IMPACTS OF NON-NATIVE FISHES ON THE FISH COMMUNITY AND THE FISHERY OF THE CIÉNAGA GRANDE DE SANTA MARTA ESTUARY, NORTHERN COLOMBIA

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Universität Bremen

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1. Fisherman with cast net in Ciénaga Grande de Santa Marta, Colombia. Photo: INVEMAR 2001
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5. Children at a fish market in Ciénaga Grande de Santa Marta, Colombia. Photo: INVEMAR 2001

IMPACTS OF NON-NATIVE FISHES ON THE FISH COMMUNITY AND THE FISHERY OF THE CIÉNAGA GRANDE DE SANTA MARTA ESTUARY, NORTHERN COLOMBIA

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A mis padres María Teresa y Orlando

A mis hermanos Orlando y Ervin

To my friends

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PRESENTATION

In 1958 Charles S. Elton published one of the most important works in Ecology: "The Ecology of Invasions by Animals and Plants". With this work he placed the cornerstone to the foundations of what is known today as invasion ecology. His book called the attention of the scientific community to a problem that nowadays is considered as one of the main threads to biodiversity.

I acknowledged the problem of species introductions in 1997. I was part of an interdisciplinary team that was assessing the status of the aquatic resources in some flood plains within the lower basin of the River Magdalena, the largest and most important river in Colombia. At that time, the Nile tilapia (*Oreochromis niloticus*) was one of the most important fishes for the local fishery. Some of the fishermen with whom I had the chance to talk during my work blamed the "Lora", as the Nile tilapia is called in the region, for the reduction of the native Bocachico (*Prochilodus magdalenae*), the most important species for the local fishery. According to them, the "Lora" was feeding on the Bocachico's fry and food. They did not know that Nile tilapia is a mouth brooder that feeds mainly on phytoplankton and detritus. So they could have confused the tilapia fry in its mouth with that of the native fish.

This comments of the fishermen, however, caught my attention and I started to look for the pathway and reason of the introduction of this fish in these ecosystems. I found out that the government agency in charge of fisheries management introduced the Nile tilapia into the lagoons because it was considered a good alternative of livelihood for the fishermen, since the main native fish populations were in decrease. I asked if there was a previous study on the possible impacts of this fish on the ecosystem, but I was told that it was not necessary, since they believed that this fish could not cause any problem. I was very surprised and became interested in helping to change this mentality of worrying only for today's problems when managing our resources. The project of which my work became part was abruptly interrupted due to lack of funds and I was unable to return to that region.

Some years after that experience, I decided to start my PhD. Searching for a topic I heard of the "boom" of Nile tilapia in Ciénaga Grande de Santa Marta (CGSM), the most important estuary in the north of Colombia. Since I had maintained an interest in species introductions, I decided to study the impacts of the non-native fishes on that ecosystem. I counted with the support of the Institute for Marine and Coastal Research (INVEMAR), in Santa Marta, which provided me a database with several types of information from periods before and after the introduction of the non-native fishes in the ecosystem. This was a golden chance that seldom occurs in the field of invasion ecology, since it is very rare to find information of the time before the introductions. Therefore I have written my Doctoral thesis on the following topic: Impacts of non-native fishes on the fish community and the fishery of the Ciénaga Grande de Santa Marta estuary, Colombia.

The study focuses on the impacts of two introduced fishes, Nile tilapia (*Oreochromis niloticus*) and snakeskin gourami (*Trichogaster pectoralis*), and has been organized in two main sections. The first is a general overview of the study and consists of several chapters providing an introduction (chapter 1) to the research problem on a global and regional scale, as well as the research topics and hypotheses, a description of the study area (chapter 2), a general methodology (chapter 3), general results and discussion (chapter 4), concluding remarks (chapter 5) and comments on management (chapter 6). The second section consists of three chapters, each of which is a manuscript that has been submitted to an international peer review journal. Since information from periods before and after introduction is available only for Nile tilapia, these manuscripts focus only on this species. The first manuscript deals with impacts on native fish abundance and catch composition (chapter 7), the second with impacts on feeding habits of native fishes (chapter 8) and the third with impacts on the fishery in terms of economic revenue and preferences for native or non-native fishes (chapter 9). Additionally, in the appendices a short terminology (Appendix A), a brief description of non-native (Appendix B) and native fishes (Appendix C) and a list of abbreviations (Appendix D) used in the text are presented.

The reader is invited to go through the next sections to learn about a study that, to my knowledge, is the first directly dealing with the impact of non-native fishes in Colombian coastal waters, but also, the first of this type in a Caribbean estuary.

ABSTRACT

In tropical coastal ecosystems very little is known about the impacts of non-native fish species on the native ichthyofauna and to the author's knowledge, there are no published studies in Caribbean estuaries. The Ciénaga Grande de Santa Marta estuary (CGSM), at the Caribbean coast of Colombia, has been affected by human intervention that altered the hydrological regime causing the loss of valuable resources. Formerly interrupted water connections were reopened in 1996-1998 to reestablish hydrological conditions, but as a side effect the occurrence of non-native fishes augmented in the estuary. Since its accidental introduction in 1995, Nile tilapia (*Oreochromis niloticus*) ranks among the most commercial resources, accounting for more than 60% of the catches until 2001, but decreasing thereafter to less than 10%. In contrast, the occurrence of snakeskin gourami (*Trichogaster pectoralis*), first registered in 1989, has been lower but more regular than that of Nile tilapia.

This study aims to determine the impacts of *O. niloticus* on the abundance, species composition, feeding habits and fishery of native fishes, and the impacts of *T. pectoralis* on the abundance of native ichthyofauna. Catch per Unit Effort (CPUE) data was used as a measure of relative abundance of different species in the ecosystem from 1994 to 2003. The data sets were divided into four periods (I=1994-1995; II=1996; III=1999-2001; IV=2002-2003). Additionally the study area was divided into four zones following an east-to-west gradient of increasing salinity.

The abundance of the native fishes combined was relatively constant and did not seem to be affected by the "boom" of Nile tilapia during the years 1999-2001. Instead, this fish represented a large addition of biomass into the system. However, on the species level, composition and abundance changed from period to period. Analyses of similarity (ANOSIM) and similarity percentage (SIMPER) revealed that *O. niloticus* modified the fish composition, dominating all zones during the period of lowest salinity (1999-2001). In contrast the native estuarine fish *Mugil incilis* was dominant in all other periods in the entire estuary. A decrease in native fish diversity coincided with high abundance of Nile tilapia. Multiple regression analyses revealed that changes in abundance of two native estuarine fishes, *Cathorops mapale* and *Megalops atlanticus,* were related to the abundance of Nile tilapia, and that changes in abundance of two native estuarine fishes, *Ariopsis bonillai* and *Elops saurus* were related to the abundance of *T. pectoralis*. However, multiple regression analyses also revealed that mostly salinity and, to a lesser extent, pH and river discharge regulate the distribution and abundance of all studied fishes, including *O. niloticus* and *T. pectoralis*.

The analyses of diet composition (e.g. index of relative importance), diet evenness (J') and diet breadth (H') in periods before and after the introduction of Nile tilapia, revealed that most native fishes and *O. niloticus* were mixed feeders with certain degree of specialization in two or three food categories. Few native fishes were either generalists or specialists. All fishes fed on the most abundant preys, which mostly belong to low levels in the food web, in both periods and changed their feeding habits according to prey abundance. Multiple regression analysis showed that mainly salinity is the factor that regulates the abundance of most common preys in the estuary. A moderate diet overlap was observed between *O. niloticus* and *Diapterus rhombeus*, but this is most likely due to high abundance of their common preys: detritus and phytoplankton.

The fishery of Nile tilapia, a relatively low-priced fish, provided a six times greater economic revenue than all native fishes together during the period 1999-2001. However, a questionnaire-based survey revealed that fishermen prefer the fishery of native estuarine fishes due to their better taste and price. An analysis on the species level showed that economic revenues derived from the most valued native species decreased during the period of highest abundance of *O. niloticus* and lowest salinity in the estuary. In contrast, the native estuarine fish *Mugil incilis* kept a relatively high price and abundance, thus providing relatively high economic revenue during the whole study period. Multiple regression analysis showed that salinity is the main factor explaining the variation of economic revenue derived from most native fishes. Nevertheless, differences in market structures have also an important influence on economic revenues.

No clear evidence has been found that indicates a negative impact of *O. niloticus* and *T. pectoralis* on the abundance and species composition of the native ichthyofauna. Additionally competition for food between *O. niloticus* and the native fishes does not seem probable due to the high abundance of their shared preys and the generalist and mixed feeding strategies of most native fishes. In fact, the fishery of *O. niloticus* represented an alternative income during a period when the most valued native fishes were scarce. However, there are indications of a high probability of negative impacts to occur: the proliferation of the Nile tilapia modified the species composition of the native fish communities dominating during a period of low salinity, and a potential impact on native benthic fish and fish biodiversity of the estuary can not be ruled out. *Oreochromis niloticus* and *T. pectoralis* have biological features that facilitate their proliferation in new environments and food resources seem not to be a limitation. However, until now their long term establishment seems to have been restricted by drastic environmental fluctuations (e.g. salinity) in the estuary. Three possible scenarios, or a combination of them, could favor the long-term proliferation of oligohaline alien fishes like *O. niloticus* and *T. pectoralis*: 1. A longer duration of relatively low salinity periods, 2. The introduction of more euryhaline strains of *O. niloticus* from aquaculture installations in the area, or 3. The adaptation of non-native fishes to the variable environmental conditions of the estuary.

The findings indicate that the establishment of alien fishes with opportunistic feeding habits in tropical estuaries with a high environmental variability is more influenced by abiotic factors than biotic interactions like competition. However, further research should be conducted to establish the role of other biotic interactions (e.g. predation, competition for space, facilitation) and human factors like overfishing on hindering naturalization of non-native fishes in this type of ecosystems. The relative constancy of the overall abundance of all native fishes combined in the estuary suggests a high resilience of this component that might be related to a high species redundancy within functional groups. Further research is needed to identify those functional groups and determine their importance for ecosystem functioning. Additionally, some gaps of knowledge in the biology of native fishes should be filled to avoid negative side effects of measures aiming to control introduced fish populations in the estuary.

ZUSAMMENFASSUNG

Aus tropischen Küstensystemen ist sehr wenig über den Einfluss von eingewanderten Arten bekannt, dies gilt besonders für karibischen Ästuare, da bis jetzt keine Untersuchungen aus diesen Gebieten veröffentlicht sind. Das Ästuar *Cíenaga Grande de Santa Marta* (CGSM) an der karibischen Küste Kolumbiens ist stark von anthropogenem Einfluss geprägt, was zu einer Änderung des hydrologischen Regimes und damit zum Verlust wertvoller Ressourcen führte. Ehemals unterbrochene Wasserverbindungen wurden in den Jahren 1996-1998 wieder geöffnet, um die ursprünglichen hydrologischen Bedingungen wieder herzustellen, mit dem Nebeneffekt, dass vermehrt eingewanderte Fischarten in dem Ästuar auftraten. Nach seiner unbeabsichtigten Einführung im Jahr 1995 gehört der Nilbuntbarsch (*Oreochromis niloticus*) bis zum Jahr 2001 zu den kommerziell am stärksten genutzten fischereilichen Ressourcen, mit einem Anteil von 60 % in den Fängen. Nach 2001 sinkt dieser Anteil auf weniger als 10 % in den Fängen. Im Gegensatz zum Nilbuntbarsch tritt der Schaufelfadenfisch (*Trichogaster pectoralis*), der erstmals 1989 festgestellt wurde, seltener, dafür aber regelmäßiger im Ästuar auf. Ziel diese Untersuchung ist es, den Einfluss von *O. niloticus* auf die Abundanz und die Zusammensetzung der heimischen Fischarten in den Fängen sowie das Fraßverhalten und die Befischung der heimischen Arten zu untersuchen. Zusätzlich soll der Einfluss von *T. pectoralis* auf die Abundanz der heimischen Ichthyofauna beschrieben werden. Es werden Daten aus Fischereifängen von 1994 bis 2003 verwendet, wobei die Fänge als Einheitsfang pro Ausfahrt (catch per unit effort, CPUE) als Maß für die relative Abundanz der verschiedenen Arten standardisiert sind. Die Daten dieser Untersuchung stammen aus vier (I-IV) verschiedenen Untersuchungszeiträumen (I = 1994-1995, II = 1996, III = 1999-2001 und IV = 2002-2003). Außerdem ist das Untersuchungsgebiet entlang eines Salinitätsgradienten im Ästuar von Ost nach West in vier Zonen eingeteilt.

Die Gesamt-Abundanz der heimischen Fischgemeinschaft war während des Untersuchungszeitraums relativ konstant und schien vom Höchstaufkommen des Nilbuntbarsches während der Jahre 1999-2001 relativ unbeeinflusst. Allerdings bedeutete das Auftreten dieser Fischart einen erheblichen zusätzlichen Eintrag von Biomasse in das System. Auf Artebene war eine Änderung in der Zusammensetzung und Abundanz der Fischarten in den Fängen zwischen den verschiedenen Untersuchungszeiträumen

feststellbar. Ähnlichkeitsanalysen (***Ana**lysis* ***o**f* ***Sim**ilarity*, ANOSIM und ***Sim**ilarity of* ***Per**centage*, SIMPER) zeigten, dass *O. niloticus* die Zusammensetzung der Artengemeinschaft beeinflusste und in allen vier Untersuchungszonen des Ästuars während Perioden mit niedrigster Salinität (1999-2001) dominierte. Im Gegensatz dazu war die heimische ästuarine Art *Mugil incilis* während des übrigen Zeitraums im gesamten Ästuar dominant. Eine Abnahme der Fischdiversität insgesamt schien im Zusammenhang mit dem Auftreten des Nilbuntbarsches zu stehen. Eine multiple Regressionsanalyse zeigte, dass Änderungen in der Abundanz zweier heimischer Fischarten, *Cathropos mapale* und *Megalops atlanticus* mit der Abundanz des Nilbuntbarsches zusammenhing, während Änderungen der Abundanz zwei weiterer einheimischer ästuariner Arten, *Ariopsis bonillai* und *Elops saurus* mit Änderung der Abundanz von *T. pectoralis* einherging. Allerdings zeigte die multiple Regressionsanalyse auch, dass die Verteilung aller untersuchten Fischarten hauptsächlich durch die Salinität sowie, wenn auch in geringerem Umfang, durch Einleitungen aus den Fluss und den pH-Wert reguliert war; dieses galt auch für *O. niloticus* und *T. pectoralis*.

Die Untersuchungen von Zusammensetzung (z.B. Index der relativen Wichtigkeit, IRI), Äquität (J`) und Diversität (H`) des Nahrungsspektrums im Zeitraum vor und nach Einführung des Nilbuntbarsches zeigten, dass die meisten heimischen Fischarten und *O. niloticus* keine eindeutige Nahrungspräferenz aufwiesen, allerdings bis zu einem gewissen Grad auf zwei oder drei Nahrungskategorien spezialisiert waren. Nur wenige der heimischen Fischarten zeigten entweder generalistisches oder spezialisiertes Nahrungsverhalten. Alle Fischarten konsumierten, unabhängig vom Auftreten *O. niloticus*, die jeweils am häufigsten vorhandene Nahrung am meistens aus den unteren Stufen des Nahrungsnetzes und änderten ihr Fraßverhalten in Abhängigkeit vom vorhandenen Nahrungsangebot. Die multiple Regressionsanalyse zeigte, dass auch das Nahrungsangebot maßgeblich durch die Salinität im Ästuar bestimmt wurde. Lediglich das Nahrungsspektrum von *O. niloticus* und *Diapterus rhombeus* wies eine leichte Überschneidung auf, was hauptsächlich auf die hohe Abundanz ihrer häufigsten Nahrungsquellen zurückzuführen war: Detritus und Phytoplankton.

Die Befischung des Nilbuntbarschs, einem Fisch mit einem relativ niedrigen Verkaufspreis, stellte im Zeitraum 1999-2001 eine sechs Mal höhere Einkommensquelle dar als die Befischung aller einheimischen Fischarten zusammen. Eine mittels Fragebögen durchgeführte Umfrage unter den Fischern ergab, dass diese dennoch bevorzugt die heimischen ästuarinen Fischarten befischten, da diese heimischen Arten aufgrund des vergleichweise besseren Geschmacks und Verkaufpreis. Eine Analyse auf Artniveau zeigte, dass die Bedeutung der bevorzugten einheimischen Fischarten als wirtschaftliche Einkommensquelle im Zeitraum höchster Abundanzen von *O. niloticus* im Zusammenhang mit niedrigster Salinität im Ästuar abnahm. Eine Ausnahme hiervon war die heimische ästuarine Art *Mugil incilis*, die nicht nur in relativ hoher Abundanz auftrat, sondern auch einen relativ hohen Verkaufspreis erzielte und damit eine wichtige wirtschaftliche Einkommensquelle während des gesamten Untersuchungszeitraumes darstellte. Auch hier ergab eine multiple Regressionsanalyse, dass die Bedeutung der meisten heimischen Fischarten als Einkommensquelle Schwankungen unterworfen war, die hauptsächlich mit Veränderungen des Salzgehaltes im Ästuar korreliert war. Schließlich spielt aber auch die Marktstruktur eine wichtige Rolle für den wirtschaftlichen Ertrag aus der Fischerei.

Die Untersuchung ergab keinen klaren Hinweis auf einen negativen Effekt der beiden eingewanderten Arten *O. niloticus* und *T. pectoralis* auf die Abundanz und Zusammensetzung der heimischen Ichthyofauna in den Fischereifängen. Eine Nahrungskonkurrenz zwischen *O. niloticus* und den heimischen Fischarten schien außerdem nicht stattzufinden. Die Nahrungsquellen, die gemeinsam genutzt wurden, sind in so hohem Umfang vorhanden, dass sie keinen limitierenden Faktor darstellten. Die Befischung von *O. niloticus* stellte viel eher eine alternative Einkommensquelle in Zeiten dar, in denen die bevorzugt befischten heimischen Arten selten vorkamen. Trotzdem gibt es Anhaltspunkte, die auf einen negativen Einfluss der eingewanderten Arten hinweisen: die schlagartige Zunahme des Nilbuntbarsches während des Zeitraums mit niedriger Salinität verändert die Artenzusammensetzung der heimischen Fischgemeinschaft im Ästuar. Ein möglicher Einfluss auf die heimischen benthischen Fischarten und die Biodiversität im Ästuar ist damit nicht auszuschließen. *Oreochromis niloticus* und *Trichogaster pectoralis* weisen biologische Merkmale auf, die eine Verbreitung dieser Arten in neuen Lebensräumen erleichtern, zumal das Nahrungsangebot im Ästuar nicht als limitierender Faktor zu wirken scheint. Die starke Variabilität der Umweltbedingungen im Ästuar (wie z.B. die Salinität) scheint aber bis jetzt eine langfristige Etablierung dieser Arten zu begrenzen.

Drei mögliche Szenarien, bzw. eine Kombination dieser wären denkbar, die die Etablierung von oligohalinen eingeführten Fischarten, wie *O. niloticus* und *T. pectoralis*, im Ästuar begünstigen würden: 1. Eine länger anhaltende Periode mit relativ niedrigem Salzgehalt, 2. Die Einführung eines mehr euryhalinen Stammes von *O. niloticus* aus der lokalen Aquakultur, oder 3. Die Adaption dieser eingewanderten Arten an die variablen Umweltbedingungen im Ästuar.

Diese Ergebnisse zeigen, dass die Etablierung eingeführter Fischarten mit opportunistischem Fraßverhalten in tropischen Ästuaren mit hoher Variabilität der Umweltbedingungen stärker von abiotischen Faktoren beeinflusst ist als von biotischen Interaktionen, wie z.B. Konkurrenz. Weitere Untersuchungen sind nötig, um zu ermitteln, welche Rolle weitere biotische Faktoren (wie z.B. Predation, Konkurrenz um Raum, gegenseitige Förderung) und anthropogene Faktoren wie Überfischung spielen, um letztlich eine Einbürgerung nicht-heimischer Arten in dieser Art von Ökosystem zu verhindern. Die relative Konstanz der Gesamt-Abundanz aller heimischen Fischarten im Ästuar lässt eine hohe Resilienz dieses Kompartiments vermuten, welche mit einer gewissen Redundanz der Arten in verschiedenen funktionellen Gruppen einher gehen könnte. Weitere Untersuchungen sind nötig, um diese funktionellen Gruppen zu identifizieren und ihre Bedeutung für die Funktion des Ökosystems zu erfassen. Außerdem gilt es, Wissenslücken in der Biologie heimischer Fischarten zu füllen, damit Maßnahmen, die die Populationen eingewanderter Fischarten kontrollieren sollen, keine negativen Auswirkungen auf die heimische Ichthyofauna haben.

RESUMEN

En ecosistemas tropicales, muy poco se conoce sobre los impactos de peces no nativos en la ictiofauna nativa, y al parecer no se han publicado aún estudios de investigación en ese campo en estuarios de la región Caribe. El estuario Ciénaga Grande de Santa Marta (CGSM), en la costa Caribe de Colombia, ha sido afectado por la intervención humana que ha alterado el régimen hidrológico causando la pérdida de valiosos recursos. Canales de conexión anteriormente interrumpidos, fueron reabiertos en 1996-1998 para reestablecer las condiciones hidrológicas del sistema, pero como efecto colateral la presencia de peces no nativos aumento en el estuario. Desde su introducción accidental en 1995, la tilapia nilótica (*Oreochromis niloticus*) figura entre los recursos más comerciales, constituyendo más del 60% de las capturas hasta el año 2001, pero disminuyendo en los años siguientes hasta menos del 10%. En contraste, la presencia del gurami piel de culebra (*Trichogaster pectoralis*), reportado por primera vez en 1989, ha sido más regular que la de la tilapia nilotica.

Este estudio tiene el propósito de determinar el impacto de *O. niloticus* en la abundancia, la composición de especies, los hábitos alimentarios y la pesquería de peces nativos; y el impacto de *T. pectoralis* en la abundancia de la ictiofauna nativa. Datos de captura por unidad de esfuerzo (CPUE) se usaron como medida de abundancia relativa de las diferentes especies en el ecosistema entre los años 1994 y 2003. Los datos fueron divididos en cuatro períodos (I=1994-1995; II=1996; III=1999-2001; IV=2002-2003). Adicionalmente el área de estudio se dividió en cuatro zonas de acuerdo con un gradiente de salinidad con incremento en dirección occidente.

La abundancia combinada de peces nativos se mantuvo relativamente constante y no parece haber sido ser afectada por el “boom” de tilapia nilótica ocurrido entre 1999 y 2001. Por el contrario, esta especie representó una considerable adición de biomasa dentro del sistema. Sin embargo a nivel de especies, la composición y abundancia cambio de período a período. Análisis de similitud (ANOSIM) y porcentaje de similitud (SIMPER) revelaron que *O. niloticus* modificó la composición de las comunidades de peces, dominando en todas las zonas en el período de menor salinidad. Por el contrario, el pez estuarino nativo *Mugil incilis* fue la especie dominante en todos los demás períodos en todo el estuario. Una

reducción de biodiversidad íctica coincidió con la alta abundancia de tilapia nilotica. Algunos análisis de regresión múltiple revelaron que los cambios en abundancia de dos peces estuarinos nativos, *Cathorops mapale* y *Megalops atlanticus,* parecen estar relacionados con la abundancia de tilapia nilótica, y los cambios en abundancia de otros dos peces estuarinos nativos, *Ariopsis bonillai* y *Elops saurus,* parecen estar relacionados con la abundancia de *T. pectoralis*. Sin embargo, otro análisis de regresión múltiple reveló que principalmente la salinidad y en menor medida, el pH y la descarga de agua dulce de los ríos, regulan la distribución y abundancia de todos los peces estudiados, incluyendo *O. niloticus* y *T. pectoralis*.

Los análisis de composición de dieta (e.g. índice de importancia relativa), equidad (J') y diversidad (H') en las dietas en períodos antes y después de la introducción de tilapia nilótica, revelaron que la mayoría de los peces nativos y *O. niloticus* tienen una estrategia mixta entre especialista y generalista, con un cierto grado de especialización en dos o tres categorías alimenticias. Muy pocos peces nativos son completamente especialistas o generalistas. En los dos períodos, todos los peces se alimentaron de las presas más abundantes del momento, las cuales en su mayoría pertenecen a niveles bajos de la red trófica. Los cambios en las dietas obedecieron a los cambios en la abundancia de las presas. El análisis de regresión múltiple mostró que la salinidad es el factor principal que regula la abundancia de las presas más comunes entre las dietas de peces en el estuario. Se encontró un sobrelapamiento moderado de las dietas de *O. niloticus* y *Diapterus rhombeus*, pero este se debió muy probablemente a la gran abundancia de las presas comunes: detritos y fitoplancton.

La pesca de tilapia nilótica, un pez de relativo bajo precio, representó seis veces mayor ingreso económico que la pesca de todas las especies nativas juntas en el período 1999-2001 en dos sitios de desembarque estudiados. Sin embargo una encuesta reveló que los pescadores prefieren las especies nativas estuarinas por su mejor precio. Un análisis a nivel de especies mostró que el ingreso económico derivado de la mayoría de las especies nativas disminuyo durante el período de mayor abundancia de *O. niloticus* y menor salinidad en el estuario. En contraste, la especie nativa *Mugil incilis* tuvo sostenidamente precio y abundancia relativamente altos, proporcionando un ingreso económico relativamente alto durante todo el período de estudio. Un análisis de regresión múltiple mostró que la salinidad parece ser también el factor principal que explica la variación en ingreso económico derivado de la mayoría de las especies nativas. Sin embargo, las diferencias en estructura de los mercados de los sitios de desembarque tienen una influencia importante en el ingreso económico.

No se encontró evidencia clara que indique que hay un impacto negativo de *O. niloticus* y *T. pectoralis* en la abundancia y composición de la ictiofauna nativa. Adicionalmente, la competencia por alimento entre *O. niloticus* y las especies nativas no parece probable debido a la gran abundancia de sus presas comunes y la estrategia mixta o generalista de la mayoría de las especies nativas. De hecho, la tilapia nilótica representó una alternativa de ingreso económico durante un período en el que la presencia de los peces nativos más valorados económicamente era escasa. Sin embargo alguna evidencia apunta hacia una alta probabilidad de que se den impactos negativos: la proliferación de tilapia nilótica modificó la composición de especies de las comunidades de peces nativos dominando durante un período de baja salinidad, y un potencial impacto en peces bentónicos nativos y la diversidad íctica del estuario no puede descartarse. *Oreochromis niloticus* y *T. pectoralis* tienen características biológicas que facilitan su proliferación en nuevos ambientes, y alimento no parece ser un limitante. Sin embargo, hasta el momento su permanencia parece estar restringida por los cambios drásticos ambientales (e.g. salinidad) en el estuario. Tres posibles escenarios, o una combinación de ellos, podrían favorecer una proliferación permanente de peces no nativos de tipo oligohalino como *O. niloticus* and *T. pectoralis*: 1. Una mayor duración de periódos de salinidad baja, 2. La introducción de linajes más eurihalinos de *O. niloticus* provenientes de cultivos en el área, o 3. La adaptación de los peces no-nativos a las variables condiciones ambientales del estuario.

Los resultados indican que el establecimiento de peces no nativos con hábitos alimenticios oportunistas en estuarios con alta variabilidad ambiental esta más influenciado por factores abióticos que por interacciones bióticas como la competencia por alimento. Sin embargo, es necesario investigar el papel de otras interacciones bióticas (e.g. predación, competencia por espacio, facilitación) y de factores humanos como la sobrepesca, en restringir la naturalización de peces no nativos en este tipo de ecosistemas. La constancia relativa de la abundancia combinada de todos los peces nativos en el estuario, sugiere que este componente posee una alta resiliencia que a su vez puede estar relacionada con una alta

redundancia de especies dentro de grupos funcionales. Se debe seguir investigando para identificar esos grupos funcionales y determinar su importancia dentro del funcionamiento del ecosistema. Adicionalmente, los vacíos de conocimiento en la biología de los peces nativos deben ser llenados para evitar efectos negativos de medidas que busquen controlar las poblaciones de peces introducidos en el estuario.

Ciénaga Grande de Santa Marta, Colombia. Photo: STS073-760-32, NASA 1995

SECTION I: OVERVIEW

1. INTRODUCTION

The spreading of a species into a new environment can be a natural process that mostly occurs in neighboring regions and over long time scales (Sax *et al.* 2005, Ricciardi 2007). However, human activities have greatly extended the geographical ranges and shortened the time scale of this process to such an extent that many of the currently introduced alien species probably would have not reached their new habitats without human mediation (Carlton & Ruiz 2005, Ricciardi 2007, Rahel 2007). Nowadays, the introduction of non-native* species is considered the second most important cause of biodiversity loss after habitat alteration: it is estimated that almost 40% of the world's known extinctions since the 17th century have been at least partially caused by the impacts of non-native species (UNEP/CBD 2004). These numbers, however, might not include cases from tropical ecosystems; although these host most of the world's biodiversity, very little is yet known about them regarding species introductions.

