2009-05-14

Towards an Ecosystem Approach for Non-Target Reef Fishes: Habitat Uses and Population Dynamics of South Florida Parrotfishes (Perciformes: Scaridae)

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Recommended Citation

Molina-Ureña, Helena, "Towards an Ecosystem Approach for Non-Target Reef Fishes: Habitat Uses and Population Dynamics of South Florida Parrotfishes (Perciformes: Scaridae)" (2009). *Open Access Dissertations*. 237.
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UNIVERSITY OF MIAMI

TOWARDS AN ECOSYSTEM APPROACH FOR NON-TARGET REEF FISHES: HABITAT USES AND POPULATION DYNAMICS OF SOUTH FLORIDA PARROTFISHES (PERCIFORMES: SCARIDAE)

By

Helena Molina-Ureña

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

Coral Gables, Florida

May 2009

UNIVERSITY OF MIAMI

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Towards an Ecosystem Approach for Non-Target Reef Fishes:
Habitat Uses and Population Dynamics of South Florida
Parrotfishes (Perciformes: Scaridae) (May 2009)

Abstract of a dissertation at the University of Miami.

Dissertation supervised by Professor Jerald S. Ault.

No. of pages in text. (299)

In the context of the precautionary approach to the sustainable use of coastal marine resources in tropical reefs, it is necessary to identify those species vulnerable to exploitation before their populations are seriously affected. The goal of this research was to develop statistically robust ecosystem-based approaches, while optimizing data acquisition on relatively unexploited fish species in South Florida reefs, i.e., parrotfishes, Family Scaridae, in Biscayne Bay (an onshore coastal bay surveyed by seasonal roller frame beam trawl surveys, 1996-2000) and Florida Keys (a coral reef tract sampled with annual Reef Fish Visual Censuses, RVC, 1997-2001), by following these steps: (I) analysis of information gaps for the stocks (or taxon) under consideration, including systematics, biogeography, population dynamics, reproductive ecology, trophodynamics, habitat use, and fisheries landings and fleet dynamics of Western Atlantic parrotfishes (Chapter 1); (II) determination of four primary research objectives from prioritization of information gap analyses of Step I: essential fish habitat, population dynamics parameter estimations, effects of exploitation, habitat protection and fisheries management on South Florida scarids, and fisheries ecology contributions to sampling and management of reef

fishes with commercial potential; (III) determination of essential fish habitats, including ontogenetic shifts, migrations, and connections between reefs and adjacent habitats subject to fisheries (Chapter 2), from integration of stratified sampling design for fisheries-independent surveys, habitat selection theory-based analyses, and length-based analyses; (IV) estimation of population dynamics and fisheries-specific parameters encompassing life history demographics from empirical data or comparisons to theoretical expectations adapted to local conditions (Chapter 3); (V) simulation modeling of a realistic range of fishing scenarios and demographic characteristics using Reef Ecosystem Exploited Fisheries Simulator (REEFS) and size-based mortality estimation (LBAR) algorithms to evaluate the efficacy of potential traditional fisheries and spatial management strategies (Chapter 4); and (VI) application of sampling optimization procedures and fisheries ecology approaches.

Nicholsina usta, *Sparisoma chrysopterum*, and *Sparisoma radians* were the top three most abundant and frequent parrotfishes in the Biscayne Bay collections. *Scarus iseri*, *Sparisoma aurofrenatum*, *Sp. viride*, and *Sp. chrysopterum* were the top four scarids in the Florida Keys RVC dataset, with an estimated combined abundance of ~36.8 x 10^6 individuals in this domain alone. Connectivity among seagrass beds, coral reefs and deep waters had three major patterns: (1) seagrass dwellers, using near shore substrates in the bay, absent in the reef, with a plausible deep-water connection (*N. usta*); (2) reef dwellers, with inshore-to-offshore ontogenetic patterns in the Florida Keys, ranging from well defined (e.g., *Sc. iseri* and *Sp. aurofrenatum*) to weak (*Sp. viride*) cross-shelf shifts; and (3) a seagrass-reef connection, using Biscayne Bay as an important recruitment ground (*Sp. chrysopterum*), in which a portion of its population may migrate through

Safety Valve onto adjacent reefs, soon after the caudal fin becomes concave (≥ 12 cm TL, ~ six months of age). Marine protected areas of the Florida Keys National Marine Sanctuary did not show effects on abundance, size composition or spatial distribution of any parrotfish studied. Simulated von Bertalanffy growth curves and observed life stage characteristics indicated that parrotfishes generally exhibit isometric growth, with extensive size overlaps among color phases and no ontogenetic changes in weight-to-length relationships. Two fisheries-oriented algorithms, REEFS and LBAR, suggested relatively short longevities ($5 \leq t_\lambda \leq 10$ years), moderate body growth curvature ($0.3 \leq K \leq 0.7$ y^{-1}); high instantaneous natural mortality rates ($0.3 \leq M \leq 0.6$ y^{-1}), and low annual survival rates ($54\% \leq A \leq 27\%$). Simulated estimates of fishing mortalities (F) ranged from 0.3 (*Sp. viride*) to 0.6 y^{-1} (*Sp. chrysopterum*), indicating low levels of exploitation, but low Spawning Potential Ratios (SPR = 23.5-26%). Proposed potential exploitation based on a legal minimum size equal to their size at first maturity and fishing rates equal or below to their natural mortality should secure SPR values at 45-48%.

DEDICATION

A Tatica y nuestra Negrita de Los Ángeles,

por otorgarme la bendición de nacer en mi querida Tiquicia, y por guiar y proteger cada segundo de mi vida.

A mis padres, Memo y Ceci,

por darme siempre las alas y la libertad para volar hacia mis sueños.

A Silvia y Ronald,

compañeros de toda mi vida, por mantenerme con los pies en la tierra y el corazón en la familia.

ACKNOWLEDGMENTS

I am profoundly grateful to my dissertation committee, Drs. Jerry S. Ault (Chairman), Steven G. Smith, Su Sponaugle, Nelson M. Ehrhardt, and James A. Bohnsack for their advice, support, encouragement, patience, guidance, mentoring, and time contributed towards my doctorate program and my dissertation.

My gratitude also goes to colleagues, peers, and friends, too numerous to name in total. John Serafy, John Fortuna, Jiangang Luo, Maria Villanueva, Liz Brooks, and Mónica Valle are hereby deeply thanked for generously sharing their knowledge with me at different stages of my dissertation work. A special acknowledgment to my lab mates Ken Lindeman, Robert Humston, Mike Larkin, Mike Feeley, Marcia Almeida, and Natalia Zurcher.

Field work was only possible thanks to the participation of Guillermo Díaz, Robert Humston, Michelle Paddack, Kerstin Grorud-Colvert, Kelly Denit, Mark Sullivan, Jim Colbo, Pedro Campuzano, Goshka Sczodrak, NOAA divers, and many more.

