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Tarpon and Other Fishes of the Western Gulf of Mexico: Proceedings from the Third International Tarpon Forum
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The cover image is the coastline along Veracruz, Mexico.

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INTRODUCTION TO THE PROCEEDINGS OF THE THIRD INTERNATIONAL TARPON FORUM HELD IN VERACRUZ, MEXICO

May 8-9, 2004

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Overview

Veracruz, Mexico, an important center of the recreational tarpon and bonefish fishery, was the site of the Third International Tarpon Forum on May 8-9, 2004. The workshop was organized by Ivonne Blandon of Texas Parks and Wildlife, and scientists from the University of Texas Marine Science Institute and Universidad Veracruzana. The forum goal was to coordinate efforts on research and restoration of tarpon, and their critical habitat throughout the Gulf of Mexico and Caribbean Sea. Tarpon supports valuable recreational fisheries in the Atlantic from North Carolina to Brazil and Africa, across the Gulf of Mexico and Caribbean Sea, and in the Pacific Ocean off Panama. Researchers around the world have worked to increase our understanding of the ecology, life history, and population dynamics of this important sportfish. This knowledge is leading to an increased awareness of management opportunities that may arise to enhance existing populations and to re-establish tarpon in areas from which fisheries have been lost. Cooperation among researchers, government agencies, and tarpon fishermen brings a spirit of optimism to the conservation and management of tarpon. This workshop was designed to foster this spirit. Researchers from Mexico, Central America, the United States, and the Caribbean presented their findings and discussed how this knowledge could enhance international management strategies.

Symposium Structure

Technical Sessions

Two days of presentations summarized results of tarpon and bonefish research and management around the Gulf of Mexico, and highlighted their ecotourism value. A Keynote on "International collaboration and opportunities for research in the Gulf of Mexico" was given by

Wes Tunnell of the Harte Institute, Texas A&M University- Corpus Christi. Other presenters were from Mexico (8), Puerto Rico (1), Venezuela (2), Florida (4) and Texas (2).

Participating organizations included: Instituto Naval (Mexico), CONANP-Marine Protected Areas (Mexico), SAGARPA Secretaria de Agricultura Ganaderia y Pesca (Mexico), Club de Yates de Veracruz (Mexico), Cooperativa de Pescadores Ecoturism- Mexico Chetumal, Cooperativa de pescadores comerciales Anton Lizardo (Mexico, Veracruz)

Roundtable Discussions

Three roundtable discussions followed the first day of the forum. The first discussion examined the current status of tarpon and bonefish research and future opportunities for collaborations. The second discussion emphasized spawning and nursery habitats, including mapping of the known habitats, discussion of the quality of those habitats and opportunities for international collaborative studies. The final discussion examined cooperation between fishermen, guides, scientists, and fishery managers. A proposal for tarpon conservation in Mexico was presented by members of the Yacht and Fishing Club of Mexico.

Acknowledgments

DEVELOPMENT OF RETINAL ARCHITECTURE IN THE ELOPOMORPH SPECIES *MEGALOPS ATLANTICUS*, *ELOPS SAURUS* AND *ALBULA VULPES* (ELOPOMORPHA: TELEOSTEI)

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ABSTRACT

Vision is critical to survival over the course of development in many marine fishes, but its relative importance in certain species (elopomorphs, for example) and at different stages of development is largely unknown. Atlantic tarpon (*Megalops atlanticus*), ladyfish (*Elops saurus*), and bonefish (*Albula vulpes*) share the leptocephalus larval form (unique to species of the teleost subdivision Elopomorpha), but diverge dramatically at metamorphosis as they enter very distinct ecological niches. To determine how ecological specialization may relate to changing retinal structure and visual function, photoreceptor organization was investigated in retinas of *M. atlanticus*, *E. saurus* and *A. vulpes* at larval settlement through juvenile stages. At settlement, *M. atlanticus* and *E. saurus* retinas had similar photoreceptor distributions, but the *A. vulpes* retina had a different arrangement of photoreceptors, possibly reflecting ecological similarities (*M. atlanticus* and *E. saurus*) and differences (*A. vulpes* vs. others) in post-settlement ecology. Larval *E. saurus* reared through metamorphosis in captivity exhibited ontogenic changes in retinal architecture that correlated with natural shifts in habitat and behavior (even though the captive environment remained static). The retinas of juvenile fishes differed dramatically in photoreceptor distributions and arrangements in different retinal regions, demonstrating that dramatic divergence in retinal morphology occurs concurrent with ecological divergence after settlement. These results demonstrate that changing retinal architecture correlates with, and may be a precursor to, changing ecology and habitat as elopomorph fishes mature. These results also form the basis for developing testable hypotheses concerning the much lacking knowledge of behavior and ecology during the early life history of these ecologically and economically important species.

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INTRODUCTION

The stability and growth of adult fish stocks depend upon recruitment and maturation of young fish as adults are removed by fishing activities and other forms of mortality. It is therefore important to develop a comprehensive understanding of the factors that affect survival during the highly vulnerable early life history stages of fishes.

Adult bonefish (*Albula vulpes*) and Atlantic tarpon (*Megalops atlanticus*) are fished intensively for sport and support economically important recreational fisheries in Florida and throughout the Caribbean. Adult ladyfish (*Elops saurus*), although not economically important, are large, highly abundant (where they occur) piscivores, undoubtedly having an important ecological impact on other fish populations. All three species spend their juvenile lives in volatile coastal habitats that are highly susceptible to anthropogenic disturbance— *M. atlanticus* and *E. saurus* in mangrove-lined estuaries and *A. vulpes* in shallow waters along sandy beaches. The optical properties of water (which affect available light quality and intensity) can be seriously affected by both natural and anthropogenic influences, especially in coastal areas. Such changes in optical qualities may interfere with the visual abilities of fishes living in these habitats. To better understand how changes in optical properties of water affect survival in young elopomorphs, it is necessary to understand how the visual systems of these fish function, and how their retinas are adapted for vision in specific photic environments. Unfortunately, to date there has been no systematic investigation of visual development in *M. atlanticus, A. vulpes, E. saurus*, or almost any other elopomorph species other than a few studies of retinal morphology in the European eel, *Anguilla anguilla* (Pankhurst 1983, Braekevelt 1984, 1985, Blaxter 1986, Braekevelt 1988 a, b).

The teleost neural retina—the portion of the eye that contains photoreceptor cells and associated neurons—contrasts sharply with the relatively static mammalian retina, in that it contains stem cells that continuously generate new neurons throughout the lifetime of the fish. This persistent neurogenesis allows the teleost retina to grow throughout life, to be modified in cell types and distributions with maturation, and to regenerate after injury (Easter and Hitchcock 2000).

Retinal morphology and function in teleosts can differ widely between ecologically distinct species, but the retina can also change significantly over the course of development within species. Habitat and behavior often change dramatically within species as fish mature

from larva to adult; retinal morphology and function may also change in a given individual as it progresses through subsequent developmental stages in which the maturing fish occupies habitats with distinct optical properties (see for example Braekevelt 1984, 1985, 1988 a, b, Bowmaker 1990, and Reckel et al. 2002). In species that remain in similar habitat throughout maturation, retinal architecture and function may change as an individual undergoes ontogenic shifts in behavior (for example as food preferences change; Shand 1997).

The overall organization of the fish retina is similar to that of other vertebrate animals, with the photoreceptive layer located at the outer margin of the neural retina adjacent to the supportive retinal pigmented epithelium (RPE, see Fig. 9). Rod and single-cone photoreceptors of teleosts are morphologically and functionally similar to those of other vertebrates (Fig. 1).
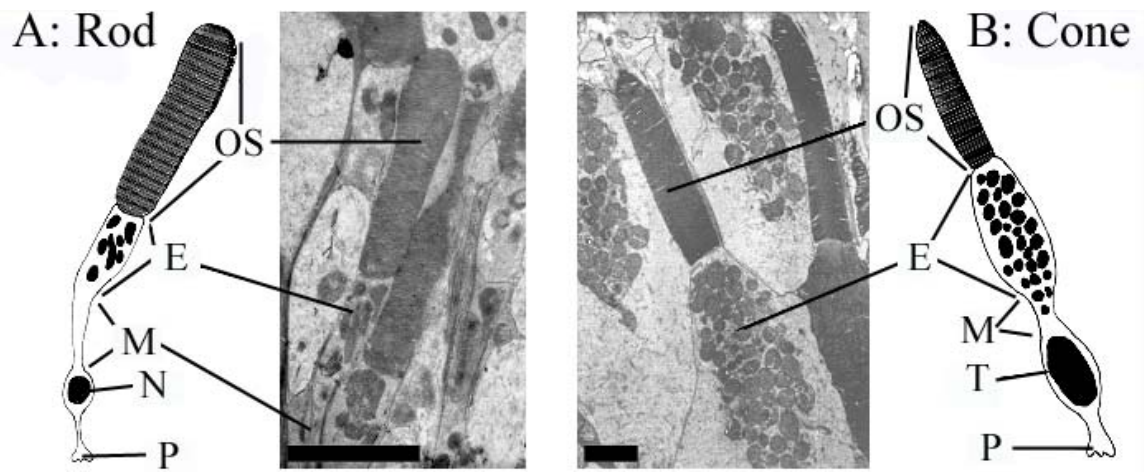
Figure 1. General structures of rod (A) and cone (B) photoreceptor cells in adult *M. atlanticus*; transmission electron micrographs (7000x) of retina fixed in buffered 2.5% glutaraldehyde/2.5% paraformaldehyde, embedded in Durcupan resin and sectioned at 70 nm. These two photoreceptor types generally differ in outer segment shape, ellipsoid diameter and shape, and nucleus shape (cone nuclei are generally more ovoid). Abbreviations: OS: outer segment, E: ellipsoid, M: myoid, N: nucleus, P: synaptic pedicel. Bar = 2.5μm.

However, teleosts also can possess double cones [two closely associated cone cells] that are present in many non-mammalian vertebrates but generally absent in higher mammals (Walls 1967). Cone cells, named for their cone-shaped outer segments, are typically responsible for high-acuity 'photopic' vision under relatively high light (i.e. daytime) conditions and provide color detection. Rod cells, named for their long rod-shaped outer segments, are generally

responsible for 'scotopic' vision under low light (i.e. nighttime) conditions; they provide high absolute sensitivity, but offer low spatial resolution relative to cones.

The retinas of almost all well-studied teleost larvae are cone-dominated by the time of the first feeding (within 1-2 days after hatching); most rod photoreceptors develop sometime later (Blaxter 1986, Evans and Fernald 1990, 1993, Evans et al. 1993, Negishi and Wagner 1995, Shand 1997, Lara 2001).   A cone-dominated retina therefore must be either adequate or necessary for first feeding (Blaxter 1986). Early cones are generally small and densely packed (Shand 1997). Since visual acuity increases with greater cone density and/or greater lens diameter (Pankhurst et al. 1993, van der Meer 1994, Shand 1994, Shand 1997), small densely packed cones should maximize visual acuity of tiny larval fish eyes in which the total number of photoreceptors and lens diameter are both small.

Elopomorph fishes share a unique larval form, called the leptocephalus, which is distinct from other teleost larvae in many ways (reviewed in Smith, 1989). Leptocephali are morphologically similar in many respects, and physiological characteristics (the facts that these larvae are isosmotic with seawater and have limited osmoregulatory abilities) indicate that most (or all) probably exist in deep stenohaline oceanic waters prior to settlement, although interspecific differences do occur in depths and regions of occurrence (Smith 1989). Due to the fragility of these larvae, most of the existing data were derived from dead specimens taken in trawls and concern primarily morphology and capture locations; thus little is known about important aspects of biology, behavior and ecology of leptocephali.

Although they have reasonably similar larvae, incredible divergent radiation occurs among elopomorph species during metamorphosis, as different species settle (i.e. make the transition from a pelagic to coastal/estuarine existence) into radically different habitats and ecological niches (consider coastal/pelagic *M. atlanticus* and demersal eels). Along with ecology, the visual systems of these fishes also likely diverge. For example, because juvenile *M. atlanticus* and *A. vulpes* occur in very different habitats, their visual requirements and abilities should also differ markedly. Thus, the goal of the research presented here was to determine how the retinas of *M. atlanticus*, *A. vulpes* and *Elops saurus* change over the course of development from larval settlement through juvenile stages. Using light microscopy and immunofluorescence to examine photoreceptor morphology and photopigment content, we found that functional architecture of the retina changes as fish mature, that these changes are distinct among species,

and that the changing retina relates to, and may be may be a precursor to changing habitats and behaviors.

METHODS

Specimen Collection

Settlement-stage *M. atlanticus* and *E. saurus* were captured during nighttime flood tides entering the Indian River Lagoon estuary through Sebastian Inlet (Brevard County, FL) from adjacent coastal waters. Larvae were collected with a 1m-diameter hoop plankton net; mesh size 0.5mm, moored from a catwalk over the inlet. Settling *M. atlanticus* larvae were captured in July 2003, and *E. saurus* in February 2004. Settlement-stage *A. vulpes* larvae were captured at night with light traps from marine reserve coastal waters off Quintana Roo, Mexico (Reserva de la Biósfera de Sian Ka'an, and Parque Marino Xcalak, Quintana Roo), and are documented in the ECOSUR database.

Juvenile *M. atlanticus* and *E. saurus* were collected from impounded mangrove marshes adjacent to the Indian River Lagoon estuary in Brevard County, FL. Habitats of both species had turbid, tannin-stained water, but *M. atlanticus* habitat was stagnant, emitted a strong odor of sulfur dioxide, and appeared to be relatively anoxic (dissolved oxygen not measured); *E. saurus* habitat was tannin-colored, but did not appear to be anoxic (based on odor and appearance). Juvenile *M. atlanticus* were collected by cast net; juvenile *E. saurus* were collected via seine net. Juvenile *A. vulpes* were also collected via seine net, but from water less than 1m deep along sandy beaches of Key Biscayne, FL.

Rearing *E. saurus* Through Metamorphosis

Three settlement-stage *E. saurus*, captured at Sebastian Inlet FL in good physical condition, were returned to the laboratory and held in a 5-gallon glass aquarium with gentle aeration. The fish were offered live *Artemia* nauplii every 2-3 days as a food source, and 50% water changes were performed weekly. *Artemia* were always available as a food source since they remained alive for 2-3 days. The timing of the first *Artemia* feeding (FAF) in the laboratory was determined when the orange-colored nauplii were first visible in the transparent gut of the fish. Two *E. saurus* were captured on 10 February 2004, and the third on 27 March 2004; two *E. saurus* were maintained in the single aquarium at any given time. To assess photoreceptor distributions and densities at the time of FAF, one fish was euthanized and prepared for light

microscopy when food was first visible in the gut. The remaining two fish were euthanized at 23 and 65 days after FAF to assess development of the visual system through metamorphosis.

Specimen and Tissue Preparation

For analysis of the effect of light and dark adaptation, fish were maintained alive in either complete darkness (or captured at night) or in bright artificial light (or captured during the day) for a minimum of 1 hour prior to ocular enucleation. The eyes of freshly euthanized juvenile fish were enucleated and dorsal aspects of eyes were immediately marked for later orientation. The anterior segment (cornea, iris, lens) of each eye was immediately removed and the eyecup (containing the retina) was placed in the appropriate fixative (see below) for a minimum of 24 hours with agitation and one change of fixative. The eyes of settlement-stage larvae were sufficiently small to allow rapid penetration of the fixative agent without cutting them open or removing them from the fish. Settlement-stage larvae were therefore immersion fixed whole and identified under a dissecting microscope, after which heads were removed and returned to fixative.

Immunofluorescence

For opsin immunocytochemistry, tissue samples were fixed in a solution of 4% paraformaldehyde and 15% picric acid in 0.1M sodium phosphate buffer at pH 7.4. Following fixation, samples were rinsed in phosphate buffered saline, infiltrated with 25% sucrose in 0.1M phosphate buffer, pH 7.4, and then embedded in Tissue-Tek and frozen at –25 C. Frozen cross-sections (16 µm) were subsequently prepared on a Leica cryostat, and sections thaw-mounted onto gelatin-coated glass microscope slides. For larval and tank-reared fish, sections were made across the entire eye in the dorso-ventral plane; for juveniles, cross-sections were made from tissue samples from different regions of the eye (nasal, temporal, dorsal, ventral). After drying at room temperature, slides were placed in fixative for 5 minutes and then rinsed in four changes of Tris-buffered saline (TBS), pH 7.4.

After rinsing, slides were incubated overnight (minimum 8 hours) at room temperature with anti-opsin antisera [CERN-906 (anti-cone) or CERN-922 (anti-rod)] diluted in TBS containing 0.25% λ-carrageenan, 1% BSA and 0.3% Triton X-100 (λ-CBT). After rinsing in four changes of TBS, slides were incubated with agitation for 1 hour at room temperature with a fluorescein-labeled secondary antibody (goat anti-rabbit IgG conjugated to fluorescein isothiocyanate; GAR-FITC; Cappel Inc., now MP Biomedicals, Irvine CA). Slides were

coverslipped with TBS as mounting solution, and viewed and digitally photographed on a Zeiss Axioskop 2 equipped with a Zeiss Attoarc 2 (HBO 100W) light source and a Pixera Penguin CL-600 camera.

Light Microscopy

For light microscopy, juvenile eyecups (cut into quadrants) and whole larval heads were fixed in a solution of 2.5% glutaraldehyde, 2.5% paraformaldehyde, and 0.008% $CaCl_2$ in 0.1M sodium cacodylate buffer, pH 7.4. After the initial fixation, tissues were post-fixed in 1% osmium tetroxide for 1 hour to improve visibility under the microscope. Tissues were then dehydrated through increasing concentrations of acetone, infiltrated with mixtures of acetone and Durcupan ACM epoxy resin (Source: Electron Microscopy Sciences, catalog number RT14040), and then embedded in Durcupan resin blocks for sectioning. After embedding, 1.0μm sections were cut on glass knives, mounted on slides and stained with a 1:1 mixture of 1% azure II in water and 1% methylene blue in 1% sodium borate.

Retinomotor Movement

In light-adapted retinas, the extents of retinomotor movements were quantified in four developmental stages of *E. saurus* (one individual each—settlement-stage, at FAF, 23 and 65 days after FAF) and in one juvenile *M. atlanticus* (for comparison). Ten locations were randomly chosen for measurements in the mid-dorsal region of the retina. The minimum extension of rods (posteriorly into the RPE) was determined by measuring the distance from the outer limiting membrane (OLM) to the base of the closest rod ellipsoid in the rod cell bundle.

Photoreceptor Density

For larval fish, 1.0μm-thick cross-sections were made across the entire eye in the dorso-ventral plane; for larger fish, 1.0μm-thick cross-sections were made from different regions of the eye (nasal, temporal, dorsal, ventral). All rod and cone nuclei were counted (regardless of size) in four adjacent 0.05mm strips from each retinal region in juvenile fish; for larvae, data were collected from four adjacent 0.05mm strips in cross sections having the greatest lens diameters (i.e., the center of the retina; cf. Pankhurst et al., 1993). Since all cells were quantified within strips of retina exactly 0.05mm in length, linear cell density (in cross-section) was recorded as number of cells/0.05mm. Counts were made at a magnification of 1000x and rectified against digital images taken of each region to be counted at lower magnification (400x); nuclei were marked on these digital images while counting using photo editing software. Immunofluorescent

labeling of rods and cones with antisera (CERN-906 and CERN-922) that label both outer segments and cell bodies (including nuclei) was initially used to determine which morphologically distinct type of nucleus belonged to each type of receptor.

Photoreceptors were quantified in the retina of one individual of each of the following: settlement-stage *M. atlanticus* and *E. saurus*, tank-reared postsettlement *E. saurus* at the three developmental stages described above, juvenile *M. atlanticus* (estimated age 3-4 months based upon size [85.3mm standard length (SL)] and date of capture: 23 November 2003), juvenile *E. saurus* (estimated age 6-7 months based upon size [192mm SL] and date of capture: 24 September 2003), and juvenile *A. vulpes* (estimated age 2-4 months, based upon size [62mm SL] and date of capture: 21 January 2004). For settlement-stage fishes and tank-reared *E. saurus*, photoreceptors were quantified only in the central retina, because the retinas were small, photoreceptor classes were less distinct at the dorsal and ventral margins, and the central retina was believed to be the primary visual axis. For juveniles, counts were made in the mid-lateral portion of each retinal region, 2/3 the distance from the center of the retina to the outer margin.

Theoretical Visual Acuity

In order to assess changes in the abilities of developing elopomorph fishes to visually discriminate prey and other objects, theoretical photopic visual acuity was estimated in settlement-stage larvae and developing *E. saurus*. The minimum separable angle in degrees (°MSA: the smallest visual angle at which two points can be discriminated as separate), was calculated based on the density of cones in the central retina and the lens diameter using the following equation from Lara (2001):

$$a = (c/2.5\ r)\ x\ (180/\pi)$$

where *a* = °MSA, *c* = distance between centers of adjacent cones, and *r* = radius of the lens. Theoretical visual acuity was calculated for settlement-stage *M. atlanticus* and *E. saurus*, and for each developmental stage of the tank-reared *E. saurus* (0, 23, 65 days after FAF).

RESULTS

Settlement-stage Larvae

Photoreceptor Density and Visual Acuity

At settlement, *M. atlanticus* (25.69mm SL) and *E. saurus* (30.30mm SL) had a similar density of rods in the central retina (Fig. 2; *M. atlanticus* 16 ± 1.00 rods/0.05mm, *E. saurus* 16 ±
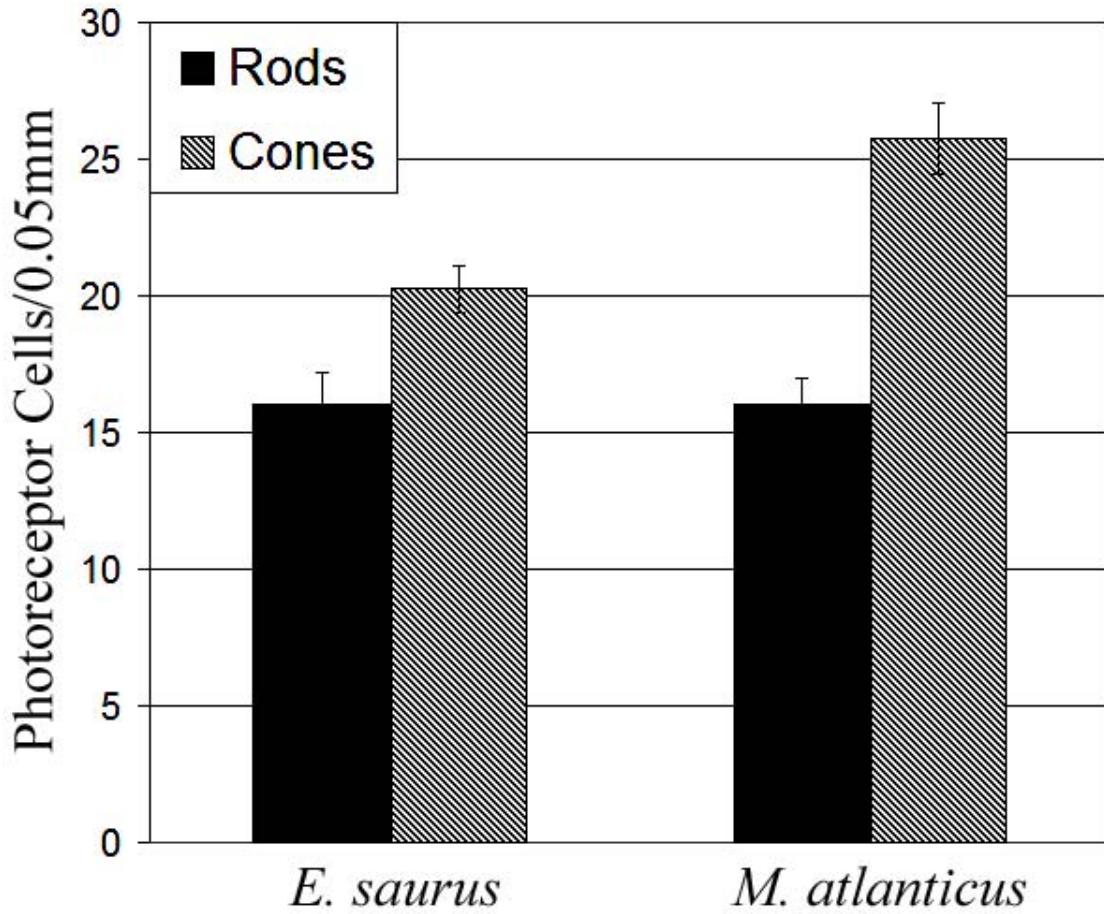
Figure 2. Photoreceptor densities in the central retina of settlement-stage *E. saurus* and *M. atlanticus*. Error bars represent standard error of the mean of four adjacent 0.05mm strips in the central retina.

1.22 rods/0.05mm), although *M. atlanticus* had a higher cone density (25.75 ± 1.31 cones/0.05mm) than *E. saurus* (20.25 ± 0.85 cones/0.05mm). *Megalops atlanticus*, however, had a smaller lens diameter (*M. atlanticus*: 0.13mm, *E. saurus*: 0.18mm). Therefore, despite the higher cone density, *E. saurus* had better calculated spatial visual acuity (*M. atlanticus*: 0.6648, *E. saurus*: 0.6164; units are degrees of minimum visual angle [°MSA] that can be discriminated, therefore a smaller number indicates better acuity).

Photoreceptor Distributions

Though rod and cone nuclei could not be clearly differentiated in peripheral regions of settlement-stage retinas, differential immunofluorescent labeling clearly demonstrated interspecific differences in relative densities of photoreceptor cell types across the retina (Figs. 3,

4). Results presented here are derived from dorso-ventral cross-sections of retina; thus, comparisons are made among dorsal, central and ventral retina.

Settlement-stage *E. saurus* (40.75mm SL) and *M. atlanticus* (23.25mm SL) had similar distributions of photoreceptors, although they appeared to differ in relative densities of rods and cones (Fig. 3A-D). Both had the greatest density of rods in the ventral retina relative to the central and dorsal retina (Fig. 4 shows *M. atlanticus* in detail). Cone cells in both species were most densely concentrated in the dorsal retina. Relative to *E. saurus*, settlement-stage *M. atlanticus* appeared to have more densely packed rods and cones throughout the retina.

Settlement-stage *A. vulpes* (48.32mm SL) differed from *E. saurus* and *M. atlanticus* in photoreceptor arrangement at settlement (Fig. 3E-F). Higher densities of both rods and cones
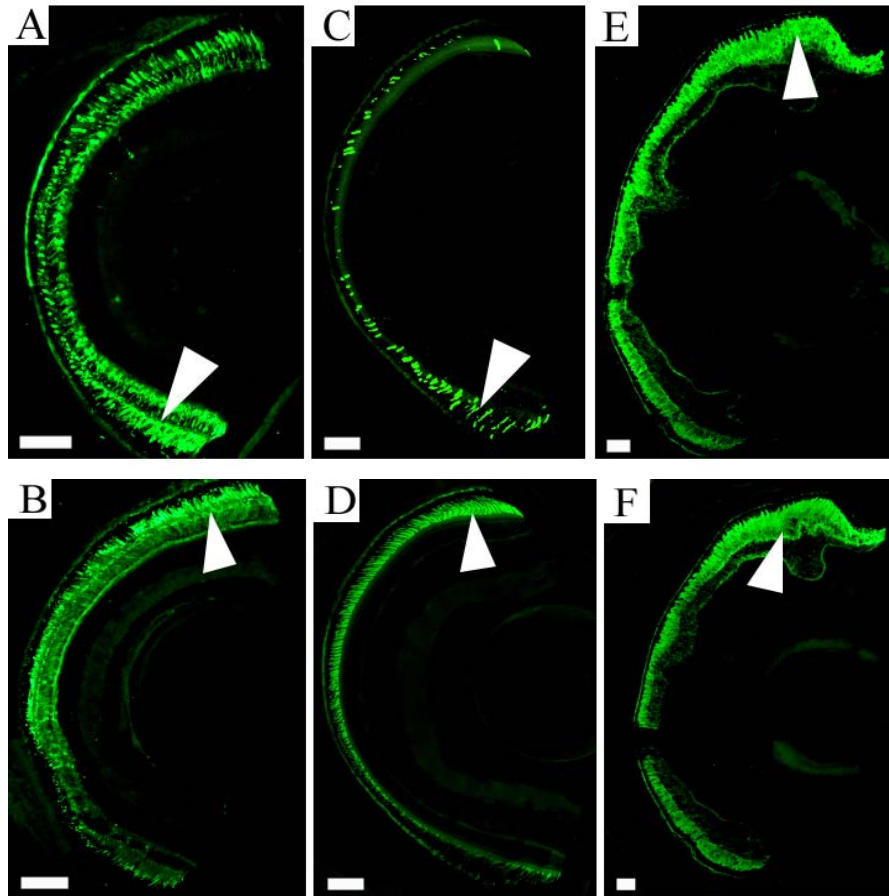
Figure 3. Relative distributions of rod and cone photoreceptors dorso-ventrally across the retina in settlement-stage *M. atlanticus* (A, B), *E. saurus* (C, D), and *A. vulpes* (E, F). A, C, E: rod cells labeled with primary antibody CERN 922 and FITC-labeled secondary; Figures B, D, F: cone cells labeled with primary antibody CERN 906 and FITC-labeled secondary. Arrows indicate the region of retina with greatest density of photoreceptors. Bar = 50μm.

were observed in the dorsal region of the *A. vulpes* retina relative to the central and ventral regions. Even so, rods were densely distributed throughout the *A. vulpes* retina compared to the sparse distribution in the middle and dorsal regions of the *E. saurus* and *M. atlanticus* retinas.

Lack of Retinomotor Movements

In all three species investigated, both rods and cones were present at settlement, but photoreceptor retinomotor movements were not apparent at this stage. That is, light and immunofluorescence microscopy revealed that rod and cone photoreceptor outer segments were located in approximately the same horizontal plane (i.e. they were not separated vertically with respect to each other as would be expected if retinomotor movements were occurring; see Fig. 4).
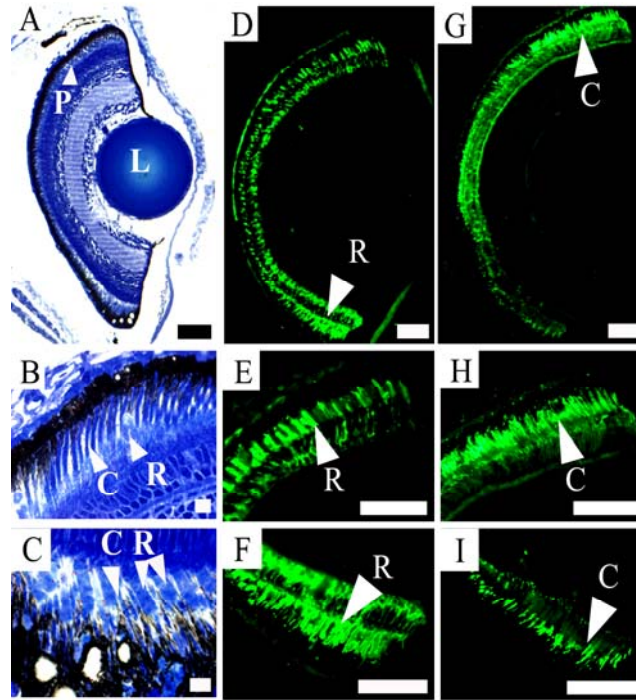
Figure 4. Distributions of rod and cone photoreceptors dorso-ventrally across the retina of settlement-stage *M. atlanticus*. A-C: Light micrographs showing overall structure of the eye and locations of rods and cones; A: Whole dorso-ventral cross section (100x); B: Dorsal (1000x); C: Ventral (1000x). D-F: Immunologically-stained rod cells, labeled with anti-rod primary antibody CERN 922 and fluorescently-labeled secondary antibody, showing greater density of rods in the ventral retina; D: Whole dorso-ventral cross-section (100x); E: Dorsal (400x); F: Ventral (400x). G-I: Immunologically-stained cone cells, labeled with anti-cone primary antibody CERN 906 and fluorescently-labeled secondary antibody, showing greater cone density in the dorsal retina; G: Whole dorso-ventral cross-section (100x); H: Dorsal (400x); I: Ventral (400x). Abbreviations: L: lens; P: photoreceptor layer; C: cone outer segments; R: rod outer segments. B-C: Bar = 5μm; A, D-I: Bar = 50μm.

Tank-Reared *E. saurus*

Photoreceptor Density and Visual Acuity

In laboratory-reared *E. saurus*, cone density decreased between settlement (20.25 ± 0.85 cones/0.05mm; 30.30mm SL) and FAF (14.25 ± 0.75 cones/0.05mm; 27.35mm SL) but changed very little thereafter (Fig. 5). There was, however, a dramatic increase in lens diameter between FAF (0.20mm) and 23 days thereafter (0.435mm lens dia.; 26.85mm SL;), and thus a rapid increase in calculated spatial visual acuity (from 0.7883°MSA at FAF to 0.3757°MSA 23 days thereafter) even though cone cell density was constant. Rod cell density, however, changed very

A **B**
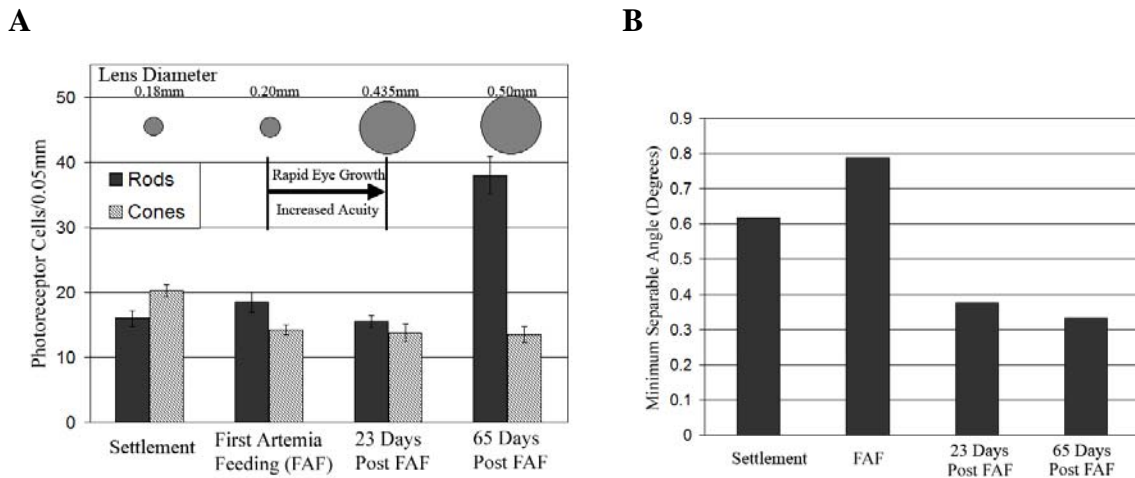
Figure 5. A: Rod and cone cell densities in the developing *E. saurus* central retina; lens diameters relate to visual acuity and are drawn to scale; error bars represent standard error of the mean. Settlement: transition period from pelagic to estuarine life; First *Artemia* feeding (FAF): first time exogenous feeding was observed in laboratory-reared specimen; 23 days after FAF; 65 days after FAF; specimens were reared from settlement-stage with a constant supply of *Artemia nauplii* for food.
B: Theoretical spatial visual acuity (MSA°) calculated from cone cell density and lens diameter; smaller bar indicates greater visual acuity (i.e. increase in acuity between FAF and 23 days past FAF, reflecting the rapid increase in lens diameter).

little between settlement and 23 days after FAF, but increased dramatically between 23 and 65 days (36mm SL) after the onset of lab feeding.