1.1. ESTABLISHMENT OF INTRODUCED SPECIES IN AQUATIC ECOSYSTEMS

Introduction of non-native species into aquatic environments is not a novel phenomenon. In Europe, for example, it may date back as far as to Roman times when the common carp, *Cyprinus carpio*, from the Danube (already introduced at that time from Asia) was used for aquaculture in Greece and Italy (Welcomme 1984). Also in colonial times (1500-1600 A.D.) it was a common practice for Europeans to transport along many Old World species to be raised in their new settlements in the New World and elsewhere (Mack 2003). Nowadays with the continuous increment of connections between distant regions in the world, species introductions have become a daily event (Carlton & Geller 1993, Lavoie *et al.* 1999, Carlton & Ruiz 2005).

The most common pathways of species introductions into aquatic systems are related to accidental events that mostly involve traffic between water bodies (Table 2). Another proportion however is related to intentional release of species whose purpose is mainly related with the improvement of revenue or enjoyment, reflecting a lack of knowledge and

* See Appendix A for definitions of related terms

awareness among resource managers when considering possible impacts of non-native species on recipient ecosystems.

Table 1: Most common pathways or vectors of introduction of non-native species into aquatic ecosystems (modified from Carlton 2001, Carlton & Ruiz 2005)

Vector or pathway	**Mechanism and type of organisms introduced**
Transport means (ships, boats, amphibious/sea planes) and related devices (navigation buoys, marina floats)	Planktonic and nektonic organisms in ballast water Attached and free-living fouling organisms on hull, rudder, propeller, seawater systems, sea chest, ballast tanks and others Organisms attached and entangled on anchors, anchor chains Benthic organisms in ballast sediment
Drilling platforms	Attached and free living fouling organisms Planktonic and nektonic organisms in ballast water
Canals	Movement of species through sea level, lock, or irrigation canals
Aquarium Industry	Invertebrates, fish, algae and sea grasses accidentally or intentionally released Organisms associated to transport media such as water or packing material that are discarded
Aquaculture and life seafood industry	Intentional or accidental release of species with their associated diseases and pathogens
Fisheries and sport fishing	Live organisms used as bait Associated organisms to shells or other parts of species or to packing materials that are discarded Organisms associated to fishing gear that is relocated
Conservation and restoration programs	Intentional release of species for stock enhancement or as forage food for other species Movement of marsh, dune, or sea grasses and their associated organisms to re-establish populations that have been diminished Intentional release of species to control pests.
Research and education	Intentional or accidental release of organisms used in scientific experiments or in school demonstrations
Tourism	Movements of organisms associated to diving or recreational equipment Transport of live organisms as souvenirs within areas with relaxed regulations
Floating marine debris	Organisms associated to human-generated debris

The initial stage of a species introduction into aquatic (and terrestrial) environments starts with the arrival of some individuals to the new ecosystem, followed by an establishment phase where they successfully reproduce until having a self-sustaining population (Colautti & MacIsaac 2004, Puth & Post 2005, Reise *et al.* 2006, Lockwood *et al.* 2007). Then they pass to a next stage where the species increases in abundance and expands its range and finally adjusts to the conditions of the new environment (Colautti & MacIsaac 2004, Puth

& Post 2005, Reise *et al.* 2006, Lockwood *et al.* 2007). Most non-native species fail to establish themselves and therefore disappear without causing big damage to the recipient ecosystem, but from the small proportion that succeeds, still an estimated 10-30% becomes pests causing major environmental problems (Williamson & Fitter 1996, Simberloff 1996, UNEP/CBD 2004). Factors that influence the success or failure of introduced species are mostly related either to biotic interactions or abiotic conditions in the recipient ecosystem or a combination of both.

Biotic interactions

Biotic interactions with resident species can either favor or hinder the establishment of non-native species in the recipient ecosystem. For example, interactions with native species such as competition or predation can constraint the establishment of alien species in the new environment (*biotic resistance hypothesis* – Elton 1958, Derivera *et al.* 2005, Mitchell *et al.* 2006). In this regard, a high biodiversity in the recipient ecosystem increases the chances of finding resident relatives (species that are taxonomically close to the introduced species) with which alien species might compete for resources and/or share predators and/or pathogens constraining in that way their establishment (*Darwin's naturalization hypothesis* – Darwin 1859, Ricciardi & Atkinson 2004, Strauss *et al.* 2006). However, a high biodiversity could also favor the establishment of alien species because if resident relatives perform already well in the ecosystem then so should the alien relative, or, high biodiversity might also imply that a high variety of resources is available in the ecosystem (Duncan & Williams 2002, Ricciardi & Mottiar 2006). Another factor favoring the success of alien species can be the lack of coevolved natural enemies (*e.g.* parasites/pathogens, predators) in the recipient ecosystem allowing introduced species the redirection of energy and resources, otherwise used for defense, to be used for reproduction and expansion (*enemy release hypothesis* – Clay 2003, Prenter *et al.* 2004). However, not only negative interactions play a role in the success of species introductions. For example, facilitative interactions like mutualism or commensalism between resident species can create/alter habitats or modify ecosystem structure thus favoring or constraining the establishment of new alien species or speeding up the expansion of old ones (*facilitation and invasional meltdown hypotheses* – Simberloff & Von Holle 1999, Bruno *et al.* 2003, Grosholz 2005, Simberloff 2006).

Abiotic factors

The fluctuation of physical or chemical variables like salinity, concentration of nutrients, substrate type or shape, among others, can promote or constraint the proliferation of alien species acting directly on physiological processes of the species or modifying the availability of habitats (Carlton 1996a, Moyle & Light 1996a,b, Menke & Holway 2006, Devin & Beisel 2007). Moderate variation of these variables (*i.e.* disturbances) create chances for (native and non-native) species to establish themselves and coexist ending up with an increase in biodiversity (*intermediate disturbance hypothesis* – Connell 1978, Hobbs & Huenneke 1992, Pausas *et al.* 2006). Human activities can alter several types of conditions and interactions in the ecosystems simultaneously leading to modification of the physical and chemical environment, as well as ecosystem structure and functioning thus facilitating the establishment of alien species (Moyle & Light a, b). However, it is difficult to separate abiotic and biotic components of an ecosystem since both types influence all processes that enable a species to persist and thrive simultaneously. Therefore the joint influence of different biotic and abiotic factors can better explain the success or failure of species introductions (Mitchell *et al.* 2006).

In summary, if the new species does not find enemies in the new environment such as pathogens/parasites, predators or strong competitors, but finds what it needs in terms of food, space, refuges, physical and chemical conditions, then its chances to succeed in establishing a self-sustaining population will increase (Carlton 1996a, Moyle & Light 1996a, Shea & Chesson 2002, Clay 2003). However, not only is finding the right resources and conditions necessary to ensure success, but good timing is also determinant (Crawley 1989, Carlton 1996a; *e.g. match-mismatch hypothesis* – Cushing 1975). In other words, favorable conditions should not only be met in the right magnitude and place but also at the right moment for a long enough period for establishment to take place. The coincidence of all these conditions creates a window that is used by the alien species for establishment and adaptation (*invasion window concept* – Johnstone 1986).

1.2. IMPACTS OF SPECIES INTRODUCTIONS ON AQUATIC ECOSYSTEMS

Although, there are differences in dispersal derived from physical differences between terrestrial and aquatic environments (*e.g.* size of habitats and distance between them – Kinlan & Gaines 2003), the ecological processes through which alien species are able to modify the structure and functioning of ecosystems are basically the same. They can be summarized in five mechanisms that act separately or in combination (see examples in Table 2):

- Predation: Introduced species that prey upon the native biota have a direct impact on the size of native populations, in some cases even bringing them to extinction (*e.g.* Nile perch in African lakes – Table 2; Ogutu-Ohwayo 1990, Moyle & Light 1996a, Mooney & Cleland 2001).

- Competition: Under conditions of resource scarcity but favorable conditions for non-native species, these can impact native populations with which they share resources (Moyle & Light 1996a). Non-native species with omnivore or opportunistic feeding habits can be very successful (*e.g.* Tilapias in African lakes – Table 2) since they can switch from one prey type to another according to their availability (Moyle & Light 1996a, Gido & Franssen 2007). Thereby alien species can outcompete native species if they drastically reduce the resources on which specialist feeders depend (Moyle & Light 1996a).

- Hybridization: Some exotic fish species can interbreed with native species producing hybrids that might be sterile or not. If they are, then there is a waste of native gametes and reduction of native reproduction. If they are not sterile, they may compete with the native parent species and reduce their survival or reproduction (Lockwood *et al.* 2007). Hybridization can even lead to extinction of native gene pools (*e.g.* tilapias in African lakes – Table 2)

- Introduction of diseases: The non-native species can bring along new parasites or pathogens into the environment against which the native species might not have a natural defense (*e.g.* salmonids in Lake Titicaca, tilapias in Lake Nicaragua – Table 2). This can lead to the depletion or even extinction of native populations.

- Habitat modification: Non-native species can physically or chemically modify, eliminate or create habitats in the recipient ecosystem (*e.g.* tilapias feeding on aquatic plants in Lake Nicaragua – Table 2), thus reducing or increasing their availability for native species (Crooks 2002, Lockwood *et al.* 2007).

Table 2: Some examples of fish introductions that developed into biological invasions, and their negative and/or positive impacts on the recipient ecosystems.

Impacted ecosystem	Non-native species	Origin	Ecological impacts	Socioeconomic impacts	References
Lakes Victoria and Kyoga (Africa)	*Lates niloticus*	Ethiopian region of Africa	Extinction of ca. 200 native fish species by predation. Deforestation due to demand of wood for smoking process of Nile perch. Changes in trophic structure that might have accelerated eutrophication.	Highly productive fishery based on Nile perch and Nile tilapia benefited mostly fishermen that could afford new fishing equipment. Fishery of native species (more varied) has almost disappeared.	Ogutu-Ohwayo (1990), Ogutu-Ohwayo & Hecky (1991), Kaufman (1992), Goudswaard *et al.* (2002)
	Oreochromis niloticus, O. leucosticus, Tilapia zilli	Mainly central Africa	Outcompeted native fish species for nursery and feeding grounds. Extinction of native tilapiine species by hybridization.		
Lake Kariba (Africa)	*Limnothrissa miodon*	Lake Tanganika, Africa	Extinction of zooplankton species by predation. Changes in food web	Productive fishery benefited human communities.	Lever (1996), Hall & Mills (2000)
Cold fresh waters worldwide	*Oncorhynchus mykiss*	Eastern Pacific (Alaska to Mexico)	Diminishing or extinction of indigenous species by predation and competition. Changes in structure of fish community.	Important economic benefits from fish culture.	Lever (1996), Cowx (1997)
Sri Lankan basins	*Oreochromis mossambicus*	Mainly central Africa	Outcompeted native cyprinids for habitat.	Improvement of fisheries.	Lever (1996), Moyle & Light (1996)
Taieri River and Lakes of New Zealand	*Salmo trutta*	Northwestern coast of Europe	Fragmented distribution and decreased abundance of native fishes like *Galaxia vulgaris* due to predation. Displacement of other native fishes by competition	Not reported in literature.	McDowall (1990), Townsend & Crowl (1991), Lever (1996),
North American Great Lakes	*Petromyzon marinus*	Northeast and northwestern Atlantic	Depletion of native trout and white fish, among others, by parasitism of *P. marinus* in the 1940's.	Great economical losses in native fishery	Mills *et al.* (1994), Cox (1999), Hall & Mills (2000)
Lake Gatun (Panama)	*Cichla ocellaris* *O. niloticus* *C. carpio*	Northern part of South America	Predation on native fishes by *C. ocellaris* altered food web. But predation on *O. niloticus* released pressure on native fishes.	Not reported in literature.	Zaret & Paine (1973), Lever (1996), Hall & Mills (2000)
Lake Titicaca (Peru, Bolivia)	*Salmo trutta, Salmo gairdneri* *Basilichthys bonariensis*	Northwestern coast of Europe Southern Argentina and Rio de la Plata	Depletion of native fish populations by competition with trout species and predation by *B. bonaerensis*. Massive fish mortality in 1981 by outbreak of a protozoan introduced with trout	Fishery of introduced salmonids did not last. Development of less diverse fishery based mainly on one native fish and *B. bonaerensis*	Villwock (1994), Lever (1996), Hall & Mills (2000)
Lake Nicaragua	*Oreochromis mossambicus, O. niloticus, O. aureus*	Mainly central Africa	Elimination of native fish habitat by feeding on aquatic plants. Depletion of native cichlids by active competition for spawning sites. Blindness in native cichlids apparently caused by a trematode parasite introduced with tilapias.	Not reported in literature.	McKaye *et al.* (1995), McCrary *et al.* (2007)

Through the above outlined mechanisms, alien species can modify the abundance and composition of native species thus modifying the structure (*i.e.* species richness, biodiversity, food web interactions, etc, *sensu* Begon *et al.* 2006) of the recipient ecosystem (Mack *et al.* 2000, Mooney & Cleland 2001, Hoffmeister *et al.* 2005). The magnitude of these impacts on ecosystem functioning (ecosystem level processes *i.e.* productivity, decomposition, flux of nutrients and water *sensu* Begon *et al.* 2006) might depend on how resilient the ecosystem is. In other words, it might depend on the capacity of the ecosystem to return to a similar state to the one it had before a disturbance (concept of resilience *sensu* Grimm & Wissel 1997), which in this case is the impact of an alien species. In this regard, current research is showing that a high biodiversity enhances the resilience of the ecosystem, since it increases the likelihood of having more than one species per functional group (set of species with a similar contribution to ecosystem processes) that would react in different ways to disturbance therefore increasing the chances of keeping the ecosystem functioning in case of species loss (Walker 1995, Gunderson 2000, Scherer-Lorenzen 2005, Hooper *et al.* 2005). Thus species introductions that lead to the elimination of an entire functional group alter the whole ecosystem functioning.

The introduction of alien species can also render benefits to resident species in the recipient ecosystem (*e.g.* through mutualistic interactions or facilitation) or to human populations (Bax *et al.* 2003, Thiltges *et al.* 2006, Sax *et al.* 2007, Vellend *et al.* 2007). For example, some of the most valued food resources (*e.g.* rice, corn, potatoes, several fish species) have been introduced in almost all regions of the world providing food and income to human populations (Pimentel *et al.* 2001, Bartley & Casal 1998). Additionally, the study of species introductions provides insights in colonization, ecosystem functioning and other ecological processes (Brown & Sax 2004, Sax *et al.* 2007). In fact, categorization of impacts under "positive" or "negative" depends on the point of view. An anthropocentric view would consider any increase of human welfare originating in a species introduction as a positive effect, but this "benefit" could be considered ecologically negative when the central point of attention is the native biota of the ecosystem (*e.g.* see examples in Table 2). The net effect of an alien species should be assessed taking into consideration all benefits and damages that can be attributed to the species with certainty as well as the spatial and temporal scales of analysis (Bartley & Casal 1998, Bax *et al.*

2003, Thielges *et al.* 2006, Reise *et al.* 2006). This two-sided nature of impacts is frequently omitted in invasion ecology and instead, perhaps as a precautionary approach, the negative impacts directly or potentially caused by alien species are overemphasized. Lessons for decision making should be learned from well known cases (see Table 2 above) in which non-native species have triggered a series of processes that ended in many cases with negative and positive consequences for the ecosystem and the human populations.

1.3. FISH INTRODUCTIONS IN NEOTROPICAL ESTUARIES

At least 20% of the world population lives within 25 km of the coast line, which is in concordance with the enormous richness in natural resources that is attributed to coastal areas (Costanza *et al.* 1997, UNDP/UNEP/WB/WRI 2000). Estuaries are among the richest ecosystems in the world in terms of valuable natural resources and services (Costanza *et al.* 1997). However, such a richness also makes these areas vulnerable to human impacts (Blaber *et al.* 2000), including introduction of non-native species (Ruiz *et al.* 1997, 1999). For a long time, it has been considered that consequences of species introductions were especially dramatic in terrestrial and fresh water ecosystems, while in marine ecosystems they were considered minimal. This belief was supported by the hypothesis that the open nature and large size of marine ecosystems provide resilience against disturbances such as pollution or bioinvasion (Ruiz *et al.* 1997). However, many cases of accidental species introductions into coastal ecosystems have demonstrated that impacts of alien species can also lead to tremendous negative impacts in these environments (Carlton 1989, Ruiz *et al.* 1997, Grosholz 2002, Bax *et al.* 2003). An example of this is the temperate estuary San Francisco Bay and Delta where at least 200 non-native species have established wild populations and altered many of the ecological communities in the estuary (Cohen & Carlton 1998).

In tropical regions still very little is known regarding the presence and impacts of non-native fishes on estuarine environments. In fact, in many tropical countries, as in other regions, one of the largest obstacles for understanding the role of alien species is that inventories of native species are still incomplete and sometimes non-native species are cryptogenic species that are considered native due to misidentifications (Grosholz 2002, Carlton 1996b). In the case of the Neotropical region (the tropical zone of the American continent) most of the studies dealing with fish introductions focus on fresh water systems and merely infer their impacts based on what the introduced species have done in similar environments elsewhere, or provide lists of non-native species with their biological features and/or historical information about their introductions (*e.g.* Erdman 1984, Contreras-B. & Escalante-C. 1984, Burger *et al.* 1992, Olivera *et al.* 1995, Alvarado & Gutiérrez 2002). Only few investigations have been published in which the ecological impacts and interactions of non-native fishes in the local ecosystems and their fisheries are well documented, but these studies also focus on fresh water environments (*e.g.* Lake Gatun and Lake Nicaragua – Table 2). This gap of research in estuarine ecosystems should be filled as soon as possible, since the increase in international ship traffic and the use of non-native species for aquaculture purposes make it very likely that an increase in species introductions in the Neotropics will be observed. Therefore, being the first research focusing on impacts of alien fishes on coastal environments of the Caribbean region, the present study is an important contribution to elucidate the effects/impacts of non-native species on tropical estuaries.

In Colombia several studies have reported the presence of non-native fishes in fresh water ecosystems and warned about potential impacts of the increasing number of introduced species on the native ichthyofauna (*e.g.* Arenas & Acero 1992, Diaz & Alvarez 1998, Alvarez & Salazar 2001). Gutiérrez (2004) collected information regarding pathways and purposes of introduction as well as the distribution of the non-native species present in continental waters. He recorded 153 exotic fish species, from which 96 are coming from a different country or continent and 57 are transferred from other basins within the country. In the same work, this author studied the biology and fishery of Nile tilapia (*Oreochromis niloticus*) in the River Sinú basin (Northern Colombia) and warned about its great potential to endanger native species. Narváez *et al.* 2005 studied the morphometric variation of Nile tilapia populations in northern Colombia, including the estuary Ciénaga Grande de Santa Marta. These authors described three different morphological types according to the environment (freshwater, estuarine and alkaline), all originating in aquaculture facilities in the region. Working with fishery data from the same estuary, Blanco *et al.* 2007 demonstrated a correspondence between the variations of Nile tilapia abundance and variability in the El Niño Southern Oscillation (ENSO) phenomenon described by salinity fluctuations. These authors also presented observational evidence for a disease outbreak in

Nile tilapia apparently linked to salinity tolerance of the species. Many of the alien fishes in the country were intentionally introduced either to increase fish production or for ornamental fish trade or aquaculture purposes and many ended in natural waters due to inadequate management of intentional introductions. Although some of these introduced fishes have already been naturalized and constitute important fishery resources in several regions of the country, there are as yet no published studies directly addressing their impacts on the native species and the ecosystems. The present study constitutes the first assessment of impacts of introduced fishes on coastal environments in Colombia.

1.4. RESEARCH TOPICS AND HYPOTHESES

The Ciénaga Grande de Santa Marta estuary (CGSM) is one of the largest estuaries in the Neotropical region and the most important at the Caribbean coast of Colombia. After human intervention altered the hydrological regime ca. 45 years ago, interrupted water connections were re-opened in 1996-1998 to re-establish hydrological conditions, but as a side effect the occurrence of non-native fishes augmented in the estuary (Botero & Salzwedel 1999). Since then Nile tilapia (*Oreochromis niloticus*) has ranked among the most commercial resources, while the snakeskin gourami (*Trichogaster pectoralis*), albeit with a lower abundance, has been present for a longer time in the estuary. This research work aims to determine the ecological impacts of the Nile tilapia and the snakeskin gourami on the native fish communities and the economic impacts of Nile tilapia on the fishery of the estuary.

<u>Ecological Impacts of Nile tilapia</u>

The environmental variations in the CGSM influence the abundance and distribution of native fishes, and salinity seems to be the factor that best describes those variations (Sánchez & Rueda 1999, Rueda 2001, Blanco *et al.* 2006). The abundance of Nile tilapia seems to be restricted by salinity variations within the estuary, increasing during the periods of fresh water conditions and decreasing dramatically during periods of high salinities (Blanco *et al.* 2007). However, the high adaptability of this species due to its biological features (fast growth, opportunistic feeding, mouth breeding and parental care among others) has allowed it to proliferate and establish self-sustaining populations in other tropical ecosystems, including coastal environments, where it has negatively impacted the native ichthyofauna (Trewavas 1983, Beveridge & McAndrew 2000, Canonico *et al.* 2005). Therefore it could be expected that in spite of the restriction imposed by environmental fluctuation (*e.g.* salinity):

Hypothesis 1: The proliferation of Nile tilapia has altered the species composition and abundance of native fish communities within the estuary.

Hypothesis 2: The temporal variation in feeding habits of native fishes is driven by competition for food with Nile tilapia.

These hypotheses are investigated in section II, chapters 7: “Role of Nile tilapia in the long term variations of abundance and species composition of the native ichthyofauna in a Caribbean estuary” and 8: “Does Nile tilapia affect the feeding habits of the native ichthyofauna of a tropical estuary? - The case of the Ciénaga Grande de Santa Marta estuary, Colombia”

Economic Impact of Nile tilapia

Environmental degradation in CGSM has led to the loss of some important resources increasing the poverty of the large human population that depends on the ecosystem for their livelihoods. Fishermen have adopted opportunistic fishing adapting their gear and effort to the abundance and distribution of the resources in CGSM (Moscarella & Pinilla 1998). The native estuarine species have always been the most important resources in the fishing trade of the region (INVEMAR 2006, Zamora 2005) and, since the variation between fresh water and marine water inflow into the CGSM is cyclic (Kaufmann & Hevert 1973), it is conceivable that native species are adapted to respond to these changes. From 1999 to 2001, Nile tilapia accounted for almost 60% of the catches in the estuary but after that it decreased into less than 10% (INVEMAR 2006). Assuming that drastic variations in environmental conditions are responsible for the decrease of Nile tilapia, it could be expected that:

Hypothesis 3: Nile tilapia, as a fishery resource, constitutes better economic revenue for the fishermen only in the short term while the native fishes represent a better alternative of income in the long term

This hypothesis is investigated in section II, chapter 9: "Has the accidental introduction of Nile tilapia economically benefited the fishery of the Caribbean estuary Ciénaga Grande de Santa Marta estuary – Colombia?"

Impact of snakeskin gourami

Although with much lower abundance than *O. niloticus*, the snakeskin gourami (*Trichogaster pectoralis*) has been present in the catches in CGSM for longer time and seems to be more tolerant to high salinities (up to 23; Arenas & Acero 1992). Moreover, it is an opportunist feeder adapted to survive in low oxygenated waters (Moyle & Cech 1988, Arenas & Acero 1992). These characteristics and its persistence in the ecosystem give it advantages to successfully establish self-sustaining populations and impact native fish populations. Therefore, it could be expected that:

Hypothesis 4: The variation in abundance of some native fishes is driven by the presence and/or abundance of *T. pectoralis*.

This research hypothesis is investigated in chapter 4.

2. STUDY AREA: THE NEOTROPICAL ESTUARY CIÉNAGA GRANDE DE SANTA MARTA

2.1. LOCATION AND DESCRIPTION

The Ciénaga Grande de Santa Marta (CGSM) is located between 10° 43’-11° 00’ N and 74° 16’-74° 35’ W (Fig. 1). It is one of the largest estuaries of the Caribbean region and one of the most important ecosystems for the regional fishery at the Northern coast of Colombia due to its extent and productivity (Sánchez & Rueda 1999, Gocke *et al.* 2003). The estuarine system is part of the deltaic plain of the Magdalena River, the largest one in Colombia, and it is separated from the sea by a 212 km^2 sand bar called Salamanca Island. The biggest marine connection is an 80-100 m wide artificial channel named Boca de la Barra (Botero & Salzwedel 1999). The estuary is connected to the Magdalena River trough a series of channels and swamps called Pajarales Lagoon Complex and also receives freshwater from the rivers Fundación, Aracataca, Sevilla and others which originate in the mountain system Sierra Nevada de Santa Marta (Fig. 1) crossing and irrigating an extensive zone of banana plantations before ending in the Ciénaga (Botero & Salzwedel 1999).

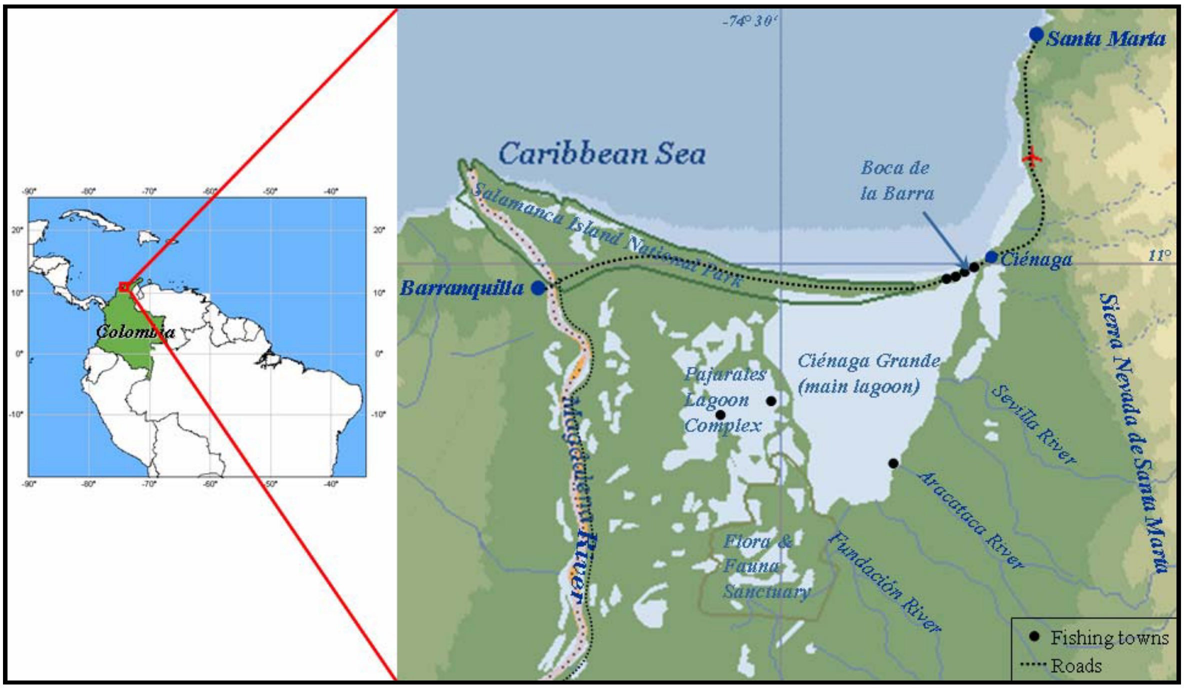

Fig. 1: Location of the Ciénaga Grande de Santa Marta estuary in South America (left) and the Caribbean coast of Colombia (right). Modified from Microsoft Encarta 2007.

The climate in the area is particularly dry (arid) with a mean air temperature of 28 °C and a dry season from December to March and a rainy season from April to November (Botero & Sazwedel 1999, Blanco *et al.* 2006). The mean annual water temperature is 30 °C and the depth varies between 1 and 7 m, the salinity between 0 and 50 (PSU – Practical Salinity Units) and the tidal amplitude between 20 and 30 cm (Polanía *et al.* 2001). The region has a hydrological deficit that ranges between -211.6 and -1146.8 mm yr^{-1} as a result of the difference between mean rainfall and mean evaporation (Blanco *et al.* 2006). Therefore, the water input from the rivers, especially the Magdalena River, is vital for the system's water budget (Kauffman & Hevert 1973, Wiedemann 1973). The water input from the Magdalena River into the CGSM estuary shows two types of flooding cycles related to the variation of rainfall in the whole basin: an annual cycle with higher water levels during the rainy season and a multi-annual cycle with extremely high water levels occurring during the rainy season every six to seven years (Kauffman & Hevert 1973). During the last decades, the flooding cycles of this river seem to be coupled to global climate events described by the occurrence of El Niño and La Niña phenomena (Restrepo & Kjerfve 2000, Blanco *et al.* 2006, 2007).