I will always be indebted to Dieter Bauer, Eileen Alicea, Amel Saied, Cynthia Ballestero, Tania Casal, Aleksandra Janik, Przemek Karwasiecki, Deanna Donohoue, Yolanda and Frank Zamora, Ana Lorena Nájera, Micky Cuesta, Sarah Frías-Torres, Tom Jamir, Pedro Campuzano, Goshka Sczodrak, Gayl Van de Bogart, Michelle Paddack, Ana Patricia Gaspar, Nuno Gracia, Gabi Kaiser and family, Yolanda and Chepito Watson, Grupo de Damas Ticas del Té, Carmita Sartain, Ivy Chow, Javier Rivera, Javier Zavala, Sahro Villarroya, Martha Moncada, Chidong Zhang, Shuyi Chen, Lora Fleming, Viva Banzon, Bob Evans, Maria Villanueva, Marlen Sotolongo, Monica Lara, and Darlene

Johnson, who always gave me a hand by generously providing a roof over my head, transportation, space to work and think, a positive attitude, warm and everlasting friendship, and vivacious conversations about science and life, among many other uplifting moments that I keep in my heart.

Long before my arrival, Kay, Helen, and Florence developed the spirit of Florida's best kept secret (our RSMAS library), while Eva Marie Kiene, Mariela Calderin, Cathy Wright, the RSMAS Graduate Studies Office, and the MBF Academic Committee, especially Dr. Lynne Fieber, helped me through administrative procedures with their best willingness and efficiency. I thank them for all the help and support.

At Universidad de Costa Rica, I thank Dr. Virginia Solís for her kindness and encouragement, as well as the staff at the Oficina de Asuntos Internacionales y Cooperación Externa, with special gratitude to Fátima Acosta, Yamileth Damazio, Dr. Manuel María Murillo, and Dr. Ana Sittenfeld.

Since my undergraduate years I found a whole new set of sisters that hold a big place in my heart, and whose personal and professional accomplishments have made me extremely proud and joyous. Despite taking different paths in life, Eugenia Arguedas, Maritza Guerrero, Xenia Lara, Sandra Torres, Carmen Roldán, Sonia Rojas, and Alexandra Sáenz, have shared a common journey with me, through laughter and tears, dances and injuries, plans and broken dreams, pride and disappointment, graduations, weddings, births, and the passing away of loved ones.

Partial funding for my doctorate program and dissertation research was provided by the NOAA Coastal Ocean Program Grant No. NA37RJ0200, NOAA National Undersea Research Center Grant No. NURC 00-19, NOAA South Florida Living Marine

Resources Program Grant No. NA67RJ0149, National Park Service Grant No. CA-528-00-024, NOAA-NMFS Coral Reef Conservation Program Grant No. NA17RJ1226, NPS DTNP/BNP CESU Grant No. H5000000494, and National Sea Grant No. R/C-E-50, a Fulbright-LASPAU scholarship, the Reitmeister Award of the Louis Aaron Reitmeister Foundation, the Lewis A. Tayler Trustee's Fund Award (Fulbright-LASPAU), three Port of Miami Propeller Club Scholarship Awards, the International Light Tackle Tournament Association Award, and the Founders Research Award (UM).

Last but not least, I want to thank my family, Molina Ureñas, Molina Arayas, and Ureña Moras, whose unconditional love, faith in me, sense of humor, and endless patience sustained me through the most difficult times of this journey.

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Introduction

Tropical reef fisheries, in general, and the Western Central Atlantic fisheries, in particular, have become a major concern because of their importance to regional subsistence and economics (Munro 1983, Sale 1991, Bohnsack and Ault 1996, Polunin and Roberts 1996, Claro et al. 2001). Understanding and managing tropical fisheries is difficult partly due to the complex biological and physical interactions, including trophodynamic relationships at the individual, population, and community levels (Sale 1991, Polunin and Roberts 1996, Ault et al. 1998, Coleman et al. 2000).

Caribbean reef fisheries can be characterized as multigear, multispecies fisheries (Munro 1996). Catches from the Caribbean Basin have largely been represented by species such as snappers (Lutjanidae), groupers (Serranidae), grunts (Haemulidae), jacks (Carangidae), sardines (Clupeidae), sharks (Elasmobranchii), triggerfishes (Balistidae), goatfishes (Mullidae), as well as squirrelfishes (Holocentridae), parrotfishes (Scaridae), surgeonfishes (Acanthuridae), and butterflyfishes (Chaetodontidae) (Munro 1983, Bohnsack et al. 1994, Claro 1994). Traditional single-species fisheries management methods are not sufficient to address such complex fisheries. The Western Central Atlantic (FAO Area 31) is reportedly undergoing the transition from predatory-species fisheries to low-trophic level fishing, as a consequence of targeting secondary species after drastic declines in the highly commercial fisheries (Pauly et al. 1998). This trend of fishing down from high quality carnivores to less valuable herbivores or planktivores, also known as "serial fishing", involves the targeting of relatively unexploited, thus not well studied, species. In the context of precautionary principle in fisheries management, it is necessary to identify those species vulnerable to exploitation before their populations start showing effects of overfishing.

This study focused on South Florida parrotfishes (Perciformes: Scaridae) for several reasons. Common knowledge assumes all scarids are herbivorous species, play diverse ecological roles in the reef ecosystems, are very abundant, and are subjected to highly variable fishing pressure. More recently, this family has been considered a key taxon in coral reef ecosystems around the world, given their major role in keeping algal communities in check (Mumby et al. 2006, Paddack et al. 2006).

The opportunity to study relatively unexploited stocks anywhere in the Caribbean basin is rare, and Florida scarid populations are assumed to be protected from fishing. To provide an integral overview of these populations, this work followed three successive steps: an analysis of information gaps, the determination of the ecosystem framework, and the prioritization of information needs on a local scale (Figure I.1).

By combining information gap analyses, fisheries theory, ecological approaches, and simulation techniques, this research was aimed at developing statistically robust approaches while optimizing data acquisition on relatively unexploited fish species in tropical reefs.

The analysis of information gaps (Chapter 1) aimed at understanding interconnections among major aspects of parrotfishes: biosystematics, biogeography, reproductive strategies, essential fish habitat, trophodynamics, population dynamics, behavior, and fisheries. The ecosystem framework developed from the gap analysis in Chapter 1 (Figure I.1) allowed the prioritization of information needed to obtain predictions of potential fishing impacts on the South Florida parrotfish populations and the reef ecosystem, based on the integration of their ecological role with local environmental and demographic conditions, while considering shifting baselines principles.

Three lines of information gaps were selected as research priorities, and the results are presented in subsequent sections. Habitat use of South Florida Keys scarids is addressed in Chapter 2. Body growth curves and developmental patterns are developed in Chapter 3. Potential fishing impacts on Florida Keys parrotfish populations are analyzed in Chapter 4. Finally, Chapter 5 refers to methodological considerations and improvements.