Retinomotor Movements

Both cones and rods were obvious throughout the *E. saurus* retina at all times post-settlement, and retinomotor movements were apparent from the time of FAF onward. The retinas of post-settlement lab-reared *E. saurus* were all in a light-adapted state—cones were retracted toward center of the eye, rods extended posteriorly toward RPE. The degree of

extension of rod cells (minimum extension from the outer limiting membrane to base of rod ellipsoid) increased between FAF (0.0199 ± 1.08E^{-3}mm) and 23 days later (0.0283 ± 7.16E^{-4}mm), and again at 65 days after FAF (0.0447 ± 2.22E^{-3}mm; Fig. 6). The extent of retinomotor movements in these earlier stages was not compared with those in juvenile *E. saurus* because all juveniles examined in this study were in a light-adapted state.
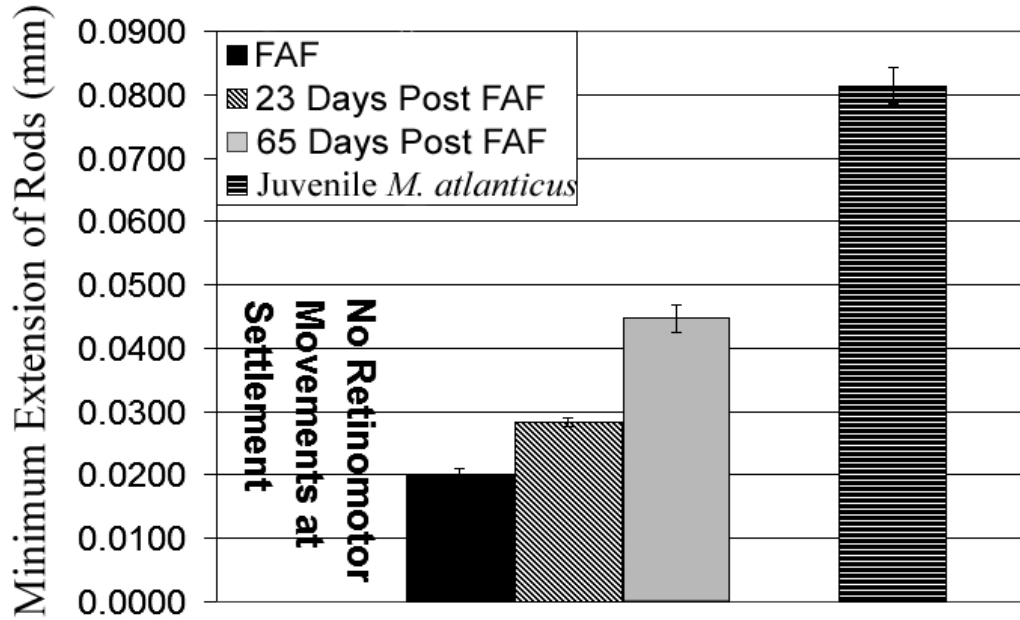
Figure 6. Degree of retinomotor movements of rod cells throughout development in *E. saurus* from settlement through 65 days after FAF; compared with degree of rod movements in juvenile *M. atlanticus*. Measurements made from the outer limiting membrane to the closest rod ellipsoid in each bundle. Error bars represent the standard error of the mean (n=10 random measurements).

In juvenile *M. atlanticus* and *E. saurus*, rod outer segments were grouped into discrete bundles. This bundling was not apparent in settlement-stage *E. saurus* or *M. atlanticus*; the earliest stage when grouped rods became apparent was in laboratory-reared specimens at 65 days post-FAF. During retinomotor movements, grouped rod outer segments apparently moved in a coordinated fashion (bundles were maintained), and cone outer segments apparently moved individually (Fig. 7).
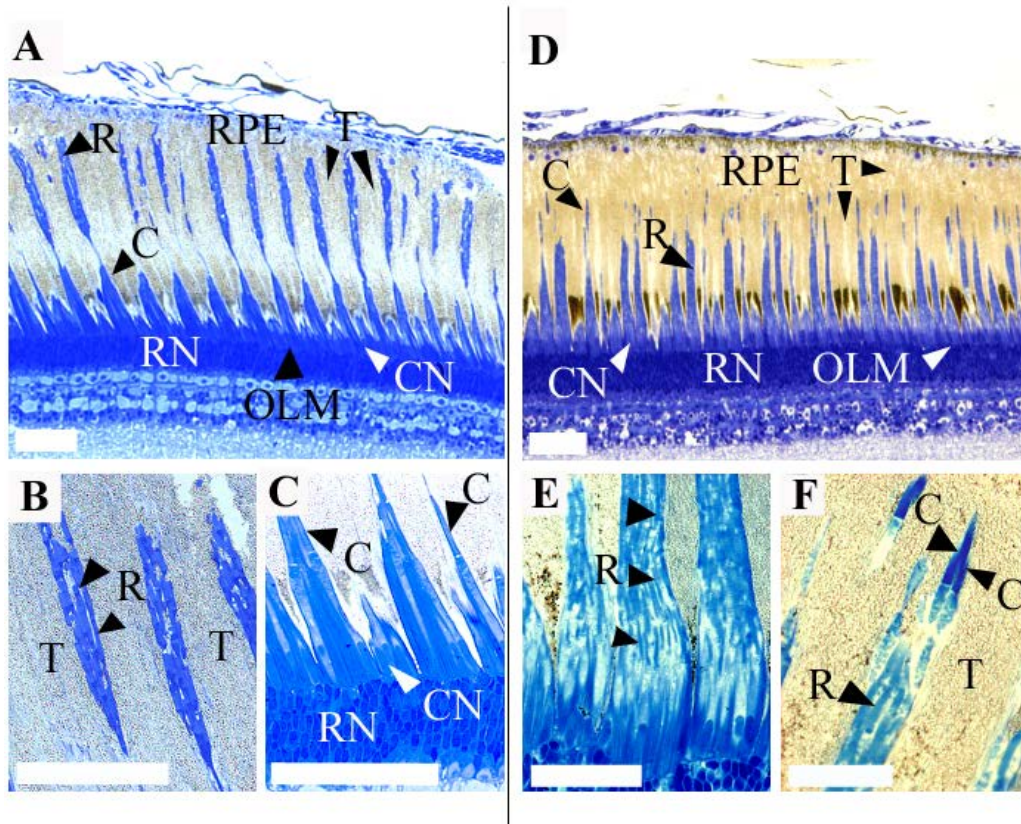
Figure 7. Photoreceptor retinomotor movements in juvenile *M. atlanticus* retina. A: Light-adapted retina with cones retracted toward the inner retina and bundled rods extended toward the RPE; reflective tapetum surrounds bundles. B, C: Higher magnification images showing extension of bundled rod outer segments and retracted clusters of cone outer segments. D: Dark-adapted retina with cones extended toward the RPE, surrounded by tapetum and rods retracted toward the inner retina. E, F: Higher magnification images showing retracted rod outer segment bundles and extended cone outer segments. Abbreviations: C: cone; R: rod; RPE: retinal pigmented epithelium; T: tapetum; RN: rod nuclei; CN: cone nuclei; OLM: outer limiting membrane. Bar = 50μm.

Juveniles

Photoreceptor Density and Visual Acuity

Photoreceptor densities in juvenile fish differed among species examined, and among retinal regions (dorsal, ventral, nasal, temporal) in a given individual (Fig. 7). *E. saurus* had the highest overall rod density throughout the retina (Avg. 133.3 ± 3.96 rods/0.05mm), and *A. vulpes* had the lowest (Avg. 51.6 ± 2.58 rods/0.05mm). *A. vulpes* had lowest rod density in the ventral (upward-looking) region; all other regions of the *A. vulpes* retina had higher but similar rod densities. In *E. saurus*, rods were most dense in the nasal (backward-looking) region, and least dense in the temporal (forward-looking) region. *Megalops atlanticus* had its highest rod density in the ventral (upward-looking) and temporal (forward-looking) regions of the retina.

Among the three species, *A. vulpes* had the greatest density of cones in all retinal regions. Within the *E. saurus* retina, cones were most dense in the nasal (10.25 ± 0.75 cones/0.05mm) and temporal (7.5 ± 0.96 cones/0.05mm) regions (backward- and forward-looking regions, respectively). The *A. vulpes* retina had its highest cone densities in these same regions (nasal: 10.0 ± 0.41; temporal: 10.25 ± 0.75 cones/0.05mm). In *M. atlanticus,* cones were most dense in the ventral (9.75 ± 1.25 cones/0.05mm) and temporal (11.0 ± 1.08 cones/0.05mm) regions (upward and forward-looking regions, respectively).

Retinal Organization and Retinomotor Movements

Stacked rod cells (outer segments in multiple layers) were observed in juveniles of all three species. In juvenile *A. vulpes* rods were densely packed, with little or no space between adjacent outer segments. Stacked rods in juvenile *M. atlanticus* and *E. saurus* formed discrete groups of densely packed cells (Fig. 8). These grouped rods were observed in both light-adapted and dark-adapted retinas, and retinomotor movements occurred with grouped rod outer segments moving in a coordinated fashion, (Fig. 9). Cone cells are not stacked and do not appear to be grouped, or at least not to the extent of rod cells.

Retinomotor movements apparently occur markedly in the juveniles of all three species, although both light and dark-adapted specimens have only been examined in *M. atlanticus* (Fig. 9). The retinas of all juvenile E. saurus and *A. vulpes* examined (collected and processed under bright light conditions) were in a light-adapted state—cones were contracted toward the center of the eye, and rods were extended toward the RPE (see Fig. 8).

Juvenile *M. atlanticus* and *E. saurus* each had a substantial light-reflective retinal tapetum lucidum (Figs. 8, 9). In dark-adapted retinas, extended cone outer segments were completely surrounded by tapetal material, removed from the light path; the outer margins of rod bundles were surrounded by tapetum with the inner margins exposed to incoming light. In light-adapted retinas, rod bundles were completely surrounded by tapetum, removed from the light path; retracted cone cells were exposed to incoming light (Fig. 9). Reflection from the tapetum ("eye shine") was readily observed in juvenile *M. atlanticus* and *E. saurus* when bright light was shone into the eyes of live fish at night. A tapetum was not apparent in juvenile *A. vulpes* retina—it was not observed in sections of retina (Fig. 8) and no eye shine was apparent.

A
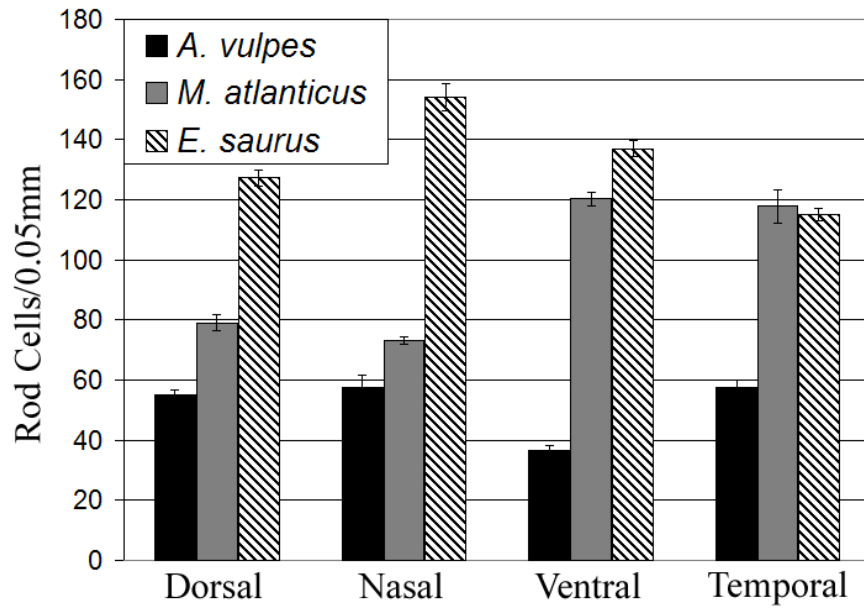
B
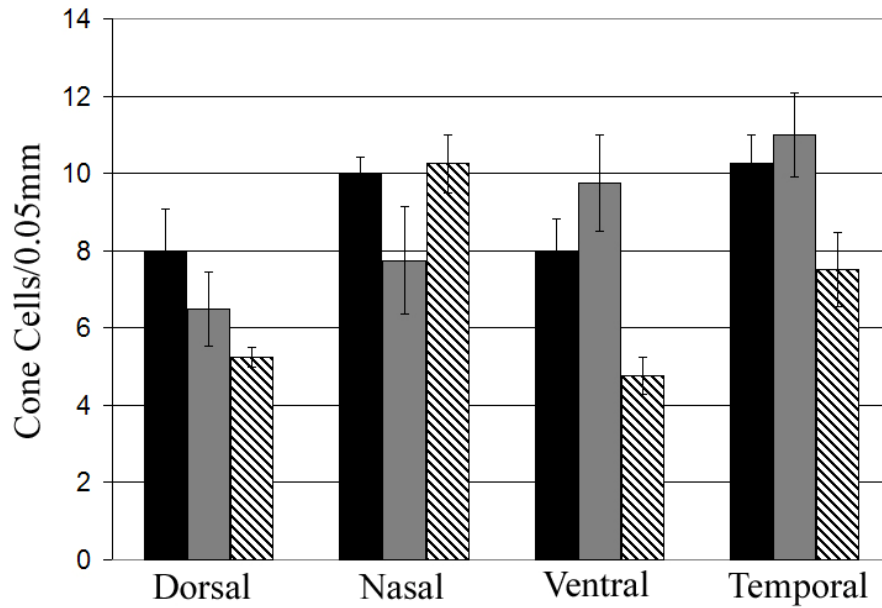
Figure 8. Distributions of rod (A) and cone (B) photoreceptors across the retina in juvenile *A. vulpes*, *E. saurus* and *M. atlanticus*. Cell nuclei were counted in four adjacent 0.05mm strips of retina; error bars represent standard error of the mean of the four strips.

Figure 8. Stacked and bundled rod photoreceptors in juvenile *M. atlanticus* light-adapted retina (A, B) with a substantial tapetum. Stacked rods in juvenile *A. vulpes* light-adapted retina (C, D): rod cells are not bundled and tapetal material is not apparent. A, C: labeled with anti-rod CERN 922 and FITC-conjugated secondary antibody. B, D: stained with 1:1 1% methylene blue/1% azure II. Abbreviations: C: cone outer segments; R: rod outer segments; T: tapetum; M: melanin. Bar = 50μm.
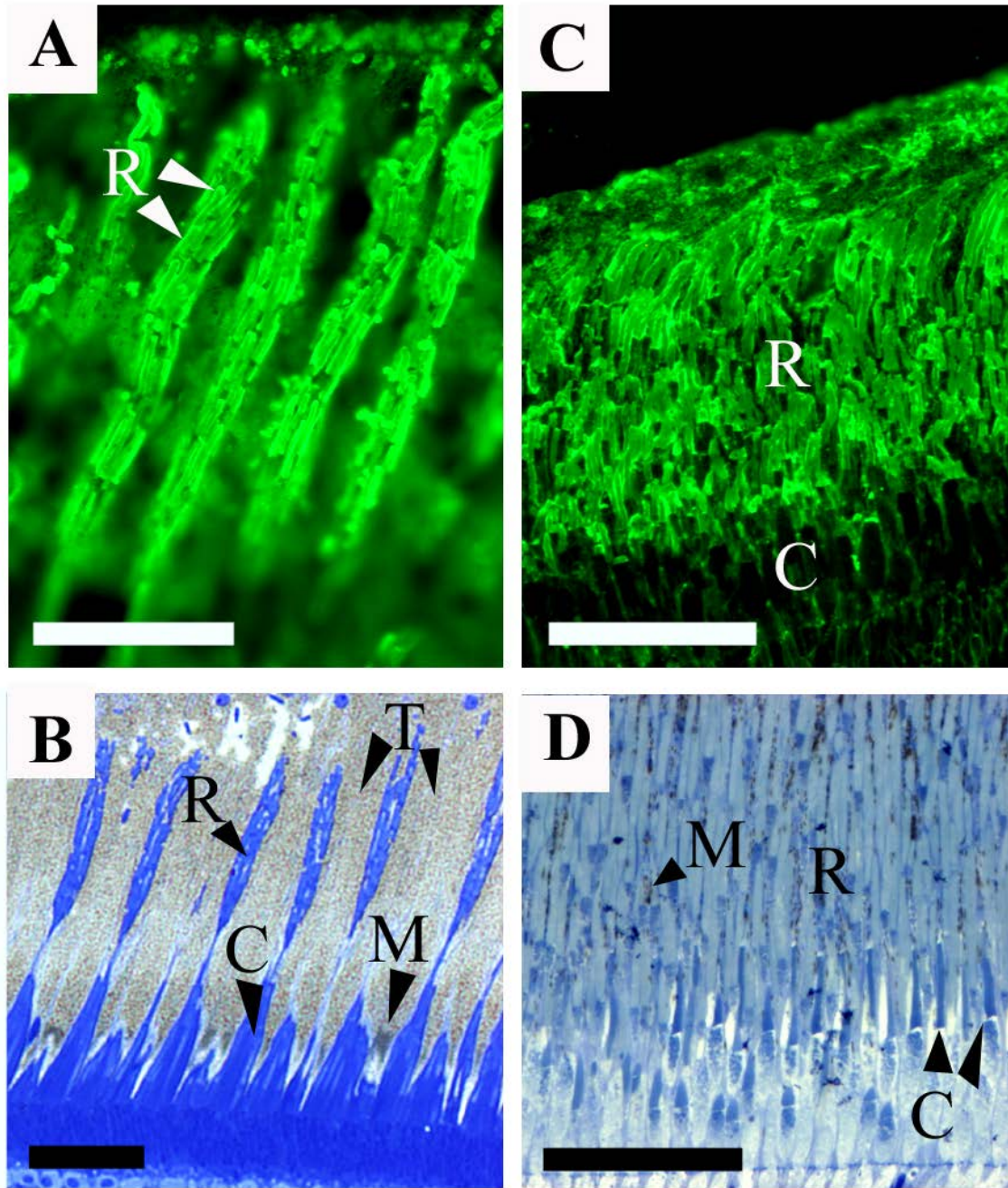
Figure 9. Stacked and bundled rod photoreceptors in juvenile *M. atlanticus* light-adapted retina (A, B) with a substantial tapetum. Stacked rods in juvenile *A. vulpes* light-adapted retina (C, D): rod cells are not bundled and tapetal material is not apparent. A, C: labeled with anti-rod CERN 922 and FITC-conjugated secondary antibody. B, D: stained with 1:1 1% methylene blue/1% azure II. Abbreviations: C: cone outer segments; R: rod outer segments; T: tapetum; M: melanin. Bar = 50μm.

DISCUSSION

Despite the fact that vision is critical to the survival of many fishes, its ecological importance and its changing roles and mechanisms over the course of development have been explored in relatively few marine species (but see for example Neave 1984, Pankhurst 1987, Evans and Fernald 1990, Evans et al. 1993, Shand 1994, 1997, Haacke et al. 2001, Lara 2001). As fishes develop from larvae to adults, changes in visual requirements occur because of ontogenic shifts in habitat, morphology and behavior. The continuously growing teleost retina (in contrast to the static mammalian retina) allows fish visual systems to change as they mature, and therefore to maintain appropriate function as habitat and feeding behavior change over the course of development. This is particularly interesting in the teleost subdivision Elopomorpha, which contains a highly diverse assemblage of species united primarily on the basis of shared larval morphology (see Smith 1989). The development of vision has been explored in only one species of elopomorph—the European eel, *Anguilla anguilla* (Pankhurst 1983, Braekevelt 1984, 1985, 1988 a, b, Pfeiler 1989). The results presented here show that retinal morphology and photopigment content (and therefore likely function as well) also change as elopomorphs mature, and suggest that changing retinal architecture is the basis for continued optimal vision as fish mature through different habitats and behaviors.

Developmental Changes in Photoreceptor Distribution

Little is known about the ecology and behavior of *M. atlanticus, E. saurus* and *A. vulpes* during settlement and early juvenile stages; far less is known about larval stages. However, careful analysis of retinal architecture and function should allow correlations to be drawn between retinal architecture and behavior, and should allow formulation of testable hypotheses about visual capabilities at different life stages.

Settlement-Stage Larvae

Photoreceptor arrangements differ in settlement-stage elopomorph fishes that are ecologically distinct as juveniles. Histologically stained semi-thin cross-sections of settlement-stage *M. atlanticus* and *E. saurus* retinas exhibited similar rod densities in the central retina, but cone density was slightly higher in M. atlanticus. Immunofluorescent labeling of rod and cone opsins confirmed that photoreceptor distributions are similar in *M. atlanticus* and *E. saurus* at settlement (although relative densities of rods and cones differ), but revealed a distinct pattern in *A. vulpes*. In *M. atlanticus* and *E. saurus*, the highest relative density of rod cells was in the

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ventral retina, with sparsely distributed rods throughout the remainder of the retina (Figs. 3, 4). Greatest cone density was observed in the dorsal retina. This pattern was even more pronounced in *E. saurus*, with far fewer rods in the central and dorsal retina than in the ventral retina (Fig. 3). Settlement-stage *A. vulpes* showed a very different pattern, with an area of increased rod and cone density in the dorsal retina. Rods and cones were present throughout in a solid layer, but the dorsal portion of the retina was greatly thickened and cones were particularly dense there. Both patterns differ from the general pattern found in many shallow living diurnal teleosts, where rod densities are greater in the dorsal retina and cone densities are greater in the ventral retina just prior to settlement (Shand 1994).

At settlement, the larvae studied here are undergoing metamorphosis and making the transition from a larval pelagic existence to a coastal/estuarine existence. It is therefore expected that the retina is in a transitional state as well and retinal organization reflects aspects of both the early larval and juvenile conditions. Little is known about the ecology of young leptocephalus larvae. Modes of feeding/nutrient acquisition in leptocephali are poorly understood (Pfeiler 1986, 1989, Smith 1989; Otake et al. 1993, Mochioka et al. 1993, Mochioka and Iwamizu 1996), but at least some leptocephali migrate vertically in the water column—toward the surface at night, and deeper during the day (Pfeiler 1989). If this is true for the species studied here, they are exposed to relatively little visible light at any time. The dense array of rods in the ventral retina (if present in younger larvae) might be an adaptation to capture the dim downwelling light from the surface. When looking up toward a dimly lit surface, the high sensitivity of rod cells may be required (but high spatial acuity not required) for detection of ambient illumination conditions, which in turn may drive the timing and extent of vertical migration.

The similar photoreceptor arrangements in *M. atlanticus* and *E. saurus* at settlement [dense rods ventrally, dense cones dorsally] likely relate to similarities in larval and post-settlement ecology between the two species; ontogenic similarities may also be attributable to the closer evolutionary relationship between M. atlanticus and *E. saurus* compared with *A. vulpes* (Forey et al. 1996, Obermiller and Pfeiler 2003). Young larvae of both species occur in deep oceanic water—both have been captured over water in excess of 100m in the Florida Straits (personal observation), and very small *M. atlanticus* leptocephali have been collected in the Yucatan Channel and the Southwestern Gulf of Mexico in waters greater than 200m depth (Smith 1980). As juveniles, both live in estuarine habitats, commonly in turbid, tannin-stained

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mangrove marshes and impounded mosquito ditches (Wade 1962, Zale 1989, personal collections). Although little is known about the feeding ecology of either species during the juvenile stage, both feed nocturnally and diurnally as adults, and juveniles and adults of both species feed at or near the surface (personal observations). Persistence of dense concentrations of rods in the ventral retina through settlement may have functional importance for feeding in the highly turbid waters that juvenile *M. atlanticus* and *E. saurus* typically inhabit. In these dimly lit waters, the high sensitivity of rods may be required to provide sufficient contrast detection for accurate predatory targeting when prey is between the fish and the surface. The results presented here show that both *M. atlanticus* and *E. saurus* maintain high ventral rod density through metamorphosis into the juvenile stage.

The explanation of cone distribution in settling *M. atlanticus* and *E. saurus* (higher in dorsal retina) is more problematic. The dorsal retina primarily receives light from deeper (and therefore darker) water. The low absolute sensitivity of cones generally would seem to preclude their utility in the dorsal retinas of fish over deep water or in highly turbid waters. It is possible that the dense array of cones in the dorsal retina is not a requirement at this stage, but is simply a result of lack of space in the small larval eyes and the need for rods in the ventral retina. Alternatively, cones in the dorsal retina may serve during daylight to detect bright specular highlights reflected from potential prey and predators below, or to detect appropriate bottom habitat for settlement.

The greater cone density in *M. atlanticus* relative to *E. saurus* (in the central retina) may relate to developmental progress of these species at settlement. Overall, *M. atlanticus* settled at a much smaller size (Avg. 22.25 mm SL, N=10) than *E. saurus* (Avg. 39.69 mm SL, N=15), and thus may be less developed at settlement. Since most teleost larvae begin life with cone-dominated (or cone-only) retinas and then rapidly add rods around the time of metamorphosis (Blaxter 1986, Evans and Fernald 1990, Shand 1997, Lara 2001), higher cone density in *M. atlanticus* may reflect settlement and onset of metamorphosis at an earlier developmental stage. Alternatively, differences in rod:cone ratios between *M. atlanticus* and *E. saurus* may represent differences in post-metamorphic ecology. Although *M. atlanticus* often inhabit more turbid waters (Zale 1989), they may feed at the surface more frequently than *E. saurus* [inferred from their upturned mouth], and thus would be exposed to higher light levels when feeding (cones function in relatively high-light environments). Additionally, juvenile *M. atlanticus* frequently

approach [and break] the surface to gulp atmospheric air (Geiger et al. 2000); *E. saurus* cannot breath air and thus do not approach the surface as frequently. The juvenile data (Fig. 7) supports this idea, showing that *M. atlanticus* maintains a much higher cone density in the ventral and temporal retinal regions than *E. saurus* after metamorphosis.

      Albula vulpes are ecologically very distinct from *M. atlanticus* and *E. saurus* as juveniles, which likely explains the very different photoreceptor distribution pattern at settlement. In contrast to the turbid estuaries inhabited by *M. atlanticus* and *E. saurus*, the juvenile *A. vulpes* examined here were collected from much clearer, more tropical waters less than 2m deep, adjacent to exposed, sandy beaches; comparable to adult *A. vulpes* habitat described by Crabtree et al. (1998). Adult *A. vulpes* feed on benthic and epibenthic prey (Crabtree et al. 1998), and the subterminal mouth and observed laboratory behaviors of juvenile *A. vulpes* suggest that they are bottom feeders as well; in stark contrast to the surface/near-surface feeding behaviors of juvenile *M. atlanticus* and *E. saurus*, respectively. It is not yet known if young *A. vulpes* larvae occur in deep oceanic waters.

      The dense array of rods and cones concentrated in the dorsal retina of *A. vulpes* during settlement may provide both high absolute sensitivity (via rods) and high visual acuity (and perhaps color vision, via cones) in the area of the retina that receives light from below. Their sub-terminal mouth indicates that settlement-stage (and juvenile) *A. vulpes* feed on items beneath them, which would be facilitated by enhanced visual function in the dorsal retina.

<div align="center">Tank-reared E. saurus</div>

      The successful capture of live settlement-stage *E. saurus* larvae in good condition, and the success of rearing them in laboratory aquaria, presented a useful opportunity to study how the elopomorph visual system makes the transition from larval to juvenile form. Despite the fact that laboratory conditions could have altered the timing of metamorphosis, our captive *E. saurus* larvae survived through metamorphosis without consuming obvious food for at least three weeks (though microscopic nutrient materials could have been absorbed or consumed), and the food consumed after metamorphosis was adequate for further development.

      Compared to settlement-stage *E. saurus*, the post-settlement individual examined immediately after the first *Artemia* feeding (FAF; 24 days after settlement), had slightly larger eyes, and exhibited slightly higher rod density and lower cone density than at settlement. These observations suggest that rod cells were being added at a faster rate than cones during

metamorphosis. Rapid addition of rods may aid with the visual transition from relatively clear oceanic waters to more turbid estuarine waters. It has also been suggested that rod pathways in the retina may increase perception of motion, which would enhance the ability to detect moving predators and prey (Wagner et al. 1998). Decreased cone density suggests decreased spatial acuity under photopic conditions.

Lens diameter was much greater in the fish examined 23 days after FAF (50 days after settlement) relative to the one examined at FAF. These fish exhibited similar rod and cone densities, so the increase in eye size means that both rods and cones must proliferate rapidly during this time. Proliferation of photoreceptors and increased lens diameter suggest that cone-based visual acuity and rod-based scotopic sensitivity both increase during this phase of maturation. Calculated visual acuity supports this idea: it essentially doubled from FAF to 23 days later (Fig. 5B). A dramatic increase in rod density (from 15.5 rods/0.05mm to 38.0 rods/0.05mm) between 23 and 65 days post-FAF might signify an increase in nocturnal feeding behavior, or it may occur in anticipation of (or concomitant with) movement into highly turbid habitat.

<div align="center">Juveniles</div>

The relatively large size of juvenile eyes allowed comparative analyses not only among species, but also among different regions of the same retina. Juvenile *M. atlanticus*, E. saurus and *A. vulpes* make interesting models for studies of visual architecture and function because, after the leptocephalus stage, they radiate dramatically in post-settlement habitat, in their overall morphology, and in their behaviors. Juvenile *M. atlanticus* and *E. saurus* often inhabit areas of high turbidity, although *M. atlanticus* can survive anoxic water better because of their ability to gulp air at the surface. Conversely, juvenile *A. vulpes* inhabit shallow, clear waters along sandy beaches. Feeding behaviors also differ: *M. atlanticus* have an upturned mouth, *E. saurus* have a more terminal mouth, and *A. vulpes* have a subterminal mouth, suggesting that these species primarily feed at the surface, midwater or just below the surface, and at the bottom, respectively.

Among the three species studied, juvenile *A. vulpes* had the lowest overall density of rods and the highest overall density of cones. Because juvenile *A. vulpes* inhabit clear shallow waters, they are exposed to very high light levels during the day, and probably to significant levels of illumination at night. High cone density, especially in dorsal, nasal, and temporal regions of the retina, likely provides high spatial acuity (and perhaps color vision) for diurnal bottom feeding,

for capturing prey stirred up by wave action, and for avoidance of mid-water predators. With the lowest rod densities of the three species, nocturnal vision in *A. vulpes* may be inferior. However, the higher density of rods in *A. vulpes* dorsal retina (lower in ventral retina) and the presence of stacked rods may provide significant nocturnal visual capacity in clear waters where even dim celestial light can penetrate the shallow depths.

Higher rod densities in juvenile *E. saurus* and *M. atlanticus* may be an adaptation allowing greater nocturnality and vision in more turbid and deeper waters. In *M. atlanticus*, the ventral and temporal regions (looking forward and upward, respectively) of the retina had the highest densities of both rods and cones. The strongly upturned mouth of *M. atlanticus* aids in their explosive predatory behavior in which they ambush prey from below (Wainwright and Bellwood 2002; personal observations); high cone and rod densities in the ventral and temporal retina should provide the best spatial resolution and absolute sensitivity under both diurnal and nocturnal feeding conditions. This photoreceptor arrangement may also aid in predator avoidance: juvenile *M. atlanticus* inhabit turbid, often anoxic waters with no other large highly mobile aquatic predators (alligators may be the only significant aquatic threat), and they often gulp air at the surface. Thus, their greatest predatory threat likely comes from above (birds), so high sensitivity and acuity in ventral and temporal regions of the retina may allow effective detection of most potential predators.

Juvenile *E. saurus* had highest rod density in the nasal retina, and highest cone densities in the nasal and temporal retina; thus, they likely have highest visual acuity and sensitivity in the forward and backward visual fields. The terminal mouth of *E. saurus* suggests that they are forward-striking predators in midwater or just below the surface (personal observations of tank-feeding support this idea). High photoreceptor densities in temporal and nasal regions of the retina should enhance spatial resolution and sensitivity in the horizontal plane in which *E. saurus* are most likely to engage prey and/or predators.

Retinomotor Movements

Cellular retinomotor movements include elongation and contraction of photoreceptor myoid regions (Fig. 1; Blaxter 1975, Kusmic and Gualtieri 2000), and dispersal and aggregation of melanin pigment granules in the retinal pigmented epithelium (RPE). These events may be adaptations that (1) allow a greater number of photoreceptor outer segments to exist in a given lateral expanse of the retina, thereby increasing visual acuity and scotopic sensitivity, (2) allow a

given class of photoreceptor to have its outer segments closer to incoming light at optimal times of day, and/or (3) shield highly sensitive rod cells from intense light during daytime (Kusmic and Gualtieri 2000). In the elopomorph fish species studied here, retinomotor movements appear to become activated during or after settlement. Thus, onset of retinomotor function may correlate either with a particular state of development in the retina, or with changing habitats and behaviors.

At settlement, *E. saurus* appeared to lack retinomotor movements, since no vertical separation between the rod and cone cell outer segments was apparent in dark-adapted retinas (if both rods and cones exhibited retinomotor activities, dark-adapted retinas should display cones in an elongated state, and rods in a contracted state). Separation was apparent, however, at the time of the first *Artemia* feeding (in tank-reared specimens), suggesting that retinomotor movements were occurring at that time.

Onset of retinomotor movements during development may provide increased cone-mediated spatial visual acuity in bright light, and rod-mediated spatial acuity in dim light (Evans and Fernald 1990). Thus, the absence of retinomotor movements may explain the existence of regions of pronounced cone or rod dominance in settlement-stage fishes (see Figs. 3 and 4). That is, the type of photoreceptor that is most useful in a particular region of the retina dominates that region of retina. Regions of specialization, such as areas of high photoreceptor cell density, occur in juvenile retinas as well, but these may not involve dominance or exclusion of one cell type over another as in larvae. For example, in juvenile *M. atlanticus*, densities of both rods and cones were highest in the ventral and temporal regions of the retina. Thus, onset of retinomotor movements may allow dense arrays of both rods and cones in a given region of the retina.

As photoreceptor densities increased through the course of settlement-to-juvenile development, so did the distances of vertical separation between rod and cone cells. In laboratory-reared *E. saurus*, a tremendous increase in rod cell density occurred between 23 and 65 days post-FAF; during this same time a similarly great increase occurred in the apparent magnitude of retinomotor movement (inferred from the distance of rod cell extension from the outer limiting membrane in dark adapted retinas). Retinomotor movements and their development are not limited to single photoreceptors, though: similar phenomena were observed in *E. saurus* and *M. atlanticus* retinas containing bundled rod photoreceptors (see Figs. 8, 9).

The timing of onset and the extent of retinomotor movements deserve careful attention-these issues and the illumination thresholds of light and dark adaptation may differ among species. If so, such interspecific differences are almost certainly of ecological importance to the species' changing habitats and behaviors. As such, changes in habitat quality may affect survival. Fish reportedly can become disoriented during periods between complete light and dark adaptation (Masuma et al. 2001). Theoretically then, survivability could be seriously affected if young fish recruit to a location where intense turbidity (due to human activities, storms, etc.) alters light quality to a degree that prevents complete light adaptation. This possibility may be less realistic in larger individuals (i.e. adults, and especially adult elopomorphs) that can easily move to more favorable habitat.

Adaptations for Low-Light Vision

Grouped and stacked rods

Grouped and stacked rod cell arrangements occur in both juvenile *E. saurus* and *M. atlanticus* (Figs. 8, 9), and preliminary analyses (data not shown) indicate this arrangement occurs in adults as well. On the other hand, bundled rods were not apparent in juvenile *A. vulpes* (Fig. 8), but the rods were highly stacked, similar to multi-bank arrangements in several species of anguilliform eels (Bozzano 2003) and mesopelagic and deep-sea fishes (Wagner et al. 1998). Rod cell bundling and stacking may be adaptations for increased visual sensitivity in low-light environments (Wagner 1990, Wagner et al. 1998, Awaiwanont et al. 2001). Tightly clustered rods may function as macroreceptors, collecting a large amount of photonic information that converges upon many fewer higher order neurons. In effect, photoreceptor bundling may sacrifice scotopic visual acuity in favor of visual sensitivity. Stacking of rods should increase photon capture and thus enhance low-light visual sensitivity as well. Although stacked and bundled rod cells are most common in mesopelagic and deep-sea fishes, several species of anchovies (common coastal fishes of the teleost Subdivision Clupeomorpha) have this arrangement as well (Awaiwanont et al. 2001).