The high productivity of its waters (0.073 - 1.25 mg C/l/h) (Gocke *et al.* 2003) together with the approximately 50,000 ha of mangrove forests (*Avicennia germinans* L., *Rhizophora mangle* L., *Laguncularia racemosa* L. and *Conocarpus erectus* L.) makes the CGSM a very rich system with about 195 species of birds, 122 of bony fishes, 98 of mollusks, 46 of mammals, 40 of reptiles and 10 of amphibians among others (Polanía *et al.* 2001, Moreno & Alvarez 2003). The ecological importance of the estuary has been nationally and internationally recognized with the creation of parks and reserves within its area. In 1964, Salamanca Island was declared national park and later in 1977, the most southern part of the Pajarales Lagoon Complex was declared Fauna and Flora Sanctuary. The Ramsar Convention on Wetlands designated the estuary as a wetland of international importance in 1998, and UNESCO as a Man and Biosphere Reserve in 2000 (CORPAMAG 2006).

2.2. HUMAN INTERVENTION AND THE INTRODUCTION OF NON-NATIVE FISHES IN CIÉNAGA GRANDE DE SANTA MARTA

Coastal villagers rely on fishes as their most important source of protein. The fishery in the system is mainly artisanal with 40,000 people depending on the estuary for their economic sustenance and 3,500 being active fishermen (Blanco *et al.* 2007). They respond to the differences in spatio-temporal abundances of fishes by using different fishing gear types such as cast nets, gill nets, encircling gill nets, seine nets and hand lines among others (Gallo 1988, Rueda & Santos-Martinez 1997, Blanco *et al.* 2007). Generally, a fishing unit consists of two fishermen, a canoe with or without engine and several fishing gears that can be used simultaneously to catch multiple target species.

The CGSM estuarine ecosystem has suffered a notorious deterioration as a result of anthropogenic alterations of hydrological conditions and exploitation of resources without appropriate management measures. A highway was built in the 1950's along the Salamanca Island to enable direct communication between the two main cities in the region, Santa Marta and Barranquilla, but this interrupted almost all sea connections of the estuary. Furthermore, a dirt road was built between the River Magdalena and the Lagoon Complex of Pajarales thereby cutting the connections to the main river. Additionally, water from the rivers that originate in the Sierra Nevada de Santa Marta has been diverted for irrigation of agricultural lands. The interruption of water flows resulted in hypersalinization of mangrove soils that led to a massive loss of mangrove forest area (~70%) and therefore to a considerable decrease of diversity and abundance of some representative fauna, including several species of fish and mollusks (Botero & Mancera 1996, Dilger & Schnetter 1997, Botero & Salzwedel 1999). Further consequences are pollution from agricultural lands and towns as well as a progressive increment of water salinity, concentration of suspended material and eutrophication. These alterations together with overfishing seem to be responsible for a decrease in fish catches in the system in the last decade (Botero & Mancera 1996, Botero & Salzwedel 1999; Rueda & Defeo 2003).

As part of a plan to recover the environmental conditions in the estuary, a monitoring research program started in 1994 and former connections to the sea and the Magdalena River were re-opened in 1996 and 1998. After that not only did the water flows increase but also the abundance of non-native fishes such as the snakeskin gourami (*Trichogaster pectoralis* Regan 1910), the Nile tilapia (*Oreochromis niloticus* Linnaeus 1757), the hybrid red tilapia (*Oreochromis* sp.) and the tambaqui (*Colossoma macropomum* Cuvier 1818) (Sánchez 1996, Bateman 1998). The hybrid red tilapia[**] appears very seldom, most probably as a result of escapes from culture ponds in the area. The tambaqui[**] was introduced into the Magdalena basin for aquaculture purposes in the 1970's, but was first registered in CGSM in the 1990's (fishermen observations). The Nile tilapia was introduced into the country also for aquaculture purposes in the 1970's, but was only registered in 1995 in the CGSM (Sánchez 1996, Gutiérrez 2004). From the introduced fishes, only the Nile tilapia has become abundant enough to acquire economic importance within the fishery in CGSM. Since 1999, *O. niloticus* ranks among the principal fish resources, accounting for almost 60% of all catches in 1999 and 2000 but dramatically decreasing since 2001 (INVEMAR 2006). The snakeskin gourami was accidentally introduced into the Magdalena basin in the 1980's as a result of ornamental trade activities, but was first registered in the estuary in 1989 (Arenas & Acero 1992). In contrast to the Nile tilapia, the snakeskin gourami has shown a very low abundance in the estuary but its occurrence has been more regular.

The Nile tilapia (*Oreochromis niloticus* Linnaeus 1757)

Photo: M.L.J. Stiassny 2003, www.fishbase.org

This fish known as Lora or Mojarra Lora in the CGSM, belongs to the family cichlidae (cichlids). It is a demersal and potamodromous fish native of the river basins of North and Central Africa. It has been introduced in almost all tropical countries in the world, mainly with aquaculture purposes. It is one of the most important fish species in the world's aquaculture with 19 % of the production in 2004 (FAO 2006). From the cultured tilapias, it

[**] See Appendix B for a brief description

is the dominant species accounting for 82 % of their production in 2004. It has a high adaptability to new environments due to characteristics such as fast growth, precocious maturation and stunting (as a response to unfavorable environmental conditions), all year round spawning (under favorable conditions), parental care, mouth brooding and highly opportunistic feeding habits (Trewavas 1983, Beveridge & McAndrew 2000). It has a relatively high salinity tolerance (up to 10 - Villegas 1990, 15 – Popma & Masser 1999, 19 - Watanabe *et al.* 1985) but it is the least euryhaline of the tilapias (Popma & Masser 1999). It can reach a maximum size of 60 cm.

The snakeskin gourami (*Trichogaster pectoralis* Regan 1910)

Photo: C. Mergus 2005, http://www.aquanostalgie.com/Poissons/trombinoscope2.php

Known as urami or terapia in the CGSM, this fish belongs to the family Osphronemidae (gouramies). It is a pelagic and potamodromous freshwater fish native of the Mekong basin in Laos, Thailand, Cambodia and Vietnam, and also the Chao Phraya basin in Asia. It is found in shallow sluggish or standing waters with a lot of aquatic vegetation. It has been introduced to many countries in the tropics for ornamental trade and/or aquaculture. As others in this family, the species is capable of breathing air through its supra branchial organs – an adaptation that allows it to survive in low oxygenated waters (Moyle & Cech 1988). It feeds mainly on aquatic plants but has also displayed opportunistic feeding, including shrimp larvae and zoobenthos (Arenas & Acero 1992). It can reach a maximum size of 25 cm.

2.3. THE NATIVE FISH COMMUNITY IN CIÉNAGA GRANDE DE SANTA MARTA

At least 130 fish species have been reported from the CGSM estuary, eight of them are cartilaginous and 122 teleost fishes (Santos-Martinez & Acero 1991) from which about 81 are commercially exploited. The structure of the fish communities in the estuary seems to be highly variable and strongly related to differences in environmental conditions (*e.g.* salinity, depth, substrate type) between zones and years of study (Sánchez 1996, Bateman 1998, Sánchez & Rueda 1999, Rueda 2001, Blanco *et al.* 2006, 2007). The greatest proportion of fishes in CGSM is composed by estuarine species, followed by coastal fishes with marine affinities and fresh water fishes with a temporal occurrence in the estuary (Santos-Martinez & Acero 1991). Most of the native fishes (about 60%) in the estuary are considered visitors (occasionally using the estuary during a phase of their life cycle) and the rest (about 40%) are considered resident species (permanently using the estuary during most or all of their life cycles) from which the majority consists in estuarine fishes (Santos-Martinez & Acero 1991, Sánchez 1996, Bateman 1998). According to the same authors, the largest proportion of resident species (about 60%) seems to spawn the whole year or have two spawning seasons, while the remaining seem to have only one. Additionally, half of the resident species seem to spawn inside the estuary and the other half in the surrounding coastal waters, however, the estuary is greatly used by juveniles (Santos-Martinez & Acero 1991, Sánchez & Rueda 1999).

The native species that historically have dominated the fishery and are considered ecologically important due to their high abundance and habits are mostly estuarine resident species (Santos-Martinez & Acero 1991, Sánchez & Rueda 1999). The majority of these fishes belong to lower categories in the food web (detritivorous, planktivorous or benthic fishes feeding mainly on invertebrates) like: *Mugil incilis* (Hancock, 1830), *Mugil liza* (Valenciennes, 1836), *Ariopsis bonillai* (Miles, 1945), *Cathorops mapale* (Betancur-R. & Acero-P., 2005), *Eugerres plumieri* (Valenciennes, 1830) and *Diapterus rhombeus* (Cuvier, 1829) (Santos-Martinez & Acero 1991, Sánchez & Rueda 1999). The other native estuarine fishes with commercial and ecological importance belong to the higher categories in the food web (piscivores or generalist carnivores) *Centropomus undecimalis* (Bloch 1792), *Megalops atlanticus* (Valenciennes, 1846), and *Elops saurus* (Linnaeus, 1766) (Santos-Martinez & Acero 1991, Sánchez & Rueda 1999). Also important but occasional visitors are the fresh water native fishes *Prochilodus magdalenae* (Steindachner 1879), *Caquetaia kraussii* (Steindachner 1878) and *Triportheus magdalenae* (Steindachner 1878)

(Santos-Martinez & Acero 1991). A brief description of some biological and/or ecological features of the most important native species can be found in the Appendix C.

3. GENERAL METHODOLOGY

3.1. DATA COLLECTION

The Institute for Marine and Coastal Research (INVEMAR) has provided three data sets corresponding to fishing, environmental and economic information that has been obtained since 1994 as part of the monitoring program mentioned before. Fishing and economic data has been collected in the landing sites by villagers especially trained for the task, while environmental data has been collected by INVEMAR researchers. Data on monthly catch (kg), landing sites, zones, fishing gears, species, number of fishing trips and prices per kg obtained by the fishermen were provided for the years 1994 to 1996 and 1999 to 2003. Additionally, monthly environmental information such as salinity (Practical Salinity Units – PSU), dissolved oxygen (mg/l), transparency (Sechi depth – m) and pH was also provided for the same time periods. Monthly data of local rainfall (mm) and river discharge (m^3/s) was provided by the National Institute for Meteorology, Hydrology and Environmental Studies (IDEAM) of Colombia.

Due to the simultaneous use of multiple fishing gears to catch many different species, the unit of effort used to compare the catches between different fishing units is the fishing trip. Catch per Unit Effort (CPUE) is then expressed as kg per fishing trip. The fishing gear cast net has been selected due to the more frequent and generalized use of this gear in the estuary. A cast net fishing unit is composed by two fishermen, one canoe, a cooling box, paddles and several cast nets of different dimensions and mesh size that can be used during the same fishing trip (Zamora 2005). Given the positive relation of CPUE with the abundance of fish stocks, this parameter can be considered an indicator of fish abundance (Richards & Schnute 1986, Haggarty & King 2006, Blanco *et al.* 2007). Therefore, CPUE of cast net fishing units is used in this study as a relative measure of abundance of fish and other organisms in CGSM – the term (relative) abundance shall be used instead of CPUE throughout the study. When the relative abundance of other species was needed (prey abundances in Chapter 9) the method diving was selected for mollusks, "releo" (a local method using a triangular bottom trawl net) for shrimps and "aros" (a local method using a submerged circular net stick to a steel arch) for swimming crabs.

Field work was conducted to collect fishes in order to get information about the feeding habits of non-native and native ichthyofauna. Ten sampling sites were chosen close to fresh water inlets in soft bottom areas of CGSM (Fig. 1, Chapter 9). Sampling was done monthly from July to December 2003, using two cast nets of 12 and 10 m of diameter and mesh size of 3 and 5 cm respectively that were operated by a local fisherman from a motor boat following a similar methodology as that used by Osorio (1988), Castaño (1989), Santos-Martinez & Arboleda (1993) and INVEMAR (2001) to make the collected data comparable to these studies. Stomachs were extracted and the contents analyzed according to the methodologies suggested by Hyslop (1980), Prejs & Colomine (1981) and Marrero (1994). Further details can be found in section II, Chapter 8.

3.2. DATA ANALYSIS

For analyses of fish abundance and catch composition, the study area was divided into 4 zones according to an east-west gradient of decreasing salinity (Giraldo *et al.* 1995) and the distinction of defined lagoon complexes: A. the main lagoon, B. the Pajarales lagoon complex, C. the sanctuary area, and D. the western side of Salamanca Island (Fig. 1, Chapter 2). Data from periods before and after introduction is available only for the non-native fish *Oreochromis niloticus*, therefore for analyses of abundance, catch composition and economic revenue the data sets were divided into 4 periods according to the abundance of this species and the mean salinity of the estuary: PI = 1994-1995 (few or no *O. niloticus* in catches; high salinities – 25.3±18 PSU); PII = 1996 (*O. niloticus* present but occurring in less than 5% of total catches; low salinities – 9.2±9.6 PSU); PIII = 1999-2001 (after re-establishment of fresh water and salt water connections and marked *O. niloticus* increase; lowest salinities – 8.1±9.5 PSU); and PIV = 2002-2003 (subsequent *O. niloticus* decrease; salinities increasing – 18.5±13.7 PSU).

Ecological impacts of Nile tilapia (*Oreochromis niloticus*)

The changes in native catch composition and fish abundance (CPUE), before (PI) and after (PII, PIII, and PIV) the introduction of Nile tilapia in the CGSM, were assessed through descriptive and multivariate analyses (Analysis of Similarity – ANOSIM, Similarity percentage Analysis – SIMPER; Clarke 1993). Forward stepwise multiple regression analysis (Zar 1996, α=0.05 or 0.025 after Bonferroni adjustment) was used to relate the abundance of six native fish species (dependent variables) with the abundance of the Nile tilapia and with environmental variables such as salinity, dissolved oxygen, pH, rainfall and river discharge (independent variables). The native fishes used in these analyses were: *Mugil incilis*, *Cathorops mapale*, *Eugerres plumieri*, *Ariopsis bonillai*, *Megalops atlanticus*, and *Elops saurus*. Further details can be found in section II, chapter 7.

The diet composition of *O. niloticus* and native fishes from years before (1988, 1989, 1993) and after (2001, 2003) the introduction of this alien fish was described based on stomach contents from the samples collected for this study (2003) and from data of previous studies (Osorio 1988, Castaño 1989, Santos-Martinez & Arboleda 1993 and INVEMAR 2001). For purposes of comparison the food items from all fish diets were arranged into common food categories (Table 2, Chapter 9). The index of relative importance (IRI; Yañez-Arancibia *et al.* 1976) was used to quantify the diet composition of the native fishes *Mugil incilis*, *Ariopsis bonillai*, *Elops saurus*, *Triportheus magdalenae*, *Diapterus rhombeus*, *Eugerres plumieri, Mugil liza*, *Cathorops mapale* and *Caquetaia kraussii*, and the Nile tilapia. Fish feeding strategies were categorized based on the values of IRI, diet breadth (Shannon-Weaner biodiversity index, H', Shannon & Weaver 1949) and diet evenness (evenness index, J', Pielou 1975). Diet overlap (Schoener index for resource overlap – Ov; Schoener 1968) was calculated between Nile tilapia and native fishes to assess the possibility of inter-specific competition. The influence of salinity, dissolved oxygen, pH and transparency on the abundance of the most frequently consumed prey was assessed through multiple regression analysis (Zar 1996, α=0.05). Further details can be found in section II, chapter 8.

Economic impact of Nile tilapia (*Oreochromis niloticus*)

The differences in the economic revenue between different periods before (PI) and after (PII, PIII, PIV) the introduction of Nile tilapia into the system were descriptively analyzed at two landing sites. In addition, a questionnaire-based survey was carried out at several landing sites to determine the fishermen's preferences for native and non-native fish. A multiple regression analysis (Zar 1996, α=0.05) was performed to establish the influence of the salinity and the economic revenue from the Nile tilapia fishery on the variation of economic revenue from the fishery of the following native fishes: *Prochilodus magdalenae*, *Centropomus undecimalis*, *Eugerres plumieri,* *Mugil incilis*, *Ariopsis bonillai*, *Elops saurus*, *Mugil liza*, *Cathorops mapale* and *Megalops atlanticus.* Further details can be found in section II, chapter 9.

Ecological impact of snake skin gourami (*Trichogaster pectoralis*)

Following the same statistical approach as in chapter 8, the influence of the abundance (CPUE) of snakeskin gourami on the abundance (CPUE) of native fishes was assessed through multiple regression analyses. Due to lack of data from the period before the introduction of *Trichogaster pectoralis*, this assessment was done only for the years 1994-1996 and 1999-2003 after its introduction. The native fishes considered for this part of the study were the same as in chapter 8: *Mugil incilis*, *Cathorops mapale*, *Eugerres plumieri*, *Ariopsis bonillai*, *Megalops atlanticus*, and *Elops saurus.* Forward stepwise Multiple Regression Analysis (Zar 1996, α=0.05 or 0.025 after Bonferroni adjustment) was conducted to determine if the variation in abundance of *T. pectoralis* (independent variable) could explain the variation in abundance of the native fish species (dependent variables). A second MRA was performed to determine the influence of environmental variables like salinity, pH and dissolved oxygen (independent variables) on the abundance of *T. pectoralis* (dependent variable). Using the zone A as a reference, dummy variables were created for zones B and D to determine the effect of zone differences on the variables. Zone C was excluded from these analyses due to lack of environmental data. Given the difficulty of establishing geographical limits to the influence of local rainfall and river input, the regional monthly mean values of these parameters were used in a third MRA as independent variables, and the regional monthly mean abundance of *T. pectoralis* as a dependent one. In all cases the statistical criterion (F) to enter variables into the models was $F > 1$.

4. GENERAL RESULTS AND DISCUSSION

4.1. ECOLOGICAL IMPACTS OF NILE TILAPIA

Species composition and abundance

The proliferation of Nile tilapia did not seem to affect the overall abundance of the native fish component of Ciénaga Grande de Santa Marta (CGSM) on a large scale, and rather seemed to be an addition to the ichthyofauna (Fig. 2 in Chapter 7). In fact, the overall abundance of the native fish component showed very low variation. This relative constancy could be indicative of high resilience of this component due to a high species redundancy, meaning that it has several fish species with similar functions and they react in different ways to the same environmental fluctuations (Walker 1995, Gunderson 2000, Hooper *et al.* 2005). Such a differential response to the environment seems to be an explanation for the observed variation in abundance and species composition of native fishes between zones and periods (see ANOSIM results & Fig. 3 in Chapter 7). This theory also explains the results of the Multiple Regression Analyses (MRA), where the abundance of the native ichthyofauna was associated to variation of salinity, pH and river discharge in different ways: The variation in abundance of the native fish *Mugil incilis* and the alien fish *Oreochromis niloticus* was negatively related to salinity, while that of the native fish *Cathorops mapale* was positively related to the same variable (Tables 2-4 in Chapter 7). Additionally, the variation in abundance of the native fishes *Ariopsis bonilllai*, *Elops saurus* and *Megalops atlanticus* was negatively related with pH, while *Eugerres plumieri* was positively associated with this variable and river discharge and negatively associated with salinity. A negative relation was found between the abundance of the native catfish *Cathorops mapale* and the alien fish *O. niloticus*, but both were associated to salinity variation as described above (Tables 2-4 in Chapter 7).

The native fish *Mugil incilis* accounted for most of the similarities within fish communities and dominated all zones except in the period of lowest salinity when it was the second dominant species after the alien fish *Oreochromis niloticus* (see SIMPER results & Fig. 3 in Chapter 7). The latter was the species that best discriminated the fish communities between periods and zones (same analysis). Additionally, fish diversity and species richness decreased in the periods when *O. niloticus* was dominant (Fig. 3 in Chapter 7). These findings could be seen as a signal of a negative impact of the Nile tilapia on the native ichthyofauna but, as it has been shown above, changes in species composition and abundance of native fishes responded rather to environmental variation than to the abundance of this alien fish. Therefore, the first hypothesis stating that, in spite of the restriction imposed by environmental fluctuation (*e.g.* salinity), the proliferation of Nile tilapia has altered the species composition and abundance of native fish communities within the estuary should be rejected, since variables such as salinity and pH seem to shape the native fish populations and constraint the long-term establishment of Nile tilapia.

The findings in this study coincide with other investigations made in tropical and sub tropical estuaries and coastal lagoons where salinity is also one of the main factors determining fish species richness, distribution and abundance in the ecosystems. Such is the case in Shellharbour lagoon in southeast Australia (Griffiths 2001), the Caeté estuary in northern Brazil (Barletta *et al.* 2005), St. Lucia estuary in South Africa (Whitfield *et al.* 2006), and Terminos lagoon in the southern Gulf of Mexico (Sosa-López *et al.* 2007).

In the absence of environmental constraints, Nile tilapia can negatively impact the native ichthyofauna as it has done in other ecosystems around the world (Costa-Pierce 2003, Canonico et al. 2005). In the African Lake Victoria for example, this species has outcompeted several native tilapiine species (Ogutu-Ohwayo 1990, Ogutu-Ohwayo & Hecky 1991). Several species of tilapias, including *O. niloticus,* have impacted the native fish communities in several lakes of Nicaragua, where they eliminated the habitat of some native fish by feeding on native aquatic plants. Additionally compete with native fish for spawning sites and seem to be responsible for an outbreak of a trematode parasite that has probably caused blindness among native cichlids (McKaye et al. 1995, McCrary et al. 2007). Peterson *et al*. (2004, 2005, 2006) call to action against the further expansion and introduction of this fish in coastal areas of Mississippi (USA) due to its rapid proliferation and high potential to compete for spawning grounds with native fish.

Feeding habits

Most of the fishes studied, including *O. niloticus*, fed on the most abundant prey types in all years (1988, 1989, 1993, 2001 and 2003). Changes in diet composition (Fig. 2 in Chapter 8) followed those of prey abundance (Fig. 3 in Chapter 8) and these responded mainly to variation in salinity within the estuary (Table 4 in Chapter 8). Three feeding strategies were distinguished: generalists, specialists and mixed feeders, with a greater occurrence of the latter (Table 3 & Fig. 2 in Chapter 8). A certain degree of specialization was however present in all diets, with a trend towards increase in the recent years (2001, 2003). The food categories detritus, sediment, unidentified plant material, zoo and phytoplankton were well represented in most of the fish diets examined except those of carnivorous fishes (Fig. 2 in Chapter 8). Blue-green algae (cyanophyceae) made up an important proportion of the diet of *O. niloticus*. The consumption of these algae is ecologically important considering that blue-green algal blooms are responsible for fish kills in the estuary (Mancera & Vidal 1994). Additionally, one of the reasons hypothesized by Blanco *et al.* (2007) for the drastic decrease of the Nile tilapia population in CGSM was a displacement of green algae (chlorophyceae) by blue-green algae within the phytoplankton component of the estuary. However, the studies of Turker *et al.* (2003) and Lu *et al.* (2006) have demonstrated that Nile tilapia is capable of effectively feeding on blue-green algae including toxic species.

The largest diet overlap (Ov=39.1) was found between the introduced *O. niloticus* and the native *Diapterus rhombeus* (Table 3 in Chapter 8) but this value is lower than 60 which is considered to be indicative of potential inter-specific competition (Zaret & Rand 1971, Langton 1982, Fjosne & Gjosaeter 1996). The considerable concentration of solids in the water column (mean: 158 mg/l ± 134.9 mg/l) that most likely reflect a considerable load of sediments and organic matter from the rivers into CGSM, and the high productivity (0.073-1.25 mg C/l/h *sensu* Gocke *et al.* 2003) reported for the system are indicative of a high abundance and probably high availability of food components like detritus, phyto- and zooplankton in the estuary. Thus, the moderate diet overlap between these two species is most likely due to the high abundance of their common preys: blue-green algae (cyanophyceae) and diatoms.

The dominance of mixed and generalist feeding among the studied fishes reflects an opportunistic strategy to adapt to the highly variable environment. An opportunistic feeding on the lower levels of the trophic web is an advantage since these food sources can be considered rarely limiting and very "cheap" in terms of energy spent for obtaining them (Gerking 1994, Peterson *et al.* 2006). Therefore a large diet overlap between native fishes and *O. niloticus* does not necessarily imply high probability of competition for food in this case. Instead, it seems to reflect a high abundance of the most common food categories in the ecosystem. Thus, the second hypothesis stating that, in spite of the restriction imposed by environmental fluctuation (*e.g.* salinity), the competition for food with Nile tilapia drives the temporal variation in feeding habits of native fishes should be rejected. Additionally, the results showed that mostly abiotic factors (*e.g.* salinity, pH; Table 4 in Chapter 8) seem to influence the abundance of the most common preys and therefore the diet variation among native fishes.

Food can hardly be a constraint for the establishment of Nile tilapia in CGSM due to its very flexible diet that allows it to shift from phytoplankton to a wider food spectrum including zooplankton, insects, small fish and plant material according to prey abundance (Balirwa 1992, 1998, Gutiérrez 2004, Njiru *et al.* 2004, Peterson *et al.* 2006). However, this opportunistic feeding is thought to be responsible for decreasing the abundance of zooplankton and large phytoplankton components thus promoting cascade effects in the trophic webs of tropical reservoirs in Brazil (Figueredo & Giani 2005, Okun *et al.* 2007). This suggests the possibility of negative impacts on the trophic structure of small and enclosed water bodies within the estuary. In bigger and interconnected water bodies the size could act as buffer to ameliorate the impact of trophic cascades. Further research is recommended in this regard.

4.2. ECONOMIC IMPACT OF NILE TILAPIA

Nile tilapia represented six times greater mean economic revenue than all native fish together during the period of lowest salinity in the estuary (Fig. 2 in Chapter 9). The economic revenues from the fishery based on the different native fishes differed among periods and landing sites (Fig. 4 in Chapter 9). Those from the fishery of some native fishes (*C. mapale, E. plumieri, Prochilodus magdalenae*) seemed to decrease when the Nile tilapia abundance increased (Fig. 4 in Chapter 9). However, the economic revenues from the fishery of both non-native and native fishes mainly correlated with the variations in salinity (Tables 2-3 in Chapter 9). Additionally, differences in location and structure of markets among landing sites seem to play an important role in the variation of the economic revenues. Although fishermen prefer native estuarine fishes due to their better taste and price, they are used to changing their target species according to the relative abundance of the fishes in the ecosystem. The drastic but short changes in the water budget of the estuary (Fig. 4 in Chapter 7) affect negatively the abundance of valued native estuarine fishes like *Ariopsis bonillai, Elops saurus* and *Cathorops mapale* (Tables 3-4 in Chapter 7). Additionally, overfishing contributes synergistically with other human activities and environmental stress to the decrease of these and other native estuarine species like *Centropomus undecimalis, Eugerres plumieri* and *Mugil liza* (Santos-Martinez & Arboleda 1993, Tíjaro *et al.* 1998, Rueda & Santos-Martinez 1999, Rivera-Monroy *et al.* 2006). Therefore, Nile tilapia a fish that has a relatively low price in the market but it is dominant during short periods of low salinity (Fig. 3 in Chapter 9) represents a temporal alternative of income when some native fish populations decrease. However, the fishery of *M. incilis*, a native estuarine fish better adapted to the environmental variation in CGSM, appears as a better alternative of income for the fishermen in the long term due to its persistence and moderately high abundance and price in all periods. Nevertheless, the stocks of this native fish also show signals of being overexploited in the estuary (Sánchez *et al.* 1998).

Based on these findings, the hypothesis stating that Nile tilapia, as a fishery resource, constitutes better economic revenue for the fishermen only in the short term, while the native fishes represent a better alternative of income in the long term should be accepted. Until now the fishery of this alien fish has provided larger economic revenue only during the short periods of low salinity when it is most abundant.

4.3. IMPACT OF SNAKESKIN GOURAMI

The snakeskin gourami (*Trichogaster pectoralis*) has been present in the catches in CGSM for a longer time than Nile tilapia, and it is also more tolerant to high salinities (up to 23) (Arenas & Acero 1992). Moreover, it is an opportunistic feeder and is adapted to low oxygenated waters, being able to breathe air (Moyle & Cech 1988, Arenas & Acero 1992). These characteristics can facilitate the establishment of this species in new environments, however in CGSM it seems to be restricted by the environmental fluctuation.

The results of multiple regression analyses showed that the variations in abundance of *T. pectoralis* were associated to the variations in the abundance of the native fishes *A. bonillai* ($r=0.14$; multiple $R^2=0.44$; $p<0.025$) and *E. saurus* ($r=0.16$; multiple $R^2=0.17$; $p<0.025$). The abundance of *T. pectoralis* responded to the variations in salinity ($r=0.25$; multiple $R^2=0.09$; $p<0.025$) and river discharge ($r=-0.25$; multiple $R^2=0.06$; $p<0.05$). The abundance of *A. bonillai* and *E. saurus* responded also to the environmental variation (pH, salinity and river discharge; Tables 3 & 4 in Chapter 7). Therefore, the positive relations found here between these native fishes and *T. pectoralis* could be explained by a similar response of the three species to the same environmental variables. Thus, the hypothesis stating that the variation in abundance of some native fishes is also driven by the presence/abundance of *T. pectoralis* should be rejected, since variations in abundance of non-native and native fishes seem to respond mostly to salinity fluctuations.