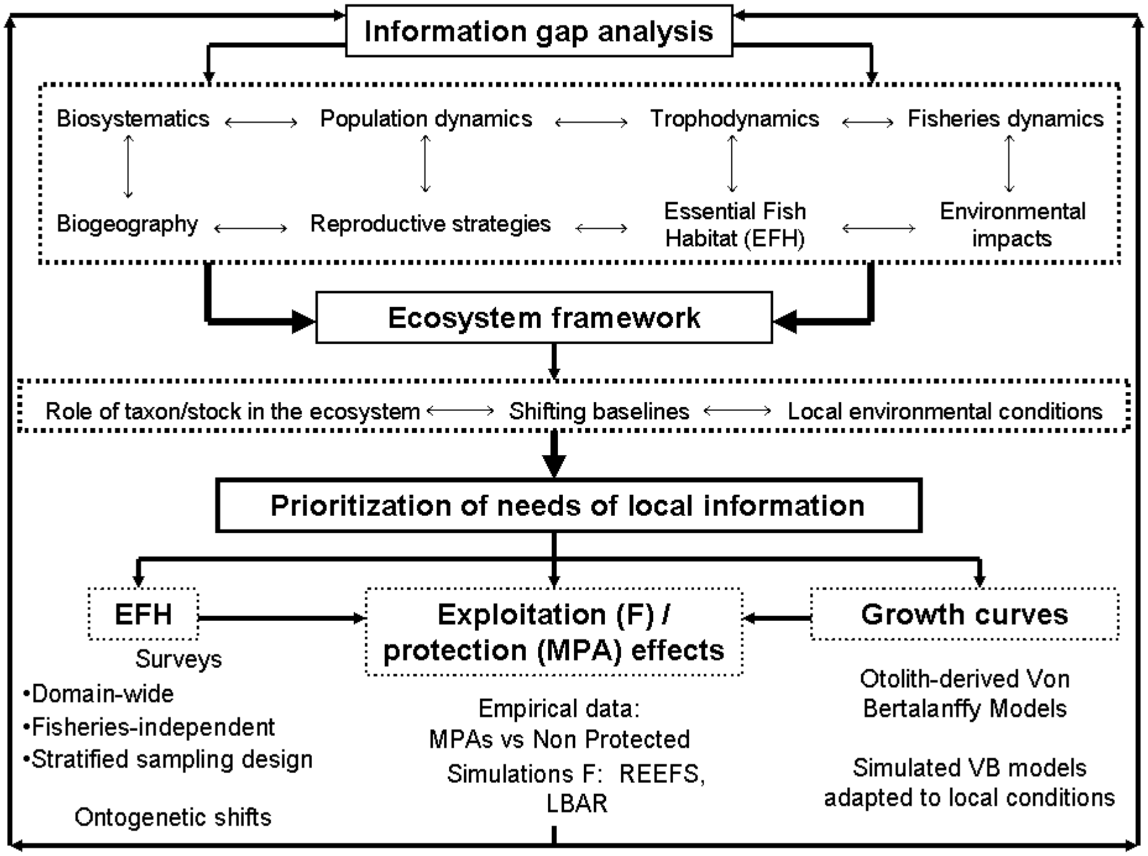

Figure I.1: Flowchart showing the phases of the present research. EFH = essential fish habitat analyses. F = fishing rate estimations. MPA = Marine Protected Areas. REEFS = Reef Ecosystem Exploited Fisheries Simulator. LBAR = length-based algorithm estimator of total mortality. VB = von Bertalanffy growth curve.

Chapter 1: Evolutionary biology of Atlantic parrotfishes: current state of knowledge

The evolutionary, reproductive, and ecological aspects of parrotfishes, one of the richest fish families on Atlantic coral reefs (Parenti and Randall 2000) were reviewed to provide an overview of the state of knowledge, debates, and information gaps about this taxon in the Atlantic Ocean and the Caribbean Sea. This chapter also explores their importance in light of evidence of the changes in coastal food webs due to overfishing (Jackson et al. 2001b), reported decline of the Caribbean coral reefs (Pandolfi et al. 2003), and the urgent need of ecosystem-based management approaches (Pandolfi et al. 2005).

1.1 Taxonomy, systematics and biogeography

Taxonomy and biosystematics of parrotfishes have been under a long-standing debate. Due to uncertainties about the monophyly of this group of species, classifications disagree at the levels of family and subfamily (Table 1.1). All parrotfishes currently belong to the family Scaridae (Rafinesque, 1810), previously known as Callyodontidae (Perciformes: Labroidei). Out of the 79 - 96 species recognized into 9 - 10 genera (Table 1.1), 23 species of 4 genera have been reported on either side of the Atlantic Ocean (Table 1.2). The most recent family-wide taxonomic review included the Venezuelan endemic species (Parenti and Randall 2000), but was published before the identification of the Brazilian endemics.

Before the beginning of this decade, most reviews of scarid biosystematics and evolutionary biology tended to disregard scientific studies from Latin American journals and researchers, missing a rich source of information that in recent years have added seven species, one Venezuelan and six Brazilian endemics (Cervigón 1994, de-Moura et al. 2001, Gasparini et al. 2003).

Furthermore, a thorough account of the history of scarid classification, going back to 1775, pointed out the controversies among early biosystematicists (Bellwood 1994). To this day, gaps in phylogenetic information confuse relationships and makes systematic ichthyology difficult for this taxon. Because the boundaries of the suborder, family, subfamily, and species levels are currently under discussion (Table 1.1), different sources of evidence will be critically reviewed in the sections below.

1.1.1 Systematics of the Family Scaridae

Osteological and myological studies encompassing up to 69 species of parrotfishes, including Atlantic representatives, concluded that Scaridae was a monophyletic family (Bellwood 1994, Monod et al. 1994, Bullock and Monod 1997). The first main character shared by parrotfishes is their functional pharyngeal toothed plate (pharyngognathy), characterized by a very unique pharyngeal jaw anatomy that sets them apart from other pharyngognathous orders. Specific traits include the lower pharyngeal jaw composed of united fifth ceratobranchials forming one functional unit (Nelson 1967, Liem and Greenwood 1981); the pharyngocleithral joint, formed by the articulation of the lower pharyngeal jaw with the cleithrum (Liem and Greenwood 1981); the loss of the gill-bearing function of the epibranchials (Gobalet 1989); and the antero-dorsal direction movement of the posterior ends of the pharyngeal plates (Liem and

Greenwood 1981, Bullock and Monod 1997). A secondary family trait, equivocally assigned as the defining one for a parrotfish by many authors, is the morphology of the front jaw dentition, which ranges from incisor-like teeth slanting forward to a fused or coalesced dental plate (Schultz 1958, Böhlke and Chaplin 1993, Nelson 1994). There is an apparent inconsistency of these two main characters, since neither one is unique to Scaridae (Bellwood and Schultz 1991). Firstly, scarid-like general morphology of the pharyngeal apparatus is seen in extant and extinct labrid species. Secondly, while other orders (e.g., tetraodontiforms) display coalesced front jaw dentition, not all scarid genera have coalesced teeth. The uniqueness of Scaridae resides in both the pharyngeal tooth development, and the patterns of the coalesced front teeth (Bellwood and Schultz 1991).

