-304
Parazenidae	<i>Cyttopsis rosea</i> (Lowe, 1843)	BaP	75.93	1.29	0.67	230-502
Parazenidae	<i>Parazen pacificus</i> (Kamohara, 1935)	BD	3.70	0.01	0.02	326-384
Percophidae	<i>Bembrops anatrostris</i> (Ginsburg, 1955)	BD	75.93	1.75	2.26	230-535
Peristediidae	<i>Peristedion ecuadorensis</i> (Teague, 1961)	BD	22.22	0.58	0.63	262-502
Peristediidae	<i>Peristedion greyae</i> (Miller, 1967)	D	40.74	0.93	1.06	230-535
Peristediidae	<i>Peristedion imberbe</i> (Poey, 1861)	BD	35.19	0.84	0.44	262-450
Peristediidae	<i>Peristedion miniatum</i> (Goode, 1880)	BD	11.11	0.34	0.40	247-530
Peristediidae	<i>Peristedion thompsoni</i> (Fowler, 1952)	BD	3.70	0.23	0.32	247-284
Peristediidae	<i>Peristedion unicuspis</i> (Miller, 1967)	BD	16.67	0.12	0.23	356-501
Poecilopsettidae	<i>Poecilopsetta beanii</i> (Goode, 1881)	BD	68.52	2.38	0.63	230-530
Polymixiidae	<i>Polymixia lowei</i> (Günther, 1859)	BD	25.93	0.57	0.69	230-443
Polymixiidae	<i>Polymixia nobilis</i> (Lowe, 1838)	BD	48.15	2.47	3.07	262-501
Serranidae	<i>Bathyanthias cubensis</i> (Schultz, 1958)	BD	5.56	0.04	0.03	262-326
Serranidae	<i>Cephalopholis fulva</i> (Linnaeus, 1758)	RA	3.70	0.03	0.01	330-350
Serranidae	<i>Hemanthias aureorubens</i> (Longley, 1935)	D	3.70	0.10	0.21	246-304
Serranidae	<i>Serranus phoebe</i> (Poey, 1851)	RA	1.85	0.04	0.01	262
Setarchidae	<i>Setarches guentheri</i> (Johnson, 1862)	BeP	46.30	3.19	2.18	230-501
Sciaenidae	<i>Protosciaena bathytatos</i> (Chao and Miller, 1975)	D	18.52	0.16	1.45	230-421
Scombroptidae	<i>Scombrops ocellatus</i> (Poey, 1860)	BD	1.85	0.49	1.36	230
Scorpaenidae	<i>Pontinus longispinis</i> (Goode and Bean, 1896)	D	35.19	2.16	2.65	230-400
Sternoptychidae	<i>Argyropelecus aculeatus</i> (Valenciennes, 1850)	BaP	31.48	0.67	0.14	247-530
Stomiidae	<i>Chauliodus sloani</i> (Bloch and Schneider, 1801)	BaP	9.26	0.06	0.01	396-430
Symphysanodontidae	<i>Symphysanodon berryi</i> (Anderson, 1970)	BD	11.11	0.48	0.72	230-326
Synodontidae	<i>Saurida normani</i> (Longley, 1935)	RA	12.96	0.08	1.05	246-384
Trachichthyidae	<i>Gephyroberyx darwini</i> (Johnson, 1866)	BeP	9.26	0.02	0.22	268-380
Trachichthyidae	<i>Hoplostethus occidentalis</i> (Woods, 1973)	BaP	53.70	3.97	2.20	230-450
Triacanthodidae	<i>Hollardia hollardi</i> (Poey, 1861)	BD	11.11	0.05	0.18	331-424
Triacanthodidae	<i>Parahollardia schmidtii</i> (Woods, 1959)	D	1.85	0.01	0.00	246
Trichiuridae	<i>Lepidopus altifrons</i> (Parin and Collette, 1993)	BeP	12.96	0.15	0.39	230-502
Triglidae	<i>Bellator brachychir</i> (Regan, 1914)	D	1.85	0.04	0.00	265
Triglidae	<i>Prionotus roseus</i> (Jordan and Evermann, 1887)	D	1.85	0.08	0.06	262
Triglidae	<i>Prionotus stearnsi</i> (Jordan and Swain, 1885)	D	3.70	0.06	0.03	262-306
Zeidae	<i>Zenopsis conchifer</i> (Lowe, 1852)	BeP	3.70	0.01	0.02	265-332
Zenionidae	<i>Zenion hololepis</i> (Goode and Bean, 1896)	BD	57.41	13.40	4.09	230-443

The nonlinear contribution of the nonparametric terms was significant in explaining the variability of bathymetric distribution of the ecological parameters only for Shannon-Wiener diversity ( $H'$ ) and Pielou's evenness ( $J'$ ) indexes ( $p < 0.05$ ). However, higher abundances ( $N \text{ km}^{-2}$ ) and biomasses ( $\text{kg km}^{-2}$ ) were found at shallower depths (200-300 m). These declined abruptly at 350 m and increased slowly again at  $> 450$  m (Fig. 2). Margalef's species richness ( $d$ ) and total species ( $S$ ) showed a decrease with depth. The values of Shannon-Wiener diversity ( $H'$ ) and Pielou's evenness ( $J'$ ) indexes decreased slowly with depth; minimum values were found between 300 and 350 m (Fig. 2).