Then it is possible to assume, that for *T. pectoralis* also the environmental variation in CGSM restricts its proliferation and, if favorable conditions are given, this species has the biological features that facilitate its establishment. However, further research is needed to determine which other environmental variables could better explain the low abundance of this species in the estuary.

The diet of the snakeskin gourami was described by Arenas & Acero (1992) based on samples taken in 1989. They found that it feeds mainly on detritus (40%) with an important consumption of fish eggs (18%) and shrimp larvae (11%). No specimens were collected during the field work in the present study and there is no recent information on its feeding habits and other ecological features in the estuary. However, assuming no major changes in its diet, these feeding habits make this species a potential threat for native shrimp and fish populations, if favorable conditions are found in the estuary for its proliferation. Therefore further research should be done also in that regard.

5. CONCLUDING REMARKS

No clear evidence was found supporting the occurrence of negative impacts of Nile tilapia (*Oreochromis niloticus*) and snakeskin gourami (*Trichogaster pectoralis*) on the native ichthyofauna and the fishery of the estuary Ciénaga Grande de Santa Marta (CGSM). The environmental fluctuation expressed in drastic changes of salinity seems to be the main factor constraining the long-term establishment of these oligohaline fishes in the estuary. Nile tilapia and snakeskin gourami have biological features that facilitate their proliferation in new environments, and, additionally, food resources seem not to be a limitation for both species in the estuary. The explosive proliferation of Nile tilapia was an addition to the native fish communities during a two year period of low salinity conditions, but a potential impact on native benthic fish and fish diversity of the estuary should be further investigated.

Three possible scenarios, or a combination of them, could favor the long-term establishment of wild populations of *O. niloticus* and *T. pectoralis*: 1. The extension of relatively low salinity periods, 2. The introduction of a more euryhaline strain of *O. niloticus* from aquaculture installations in the area, or 3. The adaptation of these non-native fishes to the variable environmental conditions of the estuary.

How feasible are these scenarios? To answer this question it is necessary to consider, in the first one, that given the moderate salinity tolerance of these alien fishes (up to 15-23 PSU, Chapter 2), the favorable conditions necessary might not require a large input of fresh water into the estuary, but rather a regular one. The salinity in CGSM is controlled by the fluctuations of freshwater vs. saline water influx, which depend on the functioning of the channels connecting the system to the river and the sea. These channels were re-opened to recover the necessary ecological conditions to maintain important resources in the estuary. If they can be kept unobstructed, the fresh water influx from the river will be more regular and therefore the occurrence of periods with very high salinities might decrease. Under such conditions the establishment of *O. niloticus* and *T. pectoralis* can be facilitated.

The second scenario is also feasible given the increasing trend of aquaculture in the country in the last decades (FAO 2006), which points to an increasing spectrum of strains to be introduced (Fitzsimmons 2000). If no further regulations are implemented to the aquaculture activities in the country, it might be just a matter of time until a more salinity tolerant strain of *O. niloticus* is introduced to the Magdalena basin and therefore reaches the CGSM.

Regarding the third scenario, laboratory assays have shown that the salinity tolerance of *O. niloticus* increases when it is exposed to gradual (*e.g.* weekly) increments of this parameter (Schofield *et al.* 2007). This added to the reports of wild populations of this fish in coastal areas with salinities up to 33 PSU (Scordella *et al.* 2003) are good indications of the high adaptability of the species.

The snakeskin gourami is not commercially cultured in Colombia and there is no information available in literature about its biological features as an introduced fish in the Neotropics. Therefore, the first scenario seems to be the most feasible for this species. Nevertheless, further research is needed to explore the real feasibility of the other two scenarios.

Nile tilapia is a profitable fish only for short periods. Therefore, this alien fish does not represent a long-term alternative to improve the economic revenue of the fishermen in the region. Instead, the native fish *Mugil incilis* can be considered a better alternative of income due to its more regular occurrence in the estuary, relatively good price and better salinity tolerance. However, its fishery should be regulated to prevent overfishing from diminishing the native fish stocks further.

In general terms, the case study of Ciénaga Grande de Santa Marta seems to lend support to some hypotheses in invasion ecology:

- Abiotic variables rather than biotic resistance seem to be the most important factors affecting the success or failure of introduced fishes in estuaries and streams (Moyle & Light 1996 a, b). Salinity seems to be the variable shaping the native and non-native fish populations in CGSM (Rueda 2001, Blanco *et al.* 2007, this study) and other tropical and subtropical estuaries (Griffiths 2001, Barletta *et al.* 2005, Whitfield *et al.* 2006, Sosa-López *et al.* 2007). In this sense, introduced fishes with a wide range of environmental tolerance (*e.g.* to salinity) should have better chances of establishment in estuaries (Marchetti *et al*. 2004, Moyle & Marchetti 2006).

- In the absence of other constraints, fishes that can feed at low trophic levels are predicted to establish long lasting populations (Moyle & Light 1996a, Gido & Franssen 2007). In the case of CGSM, the drastic salinity changes have constrained the long-term establishment of the detritivore and planktivore fishes *O. niloticus* and *T. pectoralis*.

- In systems submitted to drastic environmental changes, high species richness and biodiversity are crucial to keep the resilience in the ecosystem and therefore ecosystem functioning, since there is a higher probability of having species redundancy within functional groups (Gunderson 2000, Loreau *et al.* 2001, Hooper *et al.* 2005). Species redundancy reduces the possibilities that an entire functional group disappears after disturbance (*e.g.* drastic environmental changes, introduction of alien species; Walker 1995, Hooper *et al.* 2005). Additionally, a generalist or a mixed feeding helps the native ichthyofauna to cope with the environmental fluctuations (Trexler *et al.* 2000). This seems to be the case in CGSM, where apparently different species with similar functions respond in different ways to the same environmental changes and the most common feeding strategy is a generalist or mixed feeding. However, further research is needed to identify the different functional groups within the native ichthyofauna and their importance for processes at the ecosystem level (*e.g.* energy fluxes, nutrient cycling).

Some questions remain unanswered in this study:

- Why did only *O. niloticus* proliferate during the low salinity period (1999-2001), if this condition should have been favorable also to native fresh water fishes?

- Why if the fresh water conditions of period III (1999-2001) persisted also in period IV (2002-2003) in the western area of Salamanca Island (zone D in Fig. 1 of Chapter 8), did the "boom" of Nile tilapia occur there only in period III?

- Why has the snakeskin gourami not proliferated in the estuary during periods of favorable (low salinity) conditions?

Possible answers to the first question might be inter-specific competition for space due to the territorial behavior of *O. niloticus*, or selective predation by big native estuarine piscivores on preferred native preys. Another possible explanation could be over fishing not only in particular zones but also in the Magdalena River from where most of the fresh water fishes (including *O. niloticus*) are entering into the estuary. Galvis & Mojica (2007) found that fish resources in the Magdalena River have been depleted by overfishing to one tenth in the last 37 years.

During the period of highest abundance of Nile tilapia, most of the fishermen changed their fishing gears and methods to those that could yield the highest catch of this fish (INVEMAR 2006). It is possible that in Salamanca area, the intense fishing depleted the Nile tilapia populations to a level below the minimum that populations would need to recover. This could be a possible answer to the second question. However, there is no information on the population dynamics of this fish in those periods.

Regarding the third question, an explanation for the low abundance of snakeskin gourami during low salinity periods might also be predation by larger native fishes due to its small size (maximum 25 cm of total length – Pethiyagoda 1991) that makes it an attractive prey. Another reason could be the limited extension and high salinities (18-39; Perdomo *et al.* 1998) of the mangrove areas which constitute the most suitable habitat for *T. pectoralis* in the estuary.

The low values of the multiple regression coefficients (R^2) might indicate that analysis of additional variables could contribute new insights to understand the variation in abundance of non-native and native fishes. Therefore, it is recommendable to investigate the role of factors like overfishing, competition for space or predation for the long-term establishment of these fishes. Such knowledge is necessary to develop a plan for controlling their abundance in the estuary. Additionally, some gaps in knowledge about the biology of the native fishes should be filled to avoid that measures intending to keep out the non-native fishes affect the native ichthyofauna negatively.

A final lesson to learn from this study is that although introduction of alien species can evolve into ecological and social catastrophes (*e.g.* Lake Victoria, Table 2 in Chapter 1) it should also be considered the possibility of positive effects in the ecosystem and the human communities. Therefore, an integrated view including the ecological and social components of ecosystems is the best way to assess the impacts of species introductions.

6. SOME COMMENTS ON MANAGEMENT

Humans are perhaps the most influential component of the ecosystem, because their activities can change its structure and functioning on a bigger scale and magnitude than most other components. Ciénaga Grande de Santa Marta (CGSM) is an example of that anthropogenic influence on an ecosystem, and in certain way can be representative of what is also happening in other tropical ecosystems. Poor human populations press the coastal ecosystems for economic revenue, leading to environmental degradation and depletion of native resources. This situation increases poverty and with it also the pressure on the ecosystems. In such a scenario of resource scarcity, human populations develop the attitude "let's think only of today's revenue". In several talks with fishermen, not only in CGSM but also in other regions connected to the Magdalena river, I heard very often comments like "I know if we keep fishing in this way we will end up with no fish tomorrow, but today I need to bring some food home" or "if I don't catch it, my neighbor will, so what would be the point in stopping or reducing my fishing?", or "if I stop fishing, what else can I do? I do not know how to do anything else and can not read or write". This reveals that social problems like no access to formal education and lack of alternative jobs are in fact the main factors behind the depletion of fishery resources in the Magdalena basin (Galvis & Mojica 2007). As long as the basic needs of the inhabitants are not covered in this region, it is very difficult to think about implementing any management measure, unless this is accompanied by a simultaneous plan to improve at least the educational level of the human population and generate income alternatives.

With at least 153 species already introduced or transferred into the country (Gutiérrez 2004), measures are urgently needed to prevent more introductions and control those alien species already established. Prevention should focus mainly on interrupting the introduction pathways or vectors. "If these vectors can be effectively intercepted, alien species invasions will be reduced" (Carlton & Ruiz 2005). The control should then focus on impact evaluation (*e.g.* this study) and mitigation.

The most common pathways of species introduction in Colombia are aquaculture and ornamental trade (Gutiérrez 2004). The FAO fishery statistics (2006) show a significant growth of the aquaculture production in Colombia during the last decade, increasing from

10455 tons in 1990 to 60072 tons in 2004. The culture of Nile tilapia for example, shows the same trend with a production of 3747 tons in 1995 that increased to 8860 in 2004, according to the same source. The rapid growth of this activity certainly implies that this pathway of introduction in the country is not likely to be interrupted within the near future. Nevertheless, it is essential that regulation of this activity be implemented in the country regarding the species that can be allowed to be introduced and the type of systems to be used in their culture. The prohibition of certain species for use in aquaculture should be done based on a balanced study, that takes into consideration the negative ecological and social impacts as well as possible benefits.

Measures should be taken to control the populations of non-native fishes in the CGSM before they proliferate. A possible measure could be to regulate the amount of fresh water that enters into the system through the re-opened channels, so that salinity is kept above the tolerance limit of both introduced fish. However, it is necessary first to establish the salinity tolerance of the freshwater and marine native species to avoid disruption of their natural cycles through further intervention in the hydrological dynamics of the estuary.

In recent times in Colombia more attention has been paid to the possible impacts of species introductions than ever before and there is already a first proposal for the establishment of a national policy for prevention and control (Gutiérrez 2006). However, no studies have been published where ecological and social impacts of introduced species are addressed. Therefore, a great amount of work is still needed, especially in relation to three main aspects:

- Covering the gap of knowledge. The species inventories in many ecosystems should be still completed, including information on the biology and ecology of all species (native and non-native) reported. Additionally, more research is needed on specific impacts of all species that have already been introduced into the country. For these investigations, the establishment of a national scientific network is very important to share information between regions. The participation in such networks on the international level is also very important in order to avoid repeating efforts, since many of the non-native species have already been well studied in their original countries. There has been some advance in this aspect with the creation of a national program and database of biodiversity that includes non-native species. This program is connected to the Inter-American Biodiversity Information Network (IABIN) that compiles information on native and non-native species within the countries of the American continent.

- Increasing public awareness. In many cases resource users on all levels (*e.g.* from fishermen to restaurant visitors) do not even know the difference between a native and a non-native species, and much less the impacts of the latter on the ecosystems or human populations, or how they arrive into the country. Therefore, campaigns on the national and regional level should be done, for example, using commercials so as to address all kinds of public, specially that part of the human population with a very low level of literacy (*e.g.* fishermen). In this case, scientific work should be translated into a language and format that is understandable by the least educated. In the end, science should serve humankind and not vice versa.

- Active participation of the human community. In Colombia can be common to consider that participation of local people in a management plan is just limited to informing them of the measures that will be taken after they have been decided on the institutional level. Based on my observations and personal experience, the human community should be included in decision making from the very beginning, when the question of the necessity of a management plan is addressed for the first time. When the community participates from the initial phase they will adopt the plan as their own, and will therefore be willing to see it through.

Photos: INVEMAR 2001

SECTION II: PUBLICATIONS

7. ROLE OF NILE TILAPIA IN THE LONG TERM VARIATIONS OF ABUNDANCE AND SPECIES COMPOSITION OF THE NATIVE ICHTHYOFAUNA IN A CARIBBEAN ESTUARY”

Manuscript submitted to the Journal “Bulletin of Marine Science”

Role of Nile tilapia in the long term variations of abundance and species composition of the native ichthyofauna in a Caribbean estuary

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ABSTRACT

Changes in native fish abundance (Catch per Unit of Effort - CPUE) and species composition were assessed before and after the introduction of Nile tilapia (*Oreochromis niloticus* Linnaeus, 1757) in the Caribbean estuary Ciénaga Grande de Santa Marta (CGSM) in Northern Colombia. Multiple regression analysis was used to relate the abundance of native fish with that of non-native fish and environmental variables such as salinity, dissolved oxygen, pH, local rainfall and river discharge. Species composition and abundance of native fish was found to vary with environmental conditions in different zones but on a large scale its overall abundance remained approximately constant during all studied periods. Abundance of the native catfish *Cathorops mapale* (Betancur-R. and Acero-P., 2005) was negatively related to the abundance of *O. niloticus*, but both were related to salinity variation. Fish diversity decreased in periods when *O. niloticus* was present, but this decrease coincided with low salinity conditions. Our findings indicate that the environmental fluctuation constrains the long-term establishment of Nile tilapia in the estuary and therefore its possible effects in the abundance and species composition of the native ichthyofauna. However, it is feasible that the arrival of a more tolerant strain of this species or its future adaptation to the variable environment or a longer duration of fresh water conditions, could favor a long-term proliferation of Nile tilapia. Considering the biological features of this species, in such a case, the occurrence of negative impacts on the native fishes can not be disregarded. This is, to our knowledge, the first study investigating the impacts of *O. niloticus* on a Caribbean estuary.

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Keywords: Species composition; Colombia; estuary; non-native fish; Nile tilapia, environmental variation; fish abundance; native fish; Caribbean region; salinity.

INTRODUCTION

The introduction of new species into aquatic ecosystems has become common practice, but also a serious ecological problem: although it is intended as a solution to overcome shortage in food supply in many tropical countries, it is recognized as one of the primary threats to biodiversity (Sala et al. 2000, Bax et al. 2003, Sala and Knowlton 2006, Rahel 2007). Species introductions may result in biological invasions that dramatically affect native species through predation or grazing, competition for food or space and hybridization with native species. These and other impacts may eventually lead to alterations in the structure and function of the ecosystems and cause the loss of valuable resources (Mack et al. 2000, Mooney and Cleland 2001, Hoffmeister et al. 2005). The introduction of non-native species in Africa and the Great Lakes of North America, for example, is considered one of the main causes for the collapse of the fisheries in those regions (Ogutu-Ohwayo and Hecky 1991, Hall and Mills 2000).

Colombia's fish fauna includes at least one third of the total number of fish species known in South America (Mojica et al. 2002). It is also among the countries with the highest number of non-native fish species. Out of 153 non-native fish species recorded, 96 originated outside Colombia, while 57 have been transferred from other basins within the country (Gutierrez 2004). Many of these fishes were intentionally introduced to either increase local fishery production or for use in the ornamental fish trade, or for aquaculture purposes. Many others were accidentally introduced as a result of inadequate management of intentional introductions. Although there have been numerous warnings about the potential consequences of the increasing number of non-native fishes on the native Colombian icthyofauna, there are as yet no published studies directly addressing those impacts, even though some non-native fishes already constitute important fishery resources in several regions of the country (Diaz and Alvarez 1998, Álvarez and Salazar 2001 and Gutierrez 2004).

The Ciénaga Grande de Santa Marta (CGSM) is located at the North coast of Colombia and is one of the largest estuaries in the Caribbean Sea. This estuary is the main source of food and income for the regional fishery due to its large size (ca. 1280 km^2) and productivity (Sánchez and Rueda 1999, Gocke et al. 2003). The most important natural factors influencing the distribution and abundance of resources in the CGSM are the fresh water input from the Magdalena River (Wiedemann 1973, Kaufmann and Hevert 1973) and saltwater input from the Caribbean Sea (Sanchez and Rueda 1999, Rueda 2001, Blanco et al. 2006, 2007). Interruption of fresh and marine water input, pollution, deforestation, erosion, and over-fishing in CGSM has led to the loss of many valuable resources during the last 40 years (Botero and Mancera 1996, Botero and Salzwedel 1999, Rueda and Defeo 2003). Former waterways were re-established by dredging in 1998 with the goal of recovering former ecological conditions. Since that time, non-native fishes such as the snakeskin gourami (*Trichogaster pectoralis* Regan, 1910), the Nile tilapia (*Oreochromis niloticus* Linnaeus, 1757), the hybrid red tilapia (*Oreochromis* sp.) and the tambaqui (*Colosoma macropomum* Cuvier, 1818) increased their presence in the system (Sanchez 1996, Bateman 1998). Since 1999, *O. niloticus* has become one of the principal fishery resources, accounting for almost 60% of all catches in 1999 and 2000 (INVEMAR 2006), but decreasing to less than 10% thereafter. This drastic variation in abundance of Nile tilapia seems to be related to environmental fluctuations (e.g. salinity) in the estuary (Blanco et al 2007).

The goal of our study was to determine whether the observed spatio-temporal variation in species composition and abundance of native fish were related to the presence or abundance of the non-native fish *O. niloticus* or to environmental variability or both. We used descriptive and multivariate analysis to establish spatio-temporal trends in the changes of native fish abundance and species composition before and after the introduction of *O. niloticus*. We also used multiple regression analysis to test possible correlations between changes in native fish abundances and abundance of *O. niloticus*, salinity, pH, dissolved oxygen, and fresh water input (local rainfall and river discharge). We predicted that changes in the catches of the most abundant native fishes would be strongly related to the variation of the catches of *O. niloticus*. To our knowledge, this is the first study investigating the possible impacts of the Nile tilapia on the native ichthyofauna of a Caribbean estuary.

METHODS

STUDY SITE

The CGSM is located between 10° 43'-11° 00' N and 74° 16'-74° 35' W in the delta of the Magdalena River on the North Coast of Colombia (Figure 1). Its major connection to the Caribbean Sea is Boca de la Barra, an 80-100 m wide artificial outlet (Santos-Martinez and Acero 1991). The system receives freshwater from several rivers originating in the Sierra Nevada de Santa Marta mountain system and from the Magdalena River trough a complex of channels and swamps named Pajarales (Figure 1; Botero and Salzwedel 1999). The mean annual water temperature is 30°C and the depth in the system varies between 1 and 7 m. The salinity ranges between 0 and 40 PSU and the tidal amplitude between 20 and 30 cm (Polanía et al. 2001). The climate in the area is particularly dry (arid) with a mean air temperature of 28°C and a hydrological deficit that ranges between -211.6 and -1146.8 mm yr^{-1} resulting from the difference between mean local rainfall and mean evaporation (Botero and Salzwedel 1999, Blanco et al. 2006). Therefore, riverine water input is vital for the system's water budget (Kauffman and Hevert 1973). A dry season extends from December to March and a rainy season from April to November (Blanco et al. 2006). Of the 122 teleost fish species that have been recorded in the CGSM, 81 are commercially exploited (Polanía et al. 2001). Historically important native estuarine species include *Mugil incilis* Hancock 1830, *Cathorops mapale* Betancur-R. and Acero-P. 2005, *Eugerres plumieri* Valenciennes 1830, *Ariopsis bonillai* Miles 1945, *Megalops atlanticus* Valenciennes 1846, and *Elops saurus* Linnaeus 1766 (Santos-Martinez and Acero 1991, Sanchez and Rueda 1999).

DATA COLLECTION

The data used for this study were collected by the Institute for Marine and Coastal Research (INVEMAR) in Santa Marta, Colombia. Since 1994, monthly fishery information was collected within the framework of an ecosystem monitoring program. Data collected include weight of catch (kg), species composition of catch, effort (number of fishing trips) by gear type, and location as well as environmental information such as salinity (Practical Salinity Units – PSU), dissolved oxygen (mg/l), and pH. We also used local rainfall (mm) and river discharge (m^3/s) data provided by the National Institute for Meteorology, Hydrology and Environmental Studies (IDEAM). Catch per unit effort (CPUE) was calculated and used as a relative measure of fish abundance in the system - the term abundance shall be used throughout this study instead of CPUE. For the analyses we used fish abundance (CPUE) data from cast nets. This gear was the most consistently used over the eight-year study period and collected the widest spectrum of species when compared with all the other gear types.

DATA ANALYSIS

Our study area was divided into 4 zones: ZA. the main lagoon, ZB. the lagoon complex of Pajarales, ZC. the lagoon complex in the south-western protected area, and ZD. the western side of Salamanca Island (Figure 1). Moving east to west through these zones (A through D) represents a gradient of decreasing salinity (Giraldo et al. 1995). The change in abundance of *O. niloticus* was used as a criterion to divide the set of monthly data into four periods: PI = 1994-1995 (few or no *O. niloticus* in catches; N=58); PII = 1996 (*O. niloticus* present but occurring in less than 5% of the total catches; N=25); PIII = 1999-2001 (after reestablishment of fresh water and salt water connections and marked *O. niloticus* increase; N=34); and PIV = 2002-2003 (subsequent *O. niloticus* decrease; N=36). A Kruskal-Wallis test was done to check the significance of the difference in abundance of *O. niloticus* between these periods ($H = 195.83$, $df = 3$, $N = 327$, $p < 0.05$). Mann and Whitney U Tests were used to check the difference between all pairs of periods compared and all of them were significantly different ($p < 0.008$ after Bonferroni adjustment; Sokal and Rohlf 1995).

Fish abundance and species composition

A two way Analysis of Similarities (ANOSIM) was done to test if species composition and multispecific fish abundance significantly differed among periods and zones (factors; Clarke 1993). A Similarity Percentage (SIMPER) analysis was used to determine the species accounting for most of the similarity in abundance and species composition within periods and zones. It was used as well to determine the species that discriminate best between these grouping factors (Clarke 1993). For these analyses all fish species accounting for more than 1% of the total abundance in at least one of the eight years of the study were selected (21 species; table 1). PRIMER for Windows v. 5.2.2 (Plymouth Marine Laboratory) was used for all analyses.

Relationship of fish abundance with the environmental variables

Forward stepwise Multiple Regression Analysis (MRA; Zar 1996) was conducted to determine the extent that *O. niloticus* abundance and environmental factors explained the monthly variations in fish abundance for the 6 most abundant and commercially important native fish species (tables 2-4). Due to high correlation between salinity and abundance of *O. niloticus* (Spearman Rank Order Correlation = -0.60, $p < 0.05$), these two variables were used separately as independent variables. All data were Log+1 transformed to reach normality of the residuals and 0.025 was used as significance level (Bonferroni adjustment). In all cases the statistical criterion (F) to enter variables into the model was $F > 1$. In the first MRA, the abundances of the native species were used as dependant variables and that of *O. niloticus* as an the independent one, while in a second MRA the abundances of all fishes including *O. niloticus* were used as dependent variables, and salinity, pH and DO as independent variables. Using the zone A as a reference, dummy variables were created for zones B and D to determine the effect of zone differences in the variables in these two MRA's. Zone C was excluded from these analyses due to lack of environmental data. Given the difficulty of establishing geographical limits to the influence of local rainfall and river input, their regional monthly average values were used in a third MRA as independent variables and the regional monthly mean abundance of native fishes and *O. niloticus* as dependent ones.

RESULTS

FISH ABUNDANCE AND SPECIES COMPOSITION

The group of native fish maintained a very similar abundance over the entire study period while *O. niloticus* had a drastic variation in abundance from very low in PII and PIV to very high in PIII when it dominated the catches in the estuary (Figure 2).

A variable group of very few species (2-4) represented between 70 and 95% of the total abundance (Figure 3 A-D). The native estuarine fish *M. incilis* is the only species ranking within the most abundant in all zones and periods. The non-native fish *O. niloticus* became the most abundant species (total CPUE > 50%) in PIII in all zones except in ZA, where *M. incilis* was the most abundant. *O. niloticus* drastically decreased in PIV in all zones. The abundance of the native *C. mapale* decreased during the periods when *O. niloticus* was the most abundant fish in all zones. *E. plumieri* varied considerably from period to period, but with no apparent relation to any other species. Native freshwater fishes like *Triportheus magdalenae* Steindachner 1878, *Prochilodus magdalenae* Steindachner 1879 and *Hoplias malabaricus* Bloch 1794 appeared only in PII or PIII in ZB, ZC and ZD. Piscivorous fishes like *A. bonillai*, *M. atlanticus* and *E. saurus* increased in some zones during PIII and PIV. Fish diversity, expressed as Shanon-Weaver Index (1949), and species richness (number of species) decreased in PII in all zones (Fig. 3 A-D). Fish diversity decreased also in PIII**,** while species richness increased in PIII in all zones. Only in ZA both parameters decreased in PIV.

The two way crossed Analysis of Similarities (ANOSIM) showed significant differences in species composition and abundance between periods ($R = 0.601$, $p < 0.001$) and zones ($R = 0.49$; $p < 0.001$). This analysis also showed a significant difference ($R>0.3$; $p < 0.001$) between all pair wise comparisons (PI-PII, PI-PIII, PI-PIV, PII-PIII, PII-PIV, PIII-PIV; ZA-ZB, ZA-ZC, ZA-ZD, ZB-ZC, ZB-ZD, ZC-ZD). Furthermore, the SIMPER Analysis revealed that *M. incilis* is the fish species that best accounted for the similarity in species composition and abundance in all zones (% Similarity > 16) and periods (% Similarity > 22)**,** except in PIII. In this period *O. niloticus* accounted for the largest similarity (22%). *Oreochromis niloticus* was the species that best discriminated between most pairs of compared periods (% Dissimilarity > 12) and zones (% Dissimilarity > 10). The second species discriminating best between periods (% Dissimilarity ~ 9) and zones (% Dissimilarity ~ 10) was the native fish *C. mapale*.

RELATIONSHIP OF FISH ABUNDANCE WITH ENVIRONMENTAL VARIABLES

Salinity and river discharge are the variables with the greatest variation in the ecosystem (Figure 4 A-I). The fluctuations in salinity (Figure 4 D-E) follow an opposite pattern to those of the water discharge of Magdalena River (Figure 4 B), which is the main input of fresh water in the estuary. Zones A and B show a similar fluctuation of salinity (Figure 4D,

E) varying from high (20±14 to 35±21) in PI and PIV to low values (6±9 to 10±9) in PII and PIII. The pH (Figure 4 G-H) varies in a similar range between periods with a similar pattern in both zones, but in PIII it decreased more notoriously in ZB. No environmental data is available for PII in zone D (Figure 4 F-I), therefore conclusions regarding this zone must be considered with care. It is possible, however, to observe that the salinity range in this zone is much lower (0-5) than elsewhere and pH is similar to that of other zones. These patterns possibly also hold for the missing period.

The multiple regression analyses revealed that both the environmental variables (salinity, pH and river discharge) and the abundance of *O. niloticus* contributed to the variation in the abundance of native fish. The abundance of *O. niloticus* explained better (table 2, $p<0.025$) the variation in abundance of *C. mapale* (r= -0.45) and *M. atlanticus* (r= 0.19). When salinity, pH and dissolved oxygen were the independent variables (table 3, $p<0.025$), salinity explained better the variation in abundance of *M. incilis* (r= -0.32*), C. mapale* (r= 0.45), *E. plumieri* (r= -0.35) and *O. niloticus* (r= -0.43). The pH explained better the variations in abundance of *A. bonillai* (r= -0.50), *E. saurus* (r= -0.44) and *M. atlanticus* (r= -0.51). When river discharge and local rainfall were the independent variables (table 4, $p<0.05$), river discharge explained best the variation in abundance of *E. plumieri* (r= 0.39) and *E. saurus* (r= -0.29).