In tank-reared *E. saurus*, rod cell bundling appeared sometime between 23 and 65 days post-FAF, at about the same time that rod cell density increased dramatically (refer to Fig. 5). These concomitant changes suggest that visual sensitivity at night and/or in turbid water may increase during this time period—a time around which *E. saurus* shift to more turbid habitat, and/or may shift to nocturnality. Stacked rod cells were not apparent at 65 days post FAF, and

thus must develop later during the juvenile stage (i.e. when rod cell density increases to the extent that more than one layer is necessary).

Tapetum lucidum

The presence of a substantial tapetum lucidum in juvenile *M. atlanticus* and *E. saurus* (Figs. 8, 9) should greatly enhance photon capture (thus enhancing absolute sensitivity) by reflecting light back to the photoreceptors. The tapetum comprised most of the RPE in all regions of the eyes (dorsal, ventral, nasal, temporal) of *M. atlanticus* and *E. saurus*, with relatively very little melanin present. Tapetal material was not apparent in the juvenile *A. vulpes* retina (Fig. 8). The tapetum in tank-reared *E. saurus* appeared after the first *Artemia* feeding, and at 23 days post FAF was present only in the dorsal and central portions of the retina (only melanin was present in the mid-ventral region). By 65 days post FAF, tapetal material was only absent from the extreme ventral portion of the retina. The concurrent development of the tapetum and bundling of rods, along with a dramatic increase in rod density, suggest that scotopic visual sensitivity increases dramatically during this period of development.

The absence of bundled rods, the overall lower density of rods, and the lack of (or at least reduced) tapetum in juvenile A. vulpes suggest that scotopic (low-light) visual sensitivity in *A. vulpes* may not be as great as that in *M. atlanticus* and *E. saurus*. Lower scotopic sensitivity may relate to the clearer, shallower water that juvenile A. vulpes inhabit, and/or juvenile *A. vulpes* may not be as nocturnally active as *M. atlanticus* and *E. saurus*. Juvenile *A. vulpes* do, however, have densely-packed, stacked rods, similar to the multi-bank rod distributions found in many deep water fishes. Thus, juvenile *A. vulpes* may have higher scotopic sensitivity than some other shallow-water teleosts. The overall higher cone density throughout the *A. vulpes* retina coupled with the lower rod density indicate that photopic (daytime) acuity may be more important, and scotopic less important to juvenile bonefish in comparison with *M. atlanticus* and *E. saurus*.

Implications of Changing Visual Ecology

Metamorphosis is a critically important aspect of life history in elopomorph fishes, allowing them to invade new and distinct habitats, and to develop inter- and intraspecifically distinct modes of feeding. These new habitats necessarily have new and distinct optical qualities, novel food sources, and predatory pressures not previously encountered. Together, these changing environmental qualities necessitate change in function of the sensory systems used to gather information about the external world.

The elopomorphs studied here exhibit substantial changes in their visual systems during the course of settlement and metamorphosis—through addition of new photoreceptors and through alteration of cell type densities in specific regions of the retina. Not only does the visual system of a given species change, but also retinal architecture and therefore visual function diverge among species, allowing some to function optimally in turbid brackish water, and others in clear shallow coastal water.

While it is possible that changes in retinal architecture occur in response to environmental change (because of habitat shift, for example), it seems likely, especially given the results of the laboratory-reared *E. saurus* results reported here, that at least some changes in retinal architecture are genetically hard-wired. If settlement behavior is similarly hard-wired, then anthropogenic (or other) changes in environmental optical qualities may have serious adverse effects on recruitment and survival of larval elopomorph fishes.

ACKNOWLEDGEMENTS

LITERATURE CITED

Awaiwanont, K., W. Gunarso, M. Sameshima, S. Hayashi, G. Kawamura. 2001. Grouped, stacked rods and tapeta lucida in the retina of Japanese anchovy *Engraulis japonicus*. Fisheries Sci. 67:804-810.

Blaxter, J. H. S. 1975. The eyes of larval fish, p. 427-443. In M. A. Ali [ed], Vision in Fishes. Plenum Press, New York.

Blaxter, J. H. S. 1986. Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. Trans. Am. Fish. Soc. 115:98-114.

Bozzano, A. 2003. Vision in the rufus snake eel, Ophichthus rufus: adaptive mechanisms for a burrowing life-style. Mar. Biol. 143:167-174.

Bowmaker, J. K. 1990. Visual pigments of fishes, p. 81-107. In R. H. Douglas and B. A. Djamgoz, [eds], The visual system of fish. Chapman and Hall Ltd., London.

Braekevelt, C. R. 1984. Retinal fine structure in the European eel *Anguilla anguilla* II. Photoreceptors of the glass eel stage. Anat. Anz. 157:233-243.

Braekevelt, C. R. 1985. Retinal fine structure in the European eel *Anguilla anguilla* IV. Photoreceptors of the yellow eel stage. Anat. Anz. 158:23-32.

Braekevelt, C. R. 1988a. Retinal fine structure in the European eel *Anguilla anguilla* VI. Photoreceptors of the sexually immature silver eel stage. Anat. Anz. 166:23-31.

Braekevelt, C. R. 1988b. Retinal fine structure in the European eel *Anguilla anguilla* VIII. Photoreceptors of the sexually mature silver eel stage. Anat. Anz. 167:1-10.

Crabtree, R. E., C. Stevens, D. Snodgrass, F. Stengard. 1998. Feeding habits of bonefish, *Albula vulpes*, from the waters of the Florida Keys. Fish. Bull. 96:754-766.

Easter, S. S. Jr. and P. F. Hitchcock. 2000. Stem cells and regeneration in the retina: what fish have taught us about neurogenesis. Neuroscientist 6:454-464.

Evans, B. I. and R. D. Fernald. 1990. Metamorphosis and fish vision. J. Neurobiol. 21:1037-1052.

Evans, B. I. and R. D. Fernald. 1993. Retinal transformation at metamorphosis in the winter flounder (*Pseudopleuronectes americanus*). Visual Neurosci. 10:1055-1064.

Evans, B. I., F. I. Hárosi, R. D. Fernald. 1993. Photoreceptor spectral absorbance in larval and adult winter flounder (*Pseudopleuronectes americanus*). Visual Neurosci. 10:1065-1071.

Forey, P. L., D. T. J. Littlewood, P. Ritchie, A. Meyer. 1996. Interrelationships of elopomorph fishes, p. 175-191. In M. L. J. Stiassny, L. R. Parenti, G. D. Johnson [eds], Interrelationships of fishes. Academic Press, San Diego.

Geiger S. P., J. J. Torres, R. E. Crabtree. 2000. Air breathing and gill ventilation frequencies in juvenile tarpon, *Megalops atlanticus*: responses to changes in dissolved oxygen, temperature, hydrogen sulfide, and pH. Environ. Biol. Fish. 59:181-190.

Haacke, M. H., R. R. Melzer, H. Gebhart, U. Smola. 2001. Fine structure and development of the retina of the grenadier anchovy Coilia nasus (Engraulididae, Clupeiformes). J. Morphol. 248:41-55.

Kusmic, C. and P. Gualtieri. 2000. Morphology and spectral sensitivities of retinal and extraretinal photoreceptors in freshwater teleosts. Micron 31:183-200.

Lara, M.R. 2001. Morphology of the eye and visual acuities in the settlement-intervals of some coral reef fishes (Labridae, Scaridae). Environ. Biol. Fish. 62:365-378.

Masuma, S., G. Kawamura, N. Tezuka, M. Koiso, K. Namba. 2001. Retinomotor responses of juvenile bluefin tuna *Thunnus thynnus*. Fisheries Sci. 67:228-231.

van der Meer, H. J. 1994. Ontogenetic change of visual thresholds in the cichlid fish *Haplochromis sauvagei*. Brain Behav. Evolut. 44:40-49.

Mochioka, N., M. Iwamizu. 1996. Diet of anguilloid larvae: Leptocephali feed selectively on larvacean houses and fecal pellets. Mar. Biol. 125:447-452.

Mochioka, N., M. Iwamizu, T. Kanda. 1993. Leptocephalus eel larvae will feed in aquaria. Environ. Biol. Fish. 36:381-384.

Neave, D. A. 1984. The development of visual acuity in larval plaice (*Pleuronectes platessa* L.) and turbot (*Scophthalmus maximus* L.). J. Exp. Mar. Biol. Ecol. 78:167-175.

Negishi, K. and H. Wagner. 1995. Differentiation of photoreceptors, glia, and neurons in the retina of the cichlid fish *Aequidens pulcher*; an immunocytochemical study. Dev. Brain Res. 89:87-102.

Obermiller, L. E., E. Pfeiler. 2003. Phylogenetic relationships of elopomorph fishes inferred from mitochondrial ribosomal DNA sequences. Mol. Phylogenet. Evol. 26:202-214.

Otake, T., K. Nogami, K. Maruyama. 1993. Dissolved and particulate organic matter as possible food sources for eel leptocephali. Mar. Ecol. Prog. Ser. 92:27-34.

Pankhurst, N. W. 1983. Retinal development in larval and juvenile European eel, *Anguilla anguilla* (L.). Can. J. Zoolog. 62:335-343.

Pankhurst, N. W. 1987. Intra- and interspecific changes in retinal morphology among mesopelagic and demersal teleosts from the slope waters of New Zealand. Environ. Biol. Fish. 19:269-280.

Pankhurst, P. M., N. W. Pankhurst, J. C. Montgomery. 1993. Comparison of behavioural and morphological measures of visual acuity during ontogeny in a teleost fish, *Forsterygion varium*, Tripterygiidae (Forster, 1801). Brain Behav. Evolut. 42:178-188.

Pfeiler, E. 1986. Towards an explanation of the developmental strategy in leptocephalus larvae of marine teleost fishes. Environ. Biol. Fish. 15:3-13.

Pfeiler, E. 1989. Sensory systems and behavior of premetamorphic and metamorphic leptocephalus larvae. Brain Behav. Evolut. 34:25-34.

Reckel, F., R. R. Melzer, J. W. L. Parry, J. K. Bowmaker. 2002. The retina of five atherinomorph teleosts: photoreceptors, patterns and spectral sensitivities. Brain Behav. Evolut. 60:249-264.

Shand, J. 1994. Changes in retinal structure during development and settlement of the goatfish *Upeneus tragula*. Brain Behav. Evolut. 43:51-60.

Shand, J. 1997. Ontogenetic changes in retinal structure and visual acuity: a comparative study of coral-reef teleosts with differing post-settlement lifestyles. Environ. Biol. Fish. 49:307-322.

Smith, D. G. 1980. Early larvae of the tarpon, Megalops atlantica Valenciennes (Pisces: Elopidae), with notes on spawning in the Gulf of Mexico and the Yucatan Channel. B. Mar. Sci. 30:136-141.

Smith, D. G. 1989. Introduction to leptocephali, p. 657-668. In E. B. Böhlke [ed], Fishes of the Western North Atlantic, Part 9 Vol. 2: Leptocephali. Sears Found. Mar. Res., New Haven.

Wade, R. A. 1962. The biology of the tarpon, *Megalops atlanticus*, and the ox-eye, *Megalops cyprinoids*, with emphasis on larval development. B. Mar. Sci. Gulf & Carib. 12:545-622.

Wagner, H. 1990. Retinal structure of fishes, p. 109-157. In R. H. Douglas and B. A. Djamgoz [eds], The visual system of fish. Chapman and Hall Ltd., London.

Wagner, H., E. Fröhlich, K. Negishi, S. P. Collin. 1998. The eyes of deep-sea fish II. Functional morphology of the retina. Prog. Retin. Eye Res. 17:637-685.

Wainwright, P. C. and D. R. Bellwood. 2002. Ecomorphology of feeding in coral reef fishes, p. 33-55. In P. F. Sale [ed], Coral reef fishes. Academic Press, San Diego.

Walls, G. L. 1967. The vertebrate eye and its adaptive radiation. Hafner Pub. Co. 785 pp.

Zale, A. V. 1989. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (South Florida): *E. saurus* and Tarpon. U.S. Army Corp. Eng. Biol. Rep. 82(11.104). 13 pp.

ANALYSIS ON THE DIET OF BONEFISH, *ALBULA VULPES*, IN LOS ROQUES ARCHIPELAGO NATIONAL PARK, VENEZUELA

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ABSTRACT

The bonefish, *Albula vulpes*, is common in shallow waters of the Los Roques Archipelago National Park (LRANP), where it is a resource of great economic value due to its importance in the recreational fishery. In Venezuela, little is known about the biology of this species, in particular about its feeding habits. At least the basic knowledge on the biology and life history of this species should be achieved, since this information is needed for responsible management of its fishery. The present study is a contribution on this need, providing information on the trophic dynamics of *A. vulpes* collected in Los Roques. Feeding habits are described for this species with respect to seasonality and both fish size and sex. The stomach contents of 187 bonefish collected from November 1999 to July 2000, in shallow waters of the south western portion of the archipelago were examined. 27.2% of the stomachs examined were empty. The percentage frequency of occurrence (N), the percentage of relative frequency of abundance (F) and the percentage of relative frequency of wet weight (W) were calculated for each prey item in bonefish stomach contents. The diet was comprised primary of crustaceans, teleosts, bivalves, polychaetes and gastropods, with decapods and clupeiformes forming the most significant portion of the diet. Sex and size range of sampled bonefish *A. vulpes* (336 mm to 644 mm FL) did not show significantly differences in their diets (p = 0.406 and 0.315, respectively). However, there were significant temporal differences (p = 0.001 and p = 0.029 between months and rain/dry season). Bonefish preyed mostly on decapods and teleosts during the dry season and cold waters (November 1999-February 2000) and more gastropods during the rainy period and warmer waters (March – July 2000).

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INTRODUCTION

The recreational fishery for bonefish, *Albula vulpes* (Linnaeus, 1758), is an important economic resource in the Bahamas, Florida Keys, and much of the Caribbean (Mojica et al. 1995), including Los Roques Archipelago National Park in Venezuela (Debrot, 2001). Los Roques is one of the biggest and oldest marine parks in the Caribbean (Posada et al. 2003, Villamizar et al. 2003), as well one of the healthiest coral reef system (Kramer 2003).

Bonefish is considered a cosmopolitan species with tropical distribution. In the western Atlantic, it is distributed from North Carolina (United States) to Rio de Janeiro (Brazil), including the Caribbean Sea. In Venezuela, it is found along the coast, in shallow waters (<2m) over seagrass or sandy bottom, where it is commonly observed searching for benthic and epibenthic prey (Cervigón et al. 1991, Crabtree et al. 1998). In Los Roques, the bonefish fishery, particularly the practice of catch and release, has been increasing in recent years, with an average of 400 sports fishers visiting the archipelago every year (Ing. Jesus Durán, personal communication).

In spite of its Caribbean-wide economical importance, few studies have examined the biology and ecology of this species. The majority of investigations have focused on the metamorphosis of the leptocephalus larvae of this species. In Venezuela, the only study of *A. vulpes* describes the reproductive biology of the species (Debrot 2001).

Feeding habits of *A. vulpes* have been studied by Warmke and Erdman (1963) in Puerto Rico, who only identified the constituent molluscs of the diet. Bruger (1974) presented the frequencies of occurrence of the crustaceans found in the stomach contents of bonefish caught in South Florida, but did not quantify the other prey items. Colton and Alevizon (1983) classified prey items of *A .vulpes* collected in the Bahama islands, but they did not quantify the abundance of each item. The most complete study of bonefish feeding (Crabtree et al. 1998) described the relative importance of prey items in the diet of bonefish collected in south Florida.

The population dynamics of fishes are commonly affected by the exploitation and degradation of their habitat, and this degradation may also influence the feeding habits of fishes. Feeding studies not only permit the identification of habitat where a species feeds, but also permits an evaluation of the effects of environmental degradation on populations. It is also essential that protection strategies be established for these ecosystems.

This work represents the second contribution to the knowledge of the biology of the species for Venezuela, and to the complete description of the feeding habits of the species worldwide. Here we describe the diet of Los Roques bonefish population, examining ontogenetic and sexual differences. We also evaluate temporal differences in feeding for the examined population.

METHODS

Collections

The insular reef complex of the LRANP is located between 11°44'26" and 11°58'36" N and 66°57'26" - 66°36'25" W. Bonefish were collected by Debrot (2001) over seagrass or sandy bottom (<2 m), in the vicinity of the Dos Mosquises and La Pelona islands in the south-western portion of the Archipelago (Fig. 1). Fish were collected during November 1999 and July of 2000, using 75 m gillnet with 2 cm stretch mesh. Collected individuals were measured (fork length, FH) and sexed using macroscopic determination (Debrot 2001). Stomachs were removed and preserved in 10% formalin. Those were stored in 70% ethyl alcohol for later examination. Stomach contents of 187 specimens of *A. vulpes* were analyzed using a binocular dissecting microscope. Both wet weight and abundance was determined for each category of prey. Identification of prey was facilitated by taxonomic keys of crustaceans (Williams 1984), gastropods (Abbott and Danne 1998, Díaz and Puyana 1994, Rosenberg 1998), bivalves (Lodeiros et al. 1999), teleosts (Cervigón 1991, Cervigón et al. 1992), polychaetes (Glasby et al. 2000) and sinpunculids (Edmonds 2000).

Data Analysis

Percentage of bonefish with stomach contents was determined. Only this number of individuals was considered in further analysis. The percentage of stomach repletion grade or fullness (%RG) was calculated:

$$\%RG_i = (\%SC_i / \%SC_o) \ x \ 100$$

where, $\%RG_i$ represent the percent stomach repletion grade of stomach i and $\%SC_o$ is the percentage of wet weight of the stomach content of stomach o, where o is the examined stomach with the highest %SC. Thus,

$$\%SC_i = (1 - C_i / S_i) \ x \ 100$$

where, %SC_i represent the percent wet weight of the stomach content of stomach i, and C_i and S_i are the wet weight of the stomach i full and empty, respectively.

Prey items were quantified using several metrics:

- Percent frequency of occurrence (F),

$$F_i = (a / b) \; x \; 100$$

where, a is the number of stomachs in which the item i appeared and b is the total number of stomachs with food.

- Percentage of relative frequency of abundance (N),

$$N_i = (c / d) \; x \; 100$$

where, c represent the number of individuals of item i and d is the total number of individuals of prey items.

- Percentage of relative wet weight (W),

$$W_i = (e / f) \; x \; 100$$

where, e represents the wet weight of the individuals of item i and f is the wet weight of the individuals of the total items consumed by the examined bonefish.

Differences in feeding habits related to size, sex and month of capture were determined using the percent relative of wet weight (W). Crabtree et al. (1998) found W to more closely reflects the energetic importance of prey items in the diet than the other measures. Analysis of similarity (ANOSIM) was used to determine significant differences in diet composition (Clarke and Warwick 1994). The matrix of similarity was calculated using the complement of the dissimilarity Bray - Curtis index (Clarke 1993). Size comparisons were made between intervals of 80 mm FL, taking into account the size distribution of the bonefish population examined and observations made by Crabtree et al. (1998). It was also compared the diet between individuals bigger and smaller to 486 mm FL, because of the differences and similarities observed in the 80 mm FL intervals proposed, which were also observed by Crabtree et al. (1998).

RESULTS

Only 136 of the 187 examined bonefish stomachs contained prey (72.2%). These fishes ranged in size from 336 to 644 mm FL, with 90% between 407 and 566 mm FL (median intervals sizes; Fig. 2).
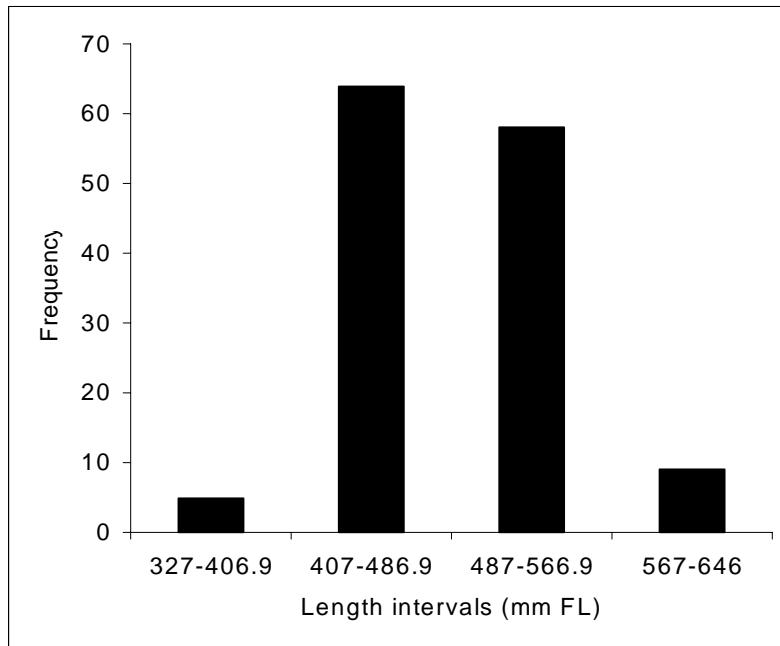
Figure 2. Size distribution of the 136 examined bonefish caught with prey items in theirs stomachs.

There was no correlation between the percentage of stomach repletion grade (%RG) and the length of the fish (Fig. 3). Monthly means and standard deviations of the RG parameter are showed in Fig. 4. April and March 1999, as well as December 2000 showed the highest percentages values, while July and February 1999 were the lowest.
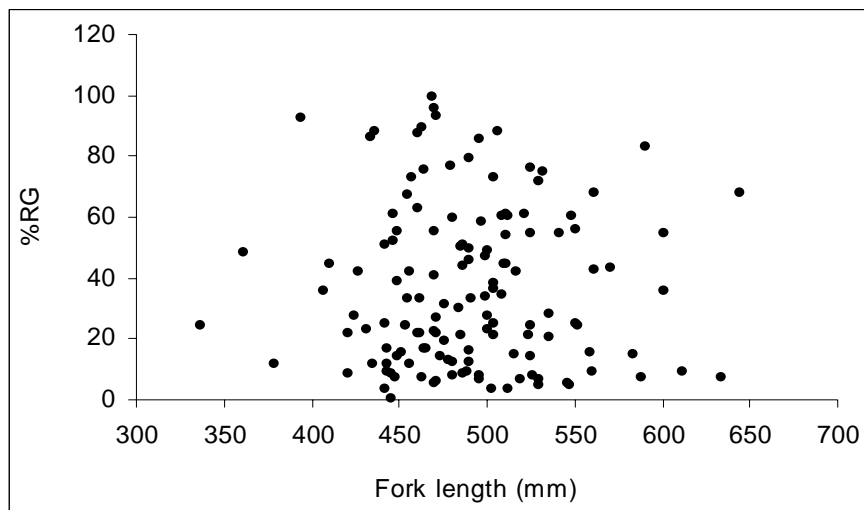
Figure 3. Correlation between the percentage of stomach repletion grade (%RG) and the fork length of the 136 bonefish caught with prey items.
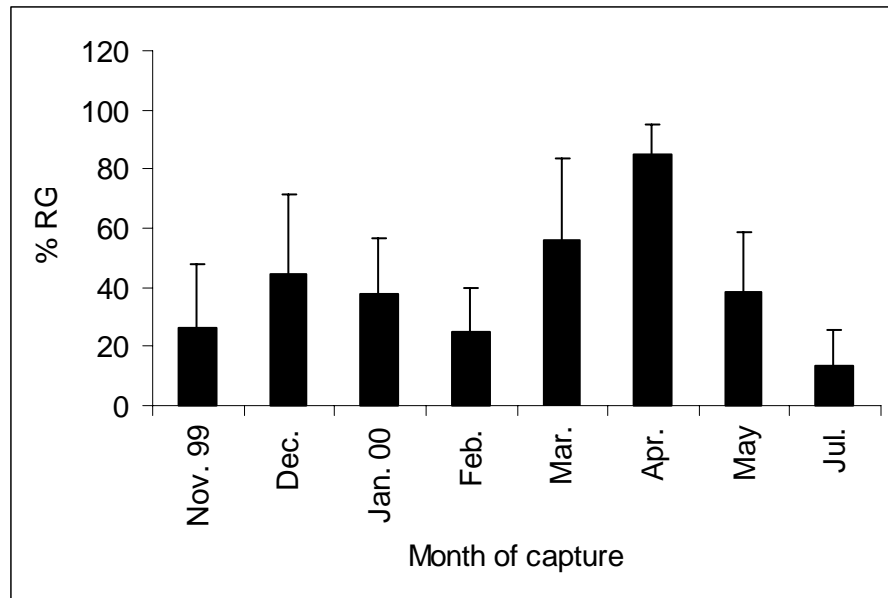
Figure 4. Monthly mean and standard deviation of the percentage of stomach repletion grade (%RG).

The diet of bonefish was composed mainly of crustaceans, teleosts, bivalves, polychaetes and gastropods (Table I). Decapods and clupeiformes dominated the diet, as expressed by values of N=34.4%, F=90.4% and W=30.9%. Crabs were the most important decapod, and were comprised of the families Xanthidae, Portunidae and Majidae. The subfamily mithracinae (Majidae) comprised the most significant taxa of the decapods, as expressed by values of N and W of 13.6 and 14.0%, respectively. The genus *Anchoa* was the most important prey item among teleosts, with values of N=9.9%, F=15.4% and W=10.3%. The bivalves were eaten at high frequency (F=44%), but their importance in the diet in terms of relative wet weight was low (W=14.7%). Bivalves of the order Veneroida were the group eaten most frequently, with values of N=9% and F=24.3%. The bivalve species of greatest importance in the bonefish diet, *Codakia orbikulatus*, with values of N=7.8%, F=15.4% and W=9.0%, belongs to this order. The species of polychaete with the highest values for all the measured parameters was *Notomastus* sp. (N=7.9%, F=10.3% and W=8.0%). Among the gastropods, *Cerithium literatum* appeared in greater quantity (N=1.8%), but *Persicula interruptolineata* and *Cosnioconcha nitens* were eaten most frequently, with values of F of 5.9% and 3.7%, respectively. Vegetal material was found in a high percentage of samples (F=40.4%), but with a low relative percent of wet weight value (W=7.1%). The most frequent seagrass species was *Syringodium* sp. (F=11.8%) (Table I).

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Table I. Food items in stomachs of bonefish, *Albula vulpes*, caught in the waters of the Archipelago Los Roques National Park, Venezuela, between November and July of 1999 and 2000 (n = 163). Prey are quantified by percentage of relative frequency of abundance (N), percentage of relative frequency of wet weight (W) and percentage of relative frequency of occurrence (F).

PREY ITEMS	N	W	F
Plant material	-	**7.1**	**40.4**
Unidentified plant material	-	6.0	19.1
Syringodium sp.	-	0.1	11.8
Halodule sp.	-	0	1.5
Thalassia testudinum	-	0.9	8.1
Miscellaneous material	2.9	9.6	17.6
Phylum Chordata			
Class Osteichthyes	**19.0**	**22.2**	**32.4**
Unidentified Osteichthyes	4.6	4.3	6.6
Order Clupeiforme	**34.4**	**31.0**	**90.4**
Engraulidae			
Anchoa sp.	9.2	10.3	15.4
Clupeidae			
Harengula humeralis	4.4	6.9	9.6
Order Anguilliforme	**0.7**	**0.7**	**0.7**
Ophichthidae			
Unidentified Ophichthinae	0.7	0.7	0.7
Subphylum Crustacea			
Class Malacostraca	**34.4**	**30.1**	**90.4**
Order Decapoda	**34.4**	**30.1**	**90.4**
Unidentified Decapoda	0.9	0.3	4.4
Unidentified Brachyura	9.5	9.4	19.1
Xanthidae			
Panopeus sp.	0.2	0.2	0.7
Eurypanopeus abbreviatus	0	0	0.7
Portunidae			
Unidentified Portuninae	2.7	2.1	12.5
Majidae			
Unidentified Mithracinae	12.7	13.7	22.1
Mithrax forceps	0.9	0.3	3.7
Unidentified Anomura	3.5	2.0	12.5
Galatheidae			
Munida sp.	0.1	0.1	1.5
Diogenidae			
Pagurites sp.	1.1	0.6	2.2
Unidentified Penalidae	0.1	0	0.7
Unidentified Penaeidae	2.8	2.2	10.3
Phylum Molusca			
Unidentified Mollusca	-	**0.9**	**7.4**
Class Gastropoda	6.3	2.8	35.3
Unidentified Gastropoda	1.7	1.3	11.0
Order Caenogastropoda	**4.3**	**1.4**	**22.1**
Marginellidae			

Persicula interruptolineata	0.6	0.1	5.9
Cerithidae			
Cerithium literatum	1.8	1.1	2.9
Columbellidae			
Unidentified Columbellidae	0.4	0.1	2.2
Cosnioconcha nitens	0.7	0.1	3.7
Columbella mercatoria	0	0	0.7
Olividae			
Olivia australis	0.8	0.1	6.6
Order Vetigastropoda	**0.3**	**0**	**2.2**
Phasianellidae			
Tricolia tessellate	0.1	0	1.5
Naticidae			
Sigatica sp.	0.1	0	0.7
Class Bivalvia	**11.3**	**14.7**	**44.1**
Unidentified Bivalvia	1.6	4.7	16.2
Order Pteroida	**0.1**	**0.1**	**1.5**
Unidentified Pectinidae	0.1	0.1	1.5
Order Veneroida	**9.0**	**9.6**	**24.3**
Lucinidae			
Lucina sp.	0.3	0	0.7
Codakia orbiculatus	7.8	9.0	15.4
Veneridae			
Unidentified Veneridae	0.6	0.1	2.9
Chione sp.	0.2	0.4	1.5
Chione cancellata	0.2	0.1	3.7
Order Arcoida	**0.5**	**0**	**1.5**
Arcidae			
Unidentified Arcidae	0.5	0	1.5
Order Mytiloida	**0.1**	**0.2**	**0.7**
Mytilidae			
Brachidontes sp.	0.1	0.2	0.7
Phylum Annelida			
Class Polychaeta	**13.4**	**10.7**	**22.8**
Unidentified Polychaeta	3.2	0.1	6.6
Unidentified Maldanidae	0.1	0.1	0.7
Unidentified Pectinaridae	1.6	2.2	2.9
Unidentified Oenonidae	0.6	0	2.2
Capitellidae			
Notomastus sp.	7.9	8.0	10.3
Phylum Sipuncula			
Class Sipunculidea	**1.0**	**1.1**	**2.2**
Order Aspidosiphoniforme	**1.0**	**1.1**	**2.2**
Unidentified Aspidosiphonidae	1.0	1.1	2.2

Differences in bonefish diet by size, sex and month of capture

For all fork length intervals, the order Decapoda dominated the diet by weight, followed by the teleosts of the order Clupeiformes (Fig. 5). In general, similarity analysis (ANOSIM) did
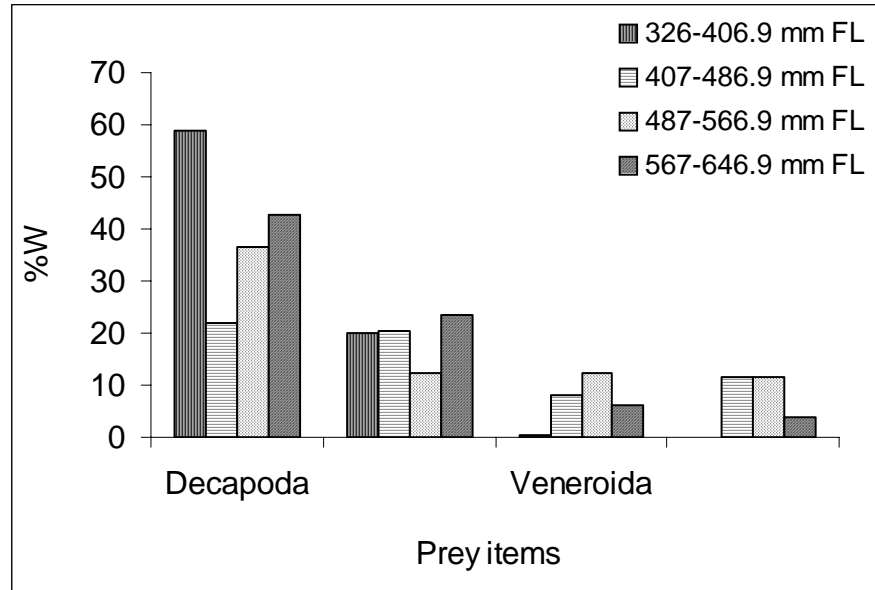
Figure 5. Differences in bonefish diet by size. Feeding habits are represented by the percentage of relative frequency of wet weight (W) for the principal prey items (orders).

not show any statistically significant difference in percentage of relative frequency of wet weight for any of the four size intervals tested, with a global value of R = 0.016 (p = 0.135). Similarity analysis conducted among fishes bigger and smaller than 486 mm FL showed no significant difference in the percentage of relative frequency of wet weight (R = 0.01; p = 0.1).

However, the 326 to 406.9 mm FL interval showed the highest value of relative frequency of wet weight for the decapods (W=58.7%), while for the teleosts the highest value of this parameter was observed for the 566 to 646.9 mm FL interval (W=23.3%). Bivalves of the order Veneroida were also eaten by all the bonefish length intervals, although with a W value much smaller than for decapods, except for the interval 486-566.9 mm FL (W=12.4%). Bonefish of the 326 to 406.9 mm FL interval did not eat polychaetes, but the 406-486.9 and 486-566.9 mm FL intervals consumed this item with a value of W of 11.5 and 11.7%, respectively, which was greater that for bivalves (Fig. 5). The gastropods had the lowest value of relative frequency of

wet weight, being consumed in a minimum percentage by the larger individuals (566 to 646.9 mm FL interval) (W=0.3%).

Similarity analysis showed no significant differences in feeding habit between the 49 males and 87 examined females (R=0.001; p = 0.406) (Fig. 6).
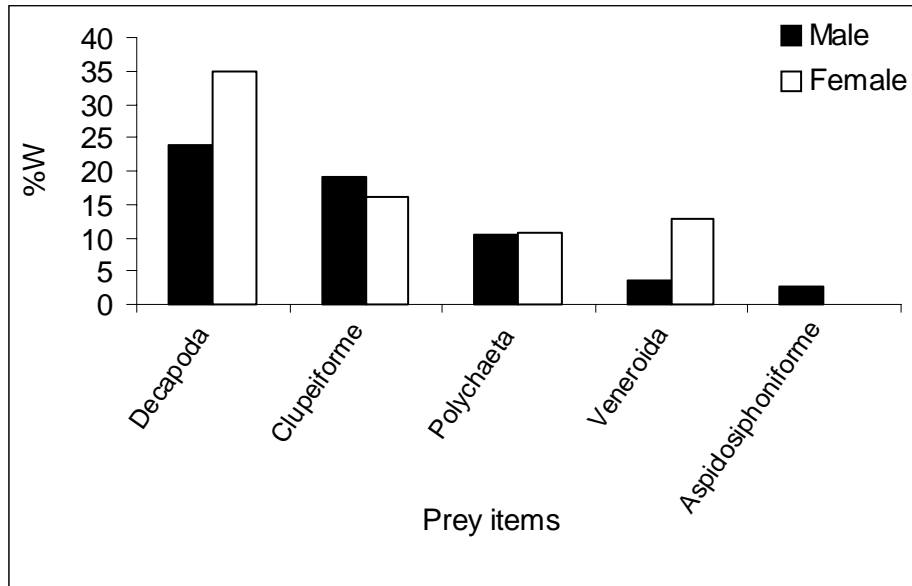
Figure 6. Differences in bonefish by (W) with sex.

In general, similarity analysis showed a statistically significant difference in bonefish feeding habits with respect to the month of capture, with a global value of R = 0.255 (p = 0.001). However, these differences were not significantly different among some months, based on the ANOSIM pairwise similarity analysis: November 1999 - April 2000 (R = -0.121; p = 0.0952), November 1999 - May 2000 (R = 0.06; p = 0.137), March - April 2000 (R = -0.063; p = 0.729) and March - May 2000 (R = 0.104; p = 0.064).

The highest consumption of decapods was during the month of December 1999 (W=61.3%), and they were not consumed at all during the months of April, May and July of 2000 (Fig. 7). Teleosts of the order Anguilliformes dominated the diet during November 1999 (W=55.0%), gastropods of the order Vetigastropoda dominated the diet in July (W=56.2%), and polychaetes were eaten only during the month of December 1999, although only with a low value of W=1.3% (Fig. 7).