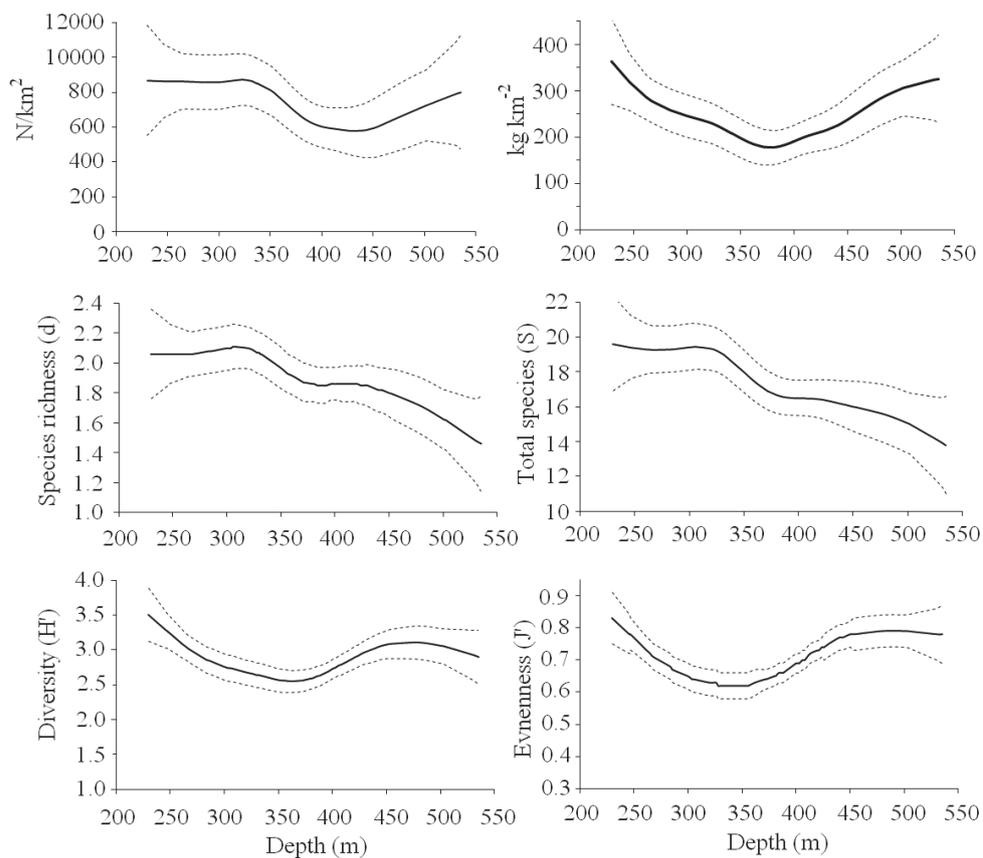


Figure 2. Modelling of functional relationships between abundance ( $N/\text{km}^2$ ), biomass ( $\text{kg}/\text{km}^2$ ), species richness ( $d$ ), total species ( $S$ ), diversity ( $H'$ ) and evenness ( $J'$ ) with depth.

Highest diversity ( $H'$ ) values were found in the northern zone of the Colombian Caribbean Sea, mainly off Riohacha (Fig. 3). In the southern zone, the high diversity index values off Cartagena and Morrosquillo gulf. Lower values of diversity were found towards the south of the study area, but the lowest values were located at the mouth of Magdalena River.

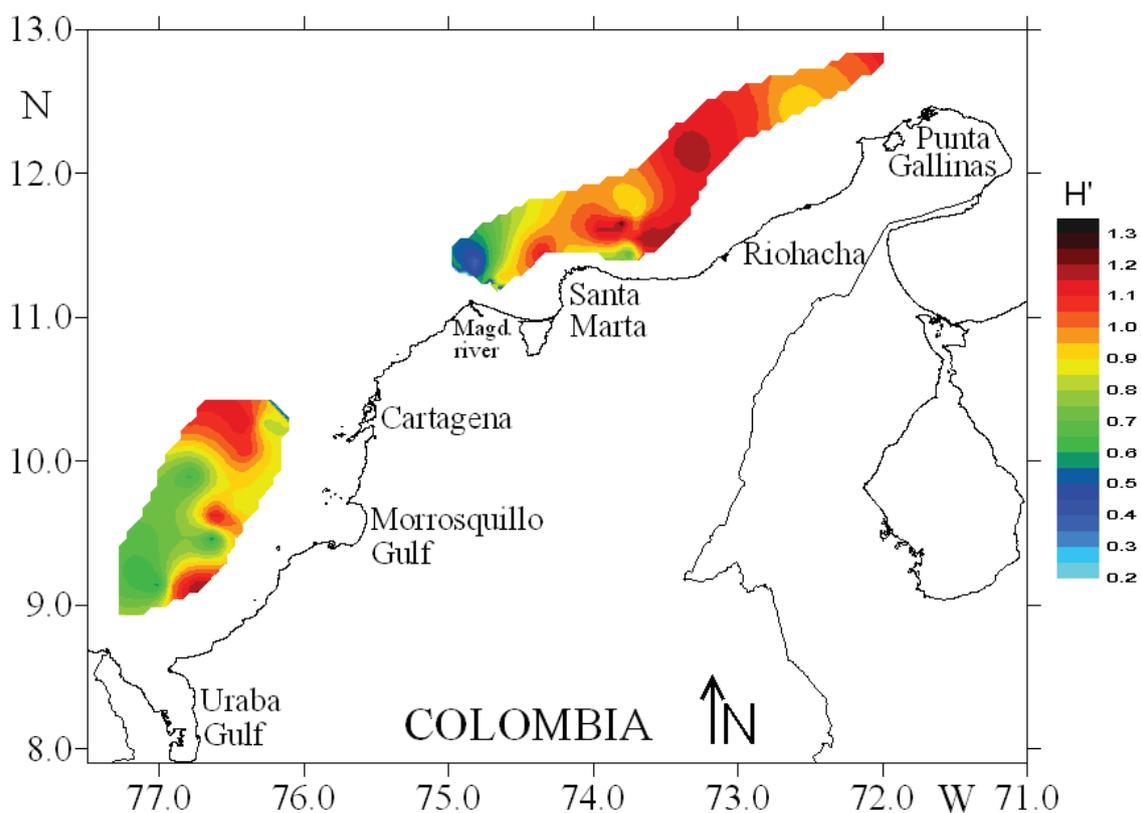


Figure 3. Spatial distribution of diversity ( $H'$ ) of deep-sea fish in the Colombian Caribbean Sea.

The dendrogram derived from the standardised values ( $\log x+1$ ) of abundance for taxonomic groups showed the presence of three clearly definable main groups across the bathymetric gradient (Bray-Curtis similarity of 45%) (Fig. 4). Cluster 1 comprises the

deepest stations (average depth 437.8 m), cluster 2 intermediate ones (388.3 m) and cluster 3 the shallower stations (292.0 m).