DISCUSSION

The hypothesis of *O. niloticus* being responsible for the fluctuation in the abundance of native ichthyofauna should be rejected since the environmental fluctuations (salinity, pH, and river discharge) seem to be the main factors determining the variation in abundance of most fish species including *O. niloticus*. However, our findings indicate that although the duration of low salinity conditions was relatively short, this non-native fish could have affected the native ichthyofauna.

On the largest spatial scale (all zones combined) the overall native fish abundance remained quite constant in the four periods studied (Figure 2). However, if the specific composition is analyzed for each period and zone (Figure 3A-D), changes in relative abundance on the species level become evident. This relative constancy of the native fish component could be indicative of a high resilience due to a high species redundancy, meaning that this component has several fish species with similar functions and they react in different ways to the same environmental fluctuations (Walker 1995, Gunderson 2000, Hooper *et al.* 2005). Such a differential response to the environment seems to explain the observed variations in species abundance and composition at smaller spatial and temporal scales (zones and periods; Fig. 3). It also explains the results of the Multiple Regression Analyses (MRA), where it is shown that abundance of the native ichthyofauna was associated to variation of salinity, pH and river discharge in different ways (Tables 2-4).

During the periods of low salinity, the inflow of unusual amounts of fresh water seems to increase the variety and size of available habitats for fresh water and euryhaline species in the estuary. In contrast, species not well adapted to these changes, seem to migrate looking for more favorable conditions or experience a decrease in their populations. This is evidenced by the increase of the number and abundance of native fresh water fishes (e.g. *P. magdalenae*, *H. malabaricus*, *T. magdalenae*) in PIII, and the decrease in abundance of native estuarine fishes (e.g. *M. incilis*, *C. mapale*) in the same period (Figure 3 A-D). The increase of piscivorous fish during the periods PIII and PIV in some zones might be a response to an increase of prey represented by non-native and native fresh water fishes (Figure 3 A-D). This might explain the positive relation between the predator *M. atlanticus* and the potential prey *O. niloticus* (Table 2).

The great adaptability of *O. niloticus* to new environmental conditions is evidenced by its high growth rate, variable maturation size and opportunistic feeding (Trewavas 1983; Balirwa 1998; Beveridge and McAndrew 2000). In strongly altered and stressed ecosystems, Nile tilapia could be a superior competitor debilitating or completely outcompeting native species (Ogutu-Ohwayo 1990, Ogutu-Ohwayo and Hecky 1991; Léveque 2002; Canonico et al. 2005). The SIMPER analysis showed that, during the period of lowest salinity (PIII), the dominance of *O. niloticus* modified the composition of the fish community that is usually dominated by the native estuarine fishes *M. incilis* and *C. mapale*. Additionally, in that same period fish diversity decreased (Fig. 3). However, changes in abundance (MRA; Tables 2-4) and species composition (Fig. 3) seem to respond mostly to environmental variation.

The negative relation between the abundances of *O. niloticus* and the native fish *C. mapale* (Figure 3, Table 2) could be indicative of interspecific competition. Both species utilize soft bottoms, the first for spawning and the second for feeding (Carpenter 2002; Froese and Pauly 2006). The abundance of both fishes, however, was related to the variations in salinity, so they could be instead responding in opposite ways to the same environmental variable. Further research should be done to establish the feasibility of competition between these two fishes.

The salinity tolerance of the tilapias is highly variable. This is evidenced by the different tolerance limits reported in different populations of Nile tilapia. In laboratory experiments, Watanabe et al. (1985) reported a salinity tolerance limit of 19 PSU, Villegas (1990) of 10 PSU and Schofield (2007) larger than 40 PSU after weekly increments. Peterson et al. (2004) reported the existence of actively reproductive populations of *O. niloticus* in coastal environments with salinities that range at about 25 PSU in Mississippi, USA. In Eastern Italy in the Lesina coastal lagoon with salinities between 22 and 33, *O. niloticus* has also established wild populations (Scordella et al. 2003). The Nile tilapia in CGSM seems to belong to a less euryhaline type since its abundance dramatically decreased when salinities increased above 15 PSU (Blanco et al. 2007). This variable environmental tolerance indicates a high adaptability of the species. Therefore, it should not be discarded that the arrival of a more tolerant strain of this fish or its adaptation to the variable environment, could favor a long term establishment of Nile tilapia in the estuary.

Negative impacts of tilapias have been reported already in several ecosystems around the world (Costa-Pierce 2003, Canonico et al. 2005). *Oreochromis niloticus* has outcompeted several native tilapiine species in the African Lake Victoria (Ogutu-Ohwayo 1990, Ogutu-Ohwayo and Hecky 1991). Tilapias, including *O. niloticus,* have impacted the native fish communities in several lakes of Nicaragua. In these lakes they eliminated the habitat of some native fish by feeding on native aquatic plants. Also compete with native fish for spawning sites and seem to be responsible for an outbreak of a trematode parasite that has probably caused blindness among native cichlids (McKaye et al. 1995, McCrary et al. 2007). The rapid proliferation of *O. niloticus* and its high potential to compete for spawning grounds with native fish (e.g. centrarchids) is considered as a threat to the US coastal areas of Mississippi (Peterson et al. 2004, 2005, 2006).

Other investigations made in tropical and sub tropical estuaries and coastal lagoons have also found that abiotic factors like salinity are the main factors determining the fish species richness, distribution and abundance in the ecosystems. Such is the case of the Shellharbour lagoon in southeast Australia (Griffiths 2001), the Caeté estuary in northern Brazil (Barletta *et al.* 2005), St. Lucia estuary in South Africa (Whitfield *et al.* 2006), and Terminos lagoon in the southern Gulf of Mexico (Sosa-López *et al.* 2007). Based on their research experience in California streams, Moyle and Light (1996) propose that "if abiotic factors are appropriate for a non-native species, then that species is likely to successfully invade, regardless of the biota already present". This statement is supported by the case of Nile tilapia in CGSM, where although having the biological advantages for its proliferation, the establishment of this fish is restricted by the lack of appropriate abiotic factors. Johnstone (1986) and Carlton (1996) pointed out that changes in the recipient ecosystem can foster adequate biological, ecological and environmental conditions creating an "invasion window" for the successful establishment of new species; however, Crawley (1989) remarked the importance of good timing of the arrival of these new species to coincide with those good environmental conditions during the time necessary. This means that if favorable conditions are met in the estuary for longer periods, *O. niloticus* could establish self-sustaining populations.

Being one of the most popular cultured fish worldwide, Nile tilapia has been introduced in many tropical countries (FAO 2006). However the impacts of this non-native fish in natural waters are not yet well studied (Canonico et al. 2003, Costa-Pierce 2003). The present study is, to our knowledge, the first one looking for the impact of this fish on the native ichthyofauna of a Caribbean estuary. Our findings indicate that the environmental fluctuation constrains the long-term establishment of Nile tilapia in the estuary and therefore its possible effects in the abundance and species composition of the native ichthyofauna. However, it is feasible that the arrival of a more tolerant strain of this species or its future adaptation to the variable environment or a longer duration of fresh water conditions, could favor a long-term proliferation of Nile tilapia. Considering the biological features of this species, in such a case, the occurrence of negative impacts on the native fishes can not be disregarded. Thus the monitoring program running in the CGSM should be continued and further complimented with experimental research to gain knowledge about other variables that could influence the interactions between the non-native and native fishes.

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Table 1: The 21 commercial species that account at least for 1% of the total Catch Per Unit of Effort (CPUE – kg fishing trip^{-1}) in at least one of the 8 years (1994-1996, 1999-2003) considered for this study. Taxonomical classification after Froese and Pauly (2006) and Nelson (2006).

Family	**Scientific name**	**Abbrev.**	**Total Catch (ton)**	**CPUE (kg fishing trip^{-1})**
Mugilidae	*Mugil incilis* Hancock 1830 [a]	Mug_in	900.9	15.1
Ariidae	*Cathorops mapale* Betancur-R. & Acero-P. 2005 [a]	Cat_9	537.0	5.7
Cichlidae	*Oreochromis niloticus* Linnaeus 1757	Ore_ni	235.8	15.6
Gerreidae	*Eugerres plumieri* Valenciennes 1830 [a]	Eug_pl	197.1	2.3
Ariidae	*Ariopsis bonillai* Miles 1945 [a]	Ari_bo	87.1	1.8
Scianidae	*Bairdiella ronchus* Cuvier 1830	Bar_ro	51.2	0.5
Elopidae	*Elops saurus* Linnaeus 1766 [a]	Elo_sa	39.1	0.8
Megalopidae	*Megalops atlanticus* Valenciennes 1846 [a]	Meg_at	38.0	1.9
Scianidae	*Micropogonias furnieri* Desmarest 1822	Mic_fu	31.8	0.5
Mugilidae	*Mugil liza* Valenciennes 1836	Mug_li	26.8	0.8
Prochilodontidae	*Prochilodus magdalenae* Steindachner 1879	Pro_ma	15.6	0.8
Engraulidae	*Anchovia clupeoides* Swainson 1839	Bna [b]	14.9	0.6
Engraulidae	*Cetengraulis edentulus* Cuvier 1829	Bna [b]	14.9	0.6
Cichlidae	*Caquetaia kraussi* Steindachner 1878	Caq_kr	10.6	0.6
Characidae	*Triportheus magdalenae* Steindachner 1878	Tri_ma	9.9	0.7
Centropomidae	*Centropomus undecimalis* Bloch 1792	Cen_un	9.9	0.2
Gerreidae	*Diapterus auratus* Ranzani 1840	MBl [b]	9.8	0.2
Gerreidae	*Diapterus rhombeus* Cuvier 1829	MBl [b]	9.8	0.2
Gerreidae	*Gerres cinereus* Walbaum 1792	MBl [b]	9.8	0.2
Erythrinidae	*Hoplias malabaricus* Bloch 1794	Hop_ma	6.5	0.8
Mugilidae	*Mugil curema* Valenciennes 1836	Mug_cu	3.8	0.2
Characidae	*Leporinus muyscorum* Steindachner 1900	Lep_mu	1.7	0.3
Characidae	*Astyanax fasciatus* Cuvier 1819	Vie [b]	1.2	0.2
Characidae	*Cyphocharax magdalenae* Steindachner 1878	Vie [b]	1.2	0.2
Characidae	*Hemibrycon* sp.	Vie [b]	1.2	0.2
Osphronemidae	*Trichogaster pectoralis* Regan 1910	Tri_pe	1.1	0.2

[a] The six (6) most abundant and commercially important native fish species
[b] Several species registered with the same code due to the difficulty for the fishermen to distinguish between species

Table 2: Forward stepwise multiple regression analysis with native fish abundances as dependent variables (Y) and the abundance of *O. niloticus* as independent variable (X). Only significant results reported ($p < 0.025$). N= 141. NS: not significant, NE: variable not in the equation, r= standardized regression coefficients.

	r			Multiple	Std. Error	p
Y	**ZB**	**ZD**	***Oreochromis niloticus***	**R^2**	**Estimate**	
Ariopsis bonillai	-0,61	-0,51	NS	0,41	0,43	0,000
Mugil incilis	NS	-0,15	NE	0,06	0,69	0,014
Elops saurus	-0,26	-0,39	NE	0,15	0,35	0,000
Cathorops mapale	-0,16	-0,51	-0,45	0,43	0,84	0,000
Eugerres plumieri	-0,46	-0,48	NE	0,29	0,66	0,000
Megalops atlanticus	NS	NS	0,19	0,60	0,45	0,027

Table 3: Forward stepwise multiple regression analysis with native and non-native fish abundances as dependent variables (Y) and Salinity (SAL), pH (units) and Dissolved Oxygen (DO - mg l^{-1}) as independent variables (X). Only significant results reported ($p < 0.025$). N= 136. NS: not significant, NE: variable not in the equation, r= standardized regression coefficients.

	r					Multiple	Std. Error	p
Y	**ZB**	**ZD**	**SAL**	**pH**	**DO**	**R^2**	**Estimate**	
Ariopsis bonillai	-0.56	-0.44	0.28	-0.50	NS	0.58	0.37	0.000
Mugil incilis	NS	NS	-0.32	NS	NE	0.12	0.68	0.002
Elops saurus	-0.22	-0.31	0.36	-0.44	0.19	0.30	0.33	0.000
Cathorops mapale	-0.27	-0.22	0.45	NS	NS	0.45	0.82	0.000
Eugerres plumieri	-0.50	-0.56	-0.35	0.32	NS	0.43	0.59	0.000
Megalops atlanticus	0.19	NE	NE	-0.51	NS	0.27	0.34	0.000
Oreochromis niloticus	0.17	-0.37	-0.43	-0.32	0.30	0.50	0.92	0.000

Table 4: Forward stepwise multiple regression analysis with native and non-native fish abundances as dependent variables (Y) and local Rainfall (mm) and River discharge (m^3 sec^{-1}) as independent variables (X). Only significant results reported ($p < 0.05$). N= 67. NS: not significant, NE: variable not in the equation, r= standardized regression coefficients.

	r		Multiple	Std. Error	p
Y	**Rainfall**	**River discharge**	**R^2**	**Estimate**	
Ariopsis bonillai	NE	NS	0.04	0.40	0.057
Mugil incilis	NE	NE	-------	-------	-------
Elops saurus	NE	-0.29	0.08	0.34	0.007
Cathorops mapale	NE	NE	-------	-------	-------
Eugerres plumieri	NS	0.39	0.15	0.57	0.001
Megalops atlanticus	NS	NE	0.01	0.61	0.290
Oreochromis niloticus	NS	NS	0.05	1.38	0.126

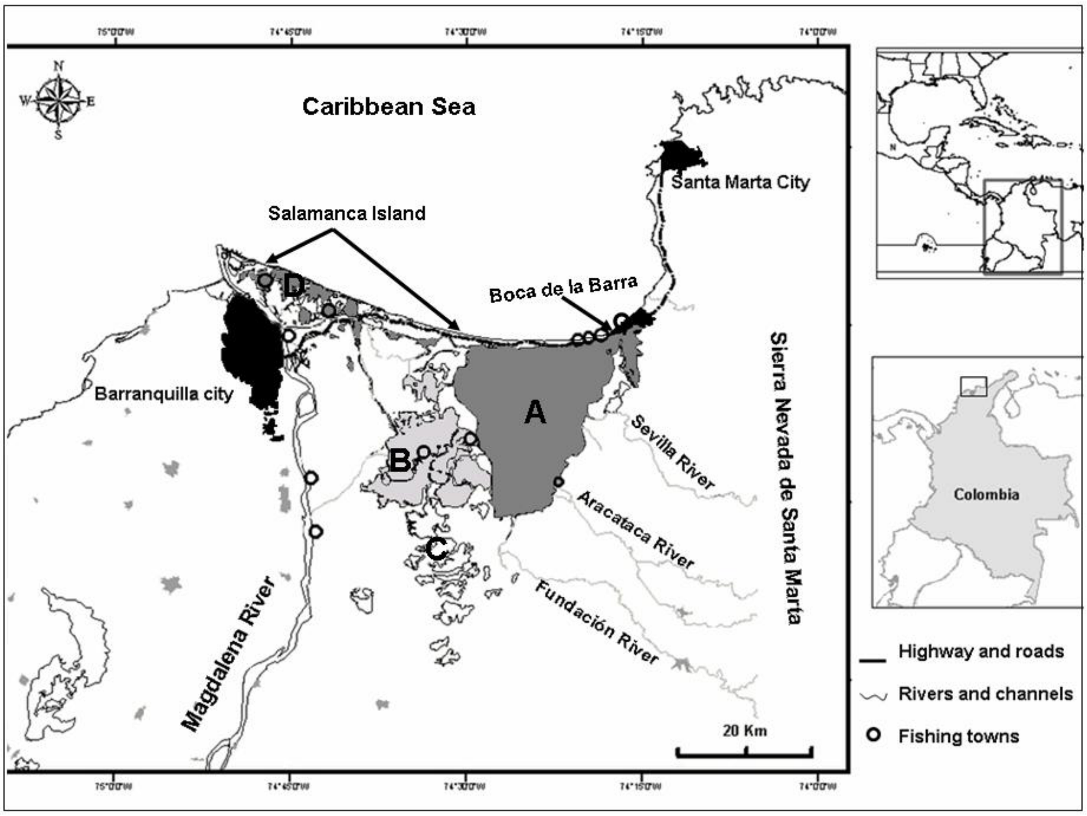

Figure1: Location of Ciénaga Grande de Santa Marta Estuary in the North Coast of Colombia. A, B, C and D are the study zones as explained in the text.

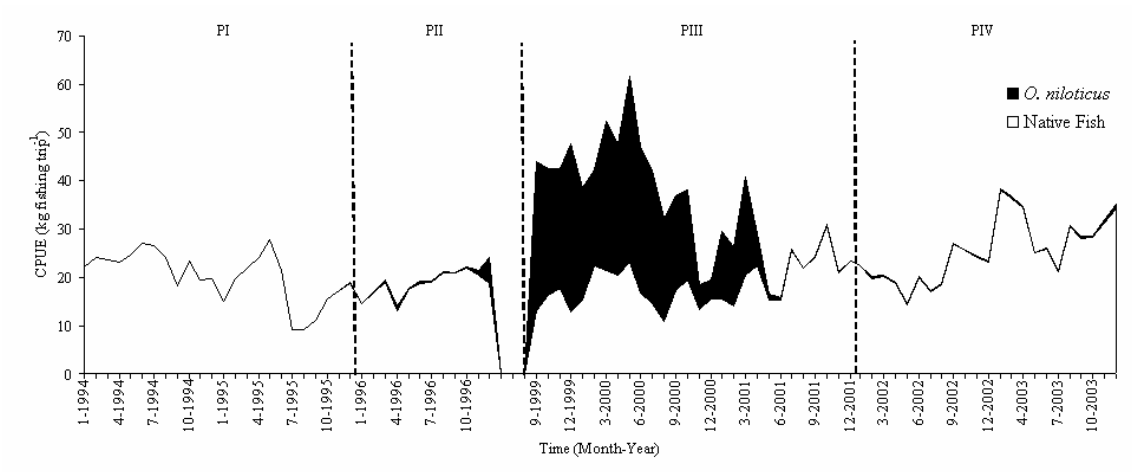

Figure 2: Changes in relative abundance – CPUE (kg fishing trip^{-1}) of non-native and native fishes during the time period of study in the whole estuary using cast net.

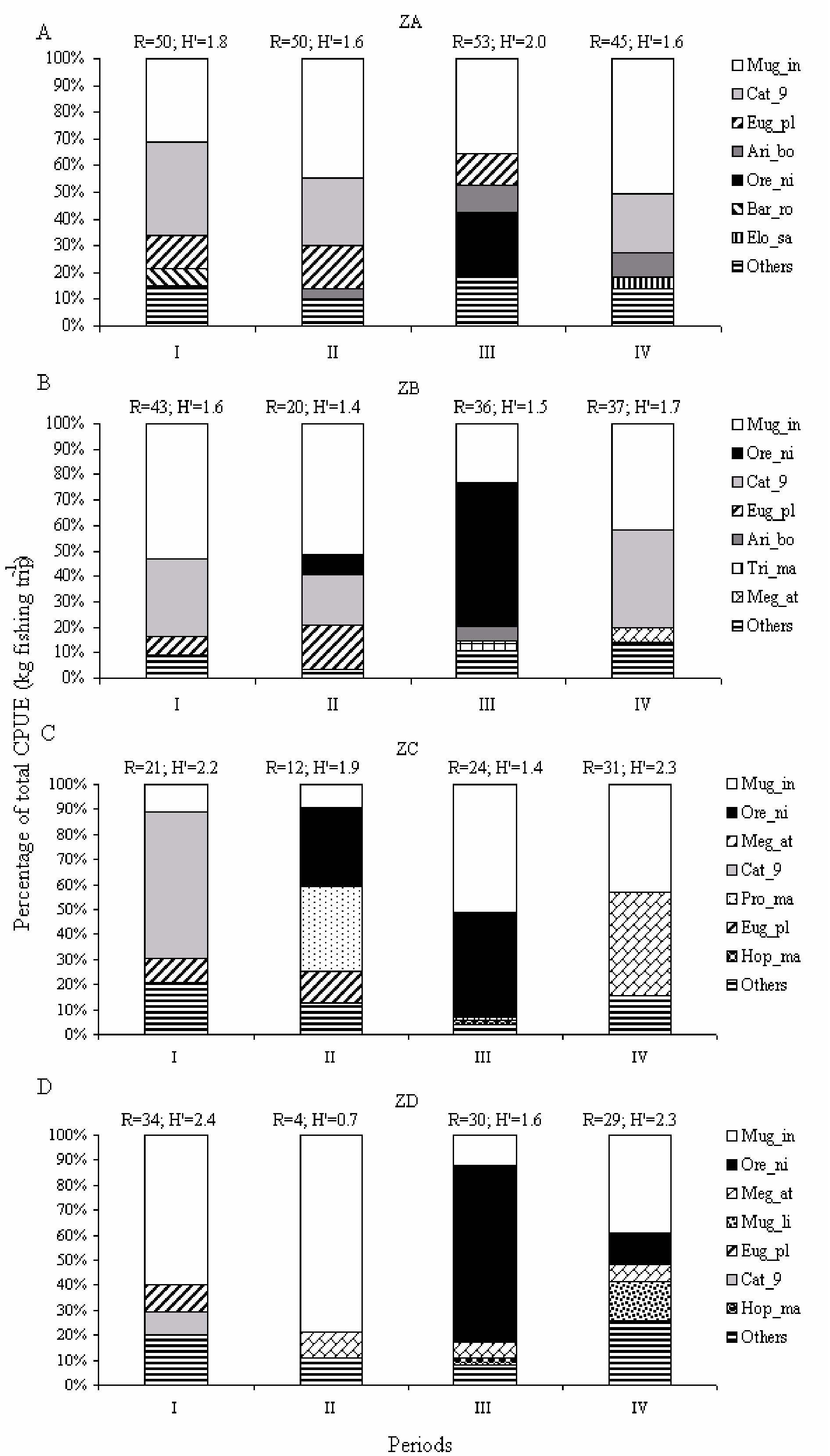

Figure 3: Changes in fish abundance, species composition, species richness (R) and fish diversity (H') in the four zones of CGSM (A, B, C, D) during the four different periods considered in this study (PI: 1994-1995; PII: 1996; PIII: 1999-2001; PIV: 2002-2003). See abbreviations of fish names in Table 1.

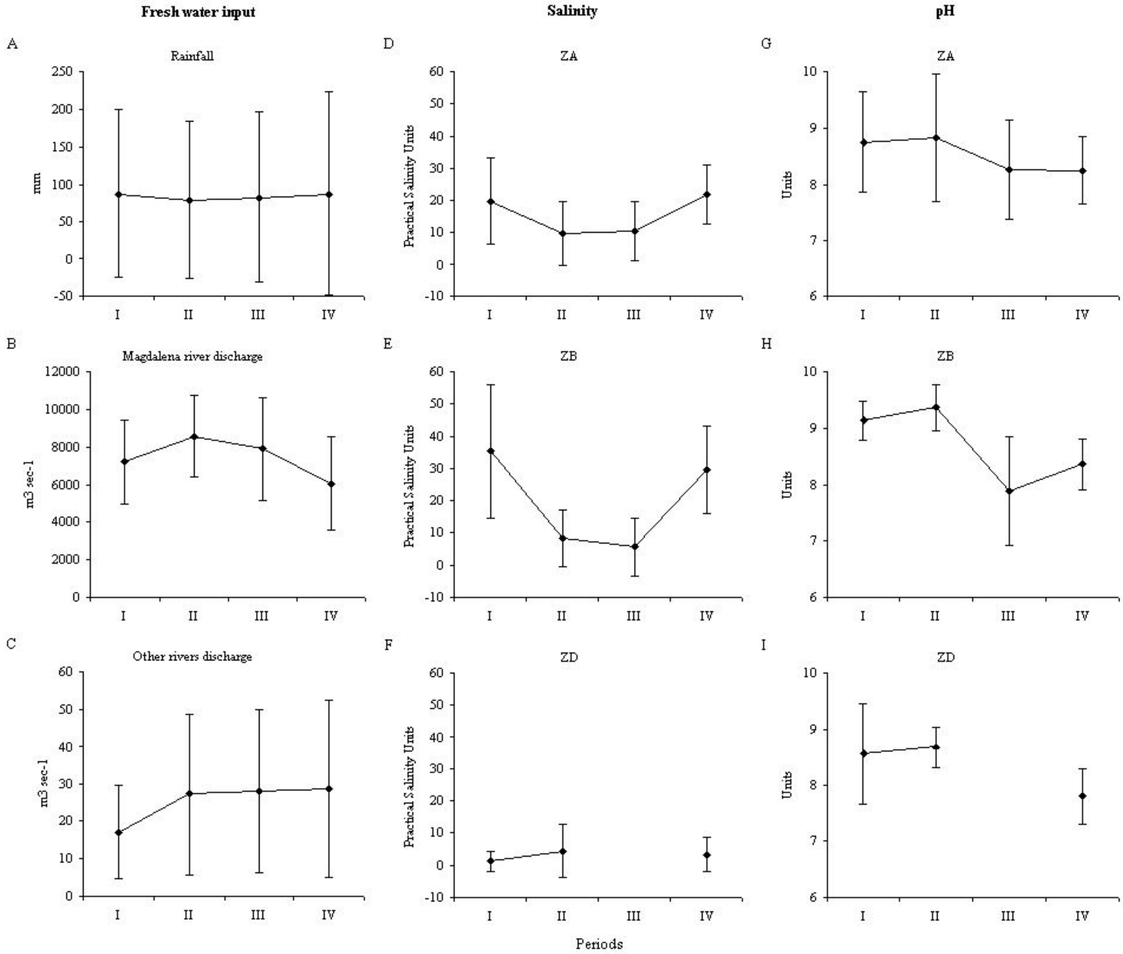

Figure 4: Variation in mean values (± standard deviation) of the main environmental parameters in CGSM during the four periods (PI: 1994-1995; PII: 1996; PIII: 1999-2001; PIV: 2002-2003) of study: (A-C) Fresh water input in the whole region; (D-F) Salinity and (G-I) pH in three of the zones of study (ZA, ZB, ZD). Zone C is not included due to lack of environmental data.

8. DOES NILE TILAPIA AFFECT THE FEEDING HABITS OF THE NATIVE ICHTHYOFAUNA OF A TROPICAL ESTUARY? - THE CASE OF THE CIENAGA GRANDE DE SANTA MARTA ESTUARY, COLOMBIA

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Does Nile tilapia affect the feeding habits of the native ichthyofauna of a tropical estuary? - The case of the Ciénaga Grande de Santa Marta estuary, Colombia

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ABSTRACT

The influence of the African Nile tilapia *Oreochromis niloticus* (Pisces: Cichlidae) on the feeding habits of the some of the most abundant and commercially used native fish species was studied in the Ciénaga Grande de Santa Marta estuary (CGSM), Northern Colombia. Most fishes fed on the most abundant prey types and changed their diet composition according to prey abundance, which responded mainly to salinity variations within the estuary. Three feeding strategies could be distinguished: generalists, specialists and mixed feeders, but a considerable degree of specialization was present in all diets, with a trend to increase in recent years. The highest diet overlap was found between *O. niloticus* and *Diapterus rhombeus*, most likely due to the high abundance of their common prey (cyanophytes and diatoms). The findings do not suggest the occurrence of competition for food between *O. niloticus* and native fishes. Instead, the changes in feeding habits of the native ichthyofauna seem to be caused by system–wide changes in prey abundance, responding to environmental variation.

Keywords: Nile tilapia; feeding habits; diet overlap; diet evenness; diet breadth; salinity

INTRODUCTION

Species introductions often result in negative impacts on the native populations and the entire ecosystem. Non-native piscivorous fishes are the ones that more often negatively impact aquatic ecosystems diminishing the native populations on which they prey upon and, in some cases bringing them to extinction (*e.g.* the non-native *Lates niloticus* L. in Lake Victoria – Africa; Ogutu-Ohwayo 1990, Moyle & Light 1996a). If resources are

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limited, non-native species that do not prey upon the native species but compete with them can also impact native populations, when the environmental conditions are favorable to the new species (Moyle & Light 1996a,b). In such a case, the successful establishment of non-native species and the survival of native ones can depend on their strategies to use resources and their capacity to respond to environmental variation, among other characteristics.