Significant differences in prey items consumed were also seen on a seasonal basis: dry season (from November 1999 to February 2000) versus rainy season (March to July 2000) ($R = 0.029$; $p = 0.029$). Bonefish ate more decapods, teleots anguilliformes, and clupeiformes in the dry season, while gastropods of the order Vetigastropoda and Caenogastropoda were eaten in higher proportion in the rainy season (Fig. 7).

DISCUSSION
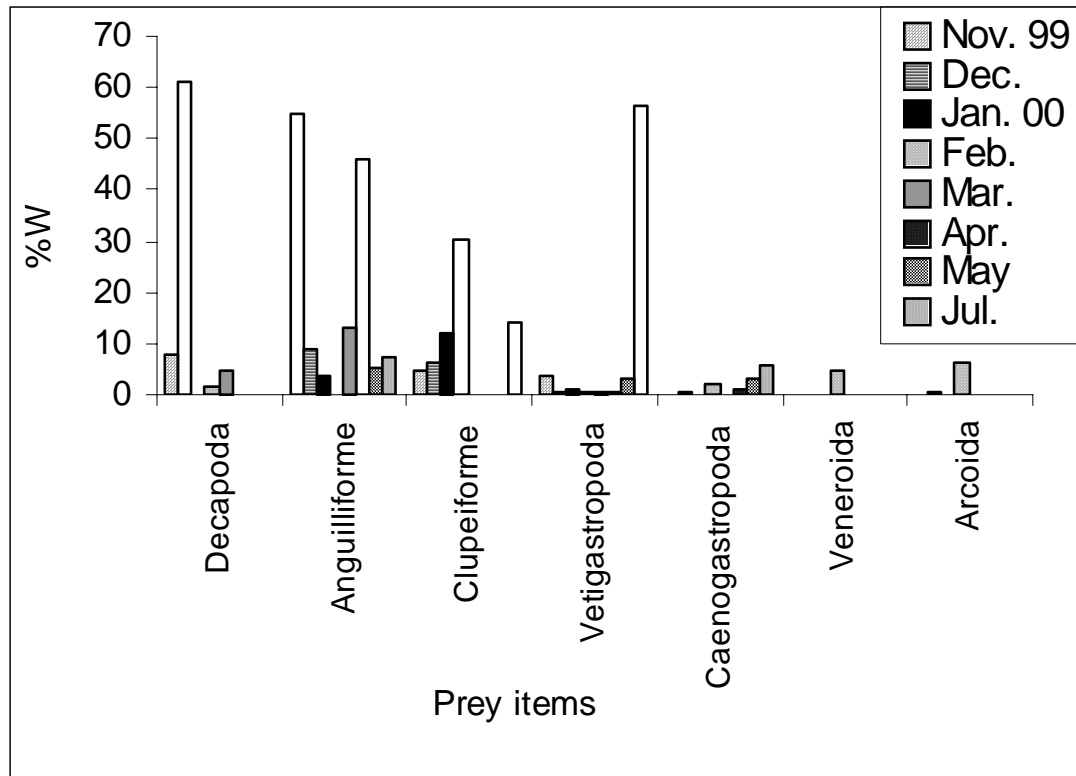
Figure 7. Differences in bonefish by (W) with month of capture.

Bonefish examined in this study ranged from 336 to 644 mm FL, but the 90% of them were in the range of 406 – 566.9 mm FL. Thus, the sampled population was composed of a significant percentage of both juveniles and adults, considering that the size at which the 50% of the population matures is 456 and 467 mm FL for females and males, respectively (Debrot 2001).

The diet of bonefish in the southwestern portion of LRANP is composed mostly of crustaceans, teleosts, bivalves, polychaetes and gastropods. Decapods and clupeiformes dominated the diet with the highest percentages for all the analyzed parameters, suggesting that

those preys really are the preferential items in the diet of this fish and should be highly available in its ecosystem. Similar results were observed for the south Florida bonefish population, where decapods dominated the diet (N=42.1%, F=88.6% and W=67.8%) (Crabtree et al. 1998).

In contrast with our observations at Los Roques, Crabtree et al. (1998) reported a higher percentage of relative frequency of abundance for molluscs (N = 51%) than for the teleosts (N = 45%) in Florida. Also, the gulf toadfish, *Opsanus beta* (Batrachoidiformes), was the most important teleosts in the diet of the south Florida bonefish population, while this item was not found in Los Roques bonefish stomachs. On the other hand, teleosts of the order Clupeiformes were not an important prey item in the south Florida bonefish population.

Molluscs (bivalves and gastropods) and polychaetes represented a significant percentage of the frequency of occurrence (F) and percentage of relative frequency of abundance (N) for Los Roques bonefish population, but the percentage of relative wet weight (W) was quite low. These differences suggest that these items are highly available as a food resource for the species in the studied environment, but they are not so important in the feeding habits of the species.

The low proportion of vegetal material seen in the bonefish stomach suggests that this item is not included as a selected item in the diet of this species. The presence of this material can be attributed to foraging for prey associated with seagrass, where *A. vulpes* is known to feed (Crabtree et al. 1998).

Colton and Alevizon (1983) analyzed the stomach contents of bonefish caught in different bottom types in the Bahamas. They found significant differences between the diet of bonefish populations related to the bottom type where they fed, suggesting that resource availability is a determining factor in the feeding habits of the species.

The areas surveyed in the present study constitute a permanent and abundant source of crustaceans, principally decapods. According to Villamizar (1993), decapods are the main prey item for most of the visitors and residents fish species in the seagrass beds of LRANP. It can be concluded that bonefish *A. vulpes* is a carnivorous opportunistic species and that resource availability seems to be the limiting factor, based on results of this study, and the observations reported by Colton and Alevizon (1983), as well by Villamizar (1993).

Crabtree et al. (1998) reported significant differences in feeding habits for bonefish in southern Florida. These authors found a positive correlation between prey size and fish length, and reported that large individuals consumed more decapods and teleosts than smaller bonefish

(< 440 mm FL). These results do not match those found in the present study where: a) no significant differences in feeding habits between large and small bonefish individuals were observed, and there was no correlation between fish size and the prey type, b) the consumption of decapods was higher in the smallest length class interval, and c) teleosts were consumed with similar W values for the small (326 – 406.9 mm FL) and the large (567 – 646.9 mm FL) bonefish.

Feeding habits for Los Roques bonefish were significantly different by time of capture, in both seasonal and monthly patterns. This was reported previously by Crabtree et al. (1988), who found significant seasonal differences for populations along the Atlantic coast of south Florida. During the dry season, when the temperature of the Caribbean Sea water is colder, bonefish ate more decapods and teleosts (Anguilliformes and Clupeiformes), while during the rainy season when water temperature is warmer, gastropods become more important in the their diet. Those monthly and seasonal differences in the bonefish diet may reflect temporal differences in prey availability related to variations in seasonal and oceanographic patterns.

In conclusion, *Albula vulpes* in the southwestern portion of LRANP is an opportunistic carnivorous species, with a diet mostly composed of decapods, teleosts, bivalves, polychaetes and gastropods. Feeding habits did not show significant differences with respect to fish length and gender, while there were significant differences with the month of capture.

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LITERATURE CITED

Abbott, R.T. and S.P. Danee. 1998. Compendium of seashells. OOYSSEY Publishing, Hong Kong. X + 411 pp.

Bruger, G.E. 1974. Age, growth, food habits and reproduction of bonefish, *Albula vulpes*, in South Florida waters. Fla. Mar. Res. Publ. 3. 20 pp.

Cervigón, F. 1991. Los peces marinos de Venezuela, Vol. 1. Fundación Científica Los Roques. Caracas, Venezuela. 425 pp.

Cervigón, F, R. Cipriani, W. Fisher, L. Garibaldi, M. Hendrickx, A.J. Lemus, R. Márquez, J.M. Poutiers, G. Robaina, and B. Rodríguez. 1992. Guía de campo de las especies comerciales marinas y de aguas salobres de la costa septentrional de Sur América, Roma FAO. 513 pp.

Clarke, K.R. 1993. Non-parametric multivariate analysis in community structure. Aust. J. Ecol. 18:117-143.

Clarke, K.R. and R.M. Warwick. 1994. Similarity-based testing for community pattern: The two-way layout with no replication. Mar. Biol. 118:167-173.

Colton, D.E. and W.S. Alevizon. 1983. Feeding ecology of bonefish in bahamian waters. T. Am. Fish. Soc. 112:178-184.

Crabtree, R.E., D. Snodgrass, C. Stevens and F.J. Stengard. 1998. Feedings habits of bonefish, *Albula vulpes*, from the waters of Florida Keys. Fish. Bull. 96:754-766.

Debrot, D. 2001. Biología reproductiva del macabí, *Albula vulpes*, en el Parque Nacional Archipiélago de Los Roques. Undergraduate Thesis. Universidad Simón Bolívar. División de Ciencias Biológicas. Caracas, Venezuela. 44 pp.

Díaz, J. M. and M. Puyana. 1994. Moluscos del caribe colombiano: Un catálogo ilustrado. Conciencias/Fundación Natura Colombia. Colombia. LXXIV + 291 pp.

Edmonds, S.J. 2000. Phylum Sipuncula, p. 375-400. In P.L. Breesley, G.J. Ross and C.J. Glasby [eds.], Polychaeta and Alliens: The Southern Synthesis. Fauna of Australia. Vol. 4A: Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing. Melbourne, Australia. XII + 465 pp.

Glasby, C.J., P.A. Hutchings, K. Fauchald, H. Paxton, G.W. Rouse, C.W. Russel, and R.S. Wilson. 2000. Class Polychaeta, p. 1-296. In P.L. Breesley, G. J. Ross and C. J. Glasby [eds.], Polychaeta and Alliens: The Southern Synthesis. Fauna of Australia. Vol. 4A: Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing. Melbourne, Australia. XII + 465 pp.

Kramer, P.A. 2003. Synthesis of coral reef health indicators for the western Atlantic: Results of the AGRRA program (1997-2000), p. 1-58. In J.C. Lang [ed.], Status of coral reef in the western Atlantic: Results of initial surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program. Atoll Research Bulletin 496.

Lodeiros, C., B.M. Espinoza and A. Prieto. 1999. Catálogo de moluscos de las costas nororientales de Venezuela: Clase Bivalvia. Edition APUDONS. 118 pp.

Mojica, R. Jr., J.M. Shenker, C.W. Harnden and D.E. Wagner. 1995. Recruitment of bonefish, *Albula vulpes*, around Lee Stocking island, Bahamas. Fish. Bull. 93:666-674.

Posada, J.M., E. Villamizar and D. Alvarado. 2003. Rapid assessment of coral reefs in the Archipiélago de Los Roques National Park, Venezuela (Part 2: fishes), p. 530-543. In J.C. Lang [ed.], Status of coral reef in the western Atlantic: Results of initial surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program. Atoll Research Bulletin 496.

Rosenberg, G. 1998. Conchology 101. A classification of the Mollusca: Class Gastropoda. Academy of Natural Sciences, Philadelphia.http://coa.acnatsci.org/ conchnet/ class-gs.html.

Villamizar, E. 1993. Evaluación de la comunidad de peces en algunas praderas de fanerógamas marinas del Parque Nacional Archipiélago de Los Roques. Ph.D. Ecology Thesis. Universidad Central de Venezuela. Instituto de Zoología Tropical. Caracas, Venezuela. 244 pp.

Villamizar, E., J.M. Posada and S. Gomez. 2003. Rapid assessment of coral reefs in the Archipiélago de Los Roques National Park, Venezuela (Part 1: stony corals and algae), p. 512-529. In J.C. Lang [ed.], Status of coral reef in the western Atlantic: Results of initial

surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program. Atoll Research Bulletin 496.

Warmke, G.L. and D.S. Erdman. 1963. Records of marine mollusks eaten by bonefish in Puerto Rican waters. The Nautilus 76:115 -120.

Williams, A.B. 1984. Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institution Press. Washington, D. C. 550 pp.
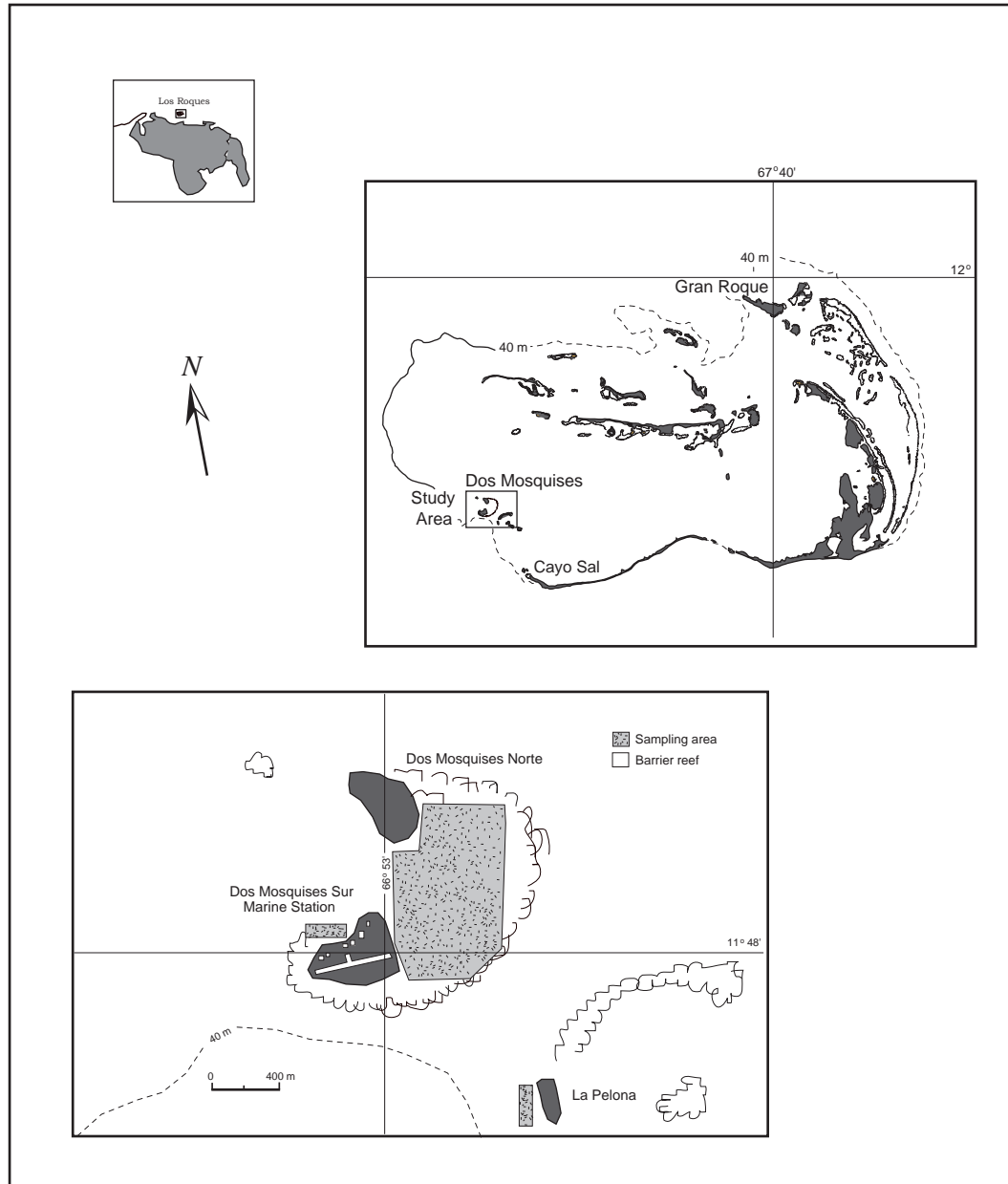
Figure 1. Sampling areas in the Los Roques Archipelago Nacional Park, Venezuela.

STUDIES IN CONSERVATION GENETICS OF TARPON (*MEGALOPS ATLANTICUS*) – III. VARIATION ACROSS THE GULF OF MEXICO IN THE NUCLEOTIDE SEQUENCE OF A 12S MITOCHONDRIAL rRNA GENE FRAGMENT

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ABSTRACT

A 351-base pair fragment amplified from the mitochondrial 12S rRNA gene of the tarpon (*Megalops atlanticus*) was sequenced in 48 individuals from off Florida, Louisiana, Texas, the Mexican Gulf of Mexico, and Chetumal in the Mexican Caribbean. Sixteen haplotypes were identified; one haplotype was most common at all sample sites with frequencies ranging from 40.0% in the Mexican Gulf to 88.89% at Chetumal. Many haplotypes exhibited high nucleotide diversity, differing from the common haplotype in sequence composition by as much as 8.8%. Inferential measures of population differentiation failed to find statistically significant structure in tarpon from the Gulf of Mexico. However, a statistically significant cline was found in the frequency of the common haplotype, with tarpon from Mexican waters exhibiting a markedly lower frequency of this haplotype than in Texas or the eastern Gulf of Mexico. This may support a hypothesis of limited stock structure, with centers of reproduction from Florida into the Caribbean and from the Bay of Campeche northward along the Mexican Gulf Coast.

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INTRODUCTION

Tarpon (*Megalops atlanticus*) is a large, long-lived, highly migratory marine fish distributed widely in western Atlantic, Caribbean, and Gulf of Mexico waters. A possibly disjunct population occurs off western Africa and a recently established population is in the eastern Pacific off Panama. Spawning offshore, females produce 0.1 to 8.0 million eggs per spawn and multiple spawnings may occur over the reproductive season (Figuerola 1996). Eggs and larvae are planktonic with pelagic development that may extend over several weeks allowing dispersal over great distances as facilitated by currents and wind (Crabtree et al. 1992). Upon reaching coastal waters leptocephali larvae undergo metamorphosis (Cyr 1991) and over the next several years utilize shallow, estuarine habitats (Zerbi 1999).

The first study on genetic variability in tarpon (McMillan-Jackson et al. 1993) examined allozymic variation in structural genes and restriction fragment length polymorphisms (RFLPs) of mitochondrial DNA (mtDNA) in a comparison of Florida tarpon with collections from the Caribbean off Venezuela and Central America, and the Atlantic off western Africa. Appreciable genetic variability combined with apparent lack of population substructure across most of the examined distribution suggested high rates of migration. The African sample was genetically depauperate with, however, several alternative markers absent or rare in the western Atlantic.

Garcia de León et al. (2002) examined a number of morphological, reproductive, and genetic traits in tarpon from the western Gulf of Mexico. The morphological and reproductive analyses found no biologically significant differences between tarpon collected along the Mexico/Texas Gulf coast. However, analyses of variation in six protein coding loci and in a fragment of the 12S/16S mitochondrial rRNA genes examined using RFLPs supported the hypothesis of a genetically subdivided tarpon stock, with samples from the upper Texas coast being differentiated from those on the lower coast and from Mexico.

These conclusions differed from those reached by Blandon et al. (2002) in an analysis of variation in RFLPs of several mtDNA fragments of tarpon collected from across the distribution of tarpon including Africa and the Pacific Ocean off Panama. As in the McMillan et al. study (1993), Blandon et al. found tarpon to be genetically diverse across its contiguous distribution in the western Atlantic and Caribbean. Evidence from analysis of molecular variance (AMOVA) suggested samples from the western Gulf of Mexico were genetically

divergent from other Gulf samples, though cluster analyses failed to find geographically coherent patterns in genetic variability within the Gulf or across the Gulf, western Atlantic, and Caribbean. African samples were genetically invariant, each individual having the common composite haplotype.

Both Garcia de León (2002) and Blandon et al. (2002) detected among-locale genetic variation in the Gulf of Mexico. However, the latter study failed to observe the abrupt break in genetic characters in the western Gulf found by Garcia de León et al. between the upper and lower Texas coast. This discrepancy may be due to a number of factors. First, the Garcia de León et al. study included both nuclear and mtDNA genetic markers, allowing a broader examination of genomic variability across the geographic limits of the study. Second, the Garcia de León et al. study was limited to RFLP data from only one mtDNA fragment, the 12S/16S rRNA segment, compared with four mtDNA fragments examined in the second study. Third, Garcia de León et al. restricted their samples to tarpon from the western Gulf of Mexico. While this may have allowed resolution of subtle genetic differences extant in the western Gulf, it also meant that no point of geographic reference existed to place those differences in perspective.

The issue of population structure in tarpon has taken on additional importance since an announcement by the Coastal Fisheries Division of Texas Parks and Wildlife Department (TPWD) that it intends to explore the possibility of culturing and stocking tarpon into Texas marine waters. This proposal is in response to severe declines in tarpon abundance and harvest since the middle of the 20th century. Stockings of hatchery spawned organisms have imposed severe challenges to the conservation of genetic diversity in enhanced populations (Allendorf et al. 1986). When genetic substructure and diversity are understood, management options such as stocking can be employed with some confidence that the genetic integrity of the target species will not be compromised. Lacking this information, mistakes may be made which have long-term negative effects on a species.

The present study attempted to resolve the differences in conclusions reached by Garcia de León et al. (2002) and Blandon et al. (2002) concerning population subdivision in Gulf of Mexico tarpon. A high resolution technique, direct sequencing of a mtDNA fragment amplified using the polymerase chain reaction (PCR), was employed. The fragment, a segment of the 12S rRNA gene, was chosen because of the apparent ability of analyses of the 12S/16S fragment to discriminate stock structure in tarpon (Garcia de León et al. 2002). Direct sequencing may be

expected to yield greater resolution of population structure compared with PCR/RFLP (Carr and Marshall 1991) and may provide insight into the differing conclusions of the two earlier studies.

METHODS

A scale was removed from tarpon encountered in catch-and-release fisheries centered in Grand Isle, Louisiana, Tampa Bay, Florida, and Chetumal, Quintana Roo, Mexico (Fig. 1).
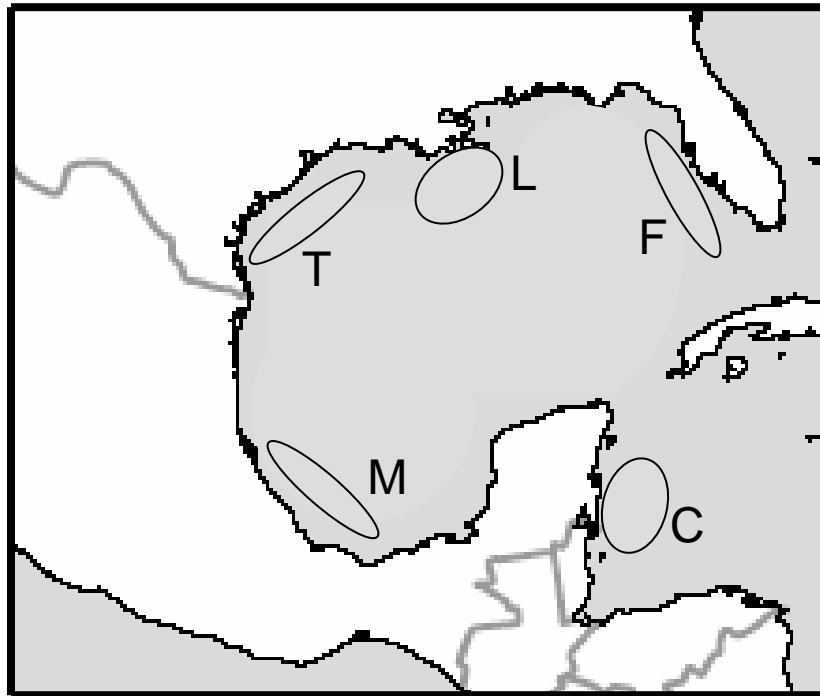
Figure 1. Sampling localities for tarpon in the Gulf of Mexico and off Chetumal in the Caribbean.

Additional scales were obtained from fish landed at tournaments at Tampico and Veracruz on the Mexican Gulf Coast and from fish encountered in TPWD routine resource sampling efforts. Scales were immediately placed in vials containing 70% ethanol. Vials were placed on ice or refrigerated at 4 C for 24 hrs following collection, after this time they were maintained at room temperature until transported to the Perry R. Bass Marine Fisheries Research Station in Palacios, Texas.

Genomic DNA was recovered from epidermis adhering to scales using the Puregene isolation kit and protocols (Gentra Systems, Minneapolis, MN). The polymerase chain reaction (PCR) was used to amplify putative 12S rRNA fragments using 16Sbr-3' and 11091' primers taken from Palumbi (1996) and modified from Kocher et al. (1989). Amplification reactions

utilized Ready-To-Go™ Beads (Amersham Pharmacia Biotech, Inc., Piscataway, NJ), to which were added approximately 100 ng of template to compose a 50 µl reaction volume. Amplification was carried out using a GeneAmp® PCR System 2400 (Applied Biosystems, Foster City, CA). The amplification protocol used was: 94 C (30 sec), 48 C (1:15 minutes), 72 C (1:30 minutes) repeated for 35 cycles. An extension period of 7 minutes at 72 C followed the final cycle. Amplification products were checked for size and purity by loading 5 µl on a 1% agarose gel, electrophoresed, and visualized with ethidium bromide. The remaining 45 µl was loaded into a 2% Seaplaque GTG agarose gel (FMC, Rockland, ME) containing ethidium bromide and electrophoresed at 44 volts. Bands were excised from the gel under UV illumination and the DNA was purified using the QIAquick PCR Purification Kit (Qiagen Inc., Valencia, CA). The DNA was resuspended in 20 µl of distilled water and quantified by comparison with mass standards. Approximately 250 ng of DNA was used for the cycle sequencing step. Sequencing was accomplished at the Molecular Genetics Core Facility of the University of Texas – Houston Medical School using the 16Sbr primer. Reverse sequencing was performed on those samples which gave questionable results on the 16Sbr primer. Samples with forward and reverse primers that did not agree were not included in subsequent analyses. Sequencing reactions employed a fluorescent dye terminator cycle sequencing kit (Perkin-Elmer Applied Biosystems, Foster City, CA) and the following thermal profile: 96°C for 5 min followed by 25 cycles of 96°C, 30 s; 50°C, 15 s; 60°C, 4 min. Sequences were resolved on an ABI 377 Stretch automated sequencer.

To assure amplification specificity, the sequence of the most common haplotype was compared with GenBank archived sequence data using the BLASTN program (Altschul et al. 1997) accessed through the National Center for Biological Information's World-Wide Web site at blast@ncbi.nlm.nih.gov. Sequences were aligned using the ClustalW program (Higgins and Sharp 1988; Thompson et al. 1994) using default settings on the BCM Search Launcher (Smith et al. 1996) provided by the Human Genome Sequencing Center of the Baylor College of Medicine and alignments were corrected manually. The program MODELTEST 3.06 (Posada and Crandall 1998) was used to establish the model of DNA evolution that best fit the sequence data and this model was employed in subsequent analyses.

Within-locality variability of mtDNA haplotypes was assessed by counts of haplotypes observed and percent of nucleotide sites that were variable. Insertion/deletion events were, for

the most part, noncontiguous and were treated as a fifth nucleotide in statistical analyses. Variation within collection regions was quantified using Nei's estimations of ĥ and $\hat{\pi}$ (Nei 1987; equations 8.5 and 10.6, respectively). The method of Jukes and Cantor (1969) was used to correct estimates of $\hat{\pi}$ for multiple mutations. Pairwise percentage sequence divergence values were estimated among haplotypes and observed mutational events were counted.

Tajima's *D* statistic (1989a) was computed using ARLEQUIN (Ver. 2.0; Schneider et al. 1999) as a measure of departure from patterns of variation expected under the neutral hypothesis due to factors such as population bottlenecks, population expansion, heterogeneity of mutation rates, and selection (Tajima 1989b). The significance of the *D*-statistic was tested by generating 1000 random samples under a hypothesis assuming selective neutrality and population equilibrium. The *P*-value assigned to the *D*-statistic for each locality represented the proportion of simulations resulting in test values less than or equal to the observation. Significance levels for multiple tests carried out simultaneously were adjusted using the sequential Bonferroni method (Rice 1989). ARLEQUIN's exact test of population differentiation was used to test for distributional homogeneity of haplotype frequencies among sampling sites. Probability values were assigned using a Markov chain procedure (Schneider et al. 1999).

Genetic distances were determined from sequence data using the Phylogeny Inference Package (PHYLIP; Version 3.5; Felsenstein 1993). The program DNADIST was used to estimate nucleotide substitution calculated assuming the Kimura 2-parameter model (Kimura 1980). The distance matrix obtained from this analysis was analyzed using the FITCH program to create least-square estimates of a phylogenetic network with unconstrained branch-lengths. Uncorrected proportional distances were computed using MEGA version 2.1 (Kumar et al. 2001) to estimate divergence among collection sites. Standard errors of the estimates were calculated by bootstrapping (500 replicates). Nucleotide sequence divergence among collection sites was estimated (Nei and Tajima 1981). Multidimensional scaling (MDS) analysis was used to explore for patterns in the distance matrix using the PROC MDS program contained in SAS (SAS Institute 1999). Relationships between haplotype frequencies and geographic location (longitude) in the Gulf of Mexico were quantified using Spearman correlation coefficients calculated using SAS (SAS Institute 1999).

RESULTS

Sequences for a ~351 base-pair fragment were obtained (Table 1). Comparisons with archived (GenBank) DNA sequences found the nearest match to be with a 12S rRNA mtDNA fragment sequenced from *Megalops cyprinoides* (Inoue et al. 2001; J. G. Inoue and M. Maya, direct submission to GenBank®), supporting the assumption that the correct fragment had been amplified and sequenced. MODELTEST 3.06 identified the Tamura and Nei (1993) model with a gamma distribution shape parameter of 1.637 as an adequate model.

Table 1. Base sequence of most common 12S mtDNA haplotype (Haplotype 1) observed in tarpon of the Gulf of Mexico. GenBank accession number = `DQ083541`.

```
CTAGCTTTAAACCCAAAGGACTTGGCGGTGCCCCAAACCCACCTAGAGGAGCCTGTTC
TACAACCGATAACCCCCGTTAAACCTCACCACTCCTAGCCAACCCCGCCTATATACCG
CCGTCGCCAGCTTACCCTATGAAGGCCCAACAGTAAGCCCAAAGAGTACAACTCAAAA
CGTCAGGTCGAGGTGTAGCGCACGAAGTGGGAAGAAATGGGCTACATTTTCTCAACCC
AGAATACTTGCGAACGACACAGTGAAACCTGAGTCCAAAGACGGATTTAGCAGTAAAA
AAGAAATAGAGAGTCTTTTTGAAACCGGCCATGGGACGCGCA
```

Sixteen haplotypes were identified (sequences for each may be obtained from the senior author). The ratio of transversions to transitions was 2.4:1. Insertion/deletion events accounted for 47.8% of observed sequence changes. The common haplotype (haplotype 1) predominated in all samples, with frequencies ranging from 40.0% in the Mexican Gulf sample to 88.89% in the Chetumal sample (Table 2). Two of the less common haplotypes, (haplotypes 7 and 8) were observed in more than one sample, all other haplotypes were restricted to a single sampling region. The number of observed haplotypes per sample ranged from two at Chetumal to six in the Mexican Gulf. The percent of nucleotide sites that were observed to be variable ranged from 0.57% at Chetumal to 9.12% in the Mexican Gulf. The latter value was inflated by the occurrence of the highly divergent haplotype 2 which was observed only in Mexican Gulf samples. For these reasons, haplotype 2 was not included in subsequent analyses of within population diversity or among population divergence. The lowest observed level of diversity, as measured by $\hat{h}$ and $\hat{\pi}$, was seen in the Chetumal sample (Table 2). The estimate of $\hat{h}$ for this Caribbean site was approximately one-third to one-quarter those estimated for Gulf of Mexico sites. Similarly, the $\hat{\pi}$ estimate for Chetumal was between 3 and 18 times lower than estimates of diversity in Gulf sites.

Table 2. Frequencies of haplotypes (sans haplotype 2) and diversity measures at 5 collection localities for tarpon in the Gulf of Mexico using a 351 bp 12S rRNA sequence. Tajima's *D* statistic (1989a) and the probability at *D* is statistically different from 0 are presented.

Haplotype	Florida	Louisiana	Texas	Mexico	Chetumal	Total
1	7	5	6	4	8	30
3				2		2
4			1			1
5		1				1
6		1				1
7	1	1				2
8	1		1			2
9					1	1
10	1					1
11	1					1
12				1		1
13				1		1
14			1			1
15			1			1
16				1		1
N	11	8	10	10	9	48
%var.	2.28	3.99	2.85	9.12	0.57	
sites	0.6182	0.6429	0.6667	0.806	0.2222	
Haplotype diversity						
±SE	0.1643	0.1841	0.1633	0.120	0.1662	
Nucleotide diversity	0.0043	0.0118	0.0089	0.014	0.0013	
±SE	0.0032	0.0075	0.0057	0.009	0.0015	
D	-1.71	-1.76	-1.97	-1.63	-1.09	
P	0.028	0.006	0.005	0.043	0.19	

Tajima's *D* values (Table 2) for Texas (*D* = -1.97) and Louisiana (D = -1.76) are significantly different from 0 when α is adjusted for multiple simultaneous comparisons (α ≤ 0.01). Values for Florida (*D* = -1.71) and Mexico (*D* = -1.63) approach statistical significance. These analyses do not support the neutral hypothesis as an explanation for polymorphisms found in the tarpon 12S rRNA fragment. The negative values reflect multiple informative sites with low frequencies which may indicate recent alterations in tarpon demographics due to population bottlenecks or expansion.

Estimates of pairwise percentage sequence divergence among haplotypes (Table 3)

demonstrated the divergence of haplotype 2 which had a mean sequence divergence of 7.09, nearly twice that of the next most divergent haplotype (haplotype 6). Haplotype 2 differs from the most common haplotype by 23 observed mutational events in the 351 nucleotides sequenced. This is more than twice that observed in any other haplotype. Due to this level of differentiation haplotype 2 was subsequently omitted from analyses of population structure.

Pairwise divergence estimates among the 5 localities ranged from 0.0006 (S.E. = 0.0012) between Chetumal and Florida to 0.0026 (S.E. = 0.0143) between Texas and Mexico samples (Table 4). The frequency of haplotype 1, the only ubiquitous haplotype identified in the survey, becomes progressively less common as one proceeds from Chetumal to Florida then westward across the Gulf of Mexico (Table 2). This cline was statistically significant (r = -1.000, P < 0.001). In Mexican waters, while still the most common haplotype, haplotype 1 was no longer found in a majority of observed tarpon.

Multidimensional scaling of Genetic affinities among the five sampling localities suggests Mexican tarpon are differentiated from tarpon sampled from Texas to Florida (Fig. 2). Tarpon from the Mexican Caribbean off Chetumal have greater genetic affinity to tarpon collected in Florida waters.
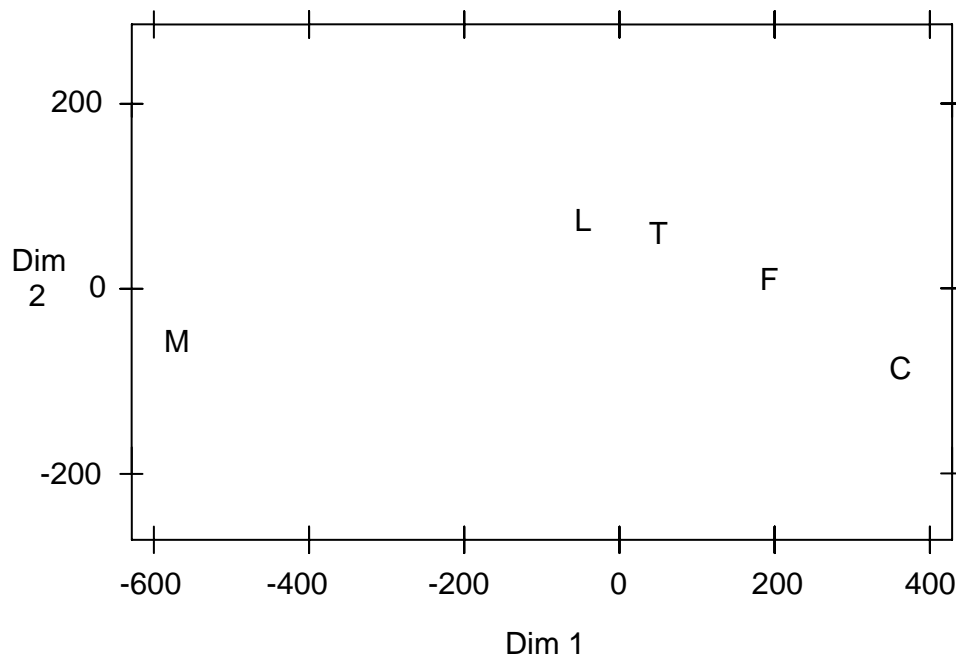

Figure 2. Multidimensional scaling analysis of genetic affinities of 5 tarpon sampling regions based on 12S rRNA sequences. Sampling regions: C = Chetumal, F = Florida, L = Louisiana, M = Mexico, T = Texas.