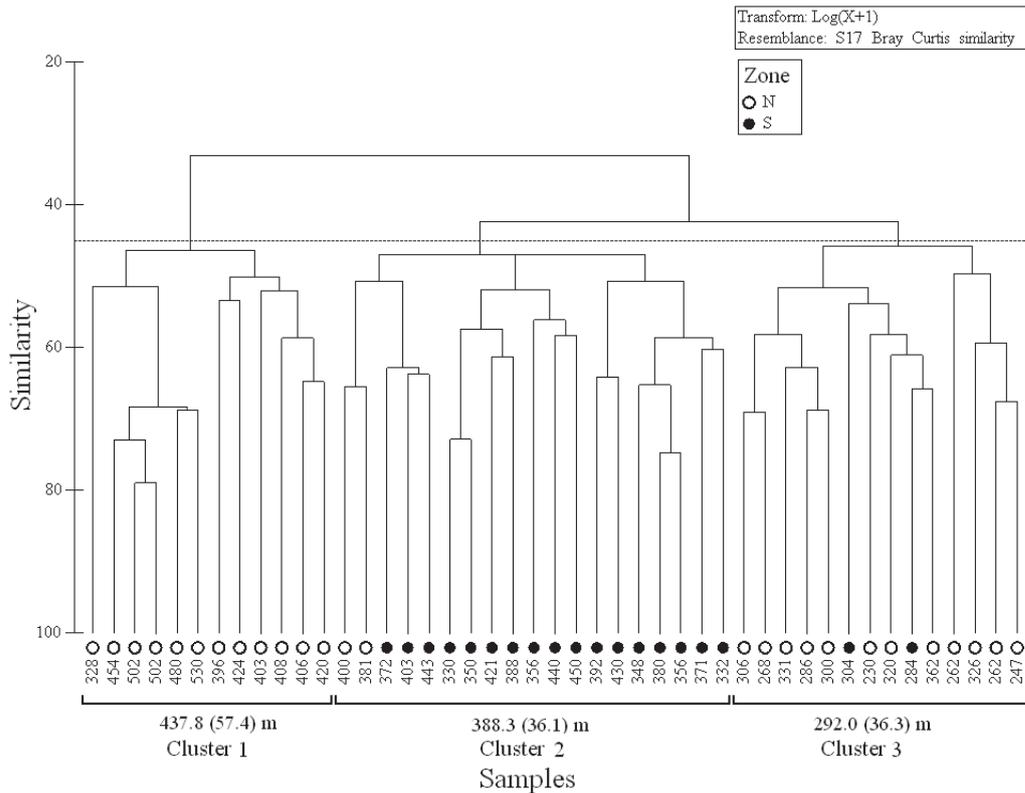


Figure 4. Dendrogram of trawl stations using group-average clustering from Bray-Curtis similarity by depth strata in terms of standardized abundance ( $N/km^2$ ) of total catches in the Colombian Caribbean Sea. The upper line indicates groups at 45% level of similarity. The mean depth (standard deviation) of each cluster is shown.

The NMDS for the deep-sea fish assemblages (Fig. 5) shows a global R of 0.667, indicating that individual stations within each cluster are more similar to each other in terms of species composition than to any station in another cluster; i.e. there is significant difference

( $p = <0.01$ ) among clusters. Also, all R values between clusters (Table 2) are close to one ( $p < 0.01$ ) and SIMPER analysis shows that the average dissimilarity is very high.

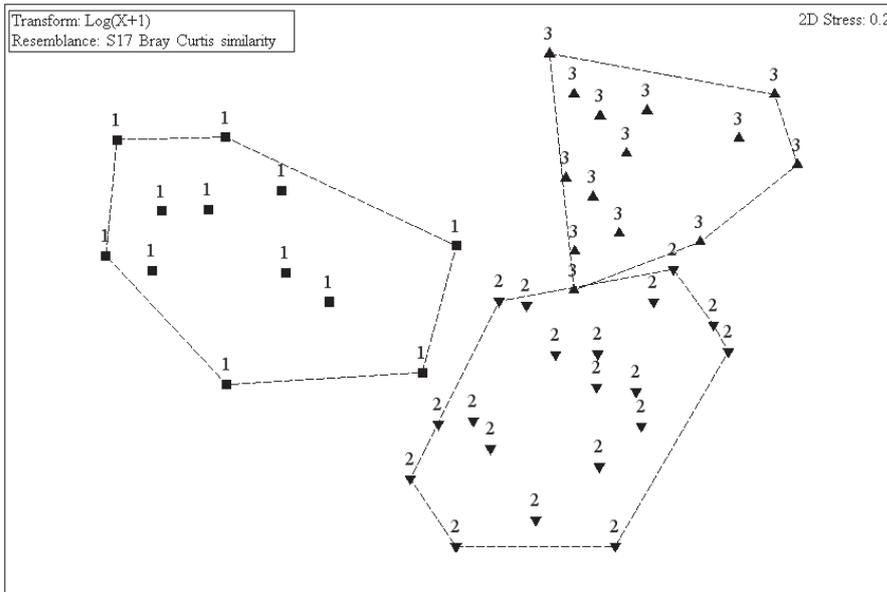


Figure 5. Non-metric multidimensional scaling (NMDS) plot for deep-sea assemblages, grouped according to cluster. The dotted line indicates 45% similarity. Global R: 0.667, significance level of sample statistic: 0.001.

Table 2. Results of ANOSIM and SIMPER analyses of differences between clusters of deep-sea assemblages.

Cluster	ANOSIM		SIMPER
	R	P	Av. Diss.
1-2	0.73	0.001	65.55
1-3	0.89	0.001	68.91
2-3	0.47	0.001	57.73

Average similarity in assemblage 1 is 51.82, and this is accounted for mainly by contributions of 5 species (*C. caelorhincus*, *M. occidentalis*, *L. barbatulum*, *E. occidentalis* and *D. atlanticus*) (Table 3). Assemblage 2 (average similarity 49.65) is principally comprised of *C. caelorhincus*, *C. suttkusi*, *Z. hololepis*, *S. argentea* and *P. beanii*. Principal species in assemblage 3 (average similarity 51.00) include *C. caelorhincus*, *S. argentea*, *P. beanii*, *N. gilli* and *B. anatrostris*. However, the main contributor species in all three assemblages is *C. caelorhincus* which accounts for 14.31%, 12.96% and 14.09%, similarity in assemblages 1, 2 and 3, respectively (Table 3).

The SIMPER analysis also confirms the existence of the three groups with very high dissimilarity values (Table 4). The dissimilarity in assemblage composition between the three assemblages is mainly caused by the fishes *M. occidentalis*, *L. barbatulum*, *Z. hololepis*, *E. occidentalis*, *H. billsamorum*, *N. gilli*, *P. longispinis*, *S. guentheri*, *C. agassizi*, *C. suttkusi* and *P. nobilis*.

Table 3. Results of the SIMPER analysis of similarity between assemblages. Species are listed in order of their contribution to the average similarity within each assemblage. Standard deviation (SD).