The hypothesis that scarids shared a common ancestor with the labrids (Schultz 1958) is confirmed by paleontology (Bellwood and Schultz 1991), cephalic osteology (Nelson 1967), dentition morphology and development (Liem and Greenwood 1981), early life history characters (Richards and Leis 1984, Colin and Bell 1991), molecular genetics (Bernardi et al. 2000, Streelman et al. 2002), and reproductive characteristics (Robertson and Warner 1978).

Below the family level, parrotfishes are a taxonomically difficult and confusing group of reef fishes (Schultz 1958, Schultz 1969, Robins et al. 1991, Parenti and Randall 2000, de-Moura et al. 2001, Humann and DeLoach 2002). The separation into two subfamilies, Sparisomatinae (comprising three Atlantic genera, *Cryptotomus*, *Nicholsina*, and *Sparisoma*) and Scarinae (including *Scarus*, and the remaining 6 genera), is mainly based on the type of bite, external dentition structure, number of rows of scales on the cheek, and molecular genetics (Schultz 1958). This division is accepted by many

(Bullock and Monod 1997, Novoa et al. 1998, de-Girolamo et al. 1999, Claro et al. 2001, Streelman et al. 2002), but not by Bellwood (1994), who found no morphological evidence to support their division because of strong indications of Sparisomatinae being a paraphyletic[1] taxon, nor by Parenti and Randall (2000) (Table 1.1). A more recent DNA sequencing study revealed two distinct lineages matching the subfamily classification, the seagrass (Sparisomatinae), and the reef (Scarinae) clades (Streelman et al. 2002). This review will address this subdivision with evidence for or against it as some of their genetic, anatomical, behavioral, and ecological traits are described and analyzed.

Individual species have been subjected to numerous misidentifications, inadequate descriptions, misnamings, misspellings, and a myriad of homonyms (Winn and Bardach 1957, Schultz 1958, Winn and Bardach 1960, Schultz 1969, Robertson and Warner 1978, Guitart 1985, Robins et al. 1991, de-Moura et al. 2001). Schultz (1958) found 354 scientific names for scarids, of which only 96 have been officially recognized. This confusion is the outcome of a combination of the protogyneous and complex polychromatic nature of scarids; the dramatic juvenile-to-adult external changes in color phases; the high interspecific overlapping and intraspecific variability of their meristics, especially the larval stages (Richards 1984); imperfect descriptions; loss of color pattern in preserved specimens; and accidental misspellings. Convergent color patterns of younger stages (e.g., *Sparisoma*[2] *rubripinne* vs. *Sp. chrysopterum*; *Scarus*[2] *taeniopterus* vs. *Sc. iseri* suggest a uniform selection for disruptive coloration, which makes it very

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[1] Term applied to a group of organisms in which all the members of the group have a common ancestor but the group does not include all the descendants of the common ancestor (e.g., "invertebrates, fishes").

[2] In order to facilitate the intergeneric comparisons, *Sparisoma* and *Scarus* spp. will be referred to as *Sp.* spp. and *Sc.* spp., respectively.

difficult to distinguish small individuals of these species (Choat and Robertson 1975, Humann and DeLoach 2002). For example, the striped parrotfish, *Scarus iseri* (Bloch, 1789), has had ten synonyms (see Integrated Taxonomic Information System[3]), with a few in wide use simultaneously, e.g., *Sc. iserti*, *Sc. croicensis* (Bloch, 1790) (Robins et al. 1991, Eschermeyer 1998).

All these confounding factors have made the development and use of identification keys based on external morphology (Guitart 1985, Cervigón 1994, Smith-Vaniz et al. 1999) very challenging, due to the lack of diagnostic external characters and the importance of live coloration in parrotfish classification (Parenti and Randall 2000). Bellwood (1994) produced the first family-wide classification of Scaridae based on cladistic analysis, a methodology absent in previous taxonomic studies of the parrotfishes.

1.1.2 Biogeography of parrotfishes

Scarid biogeography is under less intense debate, although two different theories have been proposed to account for their speciation patterns, one based on vicariance and a more recent history (Schultz 1958), and the other based on habitat use that entails an earlier origin (Streelman et al. 1997).

Schultz (1958) listed six scarid biogeographic regions (three in the Pacific, two in the Atlantic, and one in the Indian Ocean), while Bellwood (1994) considered two only, the Atlantic/Caribbean and the Indo-Pacific. The first substantiated appearance of scarids in the fossil record dates from the Middle Miocene (~13 million years ago, Mya)

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[3] Cf. http://www.itis.usda.gov/servlet/SingleRpt/SingleRpt?search_topic=TSN&search_value=614740

(Bellwood and Schultz 1991, Choat 1991). Parrotfishes are absent from the earliest coral reef fish assemblage found in the Eocene fossil record in Monte Bolca, Italy (~50 Mya) (Bellwood 1996a,1996b), while other herbivorous family, Acanthuridae, was already well represented by then (Bellwood and Schultz 1991). The absence of parrotfishes from this important fossil site has different interpretations, such as chance, patchy collections, lack of fossilization in exposed coral reefs, a more recent origin for the family (Bellwood and Schultz 1991), or the perireefal paleoenvironment condition of the Bolca deposits rather than a true coral reef ecosystem (Bellwood 1998). DNA analysis and molecular clocks, however, suggested that the major split between the seagrass and reef clades took place ~42 Mya (Streelman et al. 2002), pushing the origin of parrotfishes much earlier than first thought, and supporting the idea of considering the lack of parrotfish fossils in Monte Bolca an artifact (Bellwood 1996a,1996b). Thus, Scaridae more likely appeared 45-50 Mya.

Parrotfishes originated in the eastern Tethys Sea, the precursor of the Indo-Pacific Ocean (Streelman et al. 2002). The fossil record supports a biogeographic split 15+ Mya, driven by two major vicariance events, i.e., the closure of the eastern Tethys Sea (~13 Mya), and the formation of the Panama Isthmus (~5 Mya) (Schultz 1958). However, nuclear and mitochondrial DNA sequencing indicated that the evolution of Scaridae was driven by ecology (i.e., habitat use) rather than biogeography, based on a phylogenetic bifurcation of the reef-seagrass lineages, assigned as subfamilies, and that such separation happened ~30 My before the first scarid recorded fossil (Streelman et al. 2002). Those authors acknowledged the lack of evidence for any vicariance between the two habitats explaining the difference in species richness for each clade. However, it is probable that variations in the jaw apparatus in conjunction with feeding preferences would yield differential performances in the two habitat types, giving rise to the two seagrass-reef clades (or subfamilies).

The scarid evolutionary history was marked by four major events (Bellwood 1994) following this chronological order (Bernardi et al. 2000, Streelman et al. 2002): the family originated as seagrass-dwellers and blade browsers, later transitioning onto rocky or coral reefs (*Sparisoma* spp., inhabiting both seagrass and reef habitats, representing a transitional form). After the reef-exclusive lineage appeared, a scraping feeding mode evolved from excavators (see definitions in Table 1.2). Under this view, excavating and scraping feeding habits emerged at least twice (Scarinae and *Sparisoma*).