The sum of all environmental factors and resources that allow a species to establish a viable population in the ecosystem can be defined as its niche (Hutchinson 1957, Begon *et al.* 2006). Between sympatric species the larger the niche overlap, the greater the competition. If the shared resource is limited, this competition leads over time to either a differential resource use (resource partitioning – Schoener 1974) or the exclusion of the least fit species by the fitter one (Competitive Exclusion Principle - Gause 1934, Hardin 1960). If a high feeding niche overlap persists, it may indicate a high abundance and availability of the shared (and not limiting) resources (Tokeshi 1999). Although food is only one of the important niche factors (*e.g.* space, shelter, temperature, salinity) shaping the development of populations in an ecosystem, the fishes' feeding strategies can make the difference between success and failure when facing low food availability and presence of invaders that could potentially compete for the same food resources. Hence information regarding the feeding habits of a fish community and the diet overlap with new species can be of great importance to foresee possible negative effects caused by non-native species.

Estuaries are particularly rich ecosystems with a great variety of resources and conditions for the sustenance of important fisheries around the world (Blaber *et al.* 2000). These characteristics - and the fact that dense human populations often settle around estuaries - make them also vulnerable to species introductions (Ruiz *et al.* 1997). The estuarine lagoon system Ciénaga Grande de Santa Marta (CGSM) at the Caribbean coast of Colombia constitutes the main source of food and income for the regional fishery due to its great extension (ca. 1280 km^2) and productivity (Sánchez & Rueda 1999, Gocke *et al.* 2003). However it is also the estuary with the greatest impact of human activities in the country. The interruption of fresh and marine water inflows (due to natural events and human intervention), pollution, deforestation, erosion and over-fishing in CGSM has led to the loss of valuable resources during the last 50 years (Botero & Mancera 1996, Botero &

Salzwedel 1999). Aiming at a recovery of ecological conditions, former waterways were re-established by dredging in 1998 and thereafter the Asian snakeskin gourami (*Trichogaster pectoralis* Regan), the African Nile tilapia (*Oreochromis niloticus* L.), the hybrid red tilapia (*Oreochromis* sp.) and the transferred Amazonian tambaqui (*Colosoma macropomum* Cuvier) increased their occurrence in the system. After being first recorded in 1995, *O. niloticus* ranked among the principal fish resources, accounting for almost 60% of all catches in 1999 and 2000, while *T. pectoralis*, first recorded in 1989, has had a much lower occurrence and *C. macropomum* and *Oreochromis* sp. only sporadically appeared since 1999. Narváez *et al.* (2005) and Blanco *et al.* (2006, 2007) pointed to these non-native fish as potential disturbance factors in CGSM. Rueda (2001), Blanco *et al.* 2007 and Leal-Florez *et al.* (unpublished data) showed that the variation in the abundance of native and non-native fish in this estuary greatly correlated with the environmental fluctuation (e.g. salinity, pH, river discharge).

In the present study we aim to determine if the feeding habits of some of the most abundant native fishes have been influenced by the feeding habits of the non-native fish Nile tilapia, or if they are rather associated to the environmental variation in the CGSM ecosystem. The study is based on own survey data combined with those from published studies made in the region. Univariate indices were used to quantify diet composition, diet breadth and diet evenness for the non-native fish and the most abundant native fishes in different years before and after the introduction of *O. niloticus*. The diet overlap between Nile tilapia and native fishes was determined for recent years. The influence of the environmental variation on diet changes was assessed by the use of multiple regression analysis.

MATERIAL AND METHODS

STUDY AREA

The estuarine system Ciénaga Grande de Santa Marta is located between 10° 43’-11° 00’ N and 74° 16’-74° 35’ W in the delta of the Magdalena River, North Coast of Colombia (Fig. 1). Its major connection to the sea is Boca de la Barra, an 80-100 m wide artificial outlet (Santos-Martinez & Acero 1991). The system also receives freshwater from several rivers coming from the mountain system Sierra Nevada de Santa Marta. The mean annual water temperature is 30 °C and the water depth in the system can vary between 1 and 7 m. Salinity ranges from 0 to 40 PSU and the tidal amplitude from 20 to 30 cm (Polanía *et al.* 2001). The climate in the area is particularly dry (arid) with a mean air temperature of 28 °C which leads to a hydrological deficit between -211.6 and -1146.8 mm yr^{-1} as a result of the difference between mean rainfall and mean evaporation (Botero & Salzwedel 1999, Blanco *et al.* 2006).

The estuary has approximately 50000 ha of mangrove forests (*Avicennia germinans* L., *Rhizophora mangle* L., *Laguncularia racemosa* L. and *Conocarpus erectus* L.) and its waters are within the most productive in the tropics (0.073 - 1.25 mg C/l/h; Gocke *et al.* 2003). This is an ecologically rich system with about 195 species of birds, 122 of bony fish, 98 of mollusks, 46 of mammals, 40 of reptiles and 10 of amphibians among others (Polanía *et al.* 2001, Moreno & Alvarez 2003). At least 81 fish species are commercially exploited but catches are usually dominated by native estuarine species such as *Mugil incilis* (Hancock), *Cathorops mapale* (Betancur-R. & Acero-P.), *Eugerres plumieri* (Valenciennes), *Ariopsis bonillai* (Miles) and *Elops saurus* L. which are among the most abundant species (Sánchez & Rueda 1999, Rueda 2001). For a more comprehensive description of the CGSM see Botero & Salzwedel (1999).

DATA COLLECTION

Sampling

Ten sampling sites were chosen close to fresh water inlets in soft bottom areas of CGSM (Fig. 1). The fish were collected monthly (July-December 2003) using two cast nets of 12 and 10 m of diameter and mesh size of 3 and 5 cm, respectively. Each cast net was used 12 times in intervals of 5 min while the boat moved silently around a central point describing a circle. This methodology has been found to render the widest spectrum of fish sizes and species for this type of net in the estuary (Santos-Martinez 1989, Sánchez & Rueda 1999). Once caught, the fish were placed in labeled plastic bags and stored with ice until they died. Each fish was then injected with 4% formalin into the ventral cavities and placed again in ice until arrival in the lab where they were stored at a constant temperature of -

16°C. Salinity (Practical Salinity Units – PSU), pH and dissolved oxygen (mg l^{-1}) were measured in situ with a 320-330i/set WTW box, as well as depth (m) with a self-made plastic metric bar (3 m long) and transparency (m) with a Sechi disk. At each sampling site, 3 water samples of approximately 330 ml each were taken with a Niskin bottle at different depths (bottom, medium and surface). These samples were mixed into a labeled dark plastic bottle of 1 L for storage on ice and posterior measurement of seston (total suspended solids) and chlorophyll *a* concentration in the laboratory

Sample analysis

Water samples were processed following the standard methods for the examination of water and wastewater (APHA 1998) to determine the concentration of chlorophyll a (μg/l) and total suspended solids – seston (mg/l). After defrosting under room temperature, fishes were dried with a cloth, weighted to the nearest 0.1 g and their Standard and Total Length measured to the nearest 1 mm. The fish stomachs were extracted and then dried with absorbent paper. Their weights and volumes were measured to the nearest 0.1 g and 0.1 ml respectively. The stomachs were placed in 4 % formalin for 2 days to fix the contents and afterwards changed to 40% alcohol for storing until the contents could be extracted. After extraction of the contents, the empty stomachs were again dried with absorbent paper, and their weights and volumes were measured to the nearest 0.1 g and 0.1 ml respectively. Volume measurements were done by water displacement in sample tubes of 5 or 10 ml depending on the stomachs size. A preliminary exploration was always done in a dry Petri dish under a Stereo microscope to determine the most suitable procedure of analysis, according to the stomach content type, following Hyslop (1980), Prejs & Colomine (1981) and Marrero (1994). Only stomachs that were visually estimated to contain at least 20% of food were analyzed. The food items were identified to the lowest possible taxonomical level and their volumes estimated in percentage of the volume they covered in a Petri dish mounted on millimetric paper. When the contents were mostly composed by microscopic food items, their examination and volumetric measurement were also done using a Neubauer bright line hemacytometer. The number of units or individuals per food item was impossible to determine in most of the stomach contents due to their high level of digestion, therefore this parameter was not considered for analysis in this study.

DATA ANALYSIS

Diets composition of Nile tilapia and the native fishes

The diets of those species with at least five stomachs with food collected were analyzed. The native fishes that fulfilled this requirement were *M. incilis*, *Diapterus rhombeus* (Cuvier), *E. plumieri*, *A. bonillai, Triportheus magdalenae* (Steindachner) and *E. saurus* (Table 1). Information of diet composition, volumetric food abundance and frequency of occurrence of food categories for the native fishes and *O. niloticus* was collected from the studies of Osorio (1988), Castaño (1989), Santos-Martinez & Arboleda (1993) and INVEMAR (2001). These authors followed a similar methodology as that describe above. The compiled information (Table 1) was used to calculate different univariate indices to quantify the stomach contents and compare among different years before and after the introduction of *O. niloticus*. For the purpose of comparison, the food items from all fish diets (research works mentioned above and this study) were arranged into common food categories (Table 2). In some cases the lowest taxonomical levels had to merge with the higher ones to make the categories comparable among the different years. The importance of each food category in the diet of each fish species included in Table 1 was quantified using the Index of Relative Importance – IRI (a) as suggested by Yañez-Arancibia *et al.* (1976). This calculation includes the frequency of occurrence index (b) and the volumetric index (c) both expressed as percentage (Marrero 1994). The gravimetric index – same calculation as (c) but using weight and not volume – can also be used instead of the volumetric index in the calculation.

(a) IRI = (%F * %V) / 100

(b) %F = (Number of times that an item occurs in the stomachs of the species / Total number of stomachs analyzed for the species) * 100

(c) %V = (Sum of the volume of an item in all the stomachs where it occurs / Total volume of all food items measured in all stomachs of the species) * 100

Feeding strategies and diet variation

The Shannon-Weaver biodiversity index (H'; Shannon & Weaver 1949) was used as a diet (food niche) breadth measure (d), together with an Evennes Index (J'; Pielou 1975) (e). Large values in both indices indicate a tendency to generalized feeding and a wide niche, while small values indicate a tendency to specialization and a narrow niche (Oh *et al.* 2001).

(d) $H' = -\sum (p_{ij} * Ln.p_{ij})$,

where p_{ij} is the proportion (%V or %G) of the food item "i" in the diet of the specimen "j"

(e) $J' = H' / Ln\ S$,

where S is the number of food categories in the stomachs

Changes in the diets of the native fish species were described by comparing their diet compositions and feeding strategies from years before (1988/1989, 1993) and after (2001, 2003) the introduction of *O. niloticus* in CGSM.

Temporal variation in prey abundance and its relation to environmental variables

The Institute for Marine and Coastal Research (INVEMAR) provided data on catch per Unit of Effort (CPUE) that was used as a proxy for the monthly mean relative abundance of the prey from the periods 1994-1996 and 1999-2003. The term abundance shall be used throughout this study instead of CPUE. The data were used in groups: fishes, swimming crabs, oyster and shrimps. The prey consumed by the fishes in CGSM consists mostly of small species or individuals (Castaño 1989; this study). However the abundance of the commercial species, which are usually bigger, was used assuming that their environmental features and needs can be considered similar to those of the preys. Chlorophyll *a* and seston (suspended solids) concentrations were used as proxy for the monthly mean biomass of phytoplankton and detritus, respectively. Environmental data for the same periods of time were also provided by INVEMAR. Forward stepwise multiple regression analysis (Zar 1996) was performed to determine a set of environmental variables (independent variables) that could explain the variation of the main prey abundances (dependent variables). F>1 (α=0.05) was the statistical criterion to enter or remove variables from the equations. To avoid multiple co-linearity between independent variables (Salinity, Dissolved oxygen, pH, Transparency), only those with a tolerance greater than 0.5 were included in the analysis.

Diet Overlap between non-native and native species

The Schoener Index (Schoener 1968; here notated as O_v) was used to measure the diet overlap (f) between the native fishes and *O. niloticus* in 2001 and 2003.

(f) $O_v = 1 - 0.5 \sum |p_{ij} - p_{ik}|$,

where p_{ij} is the proportion (%V or %G) of the food item "i" in the diet of the species "j", and p_{ik} that of the species "k". 100 can be used instead of 1. A value greater than 0.6 (or 60) is considered to be indicative of potential inter-specific competition (Zaret & Rand 1971, Langton 1982, Fjosne & Gjosaeter 1996).

RESULTS

DIET COMPOSITION AND FEEDING STRATEGIES

A total of 127 stomachs were extracted but only 44 contained more than 20% of food (Table 1). Only *M. incilis* yielded sufficient numbers (24 stomachs), while *T. magdalenae* and *D. rhombeus* just yielded 6 stomachs with food to be analyzed. For the 12 fish diets analyzed (Table 1), a total of 25 food categories (Table 2) were defined combining the results in the present study with those studies already mentioned. Plant material, copepods, decapods, fishes, ostracods and detritus were the food categories most frequently found (Table 2) within the diets.

Most of the species had a wide food spectrum ranging from 2 to a maximum of 13 food items (Table 3). Diet breadth (H') ranged between 0.0 and 1.6, and evenness (J') values were throughout not greater than 0.8, suggesting a certain degree of specialization for all fish. Based on the values of these two indices (Table 3) and the diet composition (Fig. 2a-b), three main types of feeding strategies were identified: (1) a tendency to be generalist with high values in both indices and several food categories of similar importance (%IRI), (2) a tendency to be specialist with low values in both indices and the main food category with %IRI ≥ 70, and (3) a "mixed feeder" with medium to high values in both indices, showing a major tendency to be generalist but still with a considerable level of specialization regarding two to three food categories.

TEMPORAL VARIATION IN NATIVE FISH DIETS

Since no data were available on the diet composition of *T. magdalenae* before 2003, diet changes for this fish species could not be described. *Mugil incilis* was a mixed feeder with detritus, sediment and diatoms as main food categories in 1988 (Fig. 2a) while in 2003, although keeping the tendency to mixed feeding it specialized more on detritus (Fig. 2b). *Eugerres plumieri* changed from a more generalist diet based on bivalves, ostracods and decapods in 1989 (Fig. 2a) to a specialized one based on gastropods in 2001 (Fig. 2b). *Ariopsis bonillai* changed from a generalist feeding mainly on copepods, decapods and ostracods in 1989 (Fig. 2a) to a specialized feeding on fish in 2001 (Fig. 2b). *Diapterus rhombeus* shifted from being a specialized bivalve feeder in 1989 (Fig. 2a) to be a mixed feeder in 2003 (Fig. 2b) with detritus as main food category. *Elops saurus* behaved as a specialized fish feeder in both years analyzed (1993, 2001; Fig. 2a-b). *O. niloticus* seemed to be a mixed feeder with cyanophytes and diatoms as main food categories in 2001 (Fig. 2b). The two stomachs collected in 2003 content mainly plant material and in lesser extent detritus. *T. magdalenae* seemed to behave as mixed feeder in 2003 (Fig. 2b), feeding mainly on detritus and copepods.

TEMPORAL VARIATION IN PREY ABUNDANCE

The oyster *Crassostrea rizhophora* (Guilding), which has been historically the most abundant component of the group bivalves in CGSM, disappeared from the system after

1996 (Fig. 3a). Swimming crabs (Fig. 3b) increased in abundance from 1994-1996 to 1999-2000 but decrease thereafter. Shrimps (Fig. 3c) showed a considerable increase in 2000 but had a lower abundance than the group crabs in all other years. The overall abundance of fish (Fig. 3d) has been relatively constant during the years studied, but showed an important increment in 1999-2000 due to the increased abundance of non-native fishes in those years. The biomass of phytoplankton (chlorophyll a) and detritus (suspended solids) tended to increase with the salinity (Fig. 3e-g).

RELATION OF PREY ABUNDANCE WITH THE ENVIRONMENT

According to the multiple regression analysis (Table 4), salinity was the environmental variable that best explained ($p<0.05$) the variation in abundance of fish ($r=-0.43$) and the oyster ($r=0.46$) as well as the variation in biomass of phytoplankton ($r= 0.66$) and detritus ($r=0.78$). In contrast, the transparency explained best ($p<0.05$) the variation in abundance of shrimps ($r=-0.40$) and the variation of pH that of the crabs ($r=-0.54$).

DIET OVERLAP BETWEEN NON-NATIVE AND NATIVE FISH

None of the native fish diets overlapped with the diet of *O. niloticus* above 60 (Table 3), which according to Langton (1982) can be considered as a biologically significant threshold indicative of potential inter-specific competition. The largest diet overlap (Table 3) is that of *D. rhombeus* with *O. niloticus* ($O_v=39.1$) which can be considered as a moderate overlap value. The common preys in the diets of the native fishes and *O. niloticus* were cyanophytes and diatoms.

DISCUSSION

The diets of the native fishes and *O. niloticus* seem to change according to the prey abundance, and this seems to change with the observed environmental fluctuations (*e.g.* salinity) in the estuary. Most of the fishes include within their diets a great proportion of food categories from the lower levels of the trophic web. The moderate diet overlap between some native fishes and *O. niloticus* is most likely due to the high abundance and thereby the high availability of their shared preys.

In general, most of the native fishes seem to be more mixed feeders with a tendency to specialization that increased in the recent years (2001, 2003; Table 3, Fig. 2a-b). However, all fishes, including those with a specialist strategy, feed on highly abundant prey and mostly within the low trophic levels (Fig. 2a-b). All diet shifts observed over time responded to prey abundance changes (Fig. 2a-b, 3) which were mostly related to the salinity conditions in the estuary (Table 4). The shift in the diets of gerreid fishes *E. plumieri* and *D. rhombeus* are within the feeding habits described for the family (Carpenter 2002) and can be explained by the disappearance of the oyster (Fig. 3a) after 1999. This species used to form big banks providing substrate to many other species of smaller bivalves (J. Blanco, INVEMAR, pers. comm.). The reason for its disappearance in the estuary has not been studied, but it seems to be related to overfishing, river discharge and salinity changes. The mugilids are recognized as detritivore fishes (Gerking 1994, Carpenter 2002), therefore the changes in the diet of *M. incilis* in CGSM (Fig 2 a-b) are within the expected food spectrum of this family. The variation in fish abundance, with a peak in 1999-2000, could explain the high fish abundance in the stomachs of *A. bonillai* in 2001. This fish is known to be carnivorous feeding mainly on decapods and fishes (Carpenter 2002). Such plasticity in the diet spectrum allows the native fishes to adapt to the changing environmental conditions (Gerking 1994).

Oreochromis niloticus has a wide food spectrum during its life cycle that covers plankton, copepods and other small crustaceans, insect larvae, plant material and detritus (Trewavas 1983, Beveridge & Baird 2000, Peterson *et al.* 2006). In the CGSM, *O. niloticus* seems also to exploit the most abundant food resources in the estuary: detritus, vegetal material and phytoplankton (Fig. 2 b). Similarly, Gutiérrez (2004) found that Nile tilapia feeds mainly on cyanophytes, bacillariophytes and chlorophytes in the River Sinú, northern Colombia. Additionally, in the same study, a very small diet overlap with the native fish *Prochilodus magdalenae* was found. Feeding on the base of the food web gives *O. niloticus* the advantage of having a very “cheap” (in terms of energy paid for it) and almost unlimited food resource (Peterson *et al.* 2006). Thus, it appears that the moderate diet overlap observed between the native fishes and this species in CGSM is rather a sign of the great abundance and availability of their common preys than an indication of possible competition for food. However, this opportunistic feeding of *O. niloticus* is responsible of decreasing the abundance of zooplankton and large phytoplankton components thus promoting cascade effects in the trophic webs of tropical reservoirs in Brazil (Figueredo & Giani 2005, Okun et al. 2007). This suggests the possibility of future negative impacts on the trophic structure within the estuary if favorable conditions are found for the proliferation of this alien fish.

The findings in this study suggest that as long as the non-native fish *O. niloticus* maintains its feeding habits, the competition for food between this species and the native fish shall be rather low due to the high prey abundance in the estuary. The observed changes in the diets of the native ichthyofauna were rather caused by system–wide changes in prey abundance due to environmental variation than by the proliferation of the non-native fish. However Nile tilapia has proven to greatly impact faunal assemblages of other tropical aquatic systems due to its high adaptability and territorial behavior (Trewavas 1983, Ogutu-Ohwayo 1990, Ogutu-Ohwayo & Hecky 1991, McKaye *et al.* 1995, Turner & Robinson 2000, Canonico *et al.* 2005, McCrary *et al.* 2007). Thus the possibility of competition for other resources (*e.g.* spawning grounds, shelter) between *O. niloticus* and the native icthyofauna should not be excluded if there is a substantial and sustained biomass increase of this non-native fish within the estuary.

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Table 1: Fish species of which data was collected in this and former studies in the CGSM. Information on fish size and stomachs analyzed is included. L_S: Standard length, S_F: Number of stomachs with at least 20% of food, S_E: Number of empty stomachs, S_T: Total number of stomachs, F: Frequency of Occurrence (%), V: Volumetric food abundance (%), G: Gravimetric food abundance (%), IRI: Index of Relative Importance, NA: Information not available in the source.

Family	Fish species	Year	L_S (cm)		S_F	S_E	S_T	Source	Used info
			Min.	Max.					
Ariidae	*Cathorops mapale*	1989	4	34.7	37	23	60	Castaño 1989	F, V
		2003	11	16.8	2	20	22	This study	F, V
	Ariopsis bonillai	1989	3.6	27.3	25	35	60	Castaño 1989	F, V
		2001	10.0*	30.0*	57	27	84	INVEMAR 2001	F, V
		2003	6..9	26.2	0	18	18	This study	F, V
Characidae	*Triportheus magdalenae*	2003	14.4	17.2	6	7	13	This study	F, V
Cichlidae	*Caquetaia kraussii*	2003	8.2	13.5	2	8	10	This study	F, V
	Oreochromis niloticus	2001	18.0*	23.0*	9	3	12	INVEMAR 2001	F, V
		2003	11.6	11.9	2	0	2	This study	F, V
Elopidae	*Elops saurus*	1993	22.3*	83.0*	449	383	832	Santos-Martinez 1993	F, G
		2001	14.5*	32.0*	42	35	77	INVEMAR 2001	F, V
		2003	24.1	31.6	0	6	6	This study	F, V
Gerreidae	*Diapterus rhombeus*	1989	5.8	12.5	13	22	35	Castaño 1989	F, V
		2003	8.2	9.5	6	0	6	This study	F, V
	Eugerres plumieri	1989	2.5	24.6	76	120	196	Castaño 1989	F, V
		2001	12.0*	29.0*	11	23	34	INVEMAR 2001	F, V
		2003	8.2	16	0	3	3	This study	F, V
Megalopidae	*Megalops atlanticus*	1989	9.2	55.6	27	80	107	Castaño 1989	F, V
		2003	19.8	23.6	0	3	3	This study	F, V
Mugilidae	*Mugil incilis*	1988	24.0*	34.0*	NA	NA	**	Osorio 1988	IRI
		2003	11.8	27.3	24	16	40	This study	F, V
	Mugil liza	1988	40.0*	60.0*	NA	NA	**	Osorio 1988	IRI
		2003	30	33.7	2	2	4	This study	F, V

* Total length used instead of standard length
** A total of 300 stomachs analyzed of *M. incilis, M. curema* and *M. liza* all together

Table 2: Food categories used to describe the diet composition of the native and non-native fishes arrived at after combing the results of this study with those included in Table 1. A total of 12 fish diets were analyzed.

Food category	**Code**	**Number of diets with the food category**
Plant material	Veg	7
Copepoda (Crustaceans)	Cop	6
Decapods (Crustaceans: Shrimps, Crabs)	Decap	6
Detritus (unidentified organic material)	Detr	6
Teleost fishes	Fish	6
Ostracoda (Crustaceans)	Ostr	6
Cyanophyta (Protists - blue green algae)	Cyan	4
Diatoms (Protist)	Dia	4
Foraminifera (Protists)	For	4
Gastropoda (Mollusks - snails)	Gastr	4
Insects (Arthropoda)	Ins	4
Sediment	Sed	4
Bivalves (Mollusks)	Bival	3
Cladocera (Crustaceans)	Clad	3
Pieces of unidentified crustaceans	Un_Crust	3
Chlorophyta (Protists - green algae)	Chlo	2
Cirripeda (Crustaceans)	Cirr	2
Copepod eggs (Crustaceans)	Copeg	2
Polychaetes (Annelida)	Poly	2
Amphipoda (Crustaceans)	Amph	1
Insect larvae (Arthropoda)	Inslarv	1
Nematoda	Nem	1
Unidentified material	UM	1
Rotifers	Rot	1
Rotifer eggs	Roteg	1

Table 3: Diet richness (S), diet evenness (J') and diet breadth (H') for native and non-native fish in periods before (1988, 1989, 1993) and after (2001, 2003) the introduction of *O. niloticus* in CGSM. Diet overlap (O_v) between the native fish and *O. niloticus* is included.

Family	**Fish species**	**Year**	**S**	**J'**	**H' ($\log_e$)**	**Ov *O. niloticus* 2001**
Ariidae	*Ariopsis bonillai*	1989	9	0,7	1,6	-----
		2001	4	0,1	0,2	0,0
Characidae	*Triportheus magdalenae*	2003	11	0,4	1,1	29,5
Cichlidae	*Oreochromis niloticus*	2001	3	0,7	0,7	-----
Elopidae	*Elops saurus*	1993	4	0,2	0,3	-----
		2001	2	0,4	0,3	0,0
Gerreidae	*Diapterus rhombeus*	1989	8	0,3	0,7	-----
		2003	10	0,5	1,2	39,1
	Eugerres plumieri	1989	11	0,6	1,6	-----
		2001	2	0,0	0,0	0,0
Mugilidae	*Mugil incilis*	1988	5	0,8	1,2	-----
		2003	13	0,4	1,1	35,5

Table 4: Results of the forward stepwise multiple regression analysis using the regional monthly mean of the CPUE (Catch per Unit Effort) as dependent variables for each of the most frequently found preys and the monthly mean of the environmental parameters as independent variables. r: standardized regression coefficient; SAL: salinity; DO: Dissolved Oxygen (mg l^{-1}); TRA: transparency=Sechi disk depth (m). N=62

	r				**Multiple**	**Std. Error**	**p**
Y	**SAL**	**pH**	**DO**	**TRA**	**R^2**	**Estimate**	
Fish	-0.43	NE	0.33	NE	0.34	0.23	0.00001
Shrimps	NE	NE	NS	-0.40	0.20	0.56	0.00153
Crabs	NE	-0.54	NE	0.20	0.30	0.36	0.00003
Oyster	0.46	0.32	-0.35	0.40	0.58	2.17	0.00000
Phytoplankton (Chl a)	0.66	0.32	NS	0.44	0.49	1.12	0.00000
Detritus (Suspended Solids)	0.78	NE	0.25	-0.19	0.85	0.25	0.00000

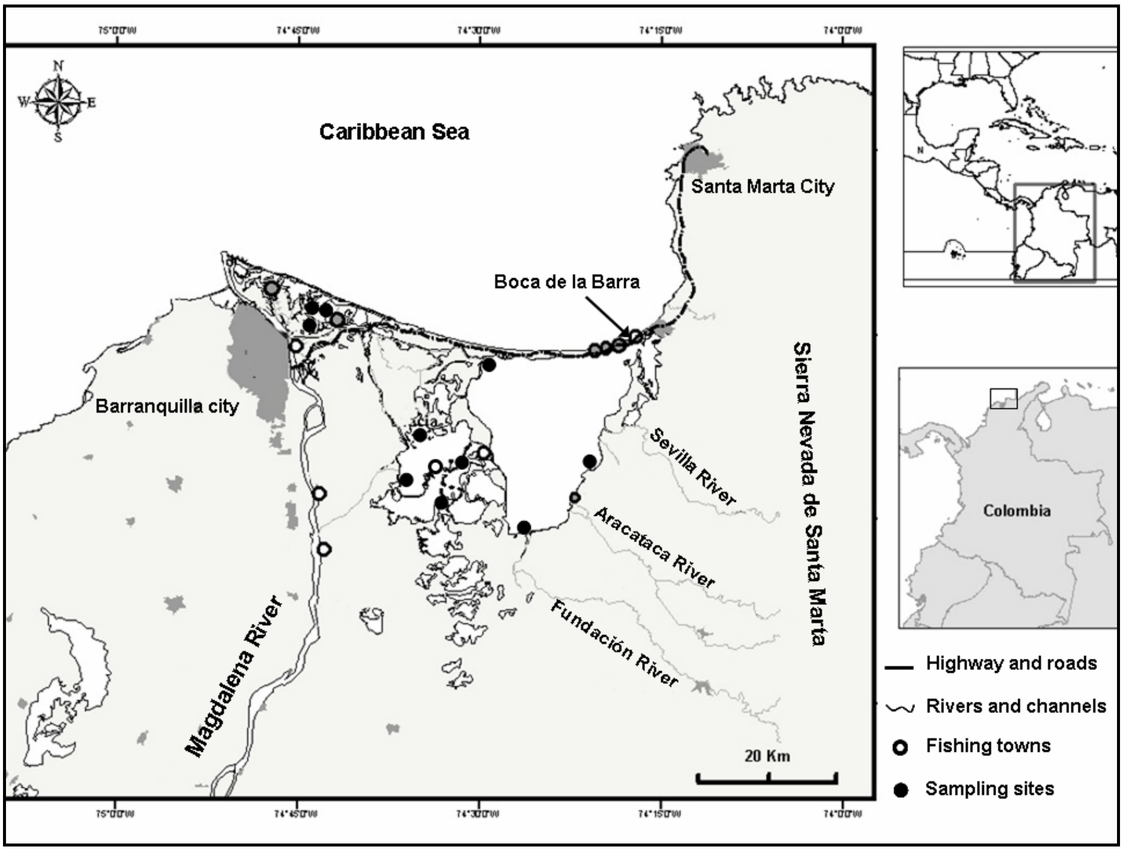

Fig. 1: Location of the estuarine ecosystem Ciénaga Grande de Santa Martha, northern Colombia, indicating its main features and the sites sampled in this study.