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Assemblage 1 (Av. Sim = 51.82)					
<i>Coelorinchus caelorhincus</i>	7.37	7.41	8.61	14.31	14.31
<i>Malacocephalus occidentalis</i>	6.42	6.20	6.18	11.96	26.26
<i>Laemonema barbatulum</i>	5.99	5.80	5.10	11.19	37.45
<i>Epigonus occidentalis</i>	4.99	3.93	1.41	7.58	45.03
<i>Dibranchus atlanticus</i>	4.75	3.91	1.84	7.54	52.57
<i>Peristedion greyae</i>	3.90	2.57	0.85	4.96	57.53
<i>Hymenocephalus billsamorum</i>	3.91	2.40	0.84	4.62	62.16
<i>Hymenocephalus italicus</i>	3.79	2.26	0.82	4.36	66.52
<i>Steindachneria argentea</i>	3.62	2.25	0.83	4.34	70.86
<i>Chaunax suttkusi</i>	3.20	1.76	0.67	3.40	74.26
<i>Gadella imberbis</i>	2.73	1.41	0.67	2.71	76.97
<i>Gurgesiella atlantica</i>	2.56	1.36	0.66	2.63	79.60
<i>Xenomystax bidentatus</i>	2.42	1.30	0.67	2.50	82.11
<i>Hydrolagus alberti</i>	2.27	1.03	0.54	1.98	84.09
<i>Epigonus pandionis</i>	2.48	0.92	0.42	1.78	85.87
<i>Anacanthobatis americanus</i>	2.00	0.72	0.42	1.38	87.25
<i>Ijimaia antillarum</i>	1.94	0.70	0.41	1.35	88.60
<i>Setarches guentheri</i>	1.92	0.67	0.41	1.29	89.89
<i>Bembrops anatirostris</i>	1.75	0.65	0.42	1.26	91.14
Assemblage 2 (Av. Sim = 49.65)					
<i>Coelorinchus caelorhincus</i>	5.96	6.43	4.27	12.96	12.96
<i>Chaunax suttkusi</i>	5.22	5.65	5.36	11.39	24.34
<i>Zenion hololepis</i>	6.12	5.55	1.41	11.18	35.53
<i>Steindachneria argentea</i>	4.09	3.64	1.20	7.34	42.87
<i>Poecilopsetta beanii</i>	4.25	3.64	1.40	7.33	50.20
<i>Chlorophthalmus agassizi</i>	4.21	3.59	1.40	7.24	57.44
<i>Polymixia nobilis</i>	3.88	2.95	1.17	5.94	63.38
<i>Setarches guentheri</i>	3.81	2.57	0.96	5.18	68.55
<i>Chlorophthalmus brasiliensis</i>	3.03	2.13	0.89	4.28	72.84
<i>Bembrops anatirostris</i>	2.86	1.92	1.03	3.87	76.71
<i>Neobythites gilli</i>	3.13	1.70	0.66	3.43	80.13
<i>Ijimaia antillarum</i>	2.58	1.56	0.76	3.14	83.27
<i>Lepophidium staurophor</i>	2.05	0.93	0.51	1.87	85.14
<i>Peristedion imberbe</i>	2.22	0.85	0.43	1.71	86.85
<i>Epigonus pandionis</i>	2.04	0.85	0.44	1.70	88.56
<i>Xenomystax bidentatus</i>	1.80	0.79	0.44	1.60	90.15
Assemblage 3 (Av. Sim = 51.00)					
<i>Coelorinchus caelorhincus</i>	7.39	7.19	4.08	14.09	14.09
<i>Steindachneria argentea</i>	6.03	5.57	2.16	10.92	25.01
<i>Poecilopsetta beanii</i>	5.59	5.30	5.45	10.39	35.40
<i>Neobythites gilli</i>	5.22	4.72	3.71	9.26	44.66
<i>Bembrops anatirostris</i>	4.95	4.42	4.77	8.67	53.33
<i>Zenion hololepis</i>	5.06	3.63	1.17	7.12	60.45
<i>Lepophidium staurophor</i>	3.73	2.70	1.48	5.29	65.74
<i>Pontinus longispinis</i>	4.20	2.67	1.13	5.23	70.97
<i>Dibranchus atlanticus</i>	3.27	2.19	0.93	4.29	75.26
<i>Polymixia lowei</i>	2.69	1.25	0.54	2.46	77.72
<i>Antigonia capros</i>	2.64	0.93	0.53	1.83	79.56
<i>Chlorophthalmus brasiliensis</i>	2.28	0.80	0.53	1.57	81.12
<i>Neopinnula americana</i>	2.02	0.78	0.53	1.54	82.66
<i>Polymixia nobilis</i>	2.52	0.77	0.43	1.51	84.17
<i>Chaunax suttkusi</i>	1.89	0.76	0.52	1.50	85.66
<i>Peristedion imberbe</i>	2.04	0.75	0.52	1.48	87.14
<i>Antigonia combatia</i>	2.51	0.70	0.43	1.38	88.52
<i>Peristedion ecuadorese</i>	1.84	0.47	0.34	0.93	89.45
<i>Peristedion greyae</i>	1.34	0.45	0.33	0.88	90.32

Table 4. Results of SIMPER analysis of dissimilarity between assemblages. Species are listed in order of their average (and SD) contribution to dissimilarity within each assemblage.

Species	Av.Diss	Diss/SD	Contrib%	Cum.%
Assem. 1 vs Assem. 2 (Av. Diss = 65.55; R= 0.73; P= 0.001)				
<i>Malacocephalus occidentalis</i>	3.76	4.67	5.74	5.74
<i>Laemonema barbatulum</i>	3.51	4.65	5.36	11.10
<i>Zenion hololepis</i>	3.05	1.71	4.65	15.75
<i>Epigonus occidentalis</i>	2.41	1.69	3.68	19.43
<i>Hymenocephalus billsamorom</i>	2.23	1.34	3.40	22.83
<i>Dibranchus atlanticus</i>	2.06	1.53	3.14	25.96
<i>Peristedion greyae</i>	2.05	1.27	3.13	29.10
<i>Hymenocephalus italicus</i>	1.98	1.32	3.02	32.12
<i>Chlorophthalmus agassizi</i>	1.96	1.52	2.98	35.10
<i>Polymixia nobilis</i>	1.89	1.48	2.88	37.98
<i>Setarches guentheri</i>	1.89	1.36	2.88	40.86
<i>Poecilopsetta beanii</i>	1.88	1.46	2.87	43.74
<i>Neobythites gilli</i>	1.73	1.14	2.63	46.37
<i>Epigonus pandionis</i>	1.68	1.09	2.56	48.93
<i>Chaunax suttkusi</i>	1.64	1.29	2.49	51.42
<i>Steindachneria argentea</i>	1.58	1.19	2.41	53.83
<i>Gadella imberbis</i>	1.56	1.14	2.39	56.21
<i>Chlorophthalmus brasiliensis</i>	1.52	1.30	2.32	58.53
<i>Gurgesiella atlantica</i>	1.52	1.14	2.32	60.85
Assem. 1 vs Assem. 3 (Av. Diss = 68.91; R=0.89; P=0.001)				
<i>Malacocephalus occidentalis</i>	3.44	4.53	5.00	5.00
<i>Laemonema barbatulum</i>	2.67	2.21	3.87	8.87
<i>Neobythites gilli</i>	2.45	2.50	3.55	12.42
<i>Zenion hololepis</i>	2.35	1.51	3.42	15.83
<i>Epigonus occidentalis</i>	2.29	1.50	3.33	19.16
<i>Hymenocephalus billsamorom</i>	2.11	1.32	3.06	22.22
<i>Poecilopsetta beanii</i>	2.10	1.77	3.04	25.26
<i>Pontinus longispinis</i>	2.01	1.49	2.92	28.18
<i>Hymenocephalus italicus</i>	2.00	1.31	2.90	31.08
<i>Lepophidium staurophor</i>	1.94	2.12	2.81	33.90
<i>Peristedion greyae</i>	1.83	1.45	2.66	36.56
<i>Bembrops anatirostris</i>	1.78	1.58	2.59	39.14
<i>Steindachneria argentea</i>	1.68	1.24	2.43	41.57
<i>Chaunax suttkusi</i>	1.56	1.25	2.27	43.84
<i>Epigonus pandionis</i>	1.51	1.03	2.19	46.03
<i>Polymixia lowei</i>	1.47	0.99	2.14	48.17
<i>Gadella imberbis</i>	1.40	1.16	2.03	50.20
<i>Dibranchus atlanticus</i>	1.38	1.41	2.01	52.21
<i>Polymixia nobilis</i>	1.38	1.04	2.01	54.22
<i>Gurgesiella atlantica</i>	1.38	1.12	2.00	56.22
<i>Xenomystax bidentatus</i>	1.35	1.18	1.96	58.18
<i>Chlorophthalmus brasiliensis</i>	1.31	1.13	1.91	60.08
Assem. 2 vs Assem. 3 (Av. Diss = 57.73; R=0.47; P=0.001)				
<i>Pontinus longispinis</i>	2.22	1.53	3.85	3.85
<i>Setarches guentheri</i>	2.03	1.34	3.51	7.35
<i>Chlorophthalmus agassizi</i>	1.97	1.43	3.41	10.77
<i>Chaunax suttkusi</i>	1.96	1.57	3.40	14.16
<i>Polymixia nobilis</i>	1.92	1.47	3.32	17.49
<i>Zenion hololepis</i>	1.82	1.08	3.15	20.64
<i>Neobythites gilli</i>	1.79	1.36	3.10	23.74
<i>Polymixia lowei</i>	1.59	1.04	2.75	26.49
<i>Dibranchus atlanticus</i>	1.58	1.30	2.73	29.22
<i>Chlorophthalmus brasiliensis</i>	1.55	1.32	2.69	31.91
<i>Lepophidium staurophor</i>	1.55	1.37	2.68	34.59
<i>Steindachneria argentea</i>	1.51	1.14	2.61	37.20
<i>Peristedion imberbe</i>	1.47	1.14	2.55	39.76
<i>Bembrops anatirostris</i>	1.47	1.30	2.55	42.31
<i>Ijimaia antillarum</i>	1.41	1.20	2.44	44.75
<i>Antigonia capros</i>	1.38	0.99	2.39	47.14
<i>Epigonus pandionis</i>	1.37	1.05	2.38	49.52
<i>Antigonia combatia</i>	1.37	0.91	2.38	51.90
<i>Neopinnula Americana</i>	1.25	1.01	2.17	54.07
<i>Xenomystax bidentatus</i>	1.22	0.96	2.12	56.19
<i>Poecilopsetta beani</i>	1.18	1.07	2.04	58.23
<i>Epigonus occidentalis</i>	1.14	0.87	1.97	60.20