Table 3. Pairwise percentage sequence divergence estimates (above diagonal) and observed number of mutational events (below diagonal) between 12S rRNA haplotypes discerned for 48 tarpon from 5 locales.

Hapl.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1		6.55	0.85	0.85	0.28	3.42	0.57	0.57	0.57	0.57	0.57	0.28	1.71	0.85	0.28	1.14
2	23		7.41	7.69	6.84	8.83	7.12	7.12	7.12	6.84	6.84	6.84	5.41	6.84	6.84	7.98
3	3	26		1.99	1.14	4.27	1.42	1.42	1.42	1.42	1.42	1.14	2.56	1.71	1.14	1.14
4	3	27	7		1.42	3.99	1.71	1.71	1.14	1.71	1.99	1.42	2.28	1.99	1.71	2.28
5	1	24	4	5		3.70	0.85	0.85	0.85	0.85	0.28	0.57	1.99	1.14	0.57	1.71
6	12	31	15	14	13		3.70	3.99	3.42	2.56	3.99	3.70	3.13	4.27	3.70	4.84
7	2	25	5	6	3	13		0.85	0.85	1.14	3.99	0.85	2.28	1.42	0.85	1.99
8	2	25	5	6	3	14	3		1.14	1.14	1.14	0.57	2.28	1.42	0.85	1.99
9	2	25	5	4	3	12	3	4		1.14	1.14	0.85	1.14	1.42	0.85	1.99
10	2	24	5	6	3	9	4	4	4		1.14	0.85	1.99	1.14	0.85	1.99
11	2	24	5	7	1	14	3	4	4	4		0.85	2.28	1.42	0.85	1.99
12	1	24	4	5	2	13	3	2	3	3	3		1.99	1.14	0.57	1.71
13	6	19	9	8	7	11	8	8	4	7	8	7		2.56	1.99	3.13
Hapl.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
14	3	24	6	7	4	15	5	5	5	4	5	4	9		1.14	2.28
15	1	24	4	6	2	13	3	3	3	3	3	2	7	4		1.71
16	4	28	4	8	6	17	7	7	7	7	7	6	11	8	6	

Table 4. Above diagonal, pairwise 12S rRNA sequence divergence discerned for 48 tarpon from 5 collection locales in the Gulf of Mexico and Caribbean. Below diagonal, standard errors.

Site	Florida	Louisiana	Texas	Mexico	Chetumal
Florida		0.0013	0.0013	0.0021	0.0006
Louisiana	0.0036		0.0016	0.0025	0.0010
Texas	0.0055	0.0068		0.0026	0.0011
Mexico	0.0116	0.0127	0.0143		0.0021
Chetumal	0.0012	0.0025	0.0043	0.0104	

DISCUSSION

Tarpon are large marine fish, capable of migrations across impressive distances. They spawn in deep water and the eggs and larvae may be transported by currents for extended periods. These life history traits predict little or no genetic subdivision in tarpon of the Gulf of Mexico. However, statistically significant clines were observed in the frequency of the most common haplotype and in measures of genetic diversity across the Gulf of Mexico, with tarpon from the westernmost Gulf of Mexico being most divergent. These results are similar to those of Garcia de León et al. (2002) who found genetic subdivision among tarpon of the western Gulf. The simplest explanation may be that a pattern of clinal change in tarpon genetic characteristics exists within the Gulf of Mexico, and that tarpon of the western Gulf are, relatively speaking, differentiated. Whether this differentiation reaches the level of distinct stock structure, as suggested by Garcia de León et al. (2002) is a matter of interpretation.

Such structure would suggest the existence of two areas of reproduction for tarpon resident in the Gulf of Mexico; one stock spawning from southern Florida south into the Caribbean and undergoing seasonal migration across the northern Gulf of Mexico (and probably north along the U.S. Atlantic coast). This is supported by tag-return data collected in the northern Gulf of Mexico where tarpon spawned off Florida then migrated during summer to feed off the mouth of the Mississippi. A western stock may reproduce in the Bay of Campeche and have seasonal migration north along the Gulf coast of Mexico and Texas (Cruz-Ayala 2002). The allozyme and mtDNA data of Garcia de León et al. (2002) suggest migrations from the two

stocks meet along the Texas coast. If such reproductive centers exist, the level of isolation is not great. Estimates of Nm between western Gulf of Mexico (Mexico) and the regions of the eastern Gulf of Mexico were low relative to estimates of tarpon migration between other points in the Gulf of Mexico, though still ranging between 10 and 63 individuals per year.

Blandon et al. (2002) recommended broodfish collected for the proposed tarpon enhancement program be tarpon obtained as near Texas as possible within the Gulf of Mexico. The results of the present study, reinforced by findings of Garcia de León et al. (2002), suggest tarpon from Mexican broodfish are inappropriate for enhancement in Texas waters, especially for stocking into upper coast Texas bays and estuaries. A further recommendation by Blandon et al. (2002) that large numbers of broodfish be employed in future stockings in Texas waters is supported by the high percentage of private and rare haplotypes found in the current study among western Gulf tarpon. It would also be prudent to have a genetic monitoring program in place to insure that the contribution of each broodfish is about equal. Recommendations aimed at protecting the genetic resources of a managed species entail a cost in effort and time; however, failure to follow these guidelines places the genetic integrity of the species at risk. This is especially true for a species with the life history characteristics of tarpon. Species undergoing local or regional declines in natural populations, such as tarpon in the western Gulf of Mexico, will be heavily impacted by a stocking program if that program is successful.

An adequate understanding of population structure of tarpon in the Gulf of Mexico is also important for the development of sound regulatory strategies. If, as suggested by Garcia de León et al. (2002) and the present study, tarpon encountered off Texas are predominantly seasonal migrants from the Bay of Campeche or from Florida, then intergovernmental management agreements are critical to the recovery of the tarpon fishery in Texas waters. Cooperative policies designed to improve nursery habitat and/or reduce directed and non-directed fishery mortality in the western Gulf of Mexico may reverse downward trends in tarpon numbers and help to reestablish the valuable recreational tarpon fishery in the western Gulf. Management options which focus on a single region, such as stocking tarpon in Texas waters, will have little effect on the strength of tarpon stocks and fisheries.

Acknowledgements

LITERATURE CITED

Allendorf, F., N. Ryman, and F. Utter. 1986. Genetics and fishery management: past, present, and future, p. 1-20. In N. Ryman and F. Utter [eds]. Population genetics and fishery management. Washington Sea Grant Program, University of Washington Press, Seattle, Washington.

Altschul, S. F., T. L. Madden, A. A. Schäffer, J. Zhang, Z. Zhang, W. Miller, and D. J. Lipman. 1997. Gapped BLAST and PSI-BLAST: a new generation of database search programs. Nucleic Acids Res. 25:3389-3402.

Cruz-Ayala, M. A. 2002. Tarpon: Tourism Resource of the Gulf of Mexico. Contrib. Mar. Sci. 35:95-96.

Blandon, I. R., R. Ward, F. J. Garcia de León, A. M. Landry, A. Zerbi, M. Figuerola, T. C. Gesteira, W. Dailey, and C. D. Acuna Leal. 2002. Studies in conservation genetics of tarpon (*Megalops atlanticus*) – I. Variation in restriction length polymorphisms of mitochondrial DNA across the distribution of the species. Contrib. Mar. Sci. 35:1-17.

Carr, S. M., and H. D. Marshall. 1991. A direct approach to the measurement of genetic variation in fish populations: applications of the polymerase chain reaction to studies of Atlantic cod, *Gadus morhus* L. J. Fish Biol. 39(Suppl.A):101-107.

Crabtree, R. E., D. C. Cyr, R. E. Bishop, L. M. Falkenstein, and J. M. Dean. 1992. Age and growth of tarpon, *Megalops atlanticus*, larvae in the eastern Gulf of Mexico, with notes on relative abundance and probable spawning areas. Environ. Biol. Fish 35: 361-370.

Cyr, E. C. 1991. Aspects of the life history of the tarpon *Megalops atlanticus* from south Florida. Unpublished Ph.D. Dissertation, University of South Carolina, Columbia.

Felsenstein, J. 1993. PHYLIP (Phylogeny Inference Package) version 3.5c. Distributed by the author. Department of Genetics, University of Washington, Seattle.

Figuerola, M. 1996. Adult snook and tarpon abundance, age, growth and reproduction in Puerto Rico estuaries and coastal waters. United States Fish and Wildlife Service Project F-33, Study II, Final Report, Washington, D. C.

Garcia de León, F. J., C. D. Acuna Leal, I. R. Blandon, and R. Ward. 2002. Studies in conservation genetics of tarpon (*Megalops atlanticus*) – II. Population structure of tarpon in the western Gulf of Mexico. Contrib. Mar. Sci. 35:18-33.

Higgins, D. G. and Sharp, P. M. (1988) CLUSTAL: a package for performing multiple sequence alignment on a microcomputer. Gene 73:237-244.

Inoue, J.G., M. Miya, K. Tsukamoto, and M. Nishida. 2001. Complete mitochondrial DNA

sequence of *Conger myriaster* (Teleostei: Anguilliformes): Novel gene order for vertebrate mitochondrial genomes and the phylogenetic implications for anguilliform families. J. Mol. Evol. 52:311-320.

Jukes, T. H., and C. R. Cantor. 1969. Evolution of protein molecules, p. 21-132. In H. N. Munro [ed.], Mammalian protein molecules. Academic Press, New York.

Kimura, M.   1980.   A simple model for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. J. Mol. Evol. 16:11-120.

Kocher, T. D., W. K. Thomas, A. Meyer, S. V. Edwards, S. Pääbo, F. X. Villablanca, and C. Wilson. 1989. Dynamics of mitochondrial DNA evolution in animals: Amplification and sequencing with conserved primers. Proc. Nat. Acad. Sci., USA 86:6196-6200.

Kumar, S., K. Tamura, I. B. Jakobsen, and M. Nei. 2001. MEGA2: Molecular Evolutionary Genetics Analysis Software. Arizona State University, Tempe.

McMillan-Jackson, A. B., T. M. Bert, and H. Cruz-Lopez. 1993. Geographic variation in allozymes, mitochondrial DNA, and morphology in the Atlantic tarpon (*Megalops atlanticus*). Section II. In R. E. Crabtree, T. M. Bert, and R. G. Taylor. Investigation into nearshore and estuarine gamefish distributions and abundance, ecology, life history, and population genetics in Florida. Florida Department of Natural Resources, FDNR\FMRI File Code: F0165-F0296-88-93-C, Tallahassee.

Nei, M. 1987. Molecular Evolutionary Genetics. Columbia University Press, New York. 512 pp.

Nei, M., and F. Tajima. 1981. DNA polymorphism detectable by restriction endonucleases. Genetics 124:701-716.

Palumbi, S. R.   1996. Nucleic Acids II: The Polymerase Chain Reaction, p. 205-247. In D. M. Hillis, C. Moritz, and B. K. Mable [eds.]   Molecular systematics, 2nd ed.   Sinauer Associates, Inc., Sunderland, Massachusetts.

Posada, D., and K. A. Crandall. 1998. MODELTEST: testing the model of DNA substitution. Bioinformatics 14:817-818.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223-225.

SAS Institute Inc. 1999. SAS/STAT user's guide, Version 8. SAS Institute Inc. Gary, North Carolina. 3884 pp.

Schneider, S., D. Roessli, and L. Excoffier. 1999. Arlequin, ver. 2.0: A Software for Population Genetic Data Analysis.   Genetics and Biometry Laboratory, University of Geneva, Geneva, Switzerland.

Smith, R. F., B. A. Wiese, M. K. Wojzynski, D. B. Davison, and K. C. Worley. 1996. BCM Search Launcher—An integrated interface to molecular biology data base search and analysis services available on the World Wide Web. Genome Res. 6:454-462.

Tajima, F.   1989a. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123:585-595.

Tajima, F. 1989b. The effect of change in population size on DNA polymorphism. Genetics 123:597-601.

Tamura, K., and M. Nei.   1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Mol. Biol. Evol. 10: 512-526.

Thompson, J. D., D. G. Higgins, and T. J. Gibson. 1994. CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, positions-specific gap penalties and weight matrix choice.   Nucleic Acids Res.

22:4673-4680.

Zerbi, A. 1999. Écologie et Biologie des Juveniles de Deux Groupes de Poissons Exploites en Peche Sportive: Le Brochet de Mer (Centropomus) et Le Tarpon (*Megalops atlanticus*) a Porto Rico. Unpublished Ph.D. Thesis, Universite D'Aix-Marsailles II, Marsailles, France.

A BRIEF DESCRIPTION OF THE BONEFISH RECREATIONAL FISHERY IN LOS ROQUES ARCHIPELAGO NATIONAL PARK, VENEZUELA

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ABSTRACT

Bonefish, Albula vulpes, supports important recreational fisheries in the Florida Keys and throughout the Caribbean. Recently, Los Roques Archipelago National Park (LRANP), located 150 km off the coast of Venezuela, has become a popular destination for bonefish sportfishers. The recreational fishery in Los Roques is relatively small, compared to other Caribbean and Florida fisheries. There are a total number of 12 licensed fishing guides in the park, but only six are currently operating. An average of 400 anglers visits the park each year. Fishing is a year round activity, but some of the highest catch rates are made from January to June. Experienced anglers average catching ten fish daily and most bonefish caught weigh one to 2 kg, and the biggest are around 4 kg.

INTRODUCTION

Bonefish, Albula spp., occur in coastal and inshore waters of tropical and subtropical seas worldwide. In Venezuela, Albula vulpes is a common species, particularly in Los Roques Archipelago National Park (LRANP; south Caribbean Sea), where large schools of bonefish inhabit the flats of this protected area (Pulido 1983, Cervigón 1991).

In a survey of 440 bonefish caught in the western portion of Los Roques Archipelago, females were significantly larger than males, ranging from 286 to 717 mm of fork length (FL; mean = 492.22 mm; s.d. = 65.36; n = 255) and males from 334 to 600 mm FL (mean = 459.36, s.d. = 35.15; n =185) (Debrot 2001). This size interval is similar to the south Florida population (228-700 and 290-700 mm FL for females and males, respectively), where females are also significantly larger than males (Crabtree et al. 1996, 1997). The smallest sexually mature female and male found in Los Roques were 351 and 424 mm FL, respectively and spawning season extends from June to January (Debrot 2001).

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Bonefish supports important recreational fisheries in the Florida Keys, the Bahamas and other Caribbean islands (Mojica et al. 1995). In the last decade, Los Roques has become one of the most popular destinations for bonefishing. This recreational fishery is a rapidly growing industry that provides an important source of income for the local economy and an alternative to traditional artisanal fisheries, such as lobster.

Although currently bonefish are not considered a meat fish, subsistence fishing has been going on for centuries in Los Roques. Fish remains from A. vulpes found in archaeological sites in Dos Mosquises island suggest that exploitation of bonefish by indigenous islanders dates back to pre-colonial times (Antczak 1999).

Since 1950, when artisanal fishers from other regions of Venezuela arrived in the archipelago, bonefish were caught in shallow water with seine nets and used as bait to fish for other valuable species, such as sharks. In the 1980´s the use of seine nets was prohibited in the Archipelago, and since then, bonefish are only caught occasionally by local fishers.

Despite its economic importance, there is currently no management plan that guarantees a sustainable practice of this activity in the Archipelago. In this paper we present a brief description of the bonefish recreational fishery in the LRANP. In the absence of any other data available on this recreational fishery, it is our belief that this information will contribute to the development of a management strategy for the bonefish recreational fishery in Los Roques.

METHODS

Study Site

LRANP is a complex reef system located 155 Km to the north off the central coast of Venezuela (11°44'45'' to 11°58'36'' N and 66°57'27'' to 66°57'27'' W), comprising an area of 2250 km2 (Fig. 1).

Los Roques Archipelago was declared a national park in 1972, in order to protect a pristine marine ecosystem dominated by coral reefs, mangrove forest, and seagrass beds. Gran Roque, the archipelago´s main island has a population of 1,200 residents and more than 50,000 tourists visit the park yearly.
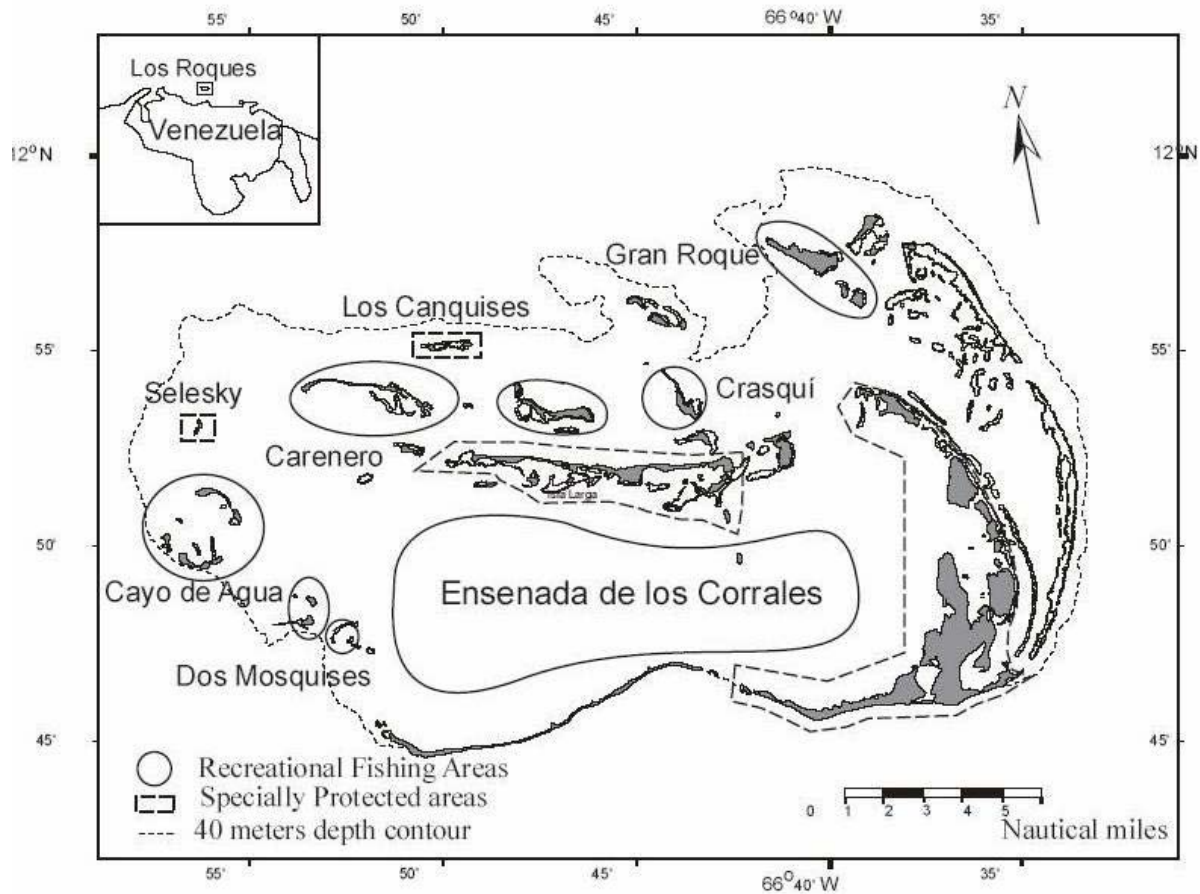
Figure 1. Map of Los Roques Archipelago National Park, Venezuela, showing the location of the main flats for bonefish recreational fishing and the areas under special protection (no take zones).

Summary of Data

This document is based on information collected from six surveys of professional fishing guides from Gran Roque and official statistics provided by authorities of the Institute of National Parks (Inparques) and Autoridad Unica de Area (AUA). A list of names, address and company affiliation of all licensed fishing guides in Los Roques was provided by Inparques. A total of 12 fishing guides were registered by the end of 2003, but only six were residing and operating in Los Roques.

We modified the set of question provided by the Bonefish Professional Guide Survey for the Florida Fishery (Ault and Humston 1999) to survey the six licensed fishing guides that were operating in Los Roques. Responses to the question were entered manually in the questionnaire.

RESULTS AND DISCUSSION

Recreational Fishery

The bonefish recreational fishery in Los Roques is relatively small, compared to other fisheries in the Caribbean and south Florida. This industry is composed of a few companies based in Gran Roque. By the end of 2003 there were seven fishing companies and only six of the 12 licensed fishing guides were working in the park.

Fishing for bonefish in Los Roques is predominantly fly fishing and catch-and -release and it is a year round activity. According to local fishing guides, some of the highest catches are made from January to June. Fishing guides reach the fishing areas using fibre glass boats (6-8 m). However, most of the fishing is done on foot, throughout the archipelago, except for the specially protected areas (no take zones), in flats, over sand, seagrass or coral bottom (Fig. 1).

According to fishing guides, most bonefish caught in Los Roques weigh one to 2 kg, but anglers often hook considerably larger fish. Several fish of 4 kg have been caught and the record is around 6 kg (13 pounds). In terms of number of catches, an average of ten fish can be caught daily by experienced anglers.

Factors affecting Bonefishing

Local fishing guides identified several threats to the recreational fishery, such as habitat degradation caused by uncontrolled tourism activities, increased fishing pressure and illegal fishing. Of these threats, the increase in fishing pressure was of the most concern for the fishing guides, who expressed the belief that some schools have abandoned their usual feeding grounds and moved to more remote flats.

Economic Importance

Tourism is the most important economic activity in the park, providing direct employment to 40% of the active population (AUA, 2000). In 2002, Los Roques received an average of US$400,000 from tourist entrance fees (Entrance Fee: US$5 per person) and from recreational fishery fees (US$2 per person/day). Additionally, the average 4 day fly-fishing trip costs around 2,325 US$, an important income which, in some cases, could benefit fishing companies, local fishing guides and lodge owners.

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LITERATURE CITED

Antczak, A. 1999. Late prehistoric economy and society of the islands off the coast of Venezuela: A contextual interpretation of the non-ceramic evidence. Ph.D. Dissertation. Institute of Archeology, University of London. 410 pp.

AUA. 2000. Características generales del visitante del Parque Nacional Archipiélago de Los Roques. Autoridad Única de Área del Parque Nacional Archipiélago de Los Roques. Departamento de Turismo. Caracas, Venezuela. Unpublished Data.

Ault, J. S. and R. Humston. 1999. Bonefish research project report #2. Univ. Miami. 41 pp.

Cervigón, F. 1991. Los Peces Marinos de Venezuela, Vol. I. Fundación Científica Los Roques. Caracas, Venezuela. 425 pp.

Crabtree, R. E., D. Snodgrass, C. H. Harnden, and C. Stevens. 1996. Age, growth and mortality of bonefish, Albula vulpes, from the waters of Florida Keys. Fish. Bull. 94:442-451.

Crabtree, R. E., D. Snodgrass, and C. H. Harnden. 1997. Maturation and reproductive seasonality in bonefish, Albula vulpes, from the waters of the Florida Keys. Fish. Bull. 95:456-465.

Debrot, D. 2001. Biología reproductiva del macabí, Albula vulpes, en el Parque Nacional Archipiélago de Los Roques. Undergraduate Thesis. Universidad Simón Bolívar. División de Ciencias Biológicas. Caracas, Venezuela. 44 pp.

Mojica, R. Jr., J. M. Shenker, C. W. Harnden, and D. E. Wagner. 1995. Recruitment of Bonefish, Albula vulpes, around Lee Stocking Island, Bahamas. Fish. Bull. 93:666-674.

Pulido, F. 1983. Hábitos alimenticios y migraciones nocturnas de algunas especies de peces entre el arrecife coralino y las praderas de fanerógamas marinas en el Archipiélago de Los Roques. Undergraduate Thesis. Universidad Simón Bolívar, División de Ciencias Biológicas. Caracas, Venezuela. 120 pp.

WHAT CAN HISTORIC TARPON SCALES TELL US ABOUT THE TARPON FISHERY COLLAPSE IN TEXAS?

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ABSTRACT

Tarpon populations attracted fishermen to the central Texas coast as early as the 1880's. During the 1920's through the 1940's, Port Aransas was known as the "Tarpon Capital of the World". By the 1950's, the vast schools of tarpon that passed along the coast for hours were essentially gone. A major unanswered question is what caused the disappearance of the historic tarpon fishery in Texas? To answer this question we need information on populations before the collapse, but no estimates of tarpon population size exist. Migratory patterns are known only in a general way with most information indicating that tarpon along the lower Texas coast were part of a population that migrated north in the summer from Mexico. Tarpon are considered sports fish in the US and Mexico and fishery data is rarely collected. It may be possible to reconstruct population characteristics from information gathered during the heyday of tarpon fishing in Texas. To that end, data written on scales posted on the walls of the historic Tarpon Inn in Port Aransas were collected and compiled. There were close to 2000 observations that have length data out of a total of ~2700 scales examined. Length and weight was recorded for 270 fish. The number of scales (catches) gradually decreases after 1940 and becomes very spotty by the late 1950s. It is possible to track length modes in the population during 1926 to 1941, providing information on the lengths of the fish and the seasonality of the catches. Looking at the entire data set, there is not a reduction in size of the fish over time but there is a notable absence of small fish during the later years. Fulton's condition based on the length and weight data might suggest reduced condition of fish after the 1950's. The data indicate that the reductions in tarpon populations may have resulted from recruitment failure, since large, old fish continued to be caught. Suggestions for future research are summarized.

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INTRODUCTION

Tarpon (*Megalops atlanticus*) are found in tropical and subtropical waters of the Atlantic and support valuable sports fisheries in Florida, Mexico and throughout the Caribbean. Recent estimates place the economic impact of the tarpon fishing industry in Florida near $1.5 billion (Doug Kelly, pers. com.). Spawning locations for tarpon are unknown and eggs have not been described. However, based on capture of larvae, spawning probably occurs from May to August in the Gulf of Mexico near Florida (Smith 1980; Crabtree et al. 1992), March to September in Puerto Rico (Zerbi et al. 2001) and throughout the year in Costa Rica (Crabtree et al. 1997) and Panama (Hildebrand 1963). Tarpon have a pelagic, leptocephalus larval stage estimated to lasts 2-3 months (Smith 1980) or 15-41 days (Cyr 1991) followed by a juvenile stage that recruits to coastal waters, mangrove lined estuaries, and rivers. Juvenile tarpon have been collected in waters of poor quality with features such as low pH, and near anaerobic conditions (Silgado 2002; Shenker et al. 1995). They can inhale atmospheric oxygen and thus tolerate oxygen-poor environments (Geiger et al. 2000; Wells et al. 2003). Juveniles grow to sexual maturity by 10 years of age but are long lived and can become large (Crabtree et al. 1997). Longevity of males is more than 30 years with lengths of over 1.5 m while females can live more than 50 years and attain lengths of over 2 m (Andrews et al. 2001).

Tarpon were abundant in the waters of the Coastal Bend in Texas as early as the 1880's. Port Aransas, Texas was considered the "Tarpon Capital of the World" from the 1920-40's when tarpon schools attracted fishermen from all over the world. By the 1960's, the large schools of tarpon that migrated along the coast were essentially gone.[1] The cause of the disappearance of the historic tarpon fishery in Texas remains a major unanswered question. Many causes for this decline have been proposed, including reductions in freshwater habitat, pollution or parasitism, reduced prey schools, and overexploitation. To understand the reason for the population decline requires information about the tarpon populations before and during the collapse, but few data from that time exists.

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[1] Dreyer recalls seeing a tarpon school in 1956 that he estimated at 5,000 fish. It was during one of the many Coastal Bend tarpon tournaments, when Dreyer and a buddy were fishing within the old Matagorda Island bombing range. The massive silvery train spanned 75 to 100 feet wide and stretched for nearly 2,000 feet, Dreyer said. He cites that same year as the leading edge of the tarpon decline in Texas. "I never saw anything like that again," Dreyer said.

Migratory patterns are known only in a general way, with most information indicating that tarpon along the Texas coast were part of a population that migrated north in the summer from Mexico and returned south when the waters began to cool in the fall. Tarpon are managed as sports fish in the U.S. and Mexico and fishery data are rarely collected. Even in Florida, where a tarpon fishery prevails, there is a lack of information concerning population structure because of the catch and release nature of the fishery (Crabtree 2002).

It may be possible to reconstruct population characteristics of the historic tarpon fishery from information gathered during the height of tarpon fishing in Texas. It was the custom at that time for fishermen to remove a scale from their fish, write the size on it and post it on the wall of the Tarpon Inn in Port Aransas, Texas (Fig. 1). Data derived from scales of individual fish mounted on the wall were used to derive estimates of population characteristics from the early 1920's through 1950's and to compare them to currently available data on tarpon from Florida and Costa Rica (Crabtree et al. 1995). Difference in population characteristics might point toward the reason for the tarpon fishery collapse.
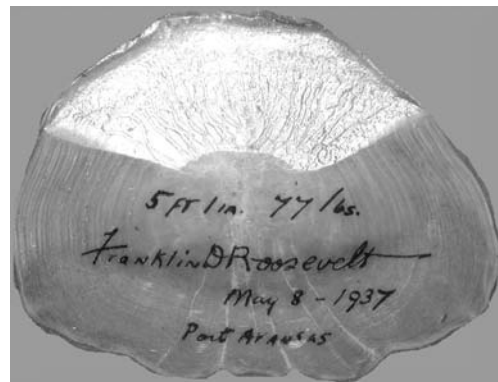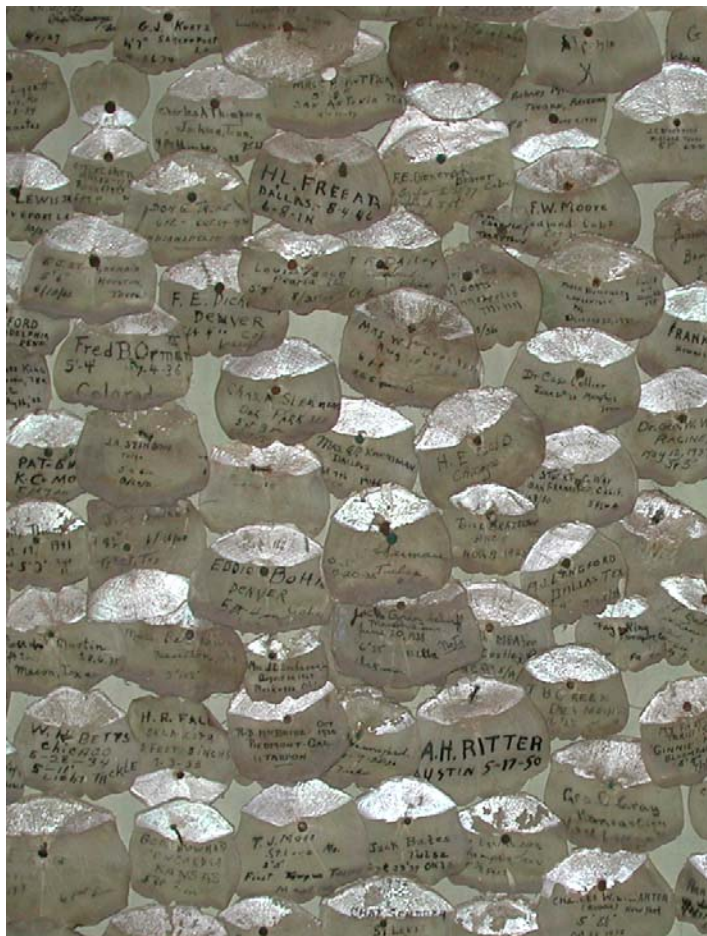

Figure 1. Wall panel of tarpon scales (left) individual scale signed by FDR from the Tarpon Inn, Port Aransas, Texas (above).

Tarpon life history characteristics suggest that overfishing on the late maturing, long-lived species could cause a decline in the population, and this might be evidenced in the scale data. The decline in fish numbers off the Texas coast might also indicate a change in migratory patterns or recruitment failure due to the lack of juveniles in response to habitat or hydrological changes. To test the recruitment failure hypothesis, we determined changes in fish size with time from the scale data. In addition we determined condition, based on length and weight data, to see if this changed over time revealing changing food or water quality conditions. Evaluating the relative contribution of different factors driving changes in abundance is difficult but insight may be gained by looking at changes in size of fish and relative condition during the time when tarpon fishing was at its peak in waters near Port Aransas.

MATERIALS AND METHODS

Data were derived from 2,700 scales of individual fish mounted on the wall at the Tarpon Inn. The data were recorded from each scale and entered into a database. Available data included fishers' names, date of the catch, length and weight of the fish. Not all data were available or legible for all 2,700 scales. Length in inches or feet was converted to cm and assumed to be total length; weight was converted from lb. to kg. To compare length-weight relationships to published data, all scale lengths were converted to fork length using a relationship of fork length to total length for Florida fish FL=-10.8096 + 0.8967TL in mm (Crabtree et al. 1995). All data herein are reported as fork length unless otherwise noted. Problems with the dataset include the general difficulties found with recreational fishery based numbers. There were no effort data, no information on discarded or released fish, not all fish caught and retained were measured, and not all scales on the wall have complete information (i.e., length, weight). Nevertheless, these data provide an interesting (although somewhat speculative) story about historical tarpon dynamics in the NW Gulf of Mexico.

A condition index, Fulton's K, was calculated based on the fork length (cm) and weight (kg) measurements calculated from the scales. The Fulton's K was calculated as weight / length^3. Fish with K>1 are heavy for their length or fatter and considered to be in good condition. Fish with K<1 are thinner and considered to be in poorer condition.

RESULTS

Scales were available from 1902 through 1998 but most of the data were from 1922-1952. Maximum annual catches of over 150 tarpon were reported in 1937-1940 (Fig. 2). The
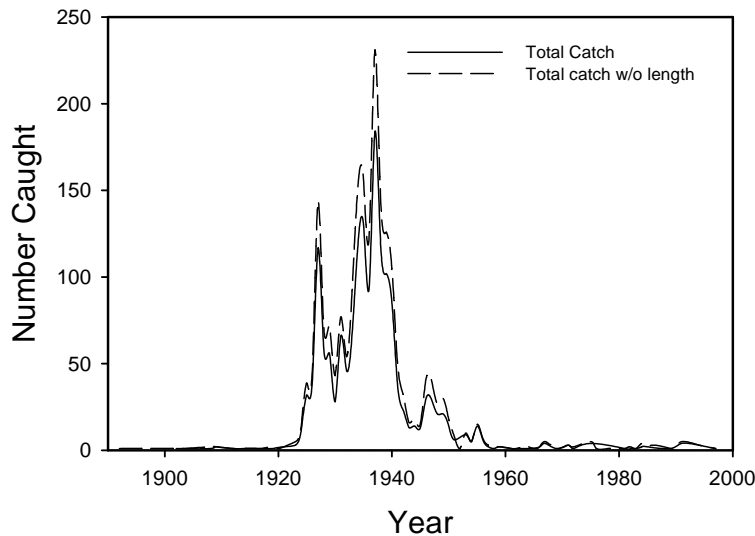
Figure 2. The number of tarpon collected each year (based on scale information) from 1902- 1998) showing the data with lengths available and all the data.

number of tarpon caught each year gradually declined after 1940 (big decline was also correlated with U.S. entry into WWII) and becomes very spotty by the late 1950's. Seventy-four percent of the scales had information on lengths of the tarpon caught and those closely follow the larger data set.