On the other hand, based on morphological studies on the Brazilian endemics, Gasparini et al. (2003) questioned two major points: the ancestral condition of browser feeding, and the simplistic criterion of seagrass-reef habitat association to classify the subfamilies.

This review considers that further evidence validates the remarks by Gaspirini and coworkers (2003), and calls for revisions on the matter. Firstly, the ancestral feeding mode will remain uncertain until scientists elucidate which labrid lineage is closest to the scarids. Secondly, exceptions within the seagrass and reef clades weaken the separation of those lineages based on habitat or feeding mode only. Thirdly, behavioral and reproductive traits, discussed in section 1.2.3 below, prove the complexity of this family.

Regarding the genus biogeography in the Americas, *Cryptotomus* and *Sparisoma* are restricted to the tropical Atlantic, while *Nicholsina* and *Scarus* occur in both the Tropical Atlantic and Tropical Eastern Pacific. Mitochondrial DNA sequences suggested that *Sparisoma* diverged from *Nicholsina* (browser) and *Cryptotomus* (browser) ~14.3 to 35 Mya, earlier than proposed by Bellwood (1994) (Bernardi et al. 2000). Cladogenesis of *Sparisoma* spp. was dated as follows (Bernardi et al. 2000): *Sp. atomarium* split from the remaining congener species 12 Mya, the Eastern Atlantic clade separated from the main lineage 10 Mya, and the remaining five *Sparisoma* formed three clades 6.5 Mya. Finally, three speciation events ocurred ~2.8-5.6 Mya: in the Western Atlantic, *Sp. chrysopterum* split from *Sp. radians*; in the Eastern Atlantic *Sp. cretense* and *Sp. strigatum* diverged; and isolated populations of *Sp. rubripinne* appeared on both sides of the Atlantic. The timing of these events coincided with accelerated extinction and accelerated speciation of Caribbean corals, 1-4 Mya. At present, no genetic studies have been conducted to elucidate the relationships of the Brazilian endemics with the rest of the scarids (de-Moura et al. 2001). The endemic scraper *Sp. tuiupiranga* is considered part of the *Sp.atomarium* clade (Gasparini et al. 2003), but more powerful genetic studies are recommended to elucidate the relationships.

1.1.3 Atlantic parrotfish species

A total of 23 Atlantic parrotfish species have been acknowledged (2 Eastern and 21 Western Atlantic), as listed in Table 1.2. Besides the validated 14 Caribbean species, a 15th western species, *Sparisoma griseorubra* (Cervigón, 1982)*,* endemic to Cubagua Island, Venezuela, has been recognized since 1993 (Cervigón et al. 1993, Cervigón 1994, Parenti and Randall 2000), but it is pending a taxonomic reassessment (de Moura, R. Museum of Zoology, University of Sao Paulo. 2003. Pers. Comm.). Six more species, *Scarus trispinosus* (Valenciennes, 1840), *Sc. zelindae* (de Moura et al., 2001), *Sparisoma amplum* (Ranzani, 1842), *Sp. frondosum* (Agassiz, 1831), *Sp. axillare* (Steindachner, 1878), and *Sp. tuiupirang*a (Gasparini, Joyeux & Floeter, 2003) were described, validated and/or acknowledged and as endemic to Brazil (de-Moura et al. 2001, Humann and DeLoach 2002, Gasparini et al. 2003, Kramer 2003), being isolated from the Caribbean by the Orinoco and Amazon river plumes.

Species keys for 14 of the Western Atlantic species (6 *Scarus* spp, 6 *Sparisoma* spp., and one species each of *Cryptotomus* and *Nicholsina*) have been available in the literature for several decades (Schultz 1958, Fischer 1978, Guitart 1985, Böhlke and Chaplin 1993, Cervigón 1994, Smith-Vaniz et al. 1999). Depending on the locality & state of preservation of the specimen, some keys are more practical than others, due to local variability in some external characters. A species key including the Venezuelan and Brazilian endemics is yet to be published.

The Atlantic species belong to four genera, listed here in evolutionary order: *Cryptotomus*, *Nicholsina*, *Sparisoma*, and *Scarus* (Schultz 1958, Winn and Bardach 1960, Randall 1983, Simoes and Andreucci 1983, Guitart 1985, Robins et al. 1986, Bellwood 1994, Cervigón 1994, Nelson 1994, Bernardi et al. 2000, Parenti and Randall 2000, de-Moura et al. 2001, Streelman et al. 2002). Evidence includes: labrid-like teeth at the front of the jaws in *Cryptotomus* and *Nicholsina* (Schultz 1958), DNA sequences (Bernardi et al. 2000, Streelman et al. 2002), mouth dentition of Brazilian parrotfishes (Simoes and Andreucci 1982, 1983), and cephalic osteology of Eastern Atlantic species (Monod et al. 1994).

Nicholsina and *Sparisoma* display a similar tooth microstructure and a primitive feeding apparatus (i.e., forwardly-slanted individualized denticles, and the presence of three rows of teeth in each pharyngeal bone), while *Scarus* presented coalesced mouth denticles, a reduced number of pharyngeal rows, and a more specialized feeding mode (Schultz 1958, Simoes and Andreucci 1982, 1983, Bellwood and Schultz 1991, Monod et al. 1994, Bullock and Monod 1997). These observations support the subfamily classification. The dentition studies, however, do not address the phylogenetic implications of their findings, while the Eastern Atlantic myo-osteological analyses only conclude that Scaridae is definitely a family apart from Labridae.

Cryptotomus, *Nicholsina*, and *Sparisoma* belong to the subfamily Sparisomatinae or seagrass clade, and *Scarus* to Scarinae or reef clade (Nelson 1994, Streelman et al. 2002), with two particularities. Firstly, García-Cagide et al. (2001) listed *Cryptotomus* as a Scarinae. Secondly, the separation of the reef-seagrass clades based on DNA sequencing, dentition, and feeding habits is not always well defined; for example, some *Sparisoma* spp. (esp. *Sp. viride*) share a dentition and cranial anatomy characteristic of the scarine clade (Streelman et al. 2002).

In summary, parrotfish systematics and evolutionary history remain subjected to debate. The morphological, ecological, and behavioral variability exhibited by these reef fishes defies traditional approaches to address their phylogeny. Alternative techniques, ranging from functional morphology to DNA sequencing and ethology, may provide a clearer picture of the evolutionary relationships among the species. By elucidating the significance of subfamily-level reef vs. seagrass differentiations happening 42 Mya, we may obtain a better understanding of the relative importance of each component of the reef and perireefal ecosystems prior to the beginning of aboriginal fishing (Jackson et al. 2001b). It is plausible that the adaptive radiation of scarids is a product of ecological segregation, sexual selection, and phenotypic plasticity rather than vicariance alone.