Total abundance was highest in shallower waters the assemblage 3 (8898.64 N/km<sup>2</sup>). It decreased with depth in assemblage 2 (6722.53 N/km<sup>2</sup>) and then increased again in assemblage 1 (7872.75 N/km<sup>2</sup>). However, these differences were statistically not significant (Table 5). The biomass values obtained in assemblage 1 were higher than in assemblage 3 and significantly lower values were found in assemblage 2 (Table 5). The biomass means showed significant differences for assemblage 1 vs. assemblage 2 and assemblage 2 vs. assemblage 3 (Table 6). Statistical analysis showed no significant differences in terms of total species (S), mean species richness (d), diversity (H') and evenness (J'). However, diversity and evenness indexes were highest in assemblage 1, with intermediate values in assemblage 3 and lowest values in the assemblage 2. Mean species richness (d) was higher in the assemblage 3 than in assemblage 1 and lower in assemblage 2. Similarly, the total number of species was high assemblages 1 and 3, and lower in assemblage 2. Mean depth showed significant differences between the assemblages (Table 5; Table 6), decreasing from assemblage 1 to assemblage 3.

Table 5. Mean abundance and values of diversity indexes and standard error ( $\pm$ SE) for species assemblages identified in the deep-sea Colombian Caribbean Sea.

Ecological parameters	Assemblage 1	Assemblage 2	Assemblage 3	p
Abundance (N km <sup>-2</sup> )	7872.75 $\pm$ 1178.10	6722.53 $\pm$ 1397.61	8898.64 $\pm$ 1491.81	0.232
Biomass (kg km <sup>-2</sup> )	342.15 $\pm$ 40.43	155.63 $\pm$ 27.05	286.30 $\pm$ 36.62	0.001
Total species (S)	44	53	55	0.316
Mean species richness (d)	1.93 $\pm$ 0.11	1.94 $\pm$ 0.08	2.15 $\pm$ 0.16	0.523
Diversity (H')	0.95 $\pm$ 0.04	0.82 $\pm$ 0.04	0.88 $\pm$ 0.07	0.139
Evenness (J')	0.76 $\pm$ 0.03	0.67 $\pm$ 0.03	0.68 $\pm$ 0.05	0.156
Depth (m)	437.75 $\pm$ 16.56	388.34 $\pm$ 8.29	291.98 $\pm$ 9.70	0.000

Table 6. Results of Nemenyi and Dunns test for differences between means of abundance and diversity values for deep-sea fish assemblages.

Assemblage	N	B	S	d	H'	J'	Depth
1 – 2	0.784	0.001	0.942	0.992	0.153	0.143	0.006
1 – 3	0.842	0.440	0.199	0.361	0.586	0.236	0.000
2 – 3	0.417	0.012	0.078	0.341	0.592	0.974	0.000

According to the bathymetric distribution fish assemblages (Fig.6), could be defined for the depth ranges between 200 m and 300 m (assemblage 3), 300 m and 400 m (assemblage 2) and 400 m and 550 m (assemblage 1). The species *C. caelorhincus* and *S. argentea* occupied all depth strata, but were most abundant in the 300 - 400 m depth stratum.

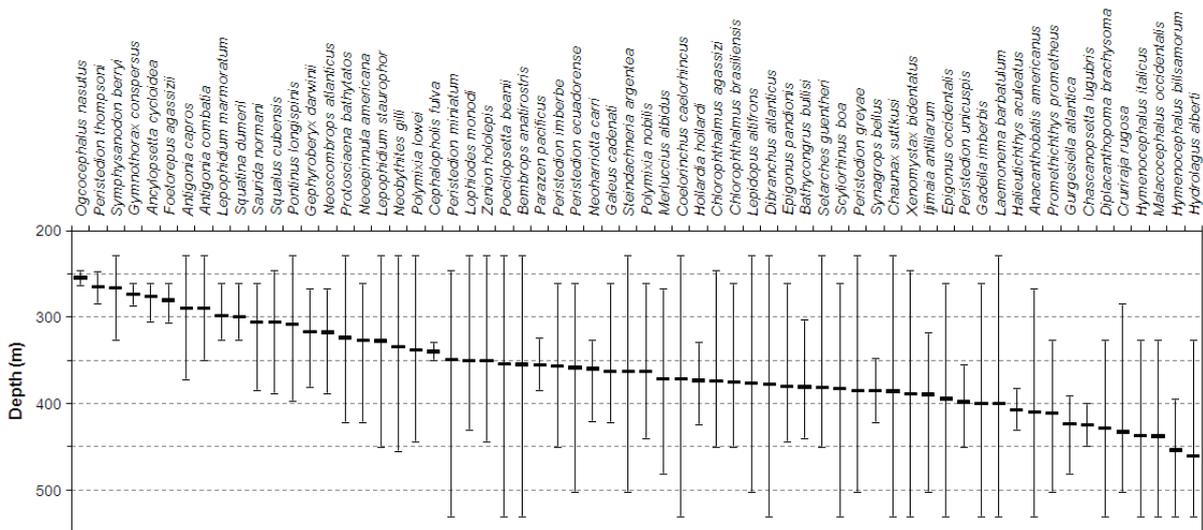


Figure 6. Bathymetric distribution of demersal deep-sea ichthyofauna in the Colombian Caribbean Sea.