Tarpon was a seasonal fishery with most catches in June and July, but large numbers were also caught in May, August, September and October (Fig. 3). There was not a lot of
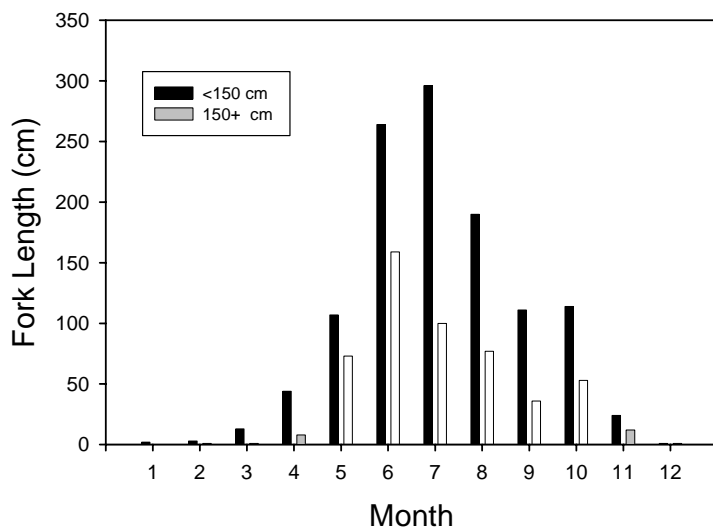
Figure 3. Number of tarpon caught per month (based on scale information) by 10-cm size ranges from 120 cm to > 200 cm.

temporal difference by size class, except the smallest fish were caught earlier than the larger fish. The largest fish were not caught until May and were gone by November.

There were close to 2000 observations that had length data out of a total of ~2,700 scales examined. Fork lengths of most fish were in the 120-160 cm size range (Fig. 4). Weight and
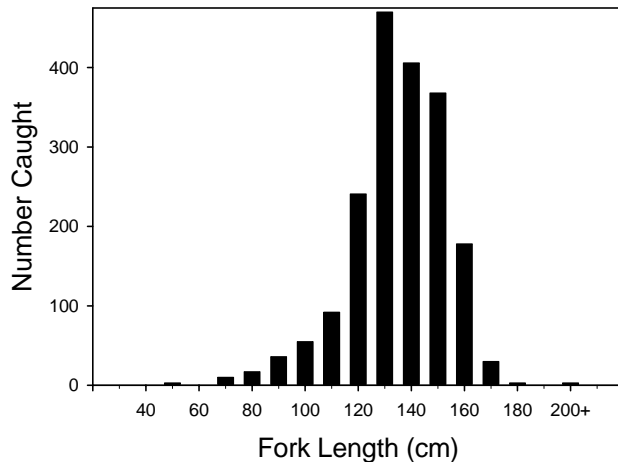
Figure 4. Number of tarpon caught by size class (based on scale data) averaged over all years.

length were recorded for 270 fish. There is a good fit to the length/weight relationship (Fig. 5) which suggests that the data were fairly accurately measured and recorded on the scales. We compared our length weight relationship to those published for tarpon in Florida and Costa Rica
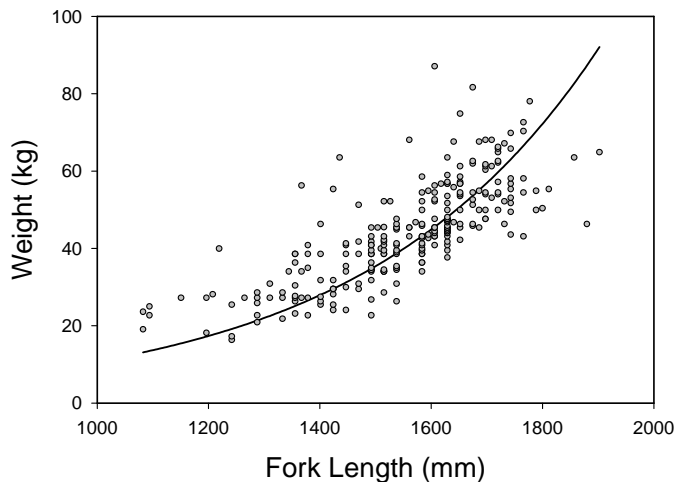
Figure 5. Fork length and weight relationship from 270 tarpon scales (r^2=0.638).

(Crabtree et al. 1995; 1997). Our fish were heavier at smaller sizes than the Florida or Costa Rica fish but fell within the length/weight range of those fish at sizes above 1,500 mm (Fig. 6).
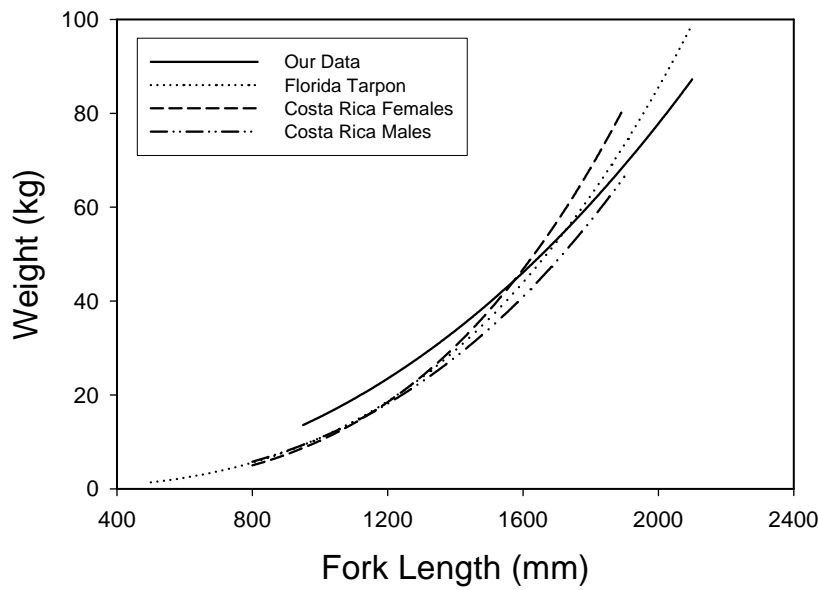
Figure 6. Fork length and weight relationship from this study and from Florida and Costa Rica tarpon populations.

Since the late 1950's there is some evidence in the data of a change in condition of tarpon caught off Port Aransas. A larger percentage of fish caught at this time are in poor condition and few have K $\geq$ 1.4 (Fig. 7).
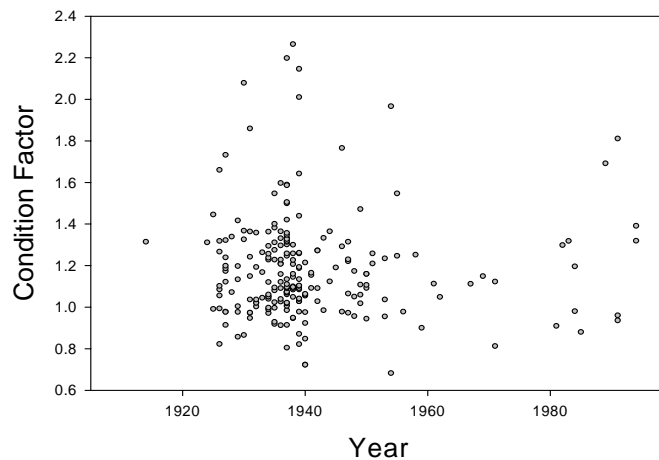
Figure 7. Condition factor based on tarpon scale length and weight data. Fish with K>1 are heavy for their length or fatter and in good condition. Fish with K<1 are thinner and in poorer condition..

It is possible to track length modes in the population during 1926 to 1941 where the vast majority of data reside and the size ranges are fairly constant (Fig. 8). But after the collapse and since 1960 there is a conspicuous lack of small fish < 130 cm while large fish remain.
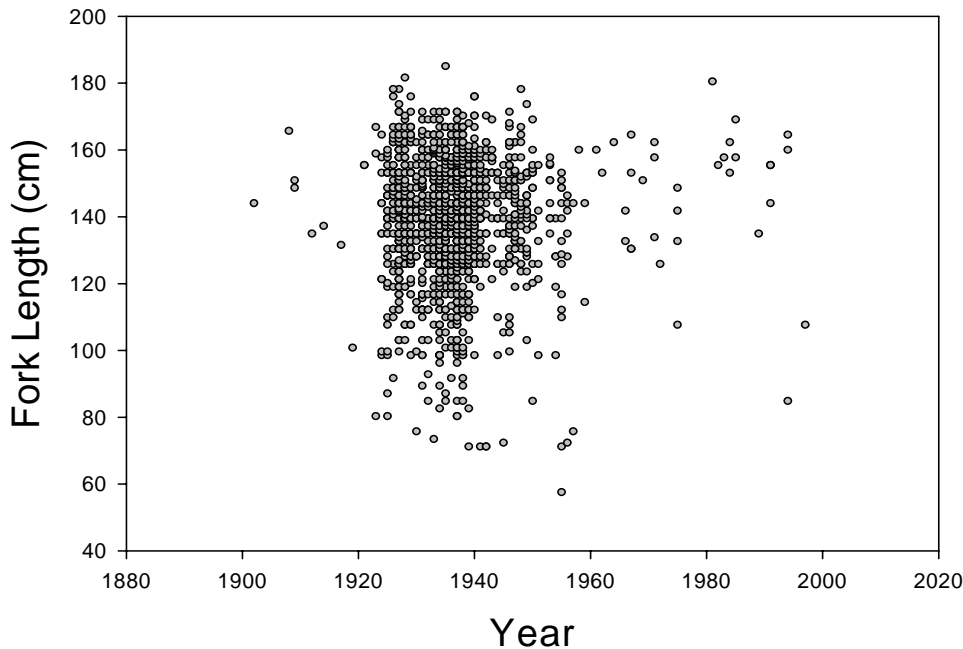
Figure 8. Tarpon lengths by year caught based on scale data

DISCUSSION

The majority of the fish lengths recorded on the scales were between 5 and 6 ½ ft. Tarpon are sexually mature at about 120 cm and smaller fish are rarely caught in the recreational fishery in Florida (Crabtree, et al. 1995) although many smaller fish were reported on the scales in the early years. There does not appear to be any obvious sign of a pending collapse based on the length modes during the period 1926-1941, such as a reduction in size range. If over-fishing were the single source of the tarpon decline, we might expect to see a reduction in the larger size classes of fish as seen in other overexploited fishes (Haedrich and Barnes 1997). These authors suggest that a reduction in mean size along with a decrease in catch (CPUE) would indicate overexploitation of the large fish. To the contrary, after the tarpon collapse and since 1960 small fish are largely absent while the large fish remain. In late July, 1999 a very large tarpon caught at Padre Island National Seashore (just south of Port Aransas) was measured and release. The fish measured 7 feet, 8 inches (208 cm FL). Radiometric aging has shown that tarpon may live up to 78 years (Andrews et al. 2001) thus old, large fish can remain in the population long after the population has been in decline. We should point out a caveat out that the lack of small fish since

1960 may be an artifact of the data if fishermen began only saving scales from large fish during this time.

There is evidence in the scale data of a possible change in condition of tarpon caught off Port Aransas. Several recent studies have linked fish condition to recruitment suggesting that high condition is associated with strong recruitment (Marshall and Frank 1999). According to Lambert and Dutil (1997), the decline in condition and energy reserves of cod over several years lowered their productivity and contributed to the collapse of the northern Gulf of St. Lawrence stock. The size of the female is directly related to egg biomass with larger fish producing greater numbers of eggs. This is especially true for long lived species as tarpon are. Reduced reproductive potential expected to result from decreased condition would ultimately reduce the number of small fish recruiting into the population.

The most parsimonious interpretation of the scale data is that there has been a lack of recruitment of young fish into the population since 1960. Genetic surveys indicate that most south Texas tarpon are closely aligned with tarpon from Mexico (Garcia de Leon et al. 2001). Texas waters are near the physiological limits imposed by low temperature on tarpon (Zale and Merrifield 1989), so that tarpon caught in Texas may have originated in Mexican nursery areas and spent a majority of the year in Mexican waters. Some have suggested that there has been a loss of nursery habitat for young tarpon in Texas and Mexico and that perhaps reductions in fresh water inflows due to damning and diversion of rivers has played a role in reducing the nursery function of estuaries. The only data on spawning sites in the western GOM are from the collection of leptocephalus larvae off the state of Veracruz near the 200-m contour by Smith (1980). He suggested that the Caribbean Yucatan and SW Gulf of Mexico, along with the SE Gulf of Mexico off Florida were major spawning grounds for tarpon. Nursery grounds in the western Gulf of Mexico, summarized by attendees at the Tarpon Forum in Veracruz in 2004 (this issue), are mangrove lined lagoons, rivers and cenotes extending from Yucatan through the state of Veracruz.

In general, nursery habitats are mud flat pools and mangrove lined lagoons. Juvenile tarpon in Puerto Rico are found in habitats with a wide range of physical conditions including high temperature, high salinity, and high pH (Zerbi 1999). Tarpon prefer shallow waters with some type of vegetation where they feed on insects or mosquito larvae, changing to a diet of fish and shrimp as they grow. In Florida, juveniles are regularly collected in marshes lining estuaries

with very poor water quality, in deep potholes, depressions, and dredged canals. (Shenker et al. 2002). Accessibility to nursery habitats may be an important consideration, and Zerbi (1999) noted colonization was highest during flood spring tides with high amplitudes.

Recruitment failure might explain the severe drop in tarpon populations in the NW Gulf of Mexico. Winemiller and Dailey (2002) used life history data for tarpon to model population dynamics under several scenarios. Their population simulations indicated that slight decreases in survival of young juveniles would have large effects on adult population abundances. Thus the accessibility and quality of nursery habitat could have a major influence on tarpon populations.

There are several avenues of research that could be useful in accessing the recruitment hypothesis. A study to determine the number of newly metamorphosed juveniles in the nursery habitats in the state of Veracruz today would provide valuable information. Are the nursery habitats accessible, is fresh water important, and what are the sources of mortality in those habitats? How many of the sub-adults (7-12 years of age; Cyr 1991) successfully leave the inshore waters and recruit to the adult population? If an estimate of numbers going into and leaving the rivers and lagoons of Veracruz were possible, then mortality during this stage could be determined. A final step would be needed to determine the survival of sub-adults from the rivers into the Gulf of Mexico. There is the also the possibility that changes in the prey base for tarpon or in the water quality of the western and northwestern Gulf of Mexico has changed so that the production of eggs has declined, but there is no base line data to determine such a change.

ACKNOWLEDGEMENTS

LITERATURE CITED

Andrews, A. H., E. J. Burton, K. H. Coale, G. M. Caillet, and R. E. Crabtree. 2001. Radiometric age validation of Atlantic tarpon, *Megalops atlanticus*. U.S. Fish. Bull. 99(3):389-398.

Crabtree, R. E. 2002. A review of recent tarpon research: what is known and what is not. Contrib. Mar. Sci. 35:101-102.

Crabtree, R. E., E. C. Cyr, C. Edward, and J. M. Dean. 1995. Age and growth of tarpon, *Megalops atlanticus*, from South Florida waters. U.S. Fish. Bull. 93(4):619-628.

Crabtree, R. E., E.C. Cyr, R. E. Bishop, L. M. Faulkenstein, and J. M. Dean. 1992. Age and growth of tarpon, *Megalops atlanticus*, with notes on relative abundance and probable spawning areas. Environ. Biol. Fish. 35:361-370.

Crabtree, R. E., C. Edward, E. C. Cyr, D. C. Chaverri, W. O. McLarney, and J. M. Dean. 1997. Reproduction of tarpon, *Megalops atlanticus*, from Florida and Costa Rican waters and notes on their age and growth. B. Mar. Sci. 61(2):271-285

Cyr, E. C. 1991. Aspects of the life history of tarpon *Megalops atlanticus* from South Florida. Unpublished Ph.D. Dissertation. University of South Carolina, Columbia 138 p.

Garcia de Leon, F. J., C. Acuna Leal, I. R. Blandon, and R. Ward. 2001. Studies in conservation genetics of tarpon (*Megalops atlanticus*)-II Population structure of tarpon in the western Gulf og Mexico. Contrib. Mar. Sci. 35:18-33.

Geiger, S. P., J. J. Torres, and R. E. Crabtree. 2000. Air breathing and gill ventilation frequencies in juvenile tarpon, *Megalops atlanticus*: Responses to changes in dissolved oxygen, temperature, hydrogen sulfide, and pH. Environ. Biol. Fish. 59(2):181-190.

Haedrich, R. L. and S. M. Barnes. 1997. Changes over time of the size structure in an exploited shelf fish community. Fisheries Res. 31:229-239.

Hildebrand, S. F. 1963. Family Elopidae, pp. 111-113 In H.B. Bigalow (ed). Fishes of the Western North Atlantic. Part 3. Sears Foundation for Marine Research, Yale University, New Haven, CT.

Lambert, Y. and J.D. Dutil. 1997. Condition and energy reserves of Atlantic cod (*Gadus morhua*) during the collapse of the northern Gulf of Lawrence stock. Can. J. Fish. Aquat. Sci. 54:2388-2400.

Marshall, C. T. and K. T. Frank. 1999. The effect of interannual variation in growth and condition on haddock recruitment. Can. J. Fish. Aquat. Sci./J. Can. Sci. Halieut. Aquat. 56(3):347-355.

Shenker, J. M., R. E. Crabtree, and G. Zarillo. 1995. Recruitment of larval tarpon and other fishes into the Indian River Lagoon. B. Mar. Sci. 57(1):284.

Shenker, J. M., E. Cowie-Mojica, R. E. Crabtree, H. M. Patterson, C. Stevens, and K. Yakubic. 2002. Recruitment of tarpon (*Megalops atlanticus*) leptocephali into the Indian River Lagoon, Florida. Contrib. Mar. Sci. 35:55-69.

Silgado, J. M. 2002. Culture of leptocephali and juvenile tarpon (*Megalops atlanticus*) collected from wild stocks off the Caribbean coast of Colombia. Contrib. Mar. Sci. 35:96-99.

Smith, D. G. 1980. Early larvae of the tarpon *Megalops atlanticus* Valenciennes (Pisces: Elopidae), with notes on spawning in the Gulf of Mexico and the Yucatan Channel. B. Mar. Sci. 30:136-141.

Wells, R. M. G., J. Baldwin, R. S. Seymour, R. V. Baudinette, K. Christian, and M. B. Bennett. 2003. Oxygen transport capacity in the air-breathing fish, *Megalops cyprinoides*: Compensations for strenuous exercise. Comp. Biochem. Physiol. 134A:45-53.

Winemiller, K. O. and W. H. Dailey. 2002. Life history strategies, population dynamics, and consequences for supplemental stocking of tarpon. Contrib. Mar. Sci. 35:81-94.

Zale, A. V. and S. G. Merrifield. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Florida): ladyfish and tarpon. Vicksburg, MS: Coastal Ecology Group; Washington, DC: National Wetlands Research Center. 17 pp.

Zerbi, A. 1999. Ecolologie et biologie des juveniles de deux groupes de poisons exploites en peche sportive: la brochet de mer (*Centropomus*) et le tarpon (*Megalops atlanticus*) a Porto Rico. Unpublished Doctoral Dissertation to the University of Marseille II, December 13, 164 pp.

Zerbi, A., C. Aliaume and J. C. Joyeux. 2001. Growth of juvenile tarpon in Puerto Rican estuaries. ICES J. Mar. Sci. 58:87-95.

THE INTERNATIONAL GRAND ISLE TARPON RODEO: TRENDS IN THE RECREATIONAL TARPON (*MEGALOPS ATLANTICUS*) FISHERY IN THE WESTERN GULF OF MEXICO

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ABSTRACT

Anecdotal evidence suggests tarpon, *Megalops atlanticus*, populations have declined in Texas and the northwestern Gulf of Mexico since the 1960s; however, quantifying and qualifying this decline is complicated by a lack of federal and state landings data. In contrast, landings at Louisiana's most renown fishing tournament, the International Grand Isle Tarpon Rodeo (IGITR), are well documented during this period and tend to contradict anecdotal evidence. Mean weight of winning entries during 1957 - 1974, 1975 - 1992, and 1993 - 2003 was 59.7 ± 18.2, 78.0 ± 7.1 and 81.2 ± 7.1 kg (mean $\pm$ SD), respectively, with these weights differing significantly (ANOVA: $F_{2,43} = 19.04$, $p < 0.01$). Post hoc testing determined the mean winning entry for 1975 - 1992 and 1993 - 2003 was significantly larger than its 1957 - 1974 counterpart (Bonferroni: $p < 0.05$). A 93.4 kg (206 lb.) tarpon landed in 1973 holds the record for the eighty-four year old tournament. Three other tarpon in excess of 90 kg have been entered since 1957; one in 2001 and two in 2002. The 691 tarpon landed at Grand Isle during these three datasets were comprised of 309, 279, and 103 individuals. Mean annual number of landings during these time intervals was 17.2 ± 13.2, 15.5 ± 7.0 and 9.4 ± 3.5, respectively. Analysis of variance indicated no significant statistical difference in number of landings for the three time datasets ($F_{2, 44} = 2.44$, $p > 0.05$). Six of the 10 largest entries since 1957 were landed between 1993 and 2003. Landings of trophy tarpon, fish in excess of 140 lb (63.5 kg) at the IGITR suggest a robust recreational fishery in the Louisiana delta.

KEY WORDS: *Megalops atlanticus*, tarpon, recreational fisheries

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INTRODUCTION

Tarpon (*Megalops atlanticus*) are widely distributed in warm temperate, subtropical and tropical waters ranging from Nova Scotia to Argentina in the western Atlantic Ocean, from Senegal to Angola in the eastern Atlantic Ocean, and proximate to Panama Canal terminus in the eastern Pacific Ocean (Hildebrand 1939, Murdy et al. 1997, Nelson 1994, Wade 1962). This highly-prized sportfish, referred to reverently by many saltwater anglers as the silverking, supports valuable recreational fisheries in Florida, Louisiana and Mexico. Seasonal migrations account for recreational fisheries in Texas, Alabama, Georgia, South and North Carolina, and Virginia while resident stocks contribute to healthy fisheries in Belize, Nicaragua, Costa Rica and a host of Caribbean nations. Venezuela, French Guiana and Brazil also have significant seasonal fisheries. Gabon, Guinea-Bissau, Sierra Leone, Angola and Liberia are increasingly popular west African destinations for tarpon anglers seeking world record and giant tarpon in excess of 200 lb (90.7 kg). The world record [130 kg (286 lb 9 oz)] was landed by Frenchman Max Domecq at Rubane, Guinea-Bissau on 19 March 2003 (Crawford 2003a). Prior to the new record, two 128.4 kg tarpon landed from Lake Maracaibo, Venezuela, and Sherbro Island, Sierra Leone in 1956 and 1991 respectively, accounted for the record (Crawford 2003b).

Despite the undeniable value of its recreational fishery, management practices for tarpon across state and international boundaries vary from heterogeneous to nonexistent. The sportfish is regarded as non-palatable in the United States, but it is available in markets in other countries largely related to their respective artisanal fisheries. There is no federal management plan related to the highly-migratory tarpon likely due to its negligible commercial value. The Marine Recreational Fisheries Statistics Survey (MRFSS) conducted by NOAA Fisheries regards the recreational tarpon fishery as a rare or special event fishery, and landings data are not documented. The MRFSS is designed as a random sample of trips and anglers, and species not frequently targeted, e.g. tarpon, permit and common snook, would have very large standard errors associated with their catch estimates. Failure of federal and state surveys to document landings and catch-per-unit effort (CPUE) render management of this species problematic. Historical and current documentation of tarpon landings throughout its range is largely restricted to tournament weighmaster logbooks, local newspaper sports pages, and regional natural history books.

Tarpon were primary target species of tournaments in Texas, Louisiana, Alabama and Florida for more than a half-century. Anecdotal evidence indicates populations in the western Gulf, particularly Texas, have declined substantially since the 1960s (Farley 2002, Grigar 1997, Kuehne 1973, Roberts 1970, Sutton 1937). Internationally-renown 'tarpon rodeos' at Port Aransas and South Padre Island, TX were renamed in the early 1970s to reflect this collapse of the Texas tarpon fishery in the early 1960s, and subsequent elimination of the fish as a category or division. In contrast, tarpon tournaments in Veracruz, MX, Grand Isle, LA, and Boca Grande, FL remain viable and continue to generate economic impacts in the millions of dollars. Approximately three decades ago, there were as many as a dozen tarpon rodeos in Louisiana alone from the Sabine River east to the Mississippi River. Four prominent rodeos continue today; Golden Meadow Tarpon Rodeo, International Grand Isle Tarpon Rodeo (IGITR), Terrebonne Sportman's League Annual Rodeo and Empire-South Pass Tarpon Rodeo.

Occasionally referred to by its Cajun French common name grande ecaille, the tarpon has a significant social and cultural history in fishing communities of Louisiana's Mississippi River delta. There is little to no prize money associated with angling tarpon at Louisiana rodeos, and angler motivation is likely the result of socialization, i.e. their recruitment to the recreational fishery. For decades, leaderboard listings at Louisiana rodeos included fathers, children and grandchildren reflecting genealogy and fishing expertise developed from one generation to the next. The golden era of tarpon fishing in Louisiana was arguably the late 1960s when angler participation and silver king landings peaked. Participants in the 1967 Golden Meadow Tarpon Rodeo numbered approximately 3000, with an unknown number of these being tarpon anglers who entered 45 silverkings. The 1966 Abbeville Tarpon Rodeo drew more than 3100 participants and logged 110 tarpon landings at its Intracoastal City, LA weigh station. During the same year, approximately 2000 anglers established the IGITR landings record of 48 silver kings (Falkner, 1967). Although there is no official documentation of angler entries in Louisiana rodeos, tarpon anglers at the tournament have waned from as many as 500 in the 1960s and early 1970s to fewer than 100 in 2003 (Grady Lloyd and Marty Bourgeois - IGITR weighmasters, personal communication).

The IGITR, the oldest contest of its kind, hosted its 84th annual event in July 2005. The first tournament was held in 1928 with 25 anglers from New Orleans, LA. Seven of the 25 fishermen landed a tarpon, and five tarpon weighed in excess of 45.4 kg (100 lb). The rodeo was

suspended in 1930 related to the Great Depression and 1942-5 during World War II (Crawford 2001). By 1948, entry categories were expanded to include tripletail, cobia, Atlantic bonito, crevalle jack, king mackerel, dolphinfish, sheepshead, red drum and spotted seatrout, and many other fish species have been added to the tournament through the years. The recreational tarpon fishery in Louisiana exists in highly dynamic environment, and the tournament reflects changes in angler behaviors, preferences and their target species. The objectives of this paper are to serve as a clearinghouse documenting weight range and landings, i.e. number of tarpon, at the IGITR, analyze weights of winning entries, i.e. the first-place tarpon, and landings for trends, and utilize these results in discussing condition of recreational tarpon fishery in Louisiana and the western Gulf of Mexico.

MATERIALS AND METHODS

Study Site

Grand Isle is a barrier island west of the Mississippi River delta at the southern terminus of LA State Highway 1 in Jefferson Parish, LA. The International Grand Isle Tarpon Rodeo is conducted annually Thursday through Saturday during the third or last weekend in July.

Weight and Landing Data

We examined weights and landings, i.e. number of tarpon landed or leadered, data from newspaper sources, tournament programs and weighmaster logs, and personal interviews and communication to quantify silverking landings at the IGITR. In addition, the primary author attended the tournament from 1999 through 2003 collecting rodeo results. For the purposes of this review, a 'landing' was defined as a tarpon entered in either the harvest or tag-and-release divisions. Rodeo results were collected and analyzed for forty-seven tournaments dating from 1957 through 2003. The results were partitioned into three periods or subsets to analyze for trends in winning entry weight, i.e. the weight of the first-place tarpon, and landings. Rodeos from 1957 through 1992 were prior to conservation measures introduced for the 1993 tournament. These thirty-six tournaments were separated into two equal subsets of eighteen years; 1957 – 1974 and 1975 – 1992. The post-conservation rodeos, spanning eleven years, were maintained in a distinct subset; 1993 – 2003.

Maximum, minimum and mean tarpon weights were calculated from the data sources. Introduction of a tag-and-release division and minimum weight standards within the tournament in the early 1990s, and changes in angler behavior and preferences rendered the comparison of

mean weights for the tarpon rodeo problematic. Effect of data subset or interval, 1957 - 1974; 1975 - 1992; and 1993 - 2003, on winning entry weight and landings (the total tarpon captured from both the harvest and tag-and-release divisions) were examined using single-factor analysis of variance (ANOVA). A significance level of $P < 0.05$ was required for rejection of the null hypotheses, i.e. no difference in mean winning weight and landings for the three subsets. Bonferroni method was used to determine *a posteriori* differences among means. Winning entry weights and landings data were found to be normally distributed and not transformed for ANOVA analysis. A single extreme outlier values (values > 1.5 interquartiles of the interquartile range) within subsets were excluded from ANOVA for weights. Outliers were limited to the winning weight value for the 1974 tournament. The 1974 IGITR was the lone event during our study in which no tarpon were landed, i.e. the weight of the winning entry was 0.0 kg. Assumptions of normal distribution and homogeneity of variances were examined using Komolgorov-Smirnov Test with Lilliefors Significance Correction and Levene's Test respectively. Data analysis was conducted using SPSS 11.5 for Windows (SPSS Inc. 2003).

RESULTS

Mean weight of winning tarpon entries for the three data subsets; 1957 - 1974, 1975 - 1992, and 1993 - 2003, was 59.7 ± 18.2, 78.0 ± 7.1 and 81.2 ± 7.1 kg respectively (mean ± SD) (Fig. 1). These mean weights differed significantly (ANOVA: $F_{2, 43} = 19.04$, $p < 0.01$). Post hoc
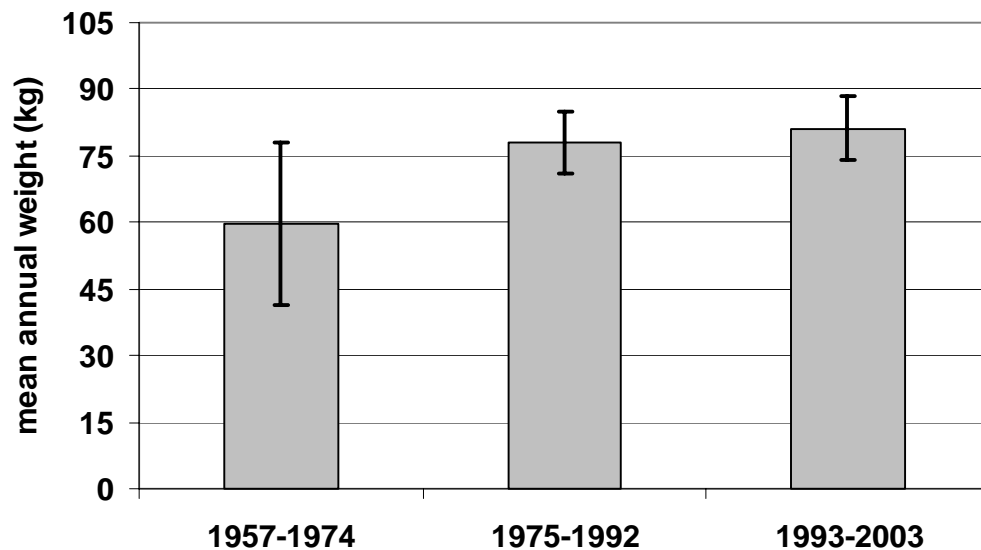
Figure 1. Mean annual winning weight (kg) and standard diviation of tarpon landings in the International Grand Isle Tarpon Rodeo during 1957-2003.

testing determined the mean winning entries for 1975 - 1992 and 1993 - 2003 were significantly larger than their 1957 - 1974 counterpart (Bonferroni: p < 0.05). Four tarpon exceeding 90 kg were landed at the IGITR during this study period; the tournament winners in 1973 and 2001, and win and place silver kings in 2002.Anglers John Guidry of Galliano, LA set the rodeo record with a 93.4 kg (206 lb) silver king in 1973, and Lee Schouest of Houma, LA won 'Most Outstanding Fish in the Rodeo' in 2001 with his 90.5 kg specimen. Six of the 10 largest entries since 1957 were landed between 1993 and 2003. Since 1974, the winning entry failed to exceed 70 kg (154 lb 5 oz) on only four occasions; 1975, 1976, 1992 and 2000, while tarpon exceeded 70 kg merely twice prior to 1974. Silver kings less than 10 kg were entered in the tournament in 1957, 1959, 1960, 1961, 1988 and 1992. No tarpon weighing less than 30 kg has been entered in the 'harvest' division since 1992 due to the introduction of a minimum weight provision in the tournament rules. However, these small tarpon would constitute a 'landing' when entered in the tag-and-release division. The greatest range in weights occurred in 1988 with the winning tarpon topping the scales at 83.0 kg and the smallest tarpon weighing 6.8 kg, a difference of 76.2 kg (Fig. 2). The 691 tarpon landed or leadered (tagged and released) at the Grand Isle rodeo
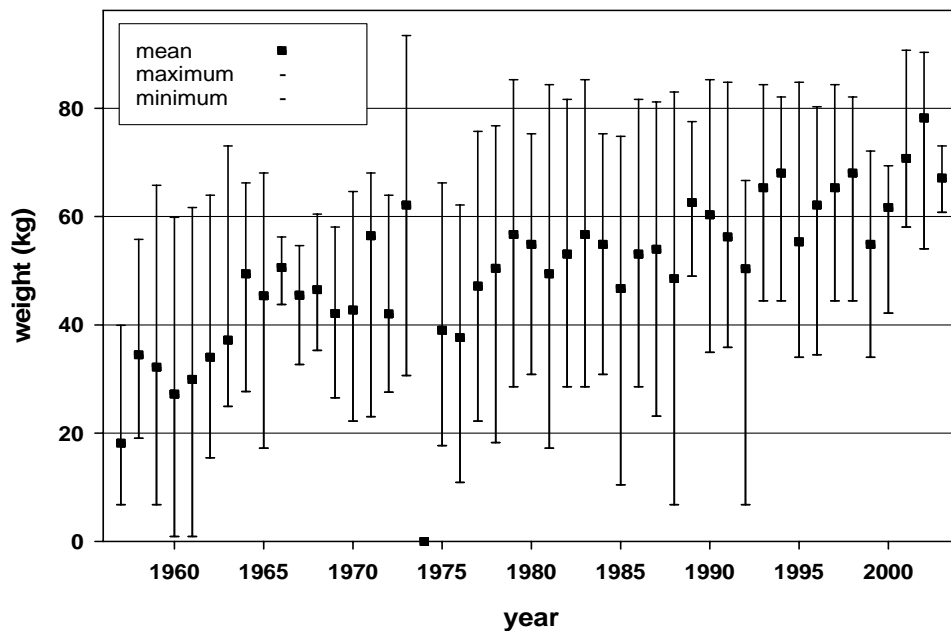
Figure 2. Annual maximum, minimum and mean weight of tarpon landings at the International Grand Isle Tarpon Rodeo, Grand Isle, LA. 1957-2003.

during the three aforementioned intervals were 309, 279, and 103 individuals respectively. Mean annual landings for 1957 - 1974, 1975 - 1992, and 1993 - 2003 were 17.2 ± 13.2, 15.5 ± 7.0 and 9.4 ± 3.5 (Fig. 3). Tarpon landings for the three data subsets did not differ significantly (ANOVA: $F_{2, 44} = 2.44$, $p > 0.05$). Annual landings peaked at 48 in 1966, and exceeded 30 in 1962, 1965, 1966 and 1988. In contrast, five or fewer tarpon were entered in 1964, 1967, 1970, 1974 and 1995 (Fig. 4).
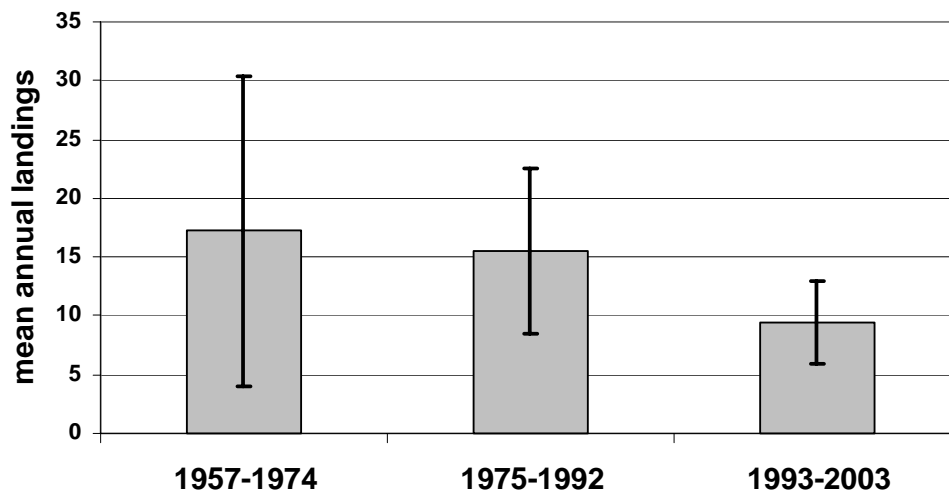
Figure 3. Mean annual number of tarpon landings at the International Grand Isle Tarpon Rodeo during 1957-2003.
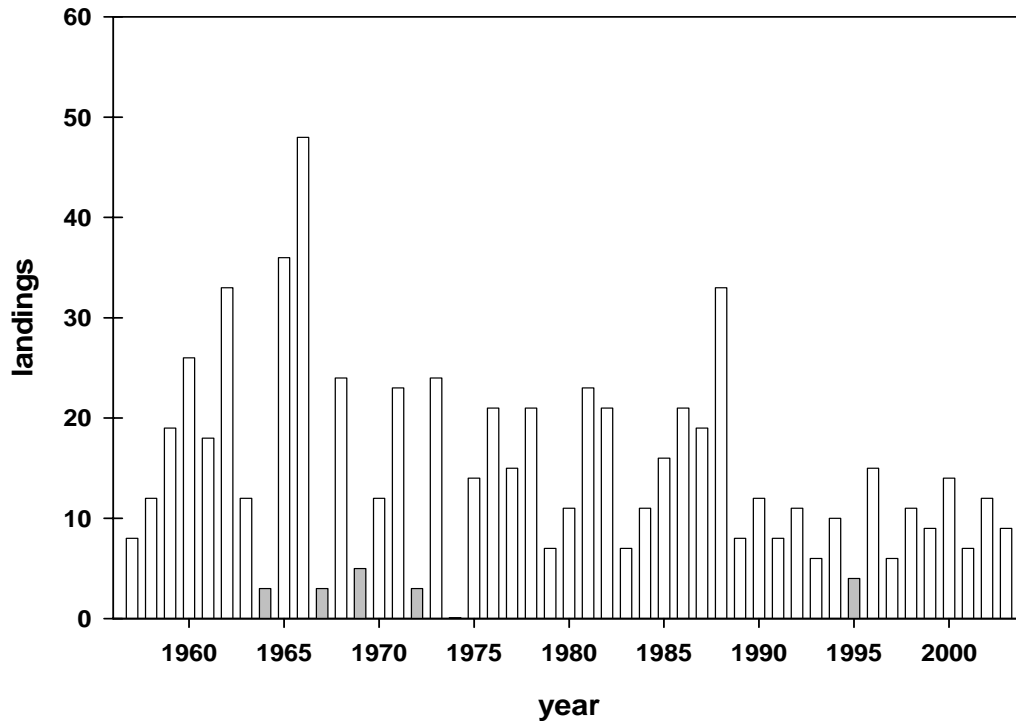
Figure 4. Annual tarpon landings at the International Grand Isle Tarpon Rodeo, Grand Isle, LA. 1957-2003.