1.2 Reproduction of Atlantic parrotfishes

Information on the reproductive strategies and patterns of the parrotfishes is vital for understanding their population dynamics, and hermaphroditism is an important factor to consider when assessing the fisheries status (cf. Chapter 4). Fortunately, scarid reproductive behavior and sexuality have been studied extensively (Winn and Bardach 1957, 1960, Randall 1963, Colin 1978, Robertson and Warner 1978, Dubin 1981, Clifton 1989, Cardwell and Liley 1991a, 1991b, Koltes 1993, Marconato and Shapiro 1996, de-Girolamo et al. 1999). All 23 species of Atlantic parrotfish are sequential hermaphrodites displaying protogyny (Robertson and Warner 1978, Cervigón 1994, de-Girolamo et al. 1999, de-Moura et al. 2001), i.e., an individual is first a female, and then transforms into a male, but does not function simultaneously as both. No gonochoric[4] species have been reported in this family, with two caveats: (a) *Sparisoma cretense* is considered a functional gonochorist with prematurational sex-change[5] (de-Girolamo et al. 1999), and (b) there are true gonochoric individuals within populations (Robertson and Warner 1978).

1.2.1 Color and sexual phases

Scarids undergo a very complex sequence of ontogenetic changes in the color patterns associated with their sexual identity. Parrotfishes may show three distinct color phases (Bellwood 1994): juvenile phase (JP), initial phase (IP), and terminal phase (TP).

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[4] Individuals that lack the genetic capacity to change sex (Warner and Robertson 1978).

[5] Testes are derived from ovaries without ever being a functional female

In general, juvenile color patterns are relatively conservative, based on a small range of colors, and show little variation among species (Bellwood 1994).

JP coloration of ten Atlantic parrotfishes does not differ from that of IPs, while being distinctively different from the older phases in 6 species: *Sp. atomarium, Sp. aurofrenatum, Sp. viride, Sc. coeruleus* (Humann and DeLoach 2002), *Sp. cretense* (de-Girolamo et al. 1999), and *Sp. tuiupiranga* (Gasparini et al. 2003). JP coloration has not been described for the St. Helena's, Venezuelan and the remaining Brazilian endemics (Cervigón 1994, de-Moura et al. 2001). Initial Phase individuals are either females or males, and can be considered subadults; IPs are characterized by a disruptive, dull coloration (brown and gray), which is advantageous for avoiding predation (Choat and Robertson 1975, Claro 1994), but can change instantly from pale to heavily mottled in some species, e.g., *Sp. chrysopterum, Sp. radians, Sp. aurofrenatum* (DeLoach 1999). Terminal Phase specimens are males that have undergone color change; TPs display a bright coloration, predominantly green and blue with cephalic and opercular markings in red, orange or blue (Choat and Robertson 1975, Robertson and Warner 1978, Warner and Robertson 1978, Bellwood 1994).

Color pattern is important for rapid sexual and intraspecific recognition, which makes the color transformation an advantage for the TP male. The cost is an increased probability of mortality by predation, due to their conspicuousness and exposed activity (Robertson and Warner 1978). *Scarus coelestinus* is the only Atlantic scarid with the same color pattern throughout its whole lifespan, which is probably a secondary adaptation.

Four sexual identities of adult parrotfishes are associated with specific color phases, namely females (IPs); primary males (IPs, TPs), referring to those which are not product of sexual transformation; secondary males (IPs, TPs), i.e., individuals resulting from sex reversal in protogyneous species; and transitional individuals (Choat and Robertson 1975, Claro 1994, Streelman et al. 1997).

Each identity tends to have a particular mating behavior (Robertson and Warner 1978) (Table 1.3). TPs are territorial (i.e., actively defend their home range against male conspecifics (de-Girolamo et al. 1999), and display pair-spawning. Male IPs do not hold territories, display group spawning and may interfere with the pair spawning of the TPs, by means of different strategies, such as *sneaking* and *streaking* (Robertson and Warner 1978). Temporary territories ranging from 2.8 to 587 m^2 occur in the congeners *Sp. cretense*, *Sp. rubripinne*, *Sp. viride*, and probably *Sp. chrysopterum* (Table 1.3).

Permanent territories have been reported for *Sc. taeniopterus, Sc. vetula, Sp. atomarium, Sp. aurofrenatum,* and *Sp. radians* (Table 1.3), suggesting that it is not a subfamily character. Some species exhibit both temporary and permanently territorial behaviors for different color phases. An ethological study in Belize suggested that the territories of *Sp. viride* and *Sc. iseri* had a reproductive goal (Mumby and Wabnitz 2002). Their agonistic behavior was intraspecific and density-dependent. However, *Sp. rubripinne* had more interspecific aggressive displays towards small *Sp. chrysopterum*. Furthermore, overall mating success of *Sp. radians* depended on territory size and male size, since spawning frequency positively correlated with territory area (Marconato and Shapiro 1996). This finding provides a plausible adaptive value of territorial behavior.

Proportions of IP males and TP males are correlated with the mating system of the species (e.g., whether it forms harems[6] or not, presence of diandry,[7] etc.), territoriality (temporary for reproductive purposes or permanent), habitat, absence of a TP in the area, androgen levels, and the overall well-being of the fish (Robertson and Warner 1978, Cardwell and Liley 1991a,1991b, Koltes 1993, van Rooij et al. 1995a, de-Girolamo et al. 1999, Allsop and West 2003b).

Population size is another factor that reportedly affects life phase proportions (Robertson and Warner 1978, Rakitin and Kramer 1996, van Rooij et al. 1996b). In a large population (e.g., in a large reef patch), a relatively larger number of females will increase chances of successful matings by group spawning or interference, thereby allowing for the presence of more IP males. Conversely, IP males would be expected to be rare in small parrotfish populations.

1.2.2 Adaptive value and costs of protogyny

It is commonly accepted that protogyny is favored by a strong sexual selection providing an advantage for a male to be bigger than the female (Choat and Robertson 1975, Warner et al. 1975, Allsop and West 2003b). A mathematical model indicated that a sex change should occur if one sex gains in fertility much more rapidly with age than the other, as is the case with parrotfishes (Warner et al. 1975). Furthermore, certain dimensionless invariants for sex reversal in protogynous species hypothetically apply regardless of fundamental biological considerations, i.e., sequential hermaphrodites

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[6] A group of females within a male territory, that mate nearly exclusively with that one male (Warner and Robertson 1978).

[7] Both primary and secondary males are present in the same population (Warner and Robertson 1978)

change sex when they are 79% of their maximum body length, and 2.5 times their age at first maturity across very different taxa (Allsop and West 2003a). Specifically, five Caribbean parrotfish species changed sex at a mean of 70 ± 11% of their maximum length (as calculated from Appendix S1 in Allsop and West (2003b). This finding is highly valuable for the theory of sex change and evolution, by emphasizing the major role fecundity plays in evolutionary processes. It provides evidence that the adaptive value of sex change transcends different lineages and absolute values of specific population dynamic parameters, while tying the process to maturity schedules and maximum size.