#### 4. Discussion

The oceans are the source of a significant amount of food produced for human consumption, but in order to suggest effective management and conservation measures, we need to know what is in the sea and how susceptible the system is to exploitation (Hart and Pearson, 2011). While the ecosystems approach to fisheries management is strongly recommended for deep-sea fisheries (FAO, 2003), there is still very little information available about the ecology of deep-sea ecosystems. This means that management strategies start from a low level of knowledge, and in consequence ecosystem-based management must adopt a highly precautionary approach (Clark, 2009). Unfortunately, scientific assessment usually begins some years after a commercial fishery has been established and in conditions where the resource is already over-fished or has collapsed (Haedrich et al., 2001; Priede et al., 2011). In contrast, this study explored an unexploited deep-sea ecosystem with the aim of identifying potential commercial fisheries (Paramo and Saint-Paul, 2011 a,b), and to provide an ecosystem baseline for subsequent development and management of a deep-sea fishery in the Colombian Caribbean Sea.

This study reveals the existence of three deep-sea fish assemblages in which depth play an important role in the differentiation of ichthyofaunal assemblage. This finding confirms observations that fish assemblages are generally associated with discrete depth ranges (Magnussen, 2002; Powell et al., 2003; Katsanevakis and Maravelias, 2009). Most of the species of the shallower assemblage have a narrow depth range, while the species of the middle depth assemblage extend their distributions over a wide depth range and are probably able to undertake large vertical migrations in the water column. Assemblages 2 (middle depth) and 3 (shallow) had some species in common, such as *C. caelorhincus*, *S. argentea* and *P. beanii*, which are all eurybathic species adapted to wide depth ranges. In

particular *C. caelorhincus* occupied all three assemblages, demonstrating its great capacity for bathymetric migrations. Macrouridae species, such as grenadiers, generally dominate over relatively flat portions of the food limited deep sea (Koslow et al., 2000) and are adapted to feeding on epibenthic and benthopelagic organisms (Merrett and Haedrich, 1997; D'Onghia et al., 2004). The composition of fish assemblages are also related to physical factors such as temperature, salinity, oxygen content, sediment conditions and other biological factors (i.e. predator and prey abundance) should also be influential in regulating the distribution of ichthyofaunal assemblages (Powell et al., 2003; Company et al., 2008). It is known that deep sea ichthyofaunal biomass (and possibly diversity as well) largely depends on the surface productivity regime (D'Onghia et al., 2004; Company et al., 2008). Clark et al., (2010) indicated the importance of water mass in defining fish assemblages. In fact, the highest diversity ( $H'$ ) was found in the Guajira region, which is strongly influenced by upwelling processes. The Colombian Caribbean Sea is characterized by northeast trade winds with surface currents flowing toward the west and south-west almost parallel to the coast. These trade winds are responsible for the upwelling that occurs in the northern zone of the study area, which increases primary productivity along the Guajira coast (Andrade et al., 2003; Paramo et al., 2003; Paramo et al., 2009). In order to further elucidate the role of primary productivity in shaping the deep-sea fish assemblages, quantitative analysis of other environmental variables (i.e. temperature, salinity, oxygen) in addition to depth, need to be conducted. Possible linkages between surface production and fish feeding through models of export flux from surface to the seafloor must definitely be included in future studies of deep-sea fish assemblages. These studies may also help to predict deep-sea fish biomass from surface production maps combined with analysis of other environmental factor. Additionally, season can be a factor in determining species

composition since some species are likely to make migrations for spawning or feeding (Clark et al., 2010). For this reason, prior to defining management zones based on the structure of assemblages, there is a need to understand the temporal stability of these deep-sea ichthyofaunal assemblages of the Colombian Caribbean Sea. Thus, assemblage analyses have the potential to provide valuable inputs for fisheries management, particularly of multispecies fisheries (Garces et al., 2006).

Many deep-sea fisheries are based on bony fish belonging to the families Macrouridae, Moridae, Brotulidae and Merlucciidae (Koslow et al., 2000) or on other cartilaginous species (FAO, 2007). However, benthic and demersal invertebrates are comparatively more important in Latin American fisheries (Arana et al., 2009). The sustainable development of these fisheries can be achieved by operating few vessels and targeting small bulk of high value species (Clark, 2009). However, Zhou et al. (2010) call for a balanced ecosystem-based fisheries management approach that might alleviate many of the ecological effects of fishing by avoiding the intensive and selective removal of particular components of the ecosystem. Balanced exploitation could increase fisheries production by utilizing additional non-target, non-vulnerable species, while reducing unsustainably high fishing pressure on current target species, thus helping to maintain sustainable fisheries, balanced ecosystems, and natural biodiversity. Following this reasoning, research into low-value species and their fisheries potential should be enhanced (Zhou et al., 2010). We strongly recommend that all stakeholders, including scientists, fisheries managers and environmental institutes establish a monitoring program of these deep-sea resources and the associated biodiversity to enable an adaptive ecosystem approach to fisheries management. One aim should be to quantify discarded biomass and study the possibilities for commercial use of these discards. The establishment of spatio-temporal regulation measures, such as marine protected areas,

should also be considered. From the point of view of conservation and fisheries management strategies, we need to know the status of deep-sea fish assemblages more fully to initiate a new deep-sea fishery in the Colombian Caribbean Sea. Conservation and protection of the habitats is therefore fundamental to develop a rational and sustainable management of the deep-sea fishery resources of the Colombian Caribbean Sea.

The code of conduct for responsible fisheries (FAO, 2009) recognizes the importance of best scientific evidence, as well as of traditional knowledge of resources and their habitats, in making decisions about the conservation and management of fisheries. However, deep-sea fisheries are generally data-poor, and many deep-water species are also difficult to age reliably (Lorance et al., 2011). Ye et al. (2011) point out that to overcome the data limitation and absence of modelling support, simple indicators have to be used to assess the current state and monitor changes of the fishery and its ecosystem. Such indicators should be observable and understandable by all stakeholders, be based on easily obtainable and reliable data, adequately reflect the condition of the resource, and have associated reference values and responsive management measures. In this sense, Shin et al., (2010) distinguished four management objectives as a means of evaluating the ecological state of marine ecosystems: conservation of biodiversity (CB), maintenance of ecosystem stability and resistance to perturbations (SR), maintenance of ecosystem structure and functioning (EF) and maintaining resource potential (RP). Eight indicators were selected to attain these objectives: total biomass of surveyed species, the inverse ratio of landings/biomass ( $1/(\text{landing}/\text{biomass})$ ), mean length of fish in the community, trophic level (TL) of landings, proportion of predatory fish, proportion of under- and moderately exploited stocks, mean lifespan, and the reciprocal of the coefficient of variation of total biomass

(1/coefficient of variation (CV) of total biomass). These indicators (and possibly others) could guide the monitoring of a deep-sea fishery off the Colombian Caribbean coast.