DISCUSSION

The IGITR data subsets, 1957 - 1974, 1975 - 1992 and 1993 - 2003, were coincidental with a general decrease in tarpon angler participation for the forty-seven tournament study. Fishing pressure, i.e. fishing effort, for tarpon peaked during 1957 through 1974 rodeos with participating anglers numbering as many as 500 annually. Although this period produced the greatest mean annual number of tarpon entered (18), average weight of winning conspecifics (59.7 kg), i.e. the first- place tarpon, was the lowest recorded among the three data subsets. This period marked the tournament's record entry of 93.4 kg in 1973, and its smallest counterpart (two tarpon at 1.75 kg) in 1960. The IGITR tournaments held from 1975 to 1992 were characterized by a reduction in number of tarpon anglers, i.e. from as many as 500 to approximately 200, and two very important modifications to fishing technique: integration of the circle hook into the recreational tarpon fishery and invention of the CoonPop® lure by Louisiana tarpon guide Captain Lance 'Coon' Schouest. Circle hooks and the coon-pop contributed to an

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increased success, or catch, rate in the proportion of tarpon landed to tarpon 'jumped' or hook-ups. These modifications to fishing technique essentially doubled tarpon landing rates over j-hooks and spoons to six silverkings for every 10 'jumped' in Louisiana (Captain Lance Schouest - Louisiana tarpon guide, personal communication). Mean annual landings for the period decreased to less than 16 tarpon coincidentally with reduced fishing effort. However, the aforementioned modifications in fishing gear and an apparent emergence of expert anglers precipitated an increase in mean weight of winning entries from 59.7 kg to 78.0 kg.

In the early 1990s, several states and the IGITR enacted conservation measures to encourage catch-and-release within the recreational tarpon fishery. Alabama, Texas and Florida introduced trophy or possession tags for the retention of tarpon in state waters, while conservation measures initiated in the 1993 tournament included: 1) a minimum entry weight of 22.7 kg (50 lb); 2) tournament honors were reduced from ten to five heaviest tarpon; and 3) a tag-and-release division established to discourage harvest of small non-competitive entries; provide anglers with a non-harvest option regardless of weight; and assist NOAA Fisheries in research regarding migratory patterns of tarpon. With the advent of the tag-and-release category, silverking landings for the 1993 - 2003 data subset included those for both the weigh-in or 'harvest' and tag-and-release divisions. Despite the tag-and-release category, mean annual landings continued its decrease from 15.5 in the prior period to 9.4 tarpon; however mean winning entry weight increased to more than 81 kg. This reduction in IGITR landings was coincidental with a general decreasing trend in tarpon fishing effort and anecdotes of reduced tarpon populations. IGITR anglers and weighmasters have expressed a greater concern for the decline in number of tarpon anglers in their Louisiana delta rather than reduced tarpon populations. Silverking fishing effort at the rodeo during the1993 to 2003 period has been estimated at 100 anglers (Grady Lloyd - IGITR weighmaster and Jeff Deblieux - LA tarpon angler, personal communication).

Tarpon have important social and cultural significance in fishing communities of Louisiana's delta, and rodeo leaderboards have seemingly recorded fishing family histories with names like Schouest, Hawthorne, Cheramie, Deblieux and Ballay appearing for decades. These expert anglers and others continued to catch trophy-quality tarpon during the final period of our study with mean winning entry weight in excess of 81 kg. However, the silverking has received intense competition from other fisheries for angler interest and angler dollars. Louisiana anglers

have had increased opportunities during the past two decades to pursue other large gamefish species and greater access to offshore waters. Recreational fisheries for wahoo and yellowfin tuna have developed within 12 km of the Louisiana delta, while other anglers target billfishes in adjacent offshore waters. Documentation of the number of tarpon anglers in the IGITR and in Louisiana's recreational tarpon fishery has varied from anecdotal to nonexistent, and has largely been dependent on the recollection of IGITR participants and Louisiana Fish and Wildlife biologists. The Louisiana Tarpon Club was reformed in 2003 with the objective of recruiting anglers and increasing public awareness of the tarpon fishery (Jeff Deblieux - LA tarpon angler, personal communication). The 1st Annual Coon-Pop Tarpon Rodeo was held in September 2003 in an effort to draw attention to tarpon and related research efforts, and recruit anglers to the seasonal fishery.

The status of tarpon stocks in the western Gulf of Mexico and throughout their range is a challenge for fishery managers. Landings of trophy tarpon at the IGITR suggest a substantial and robust fishery in the Louisiana delta. ded by good weather and calm seas, Louisiana fishermen and guides continue to report tarpon schools of thousands daily, and for the first time since 1997, Galveston, TX guides reported landings exceeding 100 tarpon in summer 2004 (Captain Lance Schouest – LA tarpon guide and Captain James Trimble - Silver King Adventures guide, personal communication). Despite its historical, cultural and economic value, the highly-migratory tarpon receives little regulatory attention and research funding. Life history and population dynamics research has contributed to a better understanding of tarpon and issues for their management in Florida, Costa Rica and Puerto Rico (Crabtree et al. 1992, 1995, 1997, Cyr 1991, Figuerola 1996), but similar research in the western Gulf is lacking. Migratory patterns and adult distribution throughout the Gulf of Mexico and the Caribbean remain poorly understood. Accurate quantification and qualification of the recreational fishery is impossible due to a lack of catch and fishing effort estimates. In the meantime, the continued stewardship of tarpon by its anglers and various non-government organizations including the Louisiana Tarpon Club, Tarpon Tomorrow and Bonefish and Tarpon Unlimited is critical to a better understanding of this enigmatic and charismatic sportfish.

'Coon' Schouest - Louisiana tarpon guide and the Schouest family, Tom Gibson - world tarpon angler and state record holder for Texas and Louisiana, Alberto Madaria - world tarpon angler, Jeff and John Deblieux - Louisiana tarpon anglers, Captains Jim Leavell and James Trimble - Texas tarpon guides, Paul Swacina - Tarpon Tomorrow and tarpon angler and Scott Alford - Texas tarpon angler, Ryan Carrico, Molly Dillender and Brandi Gates - TAMUG Marine Fisheries graduates, all the participants and organizers of International Grand Isle Tarpon Rodeo, and the silverking, *Megalops atlanticus*.

LITERATURE CITED

Crabtree, R. E., E. C. Cyr, R. E. Bishop, L. M. Falkenstein, and J. M. Dean. 1992. Age and growth of tarpon, *Megalops atlanticus*, larvae in the eastern Gulf of Mexico, with notes on relative abundance and probable spawning areas. Environ. Biol. Fish. 35:361-370.

Crabtree, R. E., E. C. Cyr, and J. M. Dean. 1995. Age and growth of tarpon, *Megalops atlanticus*, from South Florida waters. Fish. Bull. 93:619-628.

Crabtree, R. E., E. C. Cyr, D. C. Chaverri, W. O. McLarney, and J. M. Dean. 1997. Reproduction of tarpon, *Megalops atlanticus*, from Florida and Costa Rican waters and notes on their age and growth. B. Mar. Sci. 61:271-285.

Crawford, A. 2001. Tarpon rodeo stands test of time. 81st Annual International Grand Isle Tarpon Rodeo Program. 79 pp.

Crawford, R. 2003a. International Angler 65(6):11.

Crawford, R. 2003b. World record game fishes. International Game Fish Association, Dania Beach. 352 pp.

Cyr, E. C. 1991. Aspects of the life history of the tarpon, *Megalops atlanticus*, from South Florida. Ph. D. Dissertation, University of South Carolina, Columbia. 138 pp.

Falkner, J. 1967 Jul 30. Abbeville rodeo largest in the state. Baton Rouge Sunday Advocate Sect A: 12.

Farley, B. 2002. Fishing yesterday's gulf coast. Texas A&M University Press, College Station. 149 pp.

Figuerola, M. 1996. Adult snook and tarpon abundance, age, growth and reproduction in Puerto Rico estuaries and coastal waters. United States Fish and Wildlife Service, Project F-33, Study II. 57 pp.

Grigar, R. 1997. Plugger: wade fishing the gulf coast. Texas Tech University Press, Lubbock. 201 pp.

Hildebrand, S. F. 1939. The Panama Canal as a passageway for fishes, with lists and remarks on the fishes and invertebrates observed. Zoologica 24: 15-45.

Kuehne, C. M. 1973. Hurricane junction; a history of Port Aransas. St. Mary's University, San Antonio. 216 pp.

Murdy, E. O., R. S. Birdsong, and J. A. Musick. 1997. Fishes of Cheasapeake Bay. Smithsonian Institution Press, Washington. 324 pp.

Nelson, J. S. 1994. Fishes of the world, 3rd ed. John Wiley and Sons, New York. 600 pp.

Roberts, E. M. 1970. The stubborn fisherman. Creighton Publishing, Port Aransas. 234 pp.

SPSS Inc. 2003. SPSS 11.5 for Windows. Chicago, IL.

Sutton, R. L. 1937. The Silver Kings of Port Aransas and other stories. Brown-White Company, Kansas City. 338 pp.

Wade, R. A. 1962. The biology of the tarpon, *Megalops atlanticus*, and the ox-eye, *Megalops cyprinoides*, with emphasis on larval development. B. Mar. Sci. 12: 545-622.

TARPON TOURNAMENTS IN THE MEXICAN LITTORAL OF THE GULF OF MEXICO

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Tarpon (*Megalops atlanticus*) is a valuable game fish widely distributed in the Gulf of Mexico (GOM) and the Caribbean Sea. Tarpon migrations occur within approximately 50 nautical miles of shore in Mexico's GOM waters from May to September. Beginning in spring, schools of tarpon move northward and then return to southern warmer waters at the beginning of fall.

In Mexico this species is protected by law (Fishing Regulation NOM-017-PESC-1994-D.O.F. 9/05/95) and may only be legally caught during sport fishing tournaments. The tournaments are organized annually by fishing clubs or associations of sport fishermen. Fishing clubs in Mexico's GOM littoral are located in the ports of Tuxpan, Tecolutla, Veracruz, and Coatzacoalcos in the state of Veracruz, Tampico in the state of Tamaulipas, and Ciudad del Carmen in the state of Campeche. Fishing methods and registration fees are determined by each sponsoring club. Generally the registration fees range from $250.00 to US $500.00 per fisherman. The fishing method approved for these tournaments is rod and reel with motorized vessels, usually with an average of four fishermen. Fishing associations maintain records of the number of tarpon landed during each tournament and the weights of the fish winning the competition.

Anecdotal information suggests tarpon population declines in the Western Gulf of Mexico. However, a lack of quantitative data on tarpon population dynamics in the Mexican littoral zone makes it difficult for state or federal agencies to monitor population trends for this species. Tagging and genetic data suggest migratory tarpon stocks as a shared resource for different states in the GOM, and between Mexico and the United States. There are also suggestions of interconnectivity between resident and migratory populations in the GOM and adjacent areas in the Caribbean. Tournaments archives provided by Mexico's fishing

associations are an invaluable source of data useful in the effort to track trends in the tarpon population of the western GOM. This note summarizes these data.

Data collection

Tarpon tournaments records archived by fishing clubs located in the states of Campeche, Veracruz, and Tamaulipas were examined. Available data included information on landings and individual weights. The numbers of anglers and vessels participating in the tournaments were collected from the fishing club's weigh masters' log books. Records included are from tournaments in Ciudad Del Carmen, Campeche; Veracruz, Tecolutla, and Coatzacoalcos in the state of Veracruz and Tampico in the state of Tamaulipas.

Results and Discussion

Records examined from tournament archives revealed a total number of 647 tarpon landed in examined tournaments from 1995 to 2005 (Fig. 1).   Numbers landed by state ranged from 1 individual in the State of Campeche in the year 2000 to 77 individuals landed in two tournaments held in the State of Veracruz in the year 1998. Numbers landed in Veracruz (which has the most complete records) peaked between 1998 and 2001, with declines thereafter.

Mean weight of tarpon landed in tournaments in the state of Veracruz decreased during the period of 1995-2000 (Fig. 2), with weights ranging from 50.6 to 76.5 kg. Mean weight of tarpon landed in the Veracruz tournaments was 62.6 kg, 58.4 kg in the state of Tamaulipas, and 40.74 kg in the state of Campeche.   The smaller average in the Campeche tournament may reflect inclusion of immature resident fish in the tournament harvest. Catch per unit effort (CPU; Fig. 3) declined over this period in Campeche but increased over the same period in Veracruz. In Tamaulipas, CPU declined in 1997 and 1998, with recovery in 1999 and 2000.

The total number of sport fishermen participating in the tournaments in the Mexican littoral during the period of 1995-2000 was 4,617 (Fig 4). Clubs in the state of Veracruz organized four tournaments a year and the number of participants was increasing. The number of participants in the State of Tamaulipas experienced an increased number of participants in the year 1997 followed by a decreased in sport fishermen participating in the tournaments after that year. In the Ciudad del Carmen in the state of Campeche the number of participating fishermen was lower than in the other states but was relatively steady over this time period.
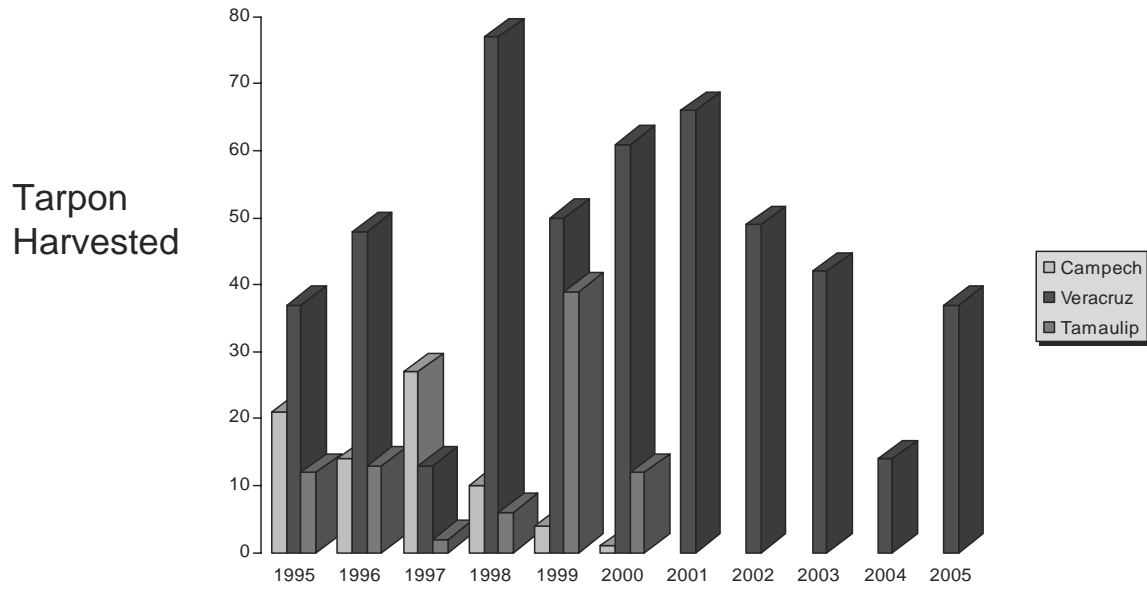
Fig 1. Number of tarpon landed in sport fishing tournaments in the states of Campeche, Veracruz, and Tamaulipas from 1995-2005.
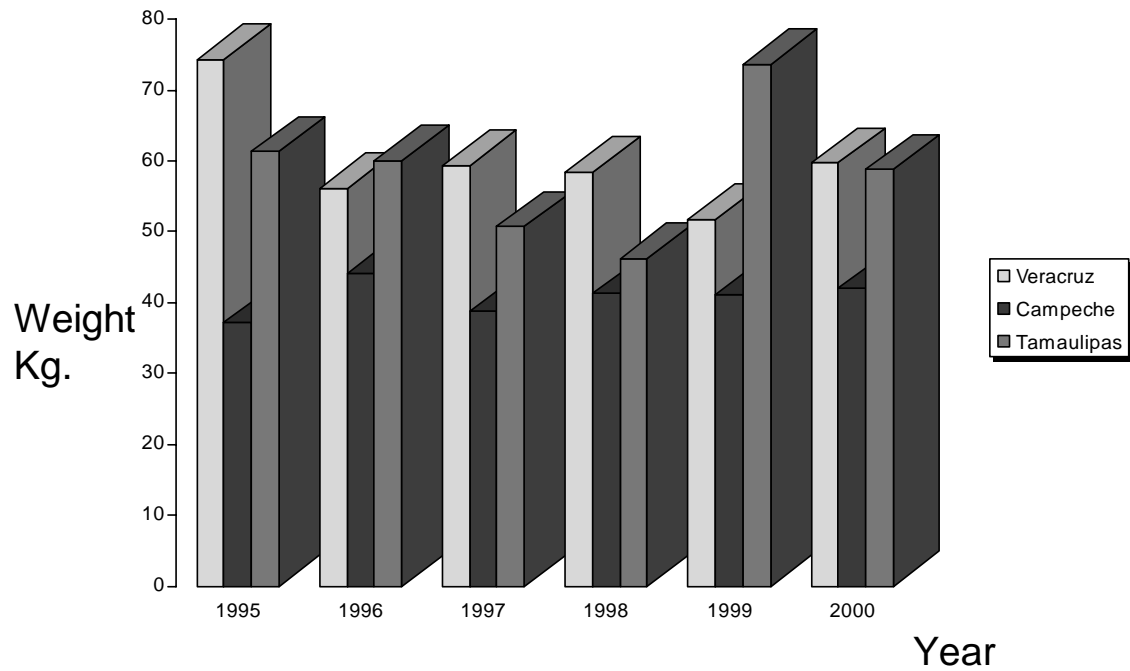
Fig 2. Mean annual weight of winning tarpon landed at tournaments in the states of Veracruz, Campeche, and Tamaulipas
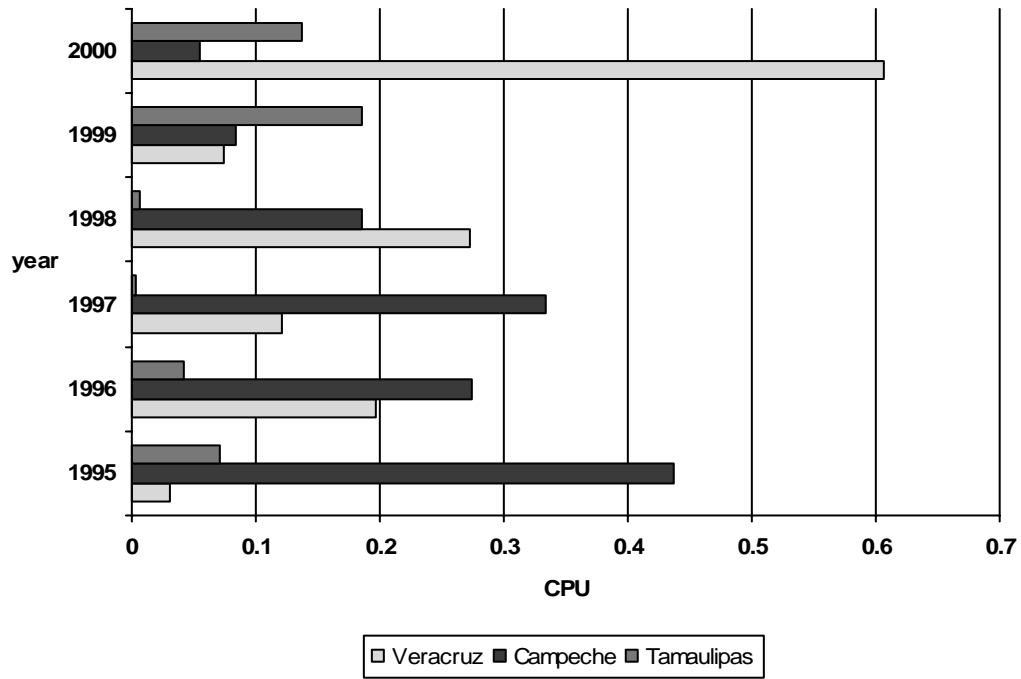
Fig 3. Catch per unit effort (CPU) calculated for tournaments in the States of Veracruz, Campeche, and Tamaulipas during the period 1995-2000.
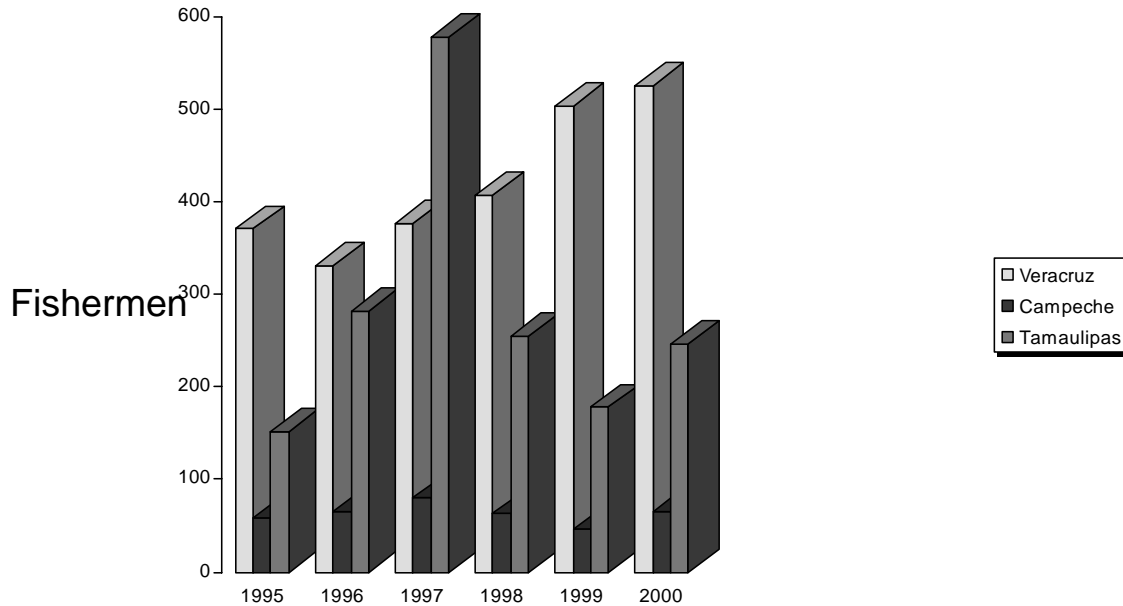
Fig 4. Number of Sportsfishermen participating in tarpon tournaments in the states of Veracruz, Campeche, and Tamaulipas.

TARPON SPORT FISHING TOURNAMENTS IN VERACRUZ 1972 – 2003: WHAT KIND OF INFORMATION IS PROVIDED?

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The first tarpon sport fishing tournament in Veracruz state coasts took place in 1953, at Tecolutla, Veracruz. Several fishing organizations perform sport fishing tournaments in the state, however, only the Veracruz Yacht Club, A. C. has preserved all the fishing tournaments records up to date. We analyzed the data from 27 fishing tournaments organized by the Veracruz Yacht Club, A. C. from 1972 to 2003 in order to know the evolution of tarpon sport fishing in this locality. The available data included some morphometrical records of those fishes carried to land, fisherman and boat names, bait used, capture zone and the used line (monofilament) diameter or resistance. The average weight of the recorded fishes increased from 32.52 kg in 1972 to 61.38 kg in 2003. The bait used has changed from artificial lures on the 70's to dead fishes from 80's to date. The fishing geographic area has changed too. In the last ten years it has moved from near the Veracruzan Reef System (Sistema Arrecifal Veracruzano SAV) to the coastal area between La Antigua River mouth and El Morro de La Mancha, a common reference point between fishermen and tourists. Finally, due the scarcity of information on tarpon fishery and population status in the Mexican portion of the Gulf of Mexico, it is important to mention the urgent need for a monitoring network and a regional data base.

LOS TORNEOS DE PESCA DEPORTIVA DE SÁBALO EN VERACRUZ-1972 - 2003

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El primer torneo de pesca deportiva de sábalo en la costa veracruzana data de 1953, el cual fue hecho en Tecolutla, Veracruz. Varias organizaciones de pescadores deportivos hacen torneos de pesca de estos peces en el estado, sin embargo, únicamente el Club de Yates de Veracruz, A.C ha conservado sus registros de pesca en los torneos hasta la actualidad. Con el objetivo de conocer la evolución de la pesca deportiva de sábalo en Veracruz se analizaron los datos registrados en 27 torneos de pesca organizados por el Club de Yates de Veracruz, A.C. desde 1972 hasta 2003. La información disponible en los archivos del club incluye algunos datos morfométricos de los peces llevados a tierra, los nombres de los pescadores y de las embarcaciones, el tipo de carnada utilizada, la zona de captura y el diámetro o resistencia de la línea (monofilamento) utilizada. El peso promedio de los peces registrados se incrementó de 32.52 kg en 1972 a 61.38 kg en 2003. La carnada utilizada ha cambiado de señuelos artificiales durante la década de los 70's a peces muertos desde los 80's hasta la fecha. El área geográfica de pesca también ha cambiado. En los últimos diez años se ha movido de las inmediaciones del Sistema Arrecifal Veracruzano (SAV) al área costera comprendida entre La Antigua y el Morro de La Mancha. Finalmente, ante la escasez de información acerca de la pesca de sábalos y el estado de sus poblaciones en la porción mexicana del Golfo de México, se hace hincapié en la

urgente necesidad de crear una red de monitoreo y un banco de datos regionales.

BONEFISH MOVEMENTS AND THEIR RELATIONSHIP TO MATURITY AND SPAWNING IN THE FLORIDA KEYS

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Since 1998 we have conducted a conventional tag-recapture program for bonefish in the Florida Keys using volunteers from the professional guides association. To date, we have tagged more than 2000 bonefish and had more than 50 recaptures. The data suggested a high proportion of tagged bonefish did not move more than 15 km from the point of release. However, several fish moved more than 65 km. The bulk of the tagged bonefish that made these heretofore unreported large-scale movements were large and sexually mature, and their movements may have been related to season and weather activity (i.e., frontal passages). The problem in exact interpretation lies in the fact that only the start and end points of the movements were known. To ameliorate that limitation, we have employed advanced technology acoustic telemetry methods to continuously monitor the movements of acoustically-tagged bonefish in a hydrophone array. In previous research (Humston et al. 2004), we described a telemetry system designed to test the hypothesis that bonefish exhibit site fidelity in selection of foraging areas in the northern Florida Keys. We found that about 70 percent of tagged fish were detected by receivers for multiple days following release, and some individuals demonstrated a high degree of site fidelity characterized by daily movements into the study area. This pattern was not consistent among all tagged fish which suggested individual variation. We found that some sexually mature animals left the study area. To better understand bonefish movements and their relationship to sexual maturity and spawning, we are currently conducting an expanded acoustic telemetry experiment with substantially increased spatial coverage of the receiver arrays to track and monitor larger-scale movements in space and time, site fidelity, habitat use and spawning migrations in the northern Florida Keys. Resultant information on habitat use, site fidelity and movement patterns are critical to design and analysis of spatial management alternatives that support conservation strategies to sustain this important fishery and ecological resource.

DESPLAZAMIENTOS DEL MACABÍ Y SUS RELACIONES CON MADURACION SEXUAL Y DESHOVE EN LOS CALLOS DE FLORIDA

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Desde 1998 se han llevado a cabo programas convencionales de marcaje y recaptura de macabís en los Callos de Florida. Hasta la fecha se han marcado más de 2000 macabís y se han

registrado mas de 50 recapturas. Los datos sugieren que una alta proporción de macabís marcados no se han desplazado más de 15 km del punto en el que fueron liberados. Sin embargo varios macabís se desplazaron mas de 65 km. El volúmen de macabís marcados que realizaron estos desplazamientos de gran escala -hasta ahora no reportados- eran animales grandes, sexualmente maduros y sus movimientos posiblemente estan relacionados con la estación y la actividad climática (i.e. vientos frontales). El problema con esta interpretacion es que de estos desplazamientos solo se conoce el punto de liberación y recaptura. Para disminuir esta limitación se han utilizado tecnología avanzada de telemetría acústica para monitorear constantemente los movimientos de macabí marcados con estos dispositivos acústicos por medio de un sistema de hidrófono. En investigaciones previas (Humston et al. 2004), se ha descrito un sistema de telemetría designado para probar la hipótesis de que los macabís seleccionan las areas de forraje en el norte de los Callos de Florida con alta fidelidad. Se determinó que el 70% de los macabís marcados eran detectados por los receptores por varios días después del marcado-liberación y algunos organismos mostraron alta preferencia por estas zonas de estudio, caracterizados por movimientos diarios a la misma área. Estos patrones no fueron consistentes en todos los organismos marcados lo cual sugiere variación entre individuos. Se encontró que algunos animales sexualmente maduros abandonaron el área de estudio. Acutalmente se esta dirigiendo una investigación con un mayor número de receptores acústicos distribuidos en una área mas extensa con el fin de poder seguir y monitorear desplazamientos a gran escala del macabí y su relación con maduración sexual, deshove, selección del habitat en el área norte de los Callos de Florida. La información adquirida del uso del habitat, predilección del área y desplazamientos son indispensables para el diseño y análisis de nuevas estrategias de manejo y conservación que sustenten esta importante pesqueria y recurso ecológico.

POP-UP ARCHIVAL TRANSMITTING TAGS TO STUDY
ATLANTIC TARPON MIGRATIONS

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Since 2001 we have been using "pop-up" PAT (passive archival transmitting) tags to map the movement-migration patterns and environmental preferences of the Atlantic tarpon (*Megalops atlanticus*) in the southeastern US, Gulf of Mexico, and Caribbean Sea. Tarpon are the focus of a valuable regional recreational fishery and are under increasingly intense exploitation pressures. The unit stock for tarpon is largely unknown, but remains perhaps the most critical piece of information needed for sound fishery management and conservation decision-making. To address the issue of stock connectivity, we began by deploying PAT tags on tarpon in locations ranging from North Carolina to central Florida, and from the Florida Keys to the west coast of Florida. Apart from data transmitted through Argos satellite network, we recovered several tags. One tag deployed in Savannah, Georgia, was recovered at Sebastian Inlet, Florida. The other deployed in Islamorada, FL, was recovered inside the Indian River Lagoon at Tropic Island, FL. In June 2003, we tagged large tarpon (> 65 kg) in Veracruz, Mexico, and remarkably, one of these tarpon migrated about 600 miles north to Corpus Christi,

Texas, in less than 30 days. On September 4, 2003, PAT tags were placed on 3 tarpon off Venice, LA, that subsequently popped-off at various locales. On October 10th the first was located about 100 miles southwest on the continental shelf; and, on November 10th a second popped off within 10 miles of the release point. We believe that the first two fish had not yet undergone extensive migrations because ocean water temperatures stayed unseasonably warm through early December 2003. However, on February 10, 2004, our third LA tag popped-off near Key West, Florida, suggesting that tarpon in the region have a bit of the snow bird in them. Here we will present an overview of our tagging efforts and show data from recovered tags that provided new insights on tarpon behavior from archived data records of fish depth, water temperature and light levels recorded at 1-minute intervals. We will show how comparisons of tag temperature and depth data with satellite-derived sea surface temperature (SST) and bathymetry data can provide accurate geo-locations of tarpon movements between release and pop-up sites. Finally, we will discuss the potential of this technology for studying behavioral movements and provide the foundation for improving management decision making to sustain this valuable fishery resource.

SEGUIMIENTO POR SATELITE PARA EL ESTUDIO DE LAS MIGRACIONES DEL SÁBALO DEL ATLÁNTICO

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Desde el año 2001 se ha estado utilizando la técnica de marcaje PAT (transimisión pasiva de datos) con el fín de identificar las rutas de migración y preferencias ambientales del sábalo del Atlántico (*Megalops atlanticus*) en el sureste de Estados Unidos, el Golfo de México y el Mar del Caribe. El sábalo es considerado de suma importancia en pesquerías locales recreativas y se encuentra sujeto a intensas presiones de pesca. La estructura del stock del sábalo es aun desconocida, siendo este dato pieza crítica necesaria para el manejo de pesquerías, conservación y toma de decisiones. Para evaluar la conectividad entre poblaciones de sábalo se realizo marcaje de organismos en distintas áreas abarcando desde Carolina del Norte hasta Florida Central, y desde los Callos de Florida hasta la costa oeste de Florida. Ademas de datos transmitidos a través del satélite Argos se recuperaron ciertas marcas. Una marca liberada en Savannah, Georgia, fue recuperada en Sebastian Inlet, Florida. Otra más liberada en Islamorada, FL, fue recuperada dentro del la Laguna "Indian river" en Tropic Island. FL. En junio del 2003 se marcaron sábalos de más de 65 Kg en Veracrúz, México, y sorprendentemente uno de estos sábalos emigró aproximadamente 600 millas al Norte de Corpus Christi, TX, en menos de 30 días. El 4 de septiembre del 2003 se marcaron tres sábalos en Venice, LA que subsecuentemente fueron encontrados en distintas areas. El primero fue localizado el 10 de Octubre 100 millas al suroeste en la plataforma continental; el segundo fue localizado el 10 de Noviembre dentro de las 10 millas de donde fue liberado. Creemos que los primeros dos organismos no realizaron migraciones extensas debido a que las temperaturas del agua permanecieron templadas (sin cambios estacionales) hasta principios de Diciembre del 2003. Sin embargo el 10 de Febrero del 2004 un tercero fue localizado en los Callos de Florida lo que sugiere que el sábalo migra hacia estas regiones durante el invierno. En este trabajo se presentan de manera general nuestros

trabajos de marcaje y en particular datos que aportan nuevos conocimientos sobre el comportamiento del sábalo en base a datos de profundidad, temperatura e intensidad lumínica medidos a intervalos de 1 minuto. Se discutira el potencial de esta tecnología de marcaje para el estudio del comportamiento migratorio siendo esto fundamental para mejorar el aprovechamiento de este invaluable recurso pesquero.