Higher vertebrates are gonochorists because their rigid sex-determination mechanism and internal fertilization render the necessary anatomical changes of sex reversal too costly bioenergetically (Choat and Robertson 1975). Protogyny is restricted to particular taxa, primarily coral reef fishes, some with complex social and reproductive behavior. Thus, strong selective forces must operate in order for a significant proportion of a population to include sex-changing forms.

Little is known about the actual cost of sex transformation (Warner et al. 1975), except that color change alone in *Sp. viride* does not demand an extreme metabolic cost (van Rooij et al. 1995b). It has been suggested that the bioenergetic investment of changing color and sex might be compensated by enhanced mating success with proportionally smaller testes (Choat and Robertson 1975, Robertson and Warner 1978, Cardwell and Liley 1991a). TPs normally have smaller gonads than IP males, in both absolute and relative terms (Choat and Robertson 1975, Robertson and Warner 1978, Cardwell and Liley 1991a). An alternative explanation to senescence or sexual function decline (Choat and Robertson 1975, Robertson and Warner 1978) is based on the assumption that TPs have ensured their reproductive success by territorial pair spawning. Thus, these individuals do not need to produce large amounts of sperm. Conversely, IP males tend to display group spawning, and higher gonadosomatic index, i.e., their testes are much bigger, because of the selective pressure of competing for female gametes (Robertson and Warner 1978). Furthermore, color phase, gonad weight, and mating patterns may be intimately related in scarids (Choat and Robertson 1975).

1.2.3 Reproductive strategies: are there subfamily patterns?

Streelman et al. (2002) suggested that social and reproductive behaviors of the Sparisomatinae and Scarinae are tightly tied to habitat (seagrass and reef clades, respectively). There are striking differences in reproductive strategies between both subfamilies, although Atlantic parrotfishes from different subfamilies share more characteristics than do within-clade species from the Indo-Pacific and Caribbean regions. Firstly, all Caribbean scarine females eventually transform into males, some maturing directly into male adults (Choat and Robertson 1975). Conversely, not all sparisomatine females, e.g., *Sp. chrysopterum, Sp. radians,* and probably *Sp. viride* and *Sp. rubripinne* change sex (Table 1.3). The presence of the gonochorist female morph can be explained by the lack of a pronounced mating hierarchy, perhaps due to the absence of permanent territoriality (Table 1.3), that allows higher reproductive success of smaller IP males (Robertson and Warner 1978). Thus, given the lack of significant differences in fertility between females and males of all sizes, there is no strong selection pressure favoring sex-changing morphs.

Secondly, some sparisomatines e.g., *Sp. chrysopterum, Sp. rubripinne, Sp. viride*, (Robertson and Warner 1978), and *Sp. cretense* (de-Girolamo et al. 1999) commonly display prematurational sex change. This character is also called secondary gonochorism (Robertson and Warner 1978, Koltes 1993, Claro 1994) because those small secondary males function in the same roles as primary males. Unlike their Indo-Pacific counterparts, no secondary gonochorists have been reported in the Caribbean Scarinae. Primary males and some secondary gonochorists, e.g., *Sp. rubripinne* tend to channel more energy into growth, and may become terminal phase more quickly (Robertson and Warner 1978). This is important when studying the growth rates and their variability within populations (cf. Chapter 3).

A third diverging pattern is that sparisomatines display monandry,[8] lacking primary males. These species have wide size overlaps between color phases and sex identities (Table 1.3), such that their color and sex phases do not appear to be closely associated. Indeed, some *Sp. rubripinne* males may retain their IP coloration throughout their lifespan (Robertson and Warner 1978). Scarines are diandrous with sex reversal occurring over a small size range (Table 1.3) and color-phase associated (Warner and Downs 1977, Robertson and Warner 1978, Streelman et al. 2002). This more straightforward reproductive history for Caribbean scarines compared to the wide range of combinations in sparisomatines could support Bellwood's (1994) misgivings about the subfamily division, because the large intra-subfamily variability of the latter resembles a complex continuum lacking of clear evolutionary paths.

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[8] All males present in a population are secondary (transformed from females) (Warner and Robertson 1978).

1.2.4 Fecundity and reproductive behavior: from harems to spawning aggregations.

Information on fecundity and sperm production is scattered, restricted to the sparisomatines, and reporting large variance of estimates (cf. Table 1.3). *Sparisoma viride* releases ~10000 eggs in a single spawning (van Rooij et al. 1995b), but the wide range of estimates, from 5500 to 68600 per female, prevented computing a fecundity curve (Koltes 1993). Fecundity studies in *Sp. cretense* from Canary Islands yielded equations shown on Table 1.3, displaying a large variability with a mean 3.35 x10^5 ovocites (range 1.7 x10^4 to 1.5x10^6 for 200-392 mm FL females) (González et al. 1993). In Puerto Rican reefs, male *Sp. radians* release a median of 8.9 x 10^6 sperm in their pair spawnings; their ~95% fertilization rate is independent of egg number, but it increases with amount of sperm (Marconato and Shapiro 1996). This ability to regulate sperm production according to female size has a three-fold adaptive value: increased probability of higher fertilization rates with more fecund females, increased reproductive success against sneaking males, and extended sperm output throughout multiple daily matings (Warner and Downs 1977). It must be noted that none of those three species reportedly displays spawning aggregations.

Harem-forming behavior does not appear to be restricted by genus or evolutionary history. Seven out of the ten Caribbean scarids studied in Panama formed harems (Robertson and Warner 1978), including species from both clades, i.e., *Cryptotomus, Sparisoma,* and *Scarus* (Table 1.3). Even though *Sp. viride, Sp. chrysopterum,* and *Sp. rubripinne* were described as non-haremic species (Robertson and Warner 1978), Mumby and Wabnitz (2002) found otherwise in Belize populations. The two latter species showed small harems with no spatial patterns, while harems of *Sp. viride* were positively correlated to territory size.

A wide array of courtship and spawning behaviors has been described for many of the Atlantic parrotfishes. Courtship rituals in general differ with social structure and number of participants (Randall 1963, Colin 1978, Robertson and Warner 1978, Dubin 1981, Colin and Bell 1991, Marconato and Shapiro 1996, Domeier and Colin 1997, de-Girolamo et al. 1999, DeLoach 1999). For example, courting territorial *Sc. taeniopterus* TPs (Dubin 1981) behave differently from mass-spawning *Sc. iseri* IPs (Colin 1978). Most species display the upward rush when spawning, hypothesized to facilitate the expulsion of gametes by the expansion of the air bladder, by the sharp flexing of the bodies, or both (Randall 1963). Reproduction-associated swimming behaviors are described in section 1.5.

Consistent spawning aggregations[9] have been reported for *Sp. rubripinne*, and *Sc. iseri* (Randall 1963, Colin 1978, Domeier and Colin 1997), as well as for four Indo-Pacific scarids. The two Caribbean species displayed year-round resident aggregations (Table 1.3) at the same spots for at least 28 and 19 years, respectively, with no apparent lunar cycle (Randall 1963, Domeier and Colin 1997). These aggregations have persisted even following major hurricanes and other natural disturbances (Colin 1996). Resident aggregations are more typical of small species, in ephemeral, frequent, and predictable episodes occurring at traditional sites near a steep drop-off. Such events entail relatively short migration distances and group spawning only (pair spawning may occur outside of the aggregation), each single event representing a small portion of the reproductive effort

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[9] Group of conspecific fish gathered for spawning , with fish densities significantly higher than those in the area during non-reproductive periods (Domeier and Colin 1997).