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## 7. General discussion

Existing fisheries management practices are failing to protect individual stocks and ecosystems; therefore fisheries management should move from single species management towards an ecosystem approach to fisheries (EAF) (Hilborn, 2011). Nevertheless, species-based approaches are also necessary to understand single populations and to analyze how they contribute to the understanding of the communities and ecosystems (Guijarro et al., 2011). A fishery consists of an ecosystem, a fishing fleet and a management system, and then an EAF should be implemented with stakeholder cooperation, provide good governance and effective enforcement (Hilborn, 2011), and be guided by key indicators of ecosystem condition (Levin et al., 2009).

The code of conduct for responsible fisheries (FAO, 2009) recognizes the importance of best scientific evidence, as well as traditional knowledge of resources and their habitat, in making decisions about the conservation and management of fisheries. However, in developing countries there is a lack of institutional capacity and budget to carry out the research into fisheries and ecosystems, required for an EAF (Mathew, 2011). Additionally, deep-sea fisheries are generally data-poor, with only landing records and rarely scientific survey data being available. Many deep-water species are also difficult to age reliably (Lorance et al., 2011). Ye et al. (2011) point that to overcome the data limitation and in the absence of modelling support, simple indicators have to be used to assess the current state of the fishery and its ecosystem and to monitor changes as they occur. Such indicators should be observable and understandable by all stakeholders, be based on easily obtainable and reliable data, adequately reflect the condition of the resource, and define associated

reference values and responsive management measures. In this sense, Shin et al. (2010) distinguished four management objectives as a means of evaluating the ecological state of marine ecosystems: conservation of biodiversity (CB), maintenance of ecosystem stability and resistance to perturbations (SR), maintenance of ecosystem structure and functioning (EF) and maintaining resource potential (RP). Eight indicators were selected to attain these objectives: total biomass of surveyed species, the inverse ratio of landings/biomass ( $1/(\text{landing}/\text{biomass})$ ), mean length of fish in the community, trophic level (TL) of landings, proportion of predatory fish, proportion of under- and moderately exploited stocks, mean lifespan, and the reciprocal of the coefficient of variation of total biomass ( $1/\text{coefficient of variation (CV) of total biomass}$ ).

The following provides a more detailed description of the indicators proposed by Shin et al. (2010), which I argue should be applied in the proposed new deep-sea fishery in the Colombian Caribbean Sea (Fig. 1) (Paramo and Saint-Paul, 2011a,b). Total biomass of surveyed species is a useful indicator of changes over time in resource potential (RP) of an ecosystem. It measures the production capacity and potential contribution of the ecosystem as an exploitable marine resource.  $1/(\text{landing}/\text{biomass})$  is an inverse measure of the level of exploitation or total fishing pressure on an ecosystem (RP). It reflects the proportion of the community production that is taken by the fishery and serves as a proxy for exploitation rate. Mean length of fish in the community allows tracking direct effects of fishing on an ecosystem (EF). The removal of larger and more fecund fish compromises population productivity. Also, the removal of larger species changes the size structure of the community and ecosystem functioning. The trophic level (TL) of landings measures the TL of species exploited by fishery represents the trophic position of the whole catch, which is expected to decrease in response to fishing (EF). Fishing can change the structure of marine

foodwebs by reducing the mean TL and potentially also ecosystem functioning by shortening the length of food chains and releasing predation on low-trophic-level organisms. The proportion of predatory fish is a measure of the diversity of fish in the community (CB) and reflects the potential effects of fishing on the functioning of marine foodwebs. The proportion of under- and moderately exploited stocks (CB), is a measure of the success of fisheries management and is used to compare the state of ecosystems. Mean lifespan is a proxy for the mean turnover rate of species and communities and is intended to reflect the stability of a system. The mean lifespan of a community will reflect the relative abundances of species with different turnover rates. It is therefore considered to be a measure of ecosystem stability and resistance to perturbations (SR).  $1/\text{coefficient of variation (CV)}$  of total biomass is adopted as a further measure of the stability of the ecosystem (SR). A low  $1/\text{CV}$  indicates low biomass stability, and thus low ecosystem stability in response to perturbations. As total biomass decreases, the area occupied by the various stocks may decrease, the stocks may be more patchily distributed, or they may occupy the same area at a lower density. Finally, an important characteristic of the indicators proposed by (Shin et al., 2010) is that they are mostly survey-based, independent of the fishery; the aim is to study the ecosystem responses to fishing pressure. Using simple yet rigorous, scientifically indicators through an ecosystem approach is a promising way to achieve real evaluation of changes in marine ecosystem status as a result of fishing activities.