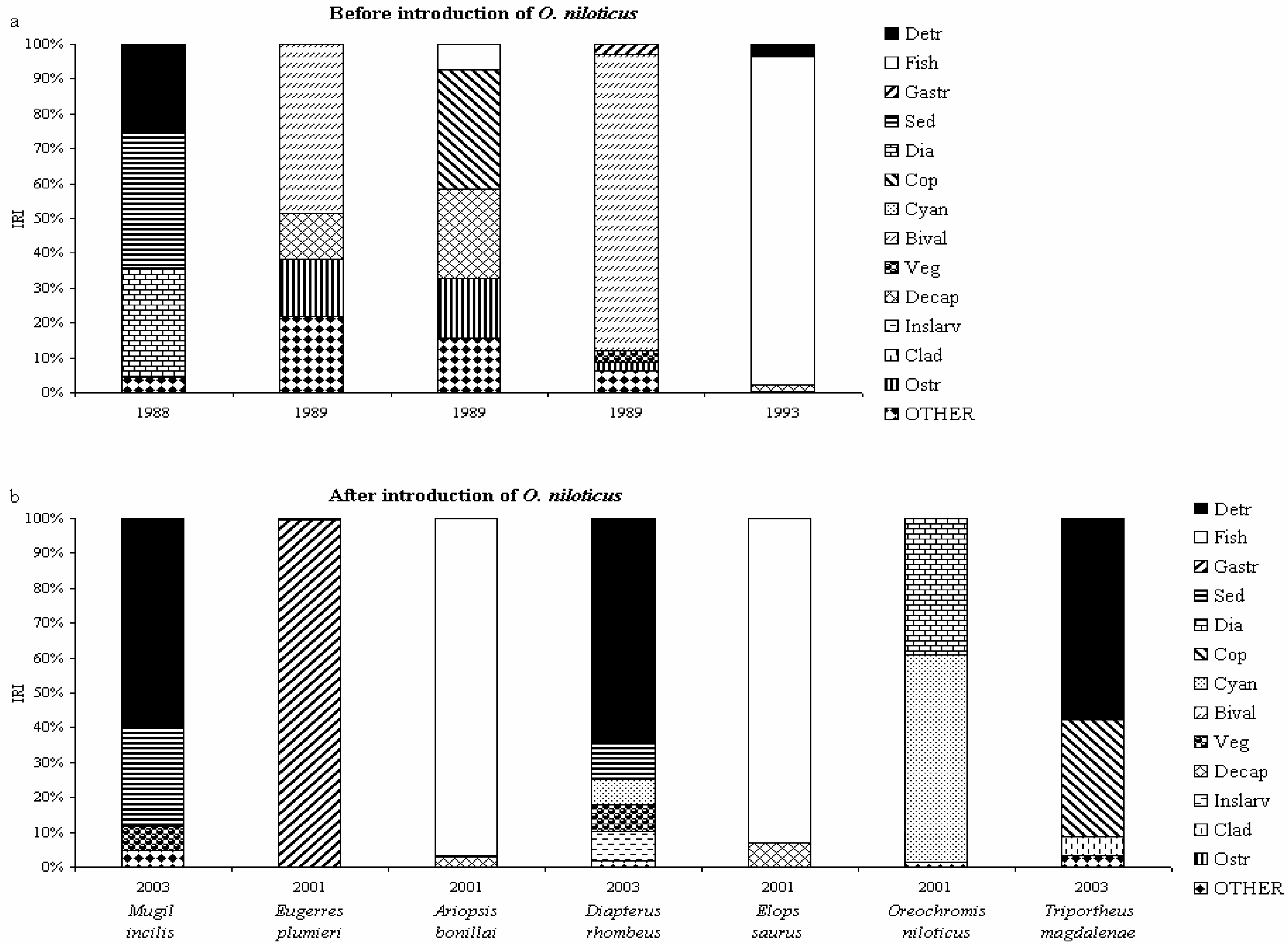

Fig. 2 (a, b): Diet composition of the most abundant native fish before (a) and after (b) the introduction of the non-native fish *O. niloticus*. The diet of the non-native fish is included in (b). The importance of the prey is quantified by the index of relative importance (IRI). See explanation of food categories in Table 2.

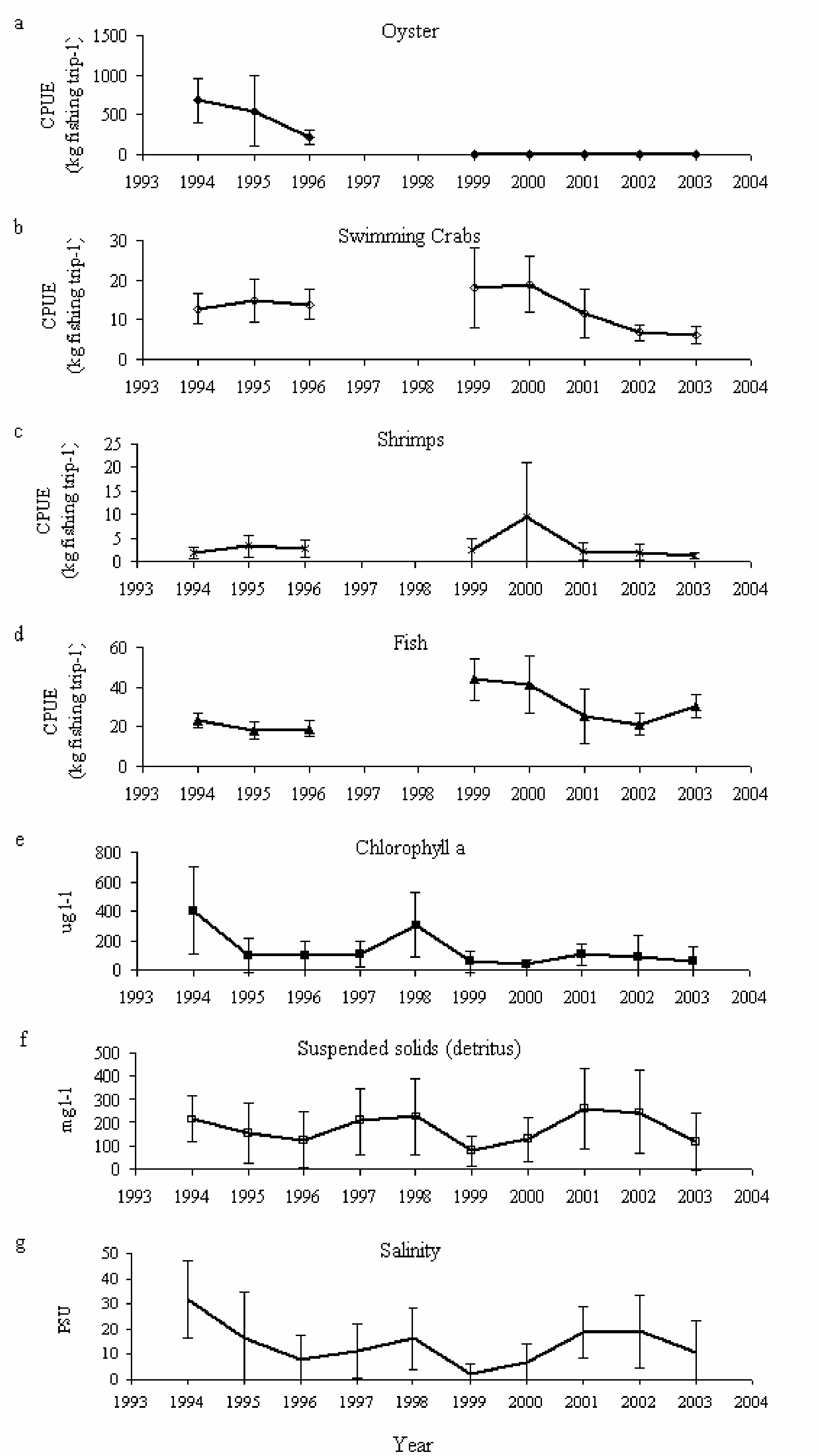

Fig. 3 (a-g): Temporal variation of the abundance of some representative preys in CGSM, using CPUE (kg/fishing trip) data of (a) the diving method for the oyster, (b) the circular trap ("aro") for the swimming crabs, (c) the midwater trawl ("releo") for shrimps, (d) cast net for the fishes as proxy for animal prey, (e) Chlorophyll a concentration as proxy for phytoplankton and (f) suspended solids as a proxy for detritus. Temporal variation of (g) Salinity (PSU) is also included for comparison. Bars represent standard deviations.

9. HAS THE ACCIDENTAL INTRODUCTION OF NILE TILAPIA ECONOMICALLY BENEFITED THE FISHERY OF THE CARIBBEAN ESTUARY CIENAGA GRANDE DE SANTA MARTA – COLOMBIA?

Manuscript submitted to the journal “Wetlands Ecology and Management”

Has the accidental introduction of Nile tilapia economically benefited the fishery of the Caribbean estuary Ciénaga Grande de Santa Marta – Colombia?

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ABSTRACT

The economic revenue derived from the fishery of native fishes and Nile tilapia was determined at two landing sites of a Caribbean estuary to find out if the non-native fish had economically benefited the fishermen in the short and long term. Gross income was used as a measure of economic revenue. In addition, a questionnaire-based survey was carried out at several landing sites to determine the fishermen's preferences for native and non-native fishes. Changes in gross income before and after the introduction of Nile tilapia were descriptively analyzed. To assess whether the Nile tilapia fishery or salinity influenced the changes in revenues derived from the native fish fishery, a multiple regression analysis was undertaken. During the period of lowest salinities in the estuary, the overall economic revenue from the fishery of Nile tilapia was two to six times larger than that of the whole fishery based on native fishes. This period coincided with a low abundance of the most valued native fishes. However, the economic revenues from the fishery of most fishes studied (including Nile tilapia) mainly responded to variations in salinity, and are greatly influenced by the differences between market structures. Although fishermen prefer native estuarine fishes due to their better price and taste, they changed to the Nile tilapia in the period when its relative abundance greatly increased. While Nile tilapia seems to be a profitable resource only during rather short intervals, the native fish *Mugil incilis*, better adapted to the environmental variation and higher salinities, appears as a better alternative for the fishermen in the long term.

Keywords: Economic revenue, estuary, non-native fish, native fish, Nile tilapia

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INTRODUCTION

Species introductions can become biological invasions that may eventually lead to alterations in the structure and function of ecosystems and the loss of valuable natural resources (Mack et al. 2000, Mooney and Cleland 2001, Hoffmeister et al. 2005). Therefore, they can negatively impact the human populations that depend on those resources for their livelihoods. For example in the African Great Lakes, the North American Great Lakes and the South American Lake Titicaca, the introduction of non-native species has caused the collapse of the fishery based on native species (Ogutu-Ohwayo and Hecky 1991, Villwock 1994, Ogutu-Ohwayo et al. 1997, Hall and Mills 2000). However, in some cases, where native resources have been depleted, species introductions may favor human populations with the provision of an alternative income (Hall and Mills 2000). In such cases it remains unclear whether these benefits would be sustainable in the long term. The well known case of the African Lake Victoria shows that short term economic benefits from the fishery of the non-native Nile perch *Lates niloticus* and the Nile tilapia *Orechromis niloticus* had, unforeseen, long term impacts like the disappearance of most of the native fish stocks with negative consequences for the livelihood of the villagers (Ogutu-Ohwayo 1990, Kaufman 1992, Goudswaard et al. 2002).

The estuary Ciénaga Grande de Santa Marta (CGSM), in Colombia, is one of the largest estuaries of the Caribbean Sea. This coastal lagoon system is the main source of food and income for the region due to its great extension (ca. 1280 km^2) and productivity (Sánchez and Rueda 1999, Gocke et al. 2003). Interruption of fresh and marine water inflows, pollution, deforestation, erosion and over-fishing in CGSM have led to the loss of valuable resources during the last 40 years (Botero and Mancera 1996, Botero and Salzwedel 1999, Rueda and Defeo 2003). This environmental degradation has greatly affected the communities whose livelihoods depend on the natural resources provided by the estuarine ecosystem. The need for sustenance of an impoverished human population has imposed a great pressure on the fishery of the region. As a result, the most commercial native fish stocks have been depleted over the last decade (Moscarella and Pinilla 1998, INVEMAR 2006). With the aim to recover the ecological conditions and therefore the economic profitability of the CGSM, former waterways were re-established by dredging in 1996-1998. Thereafter non-native fishes like the snakeskin gourami (*Trichogaster pectoralis*

Regan 1910), the Nile tilapia (*Oreochromis niloticus* Linnaeus 1757), the hybrid red tilapia (*Oreochromis* sp.) and the tambaqui (*Colosoma macropomum* Cuvier 1818) increased their occurrence in the system (Sanchez 1996, Bateman 1998). Only the fast growing and highly adaptive Nile tilapia became abundant enough to acquire an economic importance within the fishery. Since 1999, *O. niloticus* ranks among the principal fish resources, accounting for almost 60% of all catches in 1999-2000, but dramatically decreasing since 2001 (Blanco et al. 2007). These fluctuations seem to be related to salinity changes, which appear to be the main factor influencing the distribution and abundance of native (Sanchez and Rueda 1999, Rueda 2001, Blanco et al. 2006) and non-native fish in the CGSM (Blanco et al. 2007, Leal-Flórez et al. unpublished data). Our study aims to evaluate to what extend *O. niloticus* economically benefited the fishermen in the short and long terms, and to determine their preferences for tilapia versus native fish. We used the fishermen's gross income as an indicator of economic revenue obtained from fishing native and non-native fishes, and conducted a questionnaire-based survey to establish the preferences of the fishermen.

MATERIALS AND METHODS

STUDY AREA

The estuarine system Ciénaga Grande de Santa Marta is located between 10° 43'-11° 00' N and 74° 16'-74° 35' W in the Magdalena River's delta, North Coast of Colombia (Fig 1). Its major connection to the sea is Boca de la Barra, an 80-100 m wide artificial outlet (Santos-Martinez and Acero 1991). The system also receives freshwater from several rivers coming from the mountain system Sierra Nevada de Santa Marta. The climate in the area is particularly dry (arid) with a mean air temperature of 28 °C (Botero and Salzwedel 1999, Blanco et al. 2006).

Fish is the most important protein source for the coastal villagers. The fishery in the system is mainly artisanal with about 4000 active fishermen and 30000 people depending on the estuary for their livelihood (Sánchez and Rueda 1999, Blanco et al. 2007). Fishermen respond to the different spatio-temporal abundances of the resources by using diverse fishing gears like cast nets, gill nets, encircling gill nets, seine nets and lines among others

(Gallo 1988, Rueda and Santos-Martinez 1997, Rueda 2001, Blanco et al. 2007). At least 81 fish species are commercially exploited in CGSM with native species historically dominating catches. The most important native fishes include estuarine species such as the Parassi mullet *Mugil incilis* Hancock, the catfish *Cathorops mapale* Betancur-R. and Acero-P., the striped mojarra *Eugerres plumieri* Valenciennes, the New Granada sea catfish *Hexanemathichthys bonillai* Miles, the liza *Mugil liza* Valenciannes and the Tarpon *Megalops atlanticus* Valenciannes (Gallo 1988, Rueda and Santos-Martinez 1997, Sánchez and Rueda 1999, Rueda 2001). For a more comprehensive description of the ecosystem see Botero and Salzwedel (1999).

DATA COLLECTION

The fishery data used for this study have been collected by villagers trained by the Institute for Marine and Coastal Research – Santa Marta, Colombia (INVEMAR) from 1994 to 2003 within the framework of an ecosystem monitoring program. The monthly compiled information includes catch (kg), species composition, effort (number of fishing trips), gear types, prices (USD) and landing sites. Additionally, environmental data (e.g. salinity) from monthly surveys have been provided by the same institute.

Since the cast net is the most widely and constantly used fishing gear in the CGSM (Blanco et al. 2007), only fishery data related to this fishing gear was used in this study. A cast net fishing economic unit consists of two fishermen, a canoe, paddles and/or a sail, a thick long wood stick to be used as a lever, a storage box filled with ice and several cast nets of different mesh sizes and dimensions. A fishing trip lasts normally around 6 hours and it is usually made only once per day (Blanco et al. 2006, 2007). Catch per Unit Effort – CPUE (kg/fishing trip) was used as a measure of relative abundance for each fish species studied. Two landing sites were chosen due to their importance for the regional fishing trade and the availability of monthly data on prices and CPUE: Nueva Venecia (NV) and Tasajera (T). The first is a stilt village located in the Pajarales Lagoon Complex, an area with largely variable salinity where the greatest catches of Nile tilapia have been registered. The second is located on the northeastern bank of the main lagoon (Fig 1), a mostly estuarine zone, where the catches of Nile tilapia have been consistently lower.

DATA ANALYSIS

In order to take in consideration the presence/absence of the non-native fish *Oreochromis niloticus*, all data was divided into four periods (P) according to the abundance of this species: PI = 1994-1995 (few or no *O. niloticus* in catches; high salinities – 25.3±18 PSU); PII = 1996 (*O. niloticus* present but occurring in less than 5% of the total catches; low salinities – 9.2±9.6 PSU); PIII = 1999-2001 (after reestablishment of fresh water and salt water connections and marked *O. niloticus* increase; lowest salinities – 8.1±9.5 PSU); and PIV = 2002-2003 (subsequent *O. niloticus* decrease; salinities increasing – 18.5±13.7 PSU).

Fishermen's Preferences

A questionnaire-based survey consisting of open-ended questions (Table 1) was conducted between October and November 2003 at 5 landing sites with the help of trained villagers. The most commercially important and abundant native fish species to be included in posterior analyses were selected based on the results of the survey and the information available on prices and relative abundances (CPUE) for the region.

Comparison of Economic Revenue

Due to the lack of data of operational costs for the fishery between 1994 and 1999, the net income could not be calculated for all periods. Therefore this parameter was not used in this study; instead we used the gross income as a measurement of economic revenue. Monthly prices for all species of interest were converted to real prices using the consumer price index for the city of Barranquilla, the nearest big commercial center in the region. The economic revenue (a) derived from each species was calculated per month and year.

(a) Economic revenue (USD /fishing trip.) = Real price (USD/kg) * CPUE (kg/fishing trip)

To detect the general trends, a first comparison of the mean economic revenue was done for the whole fishery of *O. niloticus* and native fishes at both landing sites for the four periods. After that a more detailed comparison of economic revenues at the species level was carried out. A multiple regression analysis (MRA) was done per landing site to determine if the variation of economic revenue derived from the native species could be attributed to the variation of economic revenue from the non-native fish or to the variation of salinity or to both. The monthly economic revenue given by each native species was considered as the dependent variable. The economic revenue from *O. niloticus* and the environmental variable salinity were considered the independent variables. All data were Log+1 transformed to reach normality of the residuals.

RESULTS

FISHERMEN'S PREFERENCES

A total of 158 surveys were conducted. In general, 55% of all respondents were between 36 and 55 years of age, and 63% have between 21 and 40 years of fishing experience. For 59% and 10% of all respondents, the most valued fishes in economic terms in the period before *O. niloticus* first appeared in the catches were the estuarine fishes *Centropomus undecimalis* and *Eugerres plumieri*. The fresh water fish *Prochilodus magdalenae* was the most valuable for 17%. Other fishes like *Megalops atlanticus*, *Hexanematichthys bonillai, Mugil liza, Mugil incilis* among others were also valuable for 14% of the respondents. In the period of highest abundance of the Nile tilapia, 54% of all respondents considered *P. magdalenae* the most economically valued fish, 8% *O. niloticus*, 8% *C. undecimalis* and 2.5% *E. plumieri*. Other fishes like *M. atlanticus*, *H. bonillai, M. liza,* and *M. incilis* were mentioned by 5% of the respondents while 23% of them did not answer this question. The native estuarine fishes *C. undecimalis, E. plumieri, M. incilis, M. atlanticus* and *Cathorops mapale* were considered the most wanted fishes for fishing in the region in all periods respectively by 30%, 18%, 13%, 7% and 4% of all respondents. The native fresh water fish *P. magdalenae* and the non-native *O. niloticus* were the most wanted fishes for 14% and 4%, respectively. The reason to prefer a fish for fishing was the taste for 35% of all respondents, the high commercial value for 12% and the high abundance for 11%. A large number of respondents (38%) did not answer this question.

COMPARISON OF ECONOMIC REVENUE

During period III, the mean economic revenue obtained from the fishery of *O. niloticus* was almost 6 times greater than the revenue from the eight most commercially used native fishes together in Nueva Venecia (Fig 2a) and more than twice in Tasajera (Fig 2b). In contrast, in all other 3 periods, at both landing sites, the mean economic revenue from native species was higher than that from the non-native fishes. Additionally, the revenue in those periods is much lower than in period III (Fig 2a-b).

Coinciding with the results of the surveys, the most pricy fish species at both landing sites in all periods were the native fishes *Centropomus undecimalis*, *Prochilodus magdalenae* and *Eugerres plumieri* (Fig 3c-d). They were also the least abundant (Fig 3a-b). In contrast, the most abundant fishes *Mugil incilis*, *Cathorops mapale* and *Oreochromis niloticus* (Fig. 3a-b) were among the lowest priced ones (Fig 3c-d). In general terms, fresh water fishes like *P. magdalenae* and Nile tilapia, were more abundant in periods of low salinities (II, III) while estuarine fishes during periods of higher salinities (I, IV; Fig 3a-b). The prices for all species seemed to decrease (Fig. 3c-d) with the increase in their abundance (Fig 3a-b). However, in Nueva Venecia there are higher mean abundances (CPUE) and lower prices than in Tasajera for most of the fishes (Fig 3a-d).

The mean economic revenue provided by the fishery of native estuarine fishes (*A. bonillai*, *M. liza, M. incilis*, *C. mapale*, *E. plumieri* and *C. undecimalis*) was higher in Tasajera than in Nueva Venecia in most of the periods (Fig. 4a-b). In contrast, the mean economic revenue derived from freshwater fishes (*P. magdalenae* and *O. niloticus*) was higher in Nueva Venecia than in Tasajera (Fig 4a-b). Some differences were observed at the native species level between the periods of the highest abundance of *O. niloticus* (Period III, Fig. 3a-b) and the next period when its abundance decreased (IV, Fig. 33a-b). In Nueva Venecia (Fig. 4a) the mean economic revenue earned by fishing for *P. magdalenae*, *E. plumieri* and *C. mapale* decreased in period III while the mean economic revenue from *A. bonillai, M. liza, M. incilis* and *M. atlanticus* increased in the same period. For the next period, the mean economic revenue from *A. bonillai, M. incilis* and *E. plumieri* decreased while that from *M. liza*, *C. mapale* and *M. atlanticus* increased (Fig. 4a). In Tasajera (Fig. 4b) the mean economic revenue from *M. incilis*, *C. mapale* and *E. plumieri* decreased in

PIII, while that from *A. bonillai*, *M. liza, C. undecimalis* and *M. atlanticus* increased. In the same site, the mean economic revenue from *A. bonillai, E. plumieri, C. undecimalis* and *M. atlanticus* decreased in period IV, while that from *M. liza*, *M. incilis* and *C. mapale* increased in this period (Fig. 4b). The fishery of Nile tilapia provided larger mean economic revenue in Nueva Venecia than in Tasajera but in both sites it was much greater in period III than in period IV (Fig. 4a-b).

The MRA for Nueva Venecia (Table 2), showed that from the two independent variables the salinity explained best ($p<0.05$) the variation of monthly economic revenue given by *P. magdalenae* ($r=-0.59$), *C. mapale* ($r=0.52$), *E. plumieri* ($r=-0.35$) and *C. undecimalis* ($r=0.39$). The MRA for Tasajera (Table 3) showed that salinity ($p<0.05$) explained best the variation of monthly economic revenue provided by *M. incilis* ($r=-0.60$), *E. plumieri* ($r=0.42$) and *C. undecimalis* ($r=0.35$) while that by Nile tilapia and salinity ($p<0.05$) explained that of *C. mapale* ($r=-0.28$, $r=0.26$). Most of the multiple regression coefficients were low for both landing sites ($0.10<R^2<0.40$). For all other species, none of the two independent variables explained the variation of monthly economic revenue (Tables 4, 5).

DISCUSSION

In a context of poverty and very limited job opportunities such as that of the fishery in CGSM (Moscarella and Pinilla 1998), the arrival of a new species (Nile tilapia) with great abundance contributed to alleviate the problem of income generation for the fishermen. This happened only during periods of low salinity conditions, which are favorable to this species. However, typically estuarine native fishes such as *Centropomus undecimalis* and *Eugerres plumieri* and fresh water fishes such as *Prochilodus magdalenae* have been the most pricy species in the fishing trade in the region and they are still preferred over the non-native *O. niloticus* mostly due to their better taste. However the population stocks of those native fishes do not seem to be big enough to provide good economic revenue in all periods (Figs. 3a-b, 4a-b). The fishery of the native fish *Mugil incilis* seems to be a better alternative for more constant economic revenues since this species provided a high gross income in all periods at both landing sites (Fig. 4a-b).

In general, the variation in economic revenue responds to salinity fluctuation (Tables 2, 3) which is the variable that better describes the environmental changes (Sanchez and Rueda 1999, Rueda 2001, Blanco et al. 2006). This was expected since the economic revenue depends on both the price and the abundance of the species. The latter as well as the food abundance and availability in the ecosystem vary according to the salinity changes (Leal-Flórez et al. unpublished data). An increase in relative abundance (CPUE) of one species causes an excess supply in the market followed by price reduction. This explains the low economic revenue derived from fishing the most abundant species in certain periods (Fig 4a-b). However, not only does the abundance of a fish influence its price, other characteristics are also influential, like the access to big markets (e.g. nearness to a main road) and the consumers'/buyers' preferences, which can be determined by the taste of the fish, quality of its meat, size (e.g. for a fillet) and appearance (e.g. color). Zamora (2005) has characterized the market structure of Nueva Venecia as an oligopsony market type, where the fishermen first sell their catches to a small group of tradesmen who determine the price of the fish. The same author characterized Tasajera as a perfect market, where a big number of fishermen first sell their catches to a big group of tradesmen. These differences are related to the location of both landing sites. Nueva Venecia is a stilt village with no direct access to any road, while Tasajera is a town next to the main road connecting the biggest cities in the region. The market differences thus explain why some fishes (e.g. *H. bonillai*, *M. liza*, *E. plumieri*) with a similarly low abundance at both sites may differ in price between sites (Fig 3a-d).

The fishermen have adopted an opportunistic behavior changing their methods and gears to go after every species (including the Nile tilapia) that appears in high abundance (Moscarella and Pinilla 1998, INVEMAR 2006). This behavior responds to environmental variation (salinity changes) that favors the abundance of different fishes in different periods. Their perceptions of the best priced fishes coincided with what is shown by the comparison of prices among years. They still prefer to fish the native estuarine fishes due to their better taste and price. However, these fishes have shown a considerable decrease in abundance in the last decades that seems to be related to overfishing (Rivera-Monroy et al. 2006) and environmental variation (Rueda 2001).

The Nile tilapia is a fish with a relatively low price when compared to some native fishes, but its high abundance in periods of low salinity made it a good alternative of income for the fishermen. They were thus able to still receive economic revenue, when the catches of the high valued estuarine fishes were reduced. But the dependence of the proliferation of *O. niloticus* on low salinity conditions makes it a profitable fish only during short periods because such conditions appear due to drastic and short term changes in the water budget of the estuary. However, if the acceptance of this non-native species by the buyers would increase and if its abundance would remain at a constant high level, Nile tilapia could possibly constitute a good alternative of economic revenue in the long term. The question that arises here is if a long term establishment of *O. niloticus* in the CGSM might not negatively impact the native fishes of the ecosystem as has been shown elsewhere in other tropical ecosystems (Costa-Pierce 2003, Canonico et al. 2005).