TARPON (MEGALOPS ATLANTICUS*) AND BONEFISH (*ALBULA VULPES*)
RECREATIONAL FISHERY IN SOUTHERN QUINTANA ROO, MEXICO

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During February and March 2004 a study consisting of an evaluation of the tarpon and bonefish fishery in the communities of Calderitas, Chetumal and Xcalak in Southern Quintana Roo, Mexico was conducted. The objective of this evaluation was to characterize the tarpon and bonefish fishery in southern Quintana Roo in terms of social organization, management strategies and status of the resource based on information provided by local fishermen. Fifteen interviews were conducted with fishermen and fishermen's wives. Analysis of interviews identified two groups of fishermen in the region: a group of small-scale commercial fishermen and a group of sport fishermen (guides). The study revealed that commercial fishermen are not targeting tarpon and bonefish as directed species; the catches of these species are incidental. Tarpon and bonefish are part of a broader group of other species targeted by the recreational-sport fishermen and guides. Other species targeted for sport-recreational opportunities are snook and permit. Tarpon and bonefish are perceived by both groups of fishermen as abundant in the area. Spatial and temporal distribution of tarpon and bonefish including relative abundance is perceived as higher in the natural protected areas. Fisheries regulations are enforced by a community of fishermen that auto regulate their own activities to minimize conflicts of user groups.

LA PESCA DE SÁBALO (*MEGALOPS ATLANTICUS*) Y MACABÍ (*ALBULA VULPES*)
EN LA ZONA SUR DE QUINTANA ROO, MÉXICO

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Durante febrero y marzo de 2004 se llevó a cabo una evaluación rápida de la pesca de sábalo y macabí en las comunidades de Calderitas, Chetumal y Xcalak, todas localizadas en el sur del estado de Quintana Roo. El objetivo de la evaluación fué caracterizar la pesca de sábalo y macabí en la zona sur de Quintana Roo en términos de organización social, estado del recurso basado en el conocimiento local, y estrategias de manejo. Se aplicaron un total de 15 entrevistas

a pescadores y esposas de pescadores; 2 de ellas abiertas y 13 semiestructuradas. Lo anterior fue complementado con revisión de literatura así como con la experiencia que el primer autor del estudio tiene sobre la actividad pesquera en la zona. Existen dos grupos de pescadores en la zona sur: la pesca comercial de pequeña escala y, la pesca deportivo- recreativa. En relación a la pesca comercial, se encontró que el sábalo y el macabí no son especies objetivo dentro de la misma sino solamente especies incidentales. Con respecto a la pesca deportivo- recreativa, el sábalo y macabí forman parte de una gama de recursos destinados para este tipo de pesca y también incluyen a la palometa y al robalo. Los resultados sobre el estado del recurso usando el conocimiento local indican que, en los dos casos, sábalo y macabí son percibidos como abundantes en la zona por los pescadortes locales. Las principales áreas de pesca de sábalo y macabí se encuentran en areas naturales protegidas y dentro de éstas, la regulación de la pesca la lleva a cabo principalmente la comunidad de pescadores, ya que ellos mismos autoregulan su actividad, minimizando con ello los conflictos entre los diversos grupos locales.

TARPON REPRODUCTION IN THE LAGUNA DE OLMECA: AN URBAN LANDLOCKED LAGOON IN VERACRUZ

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The City and Port of Veracruz are located in a lagoon system composed of 21 coastal lagoons. These lagoons are located in a highly populated urban area surrounded by sand dunes. The Olmeca Lagoon is the primary subject of this study because is part of the lagoon system while at the same time is the base of urban human settlements and industrial activities. The origin of the Olmeca lagoon is a system of aquifers, and fresh water springs. The lagoon covers a surface area of approximately 43 hectares (~90 acres) with a depth of 1-2.7 m. The faunal components found in this ecosystem are: birds, mammals, reptiles and fish. The most abundant fish species are member of the families: Megalopidae, Poecilidae and Cichlidae. Fishermen reported the occurrence of juvenile and adult tarpon with a size ranging from 0.30-1.5 m TL. The Olmeca Lagoon was part of a drainage system that in the past was connected directly with the sea. However, after the construction of a highway and a 3 m concrete dam to retain water in the lagoon, the natural drainage and connection to the sea has been lost for more than 20 years. Fishermen reported adult tarpon of over 15 kg and juveniles only 25 cm TL in the same lagoon. They suspect that tarpon are reproducing in this lagoon without migration to the sea.

REPRODUCCION DE SABALOS CONFINADOS EN UNA LAGUNA QUE HA PERDIDO COMUNICACIÓN CON EL MAR COMO RESULTADO DEL DESARROLLO URBANO

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La Ciudad y Puerto de Veracruz cuenta con un Sistema Lagunar (SLCV) conformado por 21 lagunas. Que se encuentran ubicadas en una zona urbana rodeada por dunas de arena caracterizada por una alta densidad poblacional. La Laguna Olmeca, objeto del presente estudio, forma parte de este sistema lagunar y presenta en sus márgenes asentamientos humanos, industria e infraestructura urbana. Aparentemente, sólo se alimenta de agua dulce proveniente de manantiales, filtraciones de otras lagunas y lluvias, cuenta con una superficie aproximada de 43 hectáreas (cerca de 90 acres) y una profundidad que va de 1 a 2.7 metros. Entre su fauna encontramos diversas especies de peces, reptiles, mamíferos y aves. Entre los peces destacan los de la Familia *Megalopidae*; los peces del género *Poecilia* y las mojarras de la Familia *Cichlidae*, Géneros *Tilapia, Oreochromis* y *Cichlasoma. H*abitantes de la ribera de la laguna, que se dedican a la pesca reportan capturas de sábalos juveniles y adultos, de 25 a 30 cm y mas de 1.5 metros de longitud, respectivamente. La Laguna Olmeca es un vaso regulador del escurrimiento de otras lagunas del Sistema Lagunar de la Ciudad de Veracruz, que tenía comunicación directa con el mar a través de canales, que descargaban en arroyos y ríos. Estos últimos mantienen su comunicación con el mar, pero la comunicación entre la laguna y esos canales se ha perdido irremediablemente, con motivo de la construcción de infraestructura urbana. Existen dos obstáculos para organismos que quieran entrar o salir de la laguna: las compuertas construidas para controlar el nivel de agua de la laguna y la carretera construida sobre el canal que conectaba a la Laguna, que implica un desnivel de aproximadamente 2 metros de altura entre la laguna y su canal, bloqueado además con rampas y paredes de concreto. La falta de comunicación entre la laguna y el mar por más de 20 años; el reporte documentado de sábalos adultos de más de 15 Kg. de peso y de sábalos juveniles de 25 cm. de longitud, confirma que los organismos de esta especie que quedaron confinados en la laguna han alcanzado su madurez y han completado su ciclo reproductivo sin necesidad de emigrar al mar. Esta experiencia puede resultar importante como una estrategia para recuperar poblaciones de sábalos a través del confinamiento de ejemplares maduros en cuerpos de agua cerrados buscando su reproducción, para una posterior colecta y siembra de juveniles en otros cuerpos de agua donde se haya observado una drástica reducción en las existencias de sábalos.

REPORT ON THE COLLECTION OF LARVAE OF BONEFISH
ALBULA VULPES FROM THE COAST OF THE MEXICAN CARIBBEAN

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We present information about the occurrence of larvae of the bonefish Albula vulpes on the coast of the Mexican Caribbean and a preliminary analysis of its size distribution based on recent collections. All the reference material is deposited in El Colegio de la Frontera Sur (ECO-CH-LP). This material was collected from coastal waters off central and southern Quintana Roo,

Mexico, during several months between 1998 and 2004. Collections were made during the new moon using a variety of methods: standard plankton tows, light trap samples, and trawls. Out of the 2457 larvae collected, 111 were collected during 1998-2002; of these, 55% were captured in light traps, 41.4% in plankton tows and 3.6% by trawling. The remaining 2346 larvae were collected in Xcalak (1665) and Bahia Ascencion (681) in January 2004 using a new design of light trap gear. Larval abundances were highest from November to January with a minor peak in June. These results agree with the maximum larval abundances reported for Florida and the Bahamas and correspond to the reproductive season of these fishes, with a major peak between November and January. For the size analysis, standard length (LE, mm) was measured and lengths are reported to the nearest 1mm. There were differences in size distribution between the two sampling locations; in Xcalak the larvae were on average larger at 50.83 ± 3.21 mm ($\bar{x}$ ± Standard Deviation) than those from Bahia Ascencion (49.87 ± 3.10 mm). We used Maximum Likelihood Estimation, based on multinomial distribution, to estimate parameters of the normal components. In Ascencion the distribution of sizes was bimodal but this was less evident in Xcalak. We compare ours results with previous reports and the current research needs about this species are discussed.

REGISTROS DE LARVAS DE MACABÍ *ALBULA VULPES* EN COSTAS DEL CARIBE MEXICANO

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Se presenta información sobre la ocurrencia de larvas de macabí *Albula vulpes* en las costas del Caribe mexicano, asi como un primer análisis de tallas de un muestreo reciente (enero de 2004). Todo el material está depositado en la colección de larvas de peces de El Colegio de la Frontera Sur ECO-CH-LP y procede de muestreos en aguas costeras del centro y sur de Quintana Roo para algunos meses de 1998 a 2004. Los muestreos se efectuaron durante luna nueva, con varias artes: red estándar de plancton, trampa de luz y red de patin. Del total de larvas de *A. vulpes* n= 2457 recolectadas, 111 corresponden al periodo 1998-2002; de las cuales 55% fueron capturadas con trampa de luz, 41.4% con red estándar de plancton y 3.6% con red de patin. Las 2346 larvas restantes fueron recolectadas en Xcalak (1665) y Bahía Ascensión (681) en enero de 2004 con trampas de luz de diferente diseño. Las abundancias larvales mayores se registraron entre noviembre y enero, con un pulso menor en junio. Estos resultados coinciden con los de máxima abundancia larval reportada en Florida y Bahamas y corresponden a la estación reproductiva de este pez con máximos entre noviembre y enero. Para el análisis de tallas, se midió la longitud estándar (LE) al 0.1 mm más cercano. Hubo diferencias de tallas entre localidades; en Xcalak fueron capturadas larvas ligeramente mayores, 50.83 ± 3.21 mm LE ($\bar{x}$ ± desviación estándar) que en Bahía Ascensión, 49.87 ± 3.10 mm LE. Se aplicó el método de Máxima Verosimilitud, basado en la distribución multinomial, para estimar parámetros de las componentes normales. En Ascensión, la distribución de tallas fue bimodal, lo que fue menos

evidente en Xcalak. Se comparan los resultados de este estudio con reportes previos y se discuten necesidades de investigación sobre esta especie.

Summary and Recommendations

Joan Holt (UTMSI) and Yvonne Blandon (TP&W)

Highlights of the meeting

Mexico and Texas are bound by the Gulf of Mexico (GOM), by the currents, the fisheries, and the need for scientific understanding to conserve natural habitats and marine organisms. Large pelagic species such as tarpon, tuna, and billfish know no international boundaries and seasonally move throughout the GOM. Tarpon as a resource continues to be a focus of interest for many Conservation and Fishing organizations (Coastal Conservation Association, Coastal Bend Bays and Estuaries Program, Tarpon Tomorrow and Bonefish and Tarpon Unlimited), especially in Corpus Christi and Port Aransas, where tarpon were once abundant. Members of the conservation and scientific community attending the meeting explored potential causes of the tarpon collapse and possibilities for bringing tarpon back by focusing on scientific and management collaboration on this resource with Mexico.

The tagging and genetics data shows tarpon as a shared international resource; scientists and environmentalists agree on the need for international cooperation for management of this resource. Data on tarpon migration pathways collected by Dr. Jerry Ault from the University of Miami showed similar migration patterns and resident groups identified with the genetics data collected by Texas Parks and Wildlife Department. (Tarpon tagged in Florida remained in Florida or migrate north on both sides of the Florida peninsula traveling north to the Carolinas or to Louisiana. Tarpon tagged in Louisiana traveled back to Florida. Tarpon tagged in Veracruz traveled north to Texas.)

A round-table discussion took a close look at nursery habitat. Mexican fishermen and biologists identified on a map places with abundant tarpon juveniles, and sub-adults (nursery habitat) (Fig. 1). The Gulf of Mexico states of Tampico, Veracruz, Campeche, and Tabasco were identified as places with good habitat and abundant tarpon. The State of Quintana Roo on the
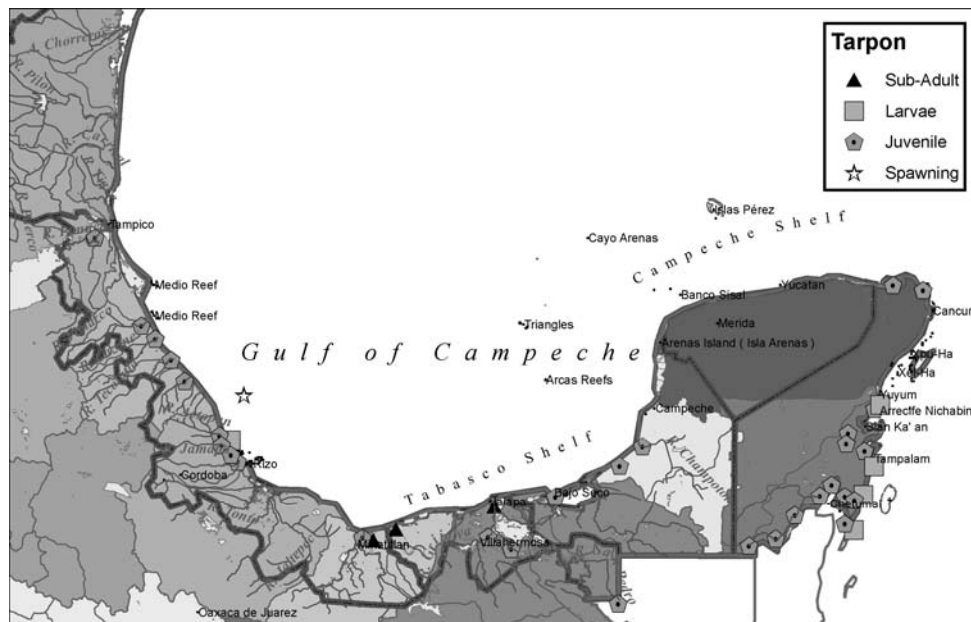

Figure 1. Map of the southwestern Gulf of Mexico identifying areas where tarpon larvae, juveniles, and sub- adults have been collected. The star denotes an area where gravid fish have been captured. Small larvae have been collected off the SW Gulf of Mexico near the 200m contour (Smith 1980 Mar Sci 30)

the Mexican Caribbean was also identified as having high numbers of metamorphosing leptocephali and juvenile tarpon. The common element was abundance of water and rich estuaries with plentiful food sources. However, most of these except for marine protected areas on the Mexican Caribbean were reported as threatened by growing coastal development, industrial activities (pollution), and human settlements. While there is no doubt that pollution and development may be a growing problem, the rivers receive tremendous flushing by the abundance of water in the region.

User group conflicts were presented during the meeting. Despite tarpon being reserved by law only for the sport fishery and protected by regulations in Mexico there are reports of high incidental catches in coastal areas of the Gulf of Mexico. Sub-adult tarpon populations, ready to join the migratory adult population face by-catch mortality in the snook and shark fishery.

Tarpon were not as abundant in the 2004 Veracruz tournament as other years. Three years ago 30 individuals were caught with similar effort in the same tournament. This year only fourteen tarpon were entered by sport fishermen in three days of fishing. The biggest fish caught was a 250 lbs gravid female. The largest fish weighed was disqualified because it was obviously caught on a long line.

Sport fishermen presented and discussed a conservation proposal for "NO KILL" tournaments. They are aware that during the tournaments gravid females are targeted. A representative from Puerto Rico offered to work with local tournament organizers to implement photo-documentation procedures which would allow the catch-and-release of tournament fish.

Recommendations

It is thought that the Tarpon fishery in Texas was closely tied to the tarpon fishery in Mexico and recent genetic and tagging data support this connection. Tarpon populations in the NW Gulf of Mexico have declined noticeably over the last several decades. There is some evidence that the failure of the tarpon fishery off Texas was tied to the loss of recruitment of young/ smaller tarpon to the population that moved north in early summer to feed on the apparently very large schools of bait fish along the NW Gulf Coast. Reasons for a loss of recruitment could be due to changes in spawning success of tarpon, changes in patterns of baitfish abundance and/or distribution, loss of spawning or nursery habitat (changing land use, urbanization), increased mortality of juvenile tarpon in the nursery grounds (marshes, mangroves and rivers) or of tarpon leaving the rivers (fishery bycatch).

Information needs and collaborative research issues
- Basic life history studies to establish fecundity, larval duration, growth rate, size at sexual maturity for tarpon.

- Identification of habitat and fisheries impacts in Mexico including:
    - Critical habitat used by small juveniles (<12 inches)
    - Estimate of number and sizes of juveniles leaving the rivers and lagoons
    - Number, size, and gender of tarpon that are part of the incidental catch for:
        - the snook fishery at the mouth of rivers and lagoons
        - the longlining fishery for sharks.

- Establish a comprehensive satellite tagging program to obtain information on adult migration, especially to determine movements during the spawning season and thereafter in the western Gulf of Mexico.

- Determine trends in migrations of anchovies, sardines, menhaden, and mullet on the Texas coast to determine if these prey items have changed over time as tarpon populations have declined.

- Establish catch and release mortality rates based on gear and fishing time to support catch and release recommendations.

- Calculate economic benefits of tarpon sports fishing for Mexico and compare to societal needs for inexpensive protein.

Management Issues

Scientific data suggest that the offshore tarpon population is composed of groups of migratory adults derived from spawning and nursery sites in many different geographic regions. Despite the cosmopolitan nature of this species, tarpon management practices in different states and countries have a tendency to be heterogeneous, with little or no coordination or communication. The scientific and conservation communities recognize the essential need to design meaningful regional conservation strategies to reestablish and maintain critical habitat to support sustainable levels of this species in the Gulf of Mexico. To that end the following management recommendations were developed:

- Design an integrative management plan for tarpon defining the status of this species as migratory and as a shared resource in the Gulf of Mexico.

- Build interagency cooperation between Mexico and the Gulf States to implement collaborative research projects on migration patterns, habitat mapping, stock assessment, and population dynamics.

- Work with conservation organizations to foster responsible fishing, especially catch and release for the migratory adults.

- Encourage and teach catch and release techniques for tarpon tournaments.

- Encourage governments to enforce laws protecting tarpon by reducing incidental catches of sub-adults.

- Support marine protected areas in tarpon spawning grounds and nursery habitat in the Gulf of Mexico and Caribbean.

- Promote the collaboration of Mexican conservation groups and fishermen to work for changes in current fish harvesting and management practices to support tarpon based ecotourism.

PROPOSAL FOR THE PROTECTION AND CONSERVATION OF TARPON (*MEGALOPS ATLANTICUS*) IN THE WATERS OF THE GULF OF MEXICO

Yuseff Barquet Tuero

Club de Yates de Veracruz.

Since the beginning of history, humans harvested fish to obtain food. Over time fisheries activities became more productive, with increased harvests per unit of fishing effort.

In Mexico, as well as in other countries of the world, the commercial fishery is a very important economic activity. We have a fleet of commercial fishing vessels equipped with high-tech gear such as global position systems (GPS) and sonar utilized in the harvest of tuna, shrimp and other species. This technology is being applied over an ever broader range of coastal fishery resources, and the fishery activities and fishing pressure have increased every year.

In the Gulf of Mexico, year after year we have observed tarpon schools migrating along the coast. These migratory schools arrive in the Mexican Gulf waters during spring, and during this period it is known that these tarpon schools are heavily impacted by the long line and other commercial fisheries.Tarpon schools are targeted, caught, and sacrificed for commercial purposes, producing a minimum income in comparison with the maximum value this species can achieve if it was utilized for sport fishery activities.

We would like to propose that the commercial tarpon fishery in the Veracruz region be eliminated. Conserving tarpon stocks will facilitate guided fishing and sport fishing opportunities that will generate tourism, income, and new business in the region.

We also propose to establish an environmental education program for commercial fishermen; a program that will focus on instruction in issues related to the tarpon sport fishery and other highly valuable recreational species. This education program will explain the economical benefits of tarpon conservation versus commercial exploitation by comparing the value of tarpon meat at the market (about $0.40 a pound) versus hundreds of dollars a day for sale of tarpon fishing guiding services. These comparisons will assist the commercial fishermen to realize that conserving tarpon provides much greater economical benefits to them while keeping commercial fishermen in compliance with the Federal law that protects tarpon.

The environmental education program for responsible commercial fishermen will be implemented by the government to provide knowledge, tools, and alternate economical activities to the commercial fishermen to achieve three main goals: 1) Conservation and protection of tarpon in the Gulf of Mexico, 2) Development of research programs on tarpon with the assistance of sport fishermen and tarpon fishing guides practicing tarpon catch and release, and 3) Integration, promotion, and commercialization of fishing guiding services and sport fisheries as a novel sector of coastal fisheries activities in the Gulf of Mexico.

A similar plan has been in place for years in Mexico in the conservation and management of whitetail deer by land owners in northern Mexico. The government gives the land owners a number of permits to be sold to hunters. Each hunter can then legally harvest one deer a year and the rancher is remunerated for allowing hunting on their land. In this case the land owner commercializes the hunting activities on his land, monitors the deer populations, and the resource benefits with economic incentives to the ranchers. The deer population has increased in

number and size and the land owner's profits are much higher than in earlier days when deer were illegally harvested for sale in markets.

Scientific management and recreational harvest of deer will serve as an example to the commercial fishermen targeting tarpon. This strategy would allow commercial fishermen to become involved in the establishment of guided fishing services with economical incentives linked to the tarpon conservation and protection.

Nine years ago during a tarpon tournament, my father Juan Jose Barquet Fitta, my cousins, Abelardo and Raul Castro Chaccur, and myself found a place at the mouth of the Antigua River that we named the "Tarpon Sanctuary", because we found there a school of tarpon so big that we cruised for up to forty miles looking at tarpon jumping and rolling in the surface of the sea. We visit this place every year and while we catch only one tarpon a year, the long liners harvest up to 40 fish in just 3 to 4 hours. The sport fishermen of the Veracruz Yacht Club are promoting catch and release only tarpon tournaments. This responsible fishing practice will change the perception of our grandparents in reference to this resource in terms of abundance and availability.

Our response to the news of tarpon population declines in the Gulf of Mexico is to think that we have a responsibility to future generations to conserve tarpon so our children and grandchildren will enjoy the capture of this magnificent fish.

We are aware of our good fortune to still enjoy tarpon fishing in our area despite the illegal fishing practices of the long-liners. We denounce the strategy of the long liners and their fishing art of aligning up to 10 vessels like a funnel with 500 illegal hooks per vessel to engulf the schools of tarpons in their feeding migration. Despite the fishing regulations protecting this species in Mexico there is no law enforcement to punish this criminal practice. We need the diligence of Federal and State institutions (SEMANAP, Navy Secretariat) to enforce the law. Enforcement efforts would be minimized if the authorities would examine the fish markets, applying the law to the salesmen purchasing, processing, or selling tarpon products. Commercial fishermen would not capture tarpon if profits from tarpon catches were eliminated.

At the Alvarado Port long liners unload tons of tarpon meat for sale. It is sad to see how the tarpon schools modify their habits because former feeding grounds are presently tarpon killing grounds. Last year we learned that at the Laguna Camaronera, a group of outlaw fishermen used purse seines to round up a school of adult tarpon while a group of free divers killed one by one the tarpons with harpoons. The sacrifice of this tarpon school yielded tons of tarpon meat that was sold at the Alvarado Port.

These cases are more abundant every day in the Mexican littoral of the Gulf of Mexico. If we do not take immediate action the consequences for the species will be devastating.

The Veracruz Yacht Club proposes to educate the commercial fishermen on the benefits and arts of tarpon sport fisheries. Our organization will promote ecotourism and guided fisheries activities, turning the Mexican coast of the Gulf of Mexico into a fishing destination. Our civic group will assist researchers, incorporating research tasks into our fishing activities for tarpon. We will ask the Mexican government to punish illegal sales of tarpon meat and tarpon products. If there is no demand for tarpon products there will not be illegal tarpon catches.

Finally, I would like to mention the conservation organization Fundacion Sabalo which was formed with the sole goal of tarpon conservation. We prepared a web-site (Fundacion Sabalo.com) to promote sport fishing activities in Veracruz. We hope this serves as a public forum for the use of different organizations to conserve and learn about tarpon.

PROPUESTA PARA LA CONSERVACIÓN DE LA ESPECIE SÁBALO (*MEGALOPS ATLANTICUS*) EN LAS AGUAS DEL GOLFO DE MÉXICO

Yuseff Barquet Tuero

Club de Yates de Veracruz

Desde el inicio de la historia del ser humano en nuestro planeta, la pesca ha sido una de las principales actividades de supervivencia, con la evolución del hombre ella ha ido mejorando para hacerse mas productiva y ofrecernos mejores rendimientos con menores esfuerzos.

En nuestro México, como en muchos países del mundo, la pesca commercial es un pilar muy importante en nuestra economía, la integran flotas de barcos pesqueros con la mas alta tecnología para la captura del atún, del camarón y de otras especies… También tenemos la pesca rivereña o de costa que año con año ha venido creciendo en nuestros litorales. Cuando nuestros amigos los pescadores comerciales toman la tecnología de un GPS o de un sonar para incrementar sus productos es aquí donde la pequeña ponencia que a continuación voy a presentarles entra en juego.

En las costas del Golfo de México durante los meses de primavera y principios del verano tenemos la visita año con año de numerosos cardúmenes de sábalo, llegan buscando la costa que todos los años recorren con crias nuevas o con cardúmenes nuevos, ellos son los eternos navegantes de una costa a la otra… y es aquí donde esa especie recibe un golpe muy fuerte al encontrarse con los long-liners y anzuelos de pescadores comerciales furtivos que al localizar estos cardúmenes reposando en la costa los acechan, capturan, sacrifican y comercializan para obtener un ingreso monetario que además de estar fuera de la ley es mínimo en comparación de lo que ellos mismos podrían obtener dedicándose a la pesca deportiva con la misma especie.

Si nosostros diseñamos un sistema de enseñanza orientado a los amigos pescadores comerciales donde nos permita instruirles en todo lo relacionado con la pesca deportiva.

Si le damos el apoyo y la difusión necesarias con nuestras autoridades competentes para que ellos puedan ofrecer dentro y fuera de nuestras fronteras este servicio …

Si logramos que se den cuenta que si comercializan sus servicios y conocimientos para llevar pescadores deportivos obtienen diez veces más dinero que comercializar la carne del sábalo pagada a 0.40 centavos de dólar en el mercado con la agravante de estar cometiendo un delito de carácter federal en nuestro país ….

Démosles las herramientas y conocimientos necesarios, además de una difusión de sus servicios, con la ayuda de nosotros y de las autoridades de nuestro México, así señores , lograremos tres objetivos a la vez:
1. La reactivacióde una parte de la pesca commercial de nuestro país que es la pesca ribereña.
2. La protección de nuestra especie en cuestión.
3. Podremos desarrollar los programas de investigación con la ayuda de estos ejemplares que se capturen y se suelten.

En nuestro país tenemos un ejemplo muy claro, es el de la protección del venado cola blanca en el norte de nuestro país, ahí la autoridad reparte permisos de caza a los dueños de los ranchos para que los comercialicen con los aficionados a la caza, ellos tienen oportunidad de

sacrificar un venado cada año, y el dueño del rancho obtiene una remuneración económica por dejar cazar en sus tierras.

Así, el dueño del rancho se ha convertido mas en guía de caza que en comercializador de su producto y la especie se ha venido protegiendo aumentando en cantidad y calidad….

No es lo mismo un venado que un sábalo, pero el caso es muy similar si lo aplicamos y le damos a nuestros amigos los pescadores comerciales las herramientas y conocimientos necesarios.

Hace alrededor de nueve (9) años durante un torneo de pesca, mi padre Juan José Barquet Fitta, los hermanso Abelardo y Raúl Castro Chaccur y su servidor, encontramos un lugar al cual llamamos "el santuario de los sábalos", este lugar es la desembocadura del Río De La Antigua.

Veníamos navegando por la costa hacia Veracruz y de pronto vimos uno, dos , siete, catorce, cuarenta y así poco a poco millas de sábalos reposando, saltando y sacando sus lomos en la superficie.

A este lugar vamos año con año a pescar sábalo deportivamente, pero no falto alguien que se dedicara a colocar palangres en esa zona y mientras nosotros sacrificamos un ejemplar. Ellos con uno de estos aparejos de pesca logran sacrificar 40 sábalos en solo tres o cuatro horas.

En el Club de Yates hemos logrado inculcado en la conciencia de nuestros socios y en nuestros amigos el deseo de liberar los ejemplares después de una buena pelea. Todavía hay personas que siguen con las ideas de nuestros abuelos cuando pensaban que no se podría acabar la especie, y ese trabajo lo seguimos enfrentando como una responsabilidad para nuestros hijos y nietos.

Nosotros los pescadores deportivos hemos constatado lo afortunados que somos en ir a estos lugares donde el sábalo llega cada año cuando vemos colocados estratégicamente artes de pesca para su captura, vemos long-liners –palangres de más de 500 anzuelos, y algunas veces contamos más de 10 embarcaciones provistas con este tipo de arte de pesca, las embarcaciones se situan en forma de embudo donde al entrar el cardúmen de sábalos por un extremo van quedando ensartados en los anzuelos, esto señores es un crimen que está penalizado por nuestras autoridades Mexicanas.

Desgraciadamente la vigilancia en estos lugares no existe, la SEMARNAP, la Secretaría de Marina y otras dependencies que se deberían de encargar de la vigilancia en estas areas pero no prestan la más minima atención.

Esta vigilancia podría ser nula si nuestras autoridades se dedicaran a proteger la especie en tierra, si en vez de estar perdiendo el tiempo en otras cuestiones hicieran una campaña para identificar y sancionar a quien compra la carne de sábalo, a quien la procesa y a quien la comercializa.   Si no hay demanda en tierra el pescador no pierde tiempo en pescar algo que sabe de antemano que no le va a dejar remuneración económica. Tengo conocimeiento de lugares como el Puerto de Alvarado donde entran toneladas de sábalo por pescadores furtivos, yo mismo he visto a pangas cargar sábalos desde los long-liners es triste ver como se van acabando a una especie y como van modificando su hábito año con año al convertir lo que antes eran lugares de estancia y comida para los sábalos converidos en lugares de sacrificio.

El año pasado tuve conocimiento de que en la región de la Laguna Camaronera, un grupo de pescadores furtivos rodearon con sus redes un cardúmen de sábalo, al tenerlos ya encerrados llegó un segundo grupo con los tanques de buceo a sacrificar uno por uno los sábalos con

harpones de punta explosiva. Esta matanza llevó al Puerto de Alvarado toneladas de estos sábalos esto es un verdadero sacrificio.

Así como este caso, podemos ver muchos más a lo largo de nuestro litoral de Golfo de México, si no hacemos algo en este momento no vamos a poder remediar las consecuencias que esto está originando. Logremos integrar un mecanismo de enseñanza para nuestros amigos los pescadores comerciales. Un mecanismo de orientación a los pescadores donde aprendan todo lo relacionado con la pesca deportiva. Un mecanismo de difusión de estos servicios a nivel mundial de nuestras comunidades deportivas.

Los pescadores comerciales se daran cuenta que los pescadores deportivos les dejarán mayores recursos que si furtivamente comercializan los sábalo. Los pescadores podrian cooperar con programas de investigación expandiendo el alcance de lose studios. Las autoridades Mexicanas podrán descansar en ese ramo dedicándose a otras areas donde en verdad se necesite este tipo de esfuerzos.

Y para terminar con esta breve intervención y agradecerles su atención quiero platicarles de un proyecto para la protección del sábalo.

En Diciembre del 2002, preparamos un portal llamado ELSABALO.com, con el objeto de promocionar la difusión de la pesca deportiva en las costas Veracruzanas, mi propósito no era otro mas que promocionar este deporte y la protección de la especie a través de la practica de captura y soltaje. Poco a poco fuí introduciendo fotografías, reseñas, información, El aspecto que desde un principio llamó mucho la atención fue la de un boletín semanal donde se informaban noticias de nuestro deporte.

De pronto el boletín tuvo tanta expectativa que se ha establecido como una fuente de información en la comunidad de pescadores deportivos, llegando a todas partes de nuestro México y otras fronteras. Pero bien, el caso es que con el boletín hemos podido ponernos contacto los principales clubes de nuestro país, estableciendo comunicación por medio del ELSABALO.com muy estrecha.

Hace un año cuando fuí contactado para participar en la organización del symposium se me ocurrió la idea de crear una fundación llamada "Fundación El Sábalo"para la conservación de la especie integrada por todos los clubes deportivos de pesca. Esta idea ha sido aceptadoa por otras organizaciones y grupos civicos y esperamos ejecutar nuestros planes y aprovecho la oportunidad para ponerlas al servicio del symposium y de todos los presentes en esta reunion, para unificar nuestras ideas y esfuerzos y enfocarlos en la conservación del sábalo.

CONTRIBUTIONS IN MARINE SCIENCE

1.   Manuscripts (3 copies) and correspondence should be sent to The Editor, Contributions in Marine Science, The University of Texas at Austin, Marine Science Institute, 750 Channel view Drive, Port Aransas, Texas 78373. Communication speed will be improved if an e-mail address and a fax number for the first or corresponding author are included.

2.   Manuscripts are invited which review or monograph any aspect of marine science. Authors should consult with the editor before submitting a manuscript. Preference is given to papers relating to the Gulf of Mexico and including the results of original research. Reviews will normally be considered from workers active in the field reviewed.

3.   All contributions are sent to outside reviewers for evaluation of scientific merit and reader interest. Manuscripts are then returned to the author for consideration of comments. Revised manuscripts should be submitted on diskette, in addition to a printed copy. Most common word processing programs are acceptable, but if there is any doubt, also include a file saved as plain text (ASCII, "text," or .TXT). Additional details on electronic submission are available on request for all authors, and is required for final copy.

4.   The submission of a manuscript will be taken to imply that it has not already been published nor is being considered for publication and if accepted by Contributions in Marine Science that it will not be published elsewhere.

5.   Manuscripts must be typewritten in English with double spacing throughout (text, literature cited, table and figure headings).

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8.   The introduction should start on page three. The major headings should be capitalized and centered on the page. For sub-headings, capitalize the initial letter of significant words. The first sub-heading should be centered, the second shouldered and the third run-on with the text.

9.   Use metric units of, or in addition to, other units. Authors should consult Style Manual for Biological Journals, The American Institute of Biological Sciences, Washington, D.C. for questions of general style and a list of acceptable abbreviations.

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     Chapter: Fogel, M.A., and L.A. Cifuentes. 1993. Isotopic fractionation during primary production, p. 73-98. In M.H. Engel and S.A. Macko [eds.], Organic Geochemistry. Plenum, New York.