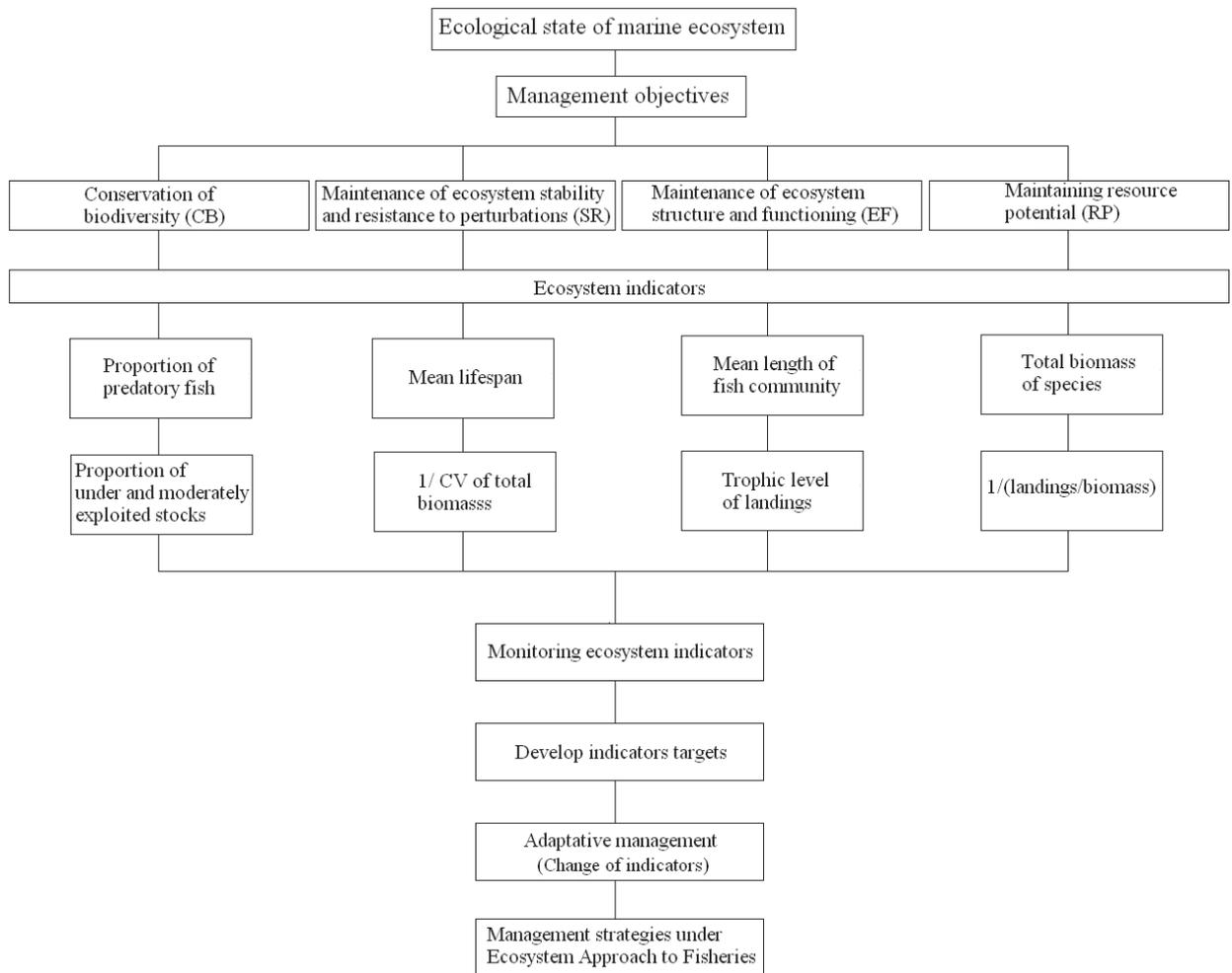


Figure 1. Management strategies under an ecosystem approach to fisheries (EAF) for deep-sea fishery in the Colombian Caribbean Sea.

Discarding is currently one of the most important topics in fisheries management (FAO, 2010). Discards are described as the proportion of the total organic material of animal origin in the catch that is thrown away or dumped at sea, for whatever reason. Bycatch is the part of a catch that is taken incidentally in addition to the target species towards which fishing effort is directed. Some or all of it may be returned to the sea as discards, usually dead or dying (FAO, 2010). However, global fishery discards have significantly declined in

recent years (Zeller and Pauly, 2005; Davies et al., 2009), apparently due to improved selectivity of fishing technology and greater utilisation of the bycatch for aquaculture and human consumption (Bellido et al., 2011). Heymans et al. (2011) modelled the deep-sea ecosystem of the Rockall area (200 miles off the west of Scotland) using Ecopath with Ecosim. They identified the lack of discard data from deepwater fisheries in the area as an important limitation and potentially a substantial source of error in the model. This emphasises the importance of having a deep knowledge and good quantification of discards to assess ecosystem status, as required for the implementation of EAF. Zhou et al. (2010) argue that less selective fishing gears may help to maintain diversity and functioning in certain marine ecosystems. They propose a balanced exploitation approach combining reduced fishing effort, less selective fishing strategies, and better use of the catch to help achieve sustainable overall yields while maintaining healthy ecosystems. Hall and Mainprize (2005) recommend diversifying the harvest and learning to utilize a wider variety of products. Fisheries production could actually increase through better use of non-target species, while reducing unsustainably high catches of target species, thereby helping to meet the challenge of increasing global food demand (Zhou et al. 2010). The biomass made available by fisheries discards returning to the seabed may produce good conditions for a short-term increase of scavenger benthic species, including fish, crabs, shrimps and other invertebrates (Bellido et al., 2011).

One important measure that should be included in the management of the proposed new deep-sea fishery in the Colombian Caribbean Sea is the implementation of spatial management, with zoning for different kinds of fishing activity and use of seasonal or temporary closures. This can be a useful tool for reducing discard rates and controlling effort exerted. Spatial management measures must be underpinned by a good knowledge of

the biology, spatial distribution and abundance of both resource species and other species impacted by fisheries, including protected species (Bellido et al., 2011). Finally, marine protected areas (MPAs) have recently emerged as a tool for marine conservation and fisheries management following an ecosystem-based approach (Worm et al. 2006; Fraser et al., 2009; Paramo et al., 2009; Jackson and Jacquet, 2011).

In this research I provide the first complete view, to date, of the pink shrimp *F. notialis* stock structure and fishery dynamics in the Colombian Caribbean Sea, based on morphometric, historic landings and biologic data. However, the shallow water shrimp fishery in the Colombian Caribbean is a typical case in which high exploitation, combined with non-existent fisheries management, have resulted in the significant depletion of stock. For that reason, the research investigated possible new fishing areas, exploring the deep sea habitats in the Colombian Caribbean Sea, to determine the potential for a viable deep-sea crustacean fishery. I propose that the deep-sea giant red shrimp (*Aristaeomorpha foliacea*), the royal red shrimp (*Pleoticus robustus*), the pink speckled deep-sea shrimp (*Penaeopsis serrata*) and the deep-sea lobster (*Metanephrops binghami*) as new fishing resources. The substantial marketability of these deep-sea crustaceans species, not only locally but also in numerous international markets, underlines the potential of these species as a new economic resource in the Colombian Caribbean Sea. However, I recommend that more scientific assessment is necessary to determine life cycle population parameters of deep-sea crustaceans and associated biodiversity, before initiating a new commercial fishery. The management of the shallow shrimp fishery and the proposed new deep-sea crustacean fishery should be based on an ecosystem approach, that considers population dynamics and structure, the optimum allocation of catches and effort, protection of nursery and spawning areas, the development of monitoring strategies (Fig. 1) by means of ecosystem indicators

(Shin et al., 2010) and the care of ecosystems through the identification of MPAs. This approach will allow an appropriate level of biodiversity and the habitat quality to be maintained, while achieving sustainable fisheries.

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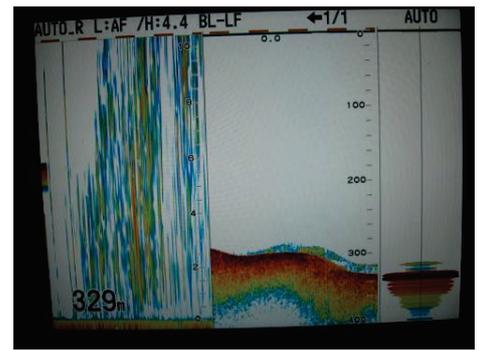
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Vessel Tee Claude used for the deep-sea surveys.



Echosounder FURUNOFCV 1150



*A. foliacea* and *P. robustus*

Catch of *A. foliacea*



*P. robustus* (up) and *A. foliacea* (low)



*A. foliacea*



*Penaeopsis serrata*

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Catch of *Metanephrops binghami*



*Metanephrops binghami*



“Desarrollo de nuevas pesquerías de aguas profundas en el Caribe colombiano hacia una producción limpia y rentable del sector pesquero usando el enfoque precautorio para la pesca responsable”



Departamento Administrativo de  
Ciencia, Tecnología e Innovación  
**Colciencias**  
República de Colombia