A possible better alternative of income in the long term seems to be the fishery of the native fish *M. incilis* due to its constant occurrence in high relative abundances (Fig 3a-b), apparent adaptability to the highly variable salinity conditions and relatively high economic revenue from its fishery in all periods (Fig. 4a-b). However, several native fishes, including this species, have already shown signals of overfishing in the estuary in the last decade (Sánchez et al. 1998). Therefore attention should be given to the fishery regulations in the system to establish measures that could ensure the maintenance of the native fish stocks and, with that, the livelihood of resource users in the long term.

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Table 1: Questions asked to the 158 respondents at the landing sites within the estuary Cienaga Grande de Santa Marta

	Questions
1	How old are you?
2	How long have you been dedicated to fishing in CGSM as an economic activity?
3	Which fish was economically most valued before the appearance of Nile tilapia* in CGSM?
4	Which fish was economically most valued when Nile tilapia* was the most captured fish in CGSM?
5	In the whole time you have been fishing, which fish has been the one everybody wants to catch the most?
6	Why has that fish been so valuable for fishing?

* Common name in Spanish (Lora) was used

Table 2: Multiple regression analysis with the monthly economic revenue derived from the fishery of native fishes as dependent variable (Y) and the monthly economic revenue from the fishery of Nile tilapia (Onil) and the monthly mean of Salinity (SAL) as independent variables (X). Same type of analysis was done with *O. niloticus* but only with Salinity as independent variable. Only significant results are reported ($p < 0.05$). N= 59. NS: not significant, r= standardized regression coefficients. Data corresponding to the landing site Tasajera.

NUEVA VENECIA	**r**		**Multiple**	**Std. Error**	**p**
Species	**Onil**	**SAL**	**R^2**	**Estimate**	
Prochilodus magdalenae	-0,33	-0,59	0,25	0,33	0,00
Ariopsis bonillai	NS	NS	0,01	0,22	0,77
Mugil incilis	-0,31	NS	0,08	0,48	0,09
Cathorops mapale	NS	0,52	0,40	0,48	0,00
Eugerres plumieri	-0,30	-0,35	0,10	0,44	0,05
Centropomus undecimalis	NS	0,39	0,16	0,01	0,01
Megalops atlanticus	NS	NS	0,05	0,17	0,26
Oreochromis niloticus	-------	-0,53	0,28	0,62	0,00

Table 3: Multiple regression analysis with the monthly economic revenue derived from the fishery of native fishes as dependent variable (Y) and the monthly economic revenue from the fishery of Nile tilapia (Onil) and the monthly mean of Salinity (SAL) as independent variables (X). Same type of analysis was done with *O. niloticus* but only with Salinity as independent variable. Only significant results are reported ($p < 0.05$). N= 62. NS: not significant, r= standardized regression coefficients. Data corresponding to the landing site Tasajera.

TASAJERA	**r**		**Multiple**	**Std. Error**	**p**
Species	**Onil**	**SAL**	**R^2**	**Estimate**	
Prochilodus magdalenae	NS	NS	0,02	0,00	0,52
Ariopsis bonillai	NS	NS	0,04	0,34	0,33
Mugil incilis	-0,24	-0,60	0,35	0,64	0,00
Cathorops mapale	-0,28	0,26	0,18	0,71	0,00
Eugerres plumieri	NS	0,42	0,18	0,53	0,00
Centropomus undecimalis	NS	0,35	0,12	0,06	0,02
Megalops atlanticus	NS	NS	0,01	0,05	0,65
Oreochromis niloticus	-------	NS	0,05	0,35	0,10

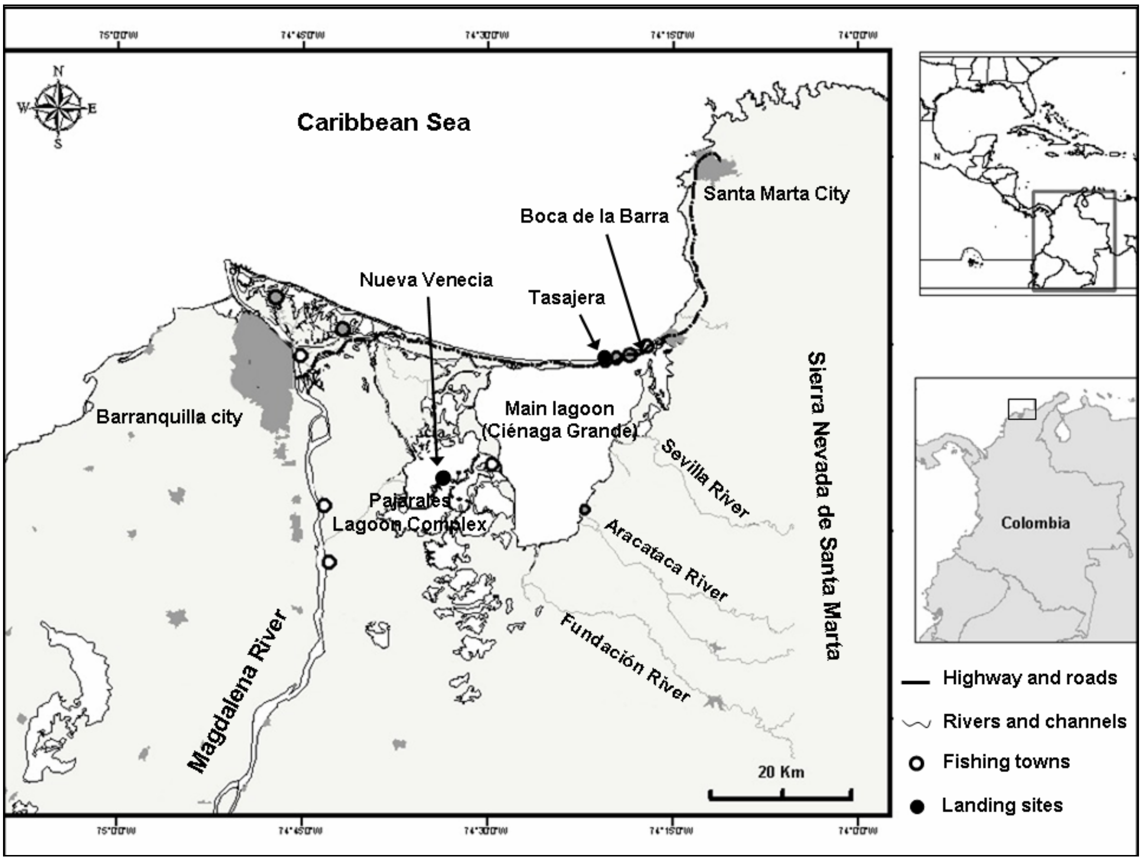

Fig 1: Location of the estuary Ciénaga Grande de Santa Marta in the north coast of Colombia.

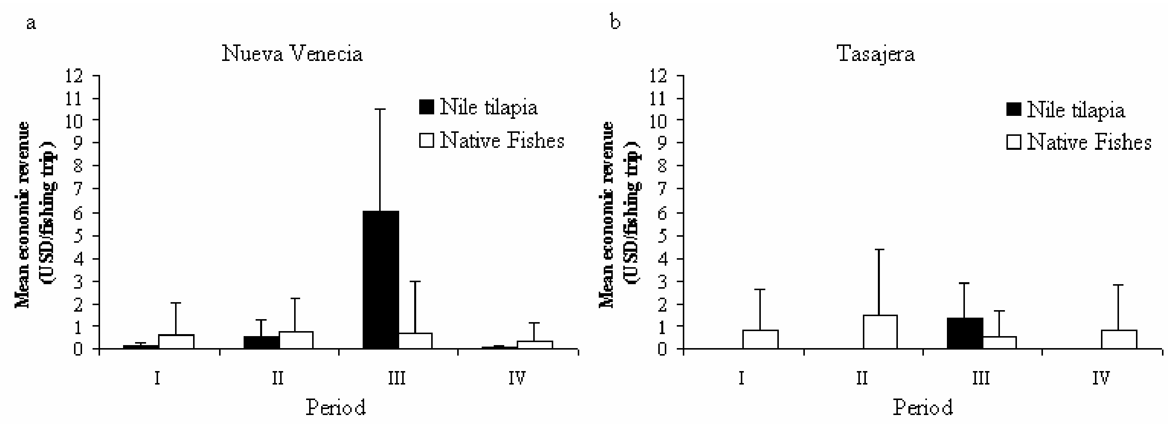

Fig. 2: Mean economic revenue (USD.kg/fishing trip) derived from the fishery of the Nile tilapia and the fishery of the eight most commercially used native fishes using cast net as fishing gear in the four periods considered in this study in the landing sites Nueva Venecia (a) and Tasajera (b). Bars represent the standard deviation.

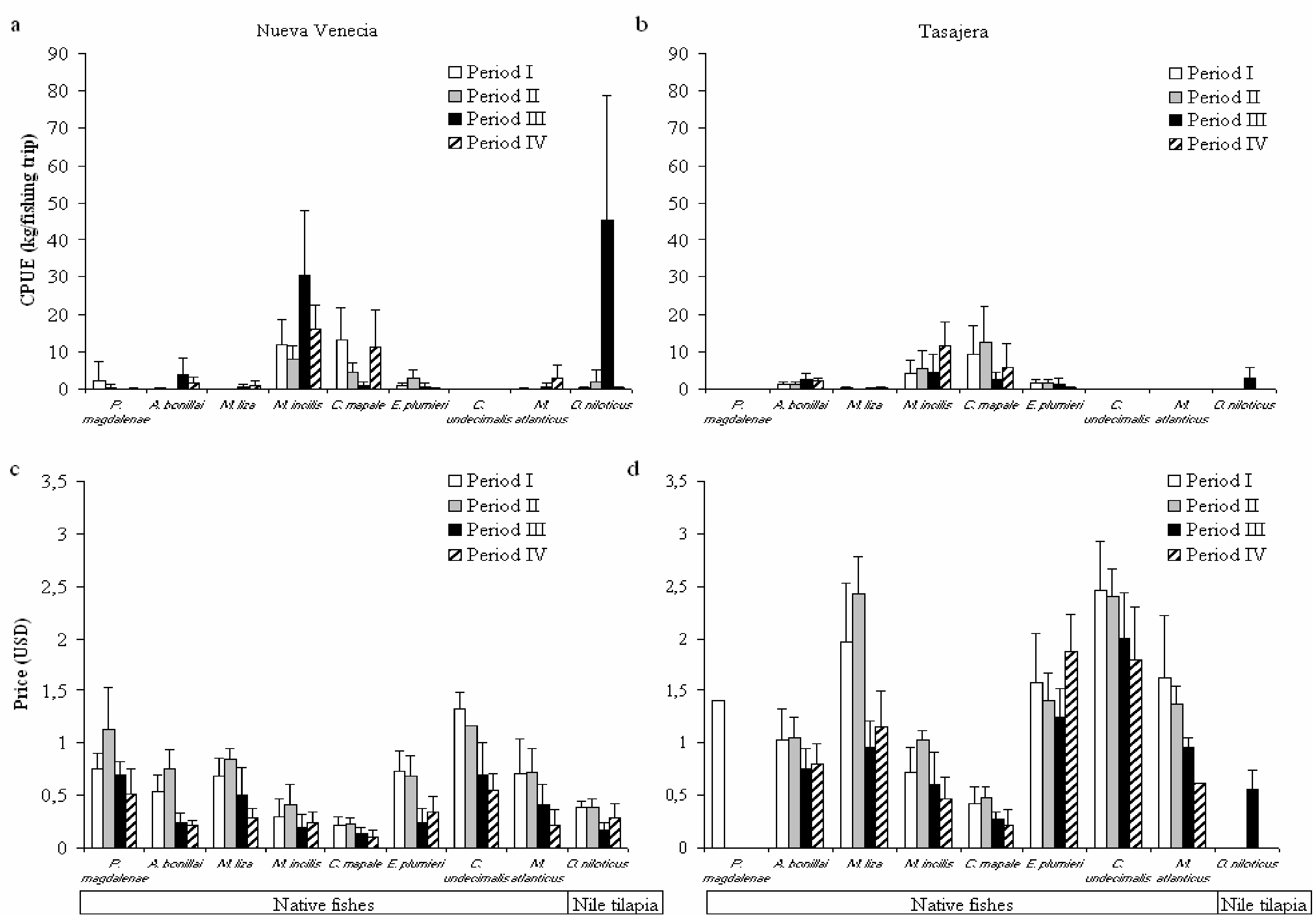

Fig 3: Mean relative abundance (CPUE – kg/fishing trip; a, b) and price (USD; c, d) of the most commercially important fishes in the four periods considered in this study for the two landing sites (Nueva Venecia and Tasajera) within CGSM. Bars represent the standard deviations.

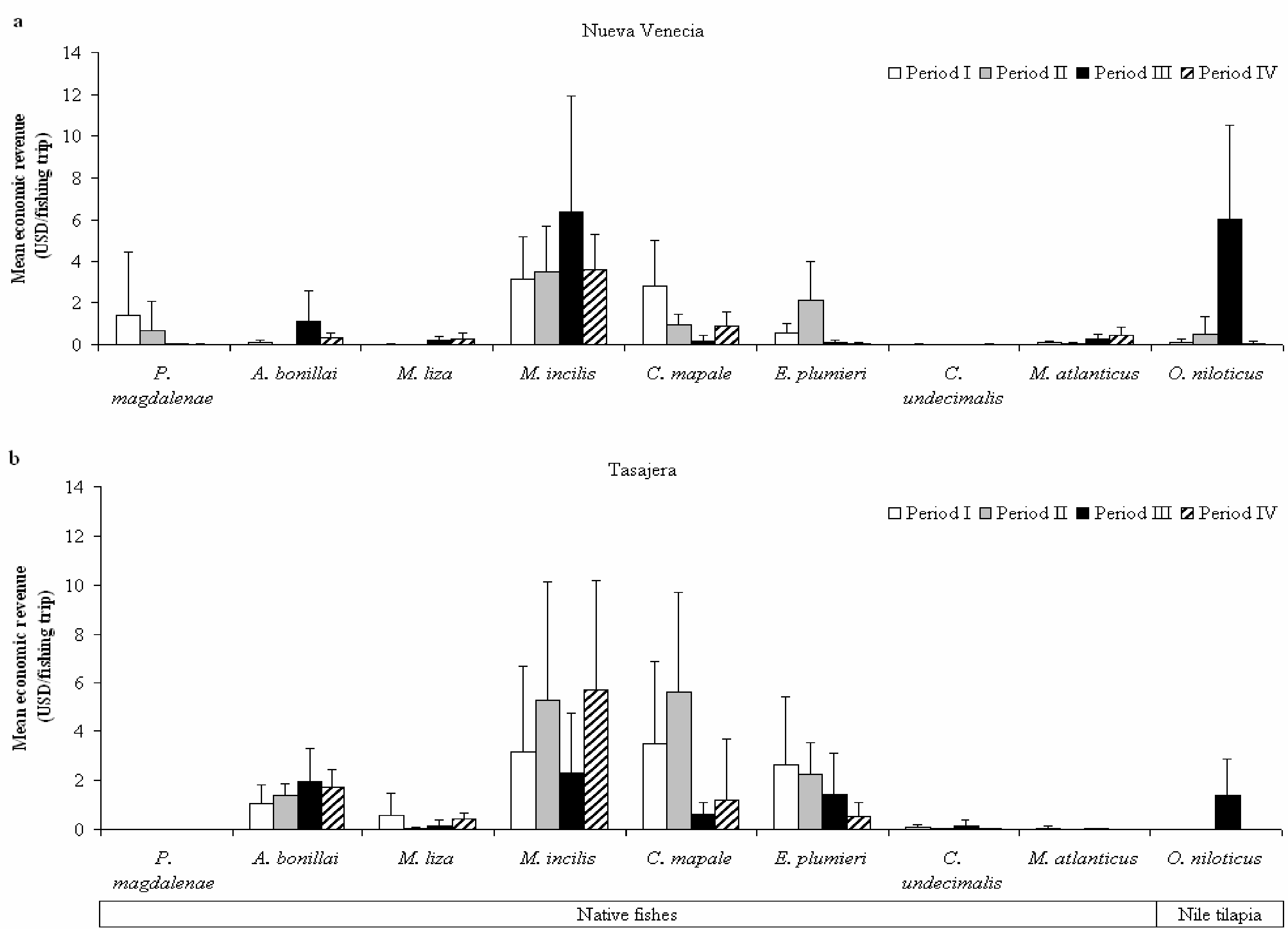

Fig. 4: Mean economic revenue (USD.kg/fishing trip) from the fishery of eight native fish species and the non-native fish *Oreochromis niloticus* for both landing sites (a: Nueva Venecia; b: Tasajera) in the four periods considered in this study. Bars represent the standard deviations.

Lagoon at the northwestern side of Salamanca Island, CGSM, Colombia. Photo: Leal-Flórez 2003

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Ciénaga Grande de Santa Marta estuary, main lagoon, sunset. Photo: Leal-Flórez 2003.

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Ciénaga Grande de Santa Marta estuary, main lagoon, sunset. Photo: Leal-Flórez 2003.

APPENDICES

APPENDIX A: TERMINOLOGY

Anadromous: Term used to designate fishes that live in the sea and ascend to rivers for spawning.

Catadromous: Term used to designate the fishes that live in freshwater but migrate to the sea for spawning.

Colonizer: Any species that reaches a new environment (Davis & Thompson 2000) out of its natural range without human mediation.

Diadromous: Term used to designate all fishes that migrate for any purpose and in any direction between freshwater and sea. This type of fishes has special adaptations to deal with the salinity changes during their migrations. It includes the terms anadromous and catadromous.

Fishbase: Online database sponsored by FAO that contains information on classification, biology and ecology of most fishes known

Introduced species: Any species intentionally or accidentally transported and released by man into an environment outside its present natural range (Welcomme 1988) unrestrictive of its impact on the new ecosystems. Terms like “non-indigenous”, “non-native”, “exotic”, “adventive”, “foreign”, “allochthonous” and “alien”, are considered as synonyms.

Invasive species: Any colonizer that has a negative impact on the new ecosystem where it is established (Davis & Thompson 2000). Not all colonizers and introduced species become invasive species.

Man and Biosphere Reserve: Protected area designated with the sponsorship of the Man and Biosphere Program of UNESCO aiming to improve the relationship of people with their environment globally.

Native species: Any species that is a member of the natural biotic community (Lever 1996) in a particular geographic area. The terms "indigenous", "autochthonous" and "endemic" are considered as synonyms.

Naturalization: Process by which an introduced species establishes self-maintaining populations in free-living state under similar conditions to those of the ecosystem from where the species is originated (Lever 1996). Naturalization begins when abiotic and biotic barriers to survival and reproduction are surmounted (Richardson *et al.* 2000).

Potamodromous: Term used to designate fishes that live in freshwater and migrate to small headwater streams to spawn. The term fluvial is sometimes used as synonymous.

Ramsar Convention: Convention on Wetlands of International Importance. An intergovernmental treaty adopted on 2 February 1971 in the Iranian city of Ramsar with the aim of protecting wetlands of importance for conservation of world's biodiversity.

Transferred species: A transferred species is any species intentionally or accidentally transported and released within its present range (Welcomme 1988), e.g. from one basin to another within the same country. The terms "transplanted species" and "translocated species" are considered as synonyms.

APPENDIX B: NON-NATIVE FISHES

The introduced fishes in the Ciénaga Grande de Santa Marta estuary are considered freshwater species. The least abundant of the non-native fishes are described below based on information compiled from Cervigón *et al.* (1993), Carpenter (2002), Nelson (2006) and Froese & Pauly (2007) among others. Common names (as used in Froese & Pauly 2007) are given in English (EN) when they are known and/or in Spanish (SP) as they are locally used. The Nile tilapia and the snakeskin gourami, which are the most abundant non-native fishes in the estuary, were described before in chapter 2.

<u>Family Cichlidae – Cichlids</u>

Oreochromis spp.

EN: Red tilapia, SP: Tilapia roja

Photo: http://gallantamnat.trustpass.alibaba.com/product/11695749/Red_Tilapia.html

Originally a hybrid between a mutant reddish-orange female of *Oreochromis mossambicus* and a normal male of *O. niloticus* that was developed in Taiwan in the late 1960's for aquaculture purposes. After that, many other strains have been developed in different regions that have also been crossed with other red tilapias of unknown origins (Popma & Masser 1999). It has been introduced in almost all tropical countries for aquaculture activities. The color makes it vulnerable to predation and fishing (J. Blanco, INVEMAR, pers. comm.) but also marketable in aquaculture.

Family Characidae – Characins

Colossoma macropomum (Cuvier 1818)

EN: Tambaqui (from Portuguese), SP: Cachama

Photo: L.L. Lovshin 1999, www.fishbase.org

Demersal, potamodromous fish that inhabits the basins of the Amazon and Orinoco Rivers. It feeds mainly on fruits and grains but its diet can also include zooplankton and insect larvae. It has been introduced for aquaculture in many countries of South America and in some of Asia. It can reach a maximum size of 108 cm.

APPENDIX C: NATIVE FISHES

The most abundant and commercially important fishes that are of interest for this study are briefly described below based on information compiled from Cervigón *et al.* (1993), Carpenter (2002), Nelson (2006) and Froese & Pauly (2007). Common names (as used in Froese & Pauly 2007) are given in English (EN) when they are known and/or in Spanish (SP) as they are locally used.

Estuarine Fishes

Family Ariidae – Sea Catfishes

Ariopsis bonillai Miles 1945
EN: New Granada sea catfish, SP: Chivo Cabezón

Photo: INVEMAR 1999

Demersal and euryhaline species found in Colombia and western Venezuela. Mostly restricted to shallow muddy bottoms in fresh and brackish waters. Males incubate eggs in the mouth. Feeds mainly on crabs. Can reach a maximum size of 80 cm but more commonly 35. Highly appreciated as food.

Cathorops mapale Betancur-R. & Acero-P. 2005
SP: Chivo Mapalé

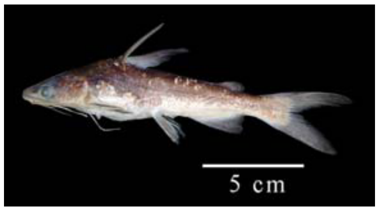

Photo: R. Betancur 2006, www.fishbase.org

Demersal and euryhaline species found in Colombia and Venezuela. Long misidentified as *Cathorops spixii*. Mostly restricted to shallow muddy bottoms in marine and brackish waters and river mouths. Males incubate eggs in the mouth. Feeds mainly on invertebrates and small fishes and detritus and algae in lesser extent. Can reach a maximum size of 31 cm. Local consumption.

Family Centropomidae – Snooks

Centropomus undecimalis Bloch 1792

EN: Common Snook, SP: Róbalo

Photo: R.A. Patzner 1999, www.fishbase.org

Found from Southern Florida to Rio de Janeiro in soft bottoms of marine and brackish waters, sometimes penetrating into fresh waters. Feeds mainly on fish and crustaceans. Can reach a maximum size of 130 cm but most commonly 50. Valued sport fish and excellent food fish.

Family Elopidae – Tenpounders

Elops saurus Linnaeus1766

EN: Ladyfish, SP: Macabí

Photo: Rodriguez-Olarte 2005, http://pegasus.ucla.edu.ve/cdbiodiversidad/GaleriaPeces.htm

Demersal fish found from Southern North Carolina to southern Brazil. Found in muddy bottoms of marine and brackish waters. Forms large schools close to the shore. Spawns offshore. Feeds on pelagic preys, mainly fish but also decapods to a lesser extent. Can reach a maximum size of 90 cm but most commonly 50. Commercialized as food fish and bait. In the recent decade sold processed for local consumption.

Family Gerreidae – Mojarras

Eugerres plumieri Valenciannes 1830

EN: Striped Mojarra, SP: Mojarra Rayada

Photo: L.O. Duarte 2002, www.fishbase.org

Demersal fish found from South Carolina to Brazil in muddy bottoms of shallow coastal waters like mangrove lined creeks and lagoons. Also enters into fresh waters. Feeds on a variety of invertebrates but mostly aquatic insects, micro-bivalves, crustaceans and detritus. Can reach a maximum size of 40 cm but most commonly 30. Highly appreciated as food, it supports important fisheries in the region.

Diapterus rhombeus Cuvier 1829

EN: Caitipa Mojarra, SP: Mojarra Blanca

Photo: L.O. Duarte 2002, www.fishbase.org

Demersal fish found from southern Gulf of Mexico and the Greater Antilles to Brazil in muddy and sandy bottoms of shallow coastal waters, including mangrove-lined lagoons. May enter freshwaters. Feeds mainly on small benthic invertebrates and plants. Can reach a maximum size of 40 cm but most commonly 30.

Family Megalopidae – Tarpons

Megalops atlanticus Valenciannes 1846

EN: Tarpon, SP: Sábalo

Photo: D. Bryan 2003, www.fishbase.org

Pelagic fish that occurs in the tropical and subtropical eastern and western Atlantic. Found in coastal waters including estuaries and mangrove-lined lagoons. Penetrates long distances into fresh waters. Its swim bladder functions as an air breathing organ, this fish is therefore adapted to living in oxygen poor waters. Exhibits a high salinity and temperature tolerance. Feeds mainly on other fishes and, less frequently on crabs. Can reach a maximum size of 220 cm, but most commonly 130. Highly appreciated as sport and food fish.

Family Mugilidae – Mullets

Mugil incilis Hancock 1830

EN: Parassi Mullet, SP: Lisa

Photo: INVEMAR 1999

Mugil liza Valenciannes 1836

EN: Liza, SP: Lebranche

Photo: Pescasubrj 2007,
http://pescasubrj.com/teste/tainha/tainha.html

Demersal fish distributed from Haiti and Panama to southeastern Brazil. Found in brackish to hyper saline waters. Spawns in small groups at the mouth of coastal rivers and creeks. Can reach a maximum size of 40 cm. Locally consumed.

Demersal fish that occurs from southern Florida to Argentina. of the western Atlantic. Found in brackish to hyper saline waters and may enter into fresh waters. Feeds on organic detritus and algae. Spawns at sea. Can reach a maximum size of 80 cm but most commonly 40. Highly appreciated as food fish.

Freshwater fishes

These are endemic fishes of northern South America.

<u>Family Prochilodontidae – Flannel-mouth characiforms</u>
Prochilodus magdalenae Steindachner 1879
SP: Bocachico

Photo: C.W. Olaya-Nieto 2002, www.fishbase.org

Demersal and potamodromous fish. Endemic of the Magdalena basin in Colombia. Considered omnivore but feeds mainly on periphyton, phytoplankton and detritus (Gutiérrez 2004). Can reach a maximum size of 50 cm but this is less common nowadays. Highly appreciated as food fish.

<u>Family Cichlidae – Cichlids</u>

Caquetaia kraussii Steindachner 1878

SP: Mojarra Peña

Photo: C.W. Olaya-Nieto 2002, www.fishbase.org

Demersal fish that inhabits the Lake Maracaibo basin in Venezuela and the rivers Atrato, Cauca and Magdalena in Colombia. Prefers marshes or swamps abundant in aquatic plants. Feeds on benthic invertebrates and other fishes. Can reach a maximum size of 26 cm.

<u>Family Characidae – Characins</u>

Triportheus magdalenae Steindachner 1878

SP: Arenca

Photo: F. Bolivar 2005, www.fishbase.org

Pelagic, potamodromous fish that is endemic to the Magdalena basin in Colombia. Feeds mainly on insects and pelagic invertebrates. Can reach a maximum size of 19 cm.

APPENDIX D: LIST OF ABBREVIATIONS

ANOSIM:	Analysis of Similarities
CBD:	Convention of Biological Diversity
CGSM:	Ciénaga Grande de Santa Marta Estuary
CORPAMAG:	Corporación Autónoma Regional del Magdalena
CPUE:	Catch Per Unit Effort
FAO:	Food and Agriculture Organization of the United Nations
ICLARM:	International Center for Living Aquatic Resources Management
INVEMAR:	Instituto de Investigaciones Marinas y Costeras, Santa Marta, Colombia
MRA:	Multiple Regression Analysis/Analyses
PI:	Period I of this study, from 1994 to 1995
PII:	Period II of this study, 1996
PIII:	Period III of this study, from 1999 to 2001
PIV:	Period IV of this study, from 2002 to 2003
PRIMER:	Plymouth Routines In Multivariate Ecological Research
PSU:	Practical Salinity Units
SIMPER:	Similarity Percentage Analysis
UNDP:	United Nations Development Program
UNEP:	United Nations Environment Program
UNESCO:	United Nations Educational, Scientific and Cultural Organization
WB:	World Bank
WRI:	World Resources Institute
ZA:	Zone A of this study, corresponding to the main lagoon
ZB:	Zone B of this study, corresponding to the Pajarales Lagoon Complex
ZC:	Zone C of this study, corresponding to the Sanctuary of Flora and Fauna
ZD:	Zone D of this study, corresponding to the Northwestern side of Salamanca Island