(Domeier and Colin 1997). There is little quantitative data to address several hypotheses explaining the spawning aggregation behavior. Some of these hypotheses list benefits such as maximization of egg dispersal, chances for larvae to find food patches, and minimization of predation as driving forces to favor this strategy (Domeier and Colin 1997). However, predation on pair-spawning gametes tends to be lower than for group spawners, probably due to the inconspicuous egg clouds of the first strategy (Colin and Bell 1991), which would counter selection for spawning aggregations. The fish's ability to learn the location and coordination is an important factor determining the occurrence of such aggregations, while fishing pressure might play a role in their disappearance (Colin 1996).

1.2.5 Spawning patterns and products

Spawning seasons are consistently protracted (usually year-round) across the western Atlantic, with peaks ranging from totally absent to reversed intensities in different areas (Table 1.4) (Colin and Bell 1991, Claro 1994, García-Cagide et al. 2001). For example, while no spawning peaks were detected in Panama (Robertson and Warner 1978), in Cuban waters, 11 out of the 16 species spawn between December and August, and only 6-7 spawn from September through November (Claro 1994). In Puerto Rico, diverse observations suggested year-round spawning activity peaking in certain months. While juveniles were found all year, the adults caught were very seldom ripe (Erdman 1977); conversely, *Sc. iseri* showed a winter spawning peak in Puerto Rico, but was most active during summer in Jamaica (Colin 1978, Colin and Clavijo 1988). Lunar and tidal rhythms are not well defined in most of these species (Colin and Clavijo 1988, van Rooij et al. 1996b), a phenomenon perhaps attributable to the absence of strong, predictable tidal currents in the region. Despite larval stages showing lunar cycles, neither *Sc. iseri, Sc. taeniopterus, Sp. aurofrenatum,* or *Sp. viride* spawning displayed any lunar activity in Puerto Rico, although *Sc. vetula* apparently spawn near full or new moon only (Colin and Clavijo 1988). A temperate species, *Sp. cretense*, showed a well-defined reproductive season in the summer months (Table 1.4) with daily spawning activity in the Mediterranean (de-Girolamo et al. 1999). Unfortunately, there is less information on the large-bodied species, which may have a greater role in the trophic structure because of their larger biomass, and that may be the most impacted by fishing and habitat loss. *Scarus coelestinus* and *Sc. guacamaia* were summer spawners in Bermuda, at the northern end of their distribution (Winn and Bardach 1960, Winn et al. 1964), while *Sc. coeruleus* displayed reproductive activity during January in Jamaica (Reeson 1983). The only reported spawning activity for *N. usta* is in Venezuela (Cervigón 1994), probably one of its southernmost populations and where this species is very abundant (Table 1.4).

Daily patterns vary among species regardless of genus. Most Atlantic scarids are afternoon spawners (Table 1.3), though a few display morning spawning activity (Table 1.3), perhaps following tidal cycles (Colin and Clavijo 1988). However, Florida populations of *Sp. viride* have been observed spawning throughout the day (Paddack, M. University of Miami. 2004. Pers. Comm.).

All scarid eggs are pelagic, and their shape may loosely follow a subfamily division (Richards and Leis 1984, Bellwood 1994). Like the labrids, *Sparisoma* spp. have spherical eggs (a plesiomorphic state[10]), while *Scarus* spp. and other scarine genera have fusiform eggs (Winn and Bardach 1960, Randall 1963, Erdman 1977, Bellwood 1994, Cervigón 1994). The exception is the Indo-Pacific *Bolbometopon*, a scarine with

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[10] Plesiomorphy: A primitive character state for the taxa under consideration

spherical eggs (Colin and Bell 1991, Bellwood 1994). The larvae are pelagic as well (Aboussouan 1969, Richards 1984, Richards and Leis 1984, Ramírez-Mella and García-Sais 2003). Under laboratory conditions, *Sp. rubripinne* hatched 25 hours after fertilization at 26 C, and used up their yolk sac in three days. The larvae would orient itself with the head up, and exhibit mainly upward movements during the first 6 days of age (Randall and Randall 1963).

Hybridization in parrotfishes has rarely been addressed, but timing of spawning seems to be an important isolation mechanism. *Scarus iseri* and *Sc. taeniopterus* are strikingly similar species in IP and TP colorations, habitat, social behavior, etc., but no hybrids have been reported (Dubin 1981). Instead, these congeners represent a dramatic example of convergence. Their sympatric genetic isolation is achieved by differential spawning hours during the day, mid-to-late afternoon vs. early- midmorning, respectively (Table 1.3). Intergeneric hybrids might be less likely, given the egg morphology differences probably acting as a fertilization barrier. Unfortunately, no genetic population studies have been conducted yet to address this issue, considering the astounding geographic variation in color patterns found in fish of the same species.

It is a challenging task to summarize reproduction of the Atlantic parrotfishes into a few well-defined patterns. Firstly, from an adaptive perspective, numerous sexual identities and coexisting behaviors within a single population are common in parrotfishes, a strategy that will remain as long as those types are successful in different habitats (Robertson and Warner 1978). Secondly, despite the high complexity in the reproductive biology of scarids, dimensionless life history theory can be applied to understand and predict events such as age and size of sex reversal, within an approach that disregards variations in many biological aspects(Allsop and West 2003a, Allsop and West 2003b). These principles can be very useful for fisheries management approaches when field information on specific taxa is not available. Thirdly, scarines are strikingly different from the sparisomatines regarding monandry, prematurational sex change, ontogeny of sex and color transformations, DNA sequencing, and preferred bottom substrate. Other characteristics, such as spawning aggregation behavior and spawning time of day, transcend subfamily division, genera, genetic clades, and biogeographical region. These traits are probably driven by selective forces related to local ecological pressures. The sympatric speciation sustained by differential spawning hours during the day partially allows a high species richness in the same reef patch.

1.3 Relative abundances of parrotfishes in tropical reefs

Herbivore taxa account for a large component of the coral reef biota. In Caribbean reef flats, herbivorous species may represent as much as 49% of the fish community biomass, 28% by density, and ~19% of the species (Claro 1994). Parrotfishes are one of the four most diverse and abundant herbivorous families in tropical reefs (Bellwood and Schultz 1991, Choat 1991, Claro 1994), representing 2.3% of the 444 reef fish species in the Northwest Atlantic (Robertson 1998). Scarids dominated the fish communities on Caribbean reef flats (Winn and Bardach 1960, Randall 1963, Fischer 1978, Randall 1983, Reeson 1983, Claro 1994, Claro et al. 2001) before they were fished to replace the declining catches of top predators in certain areas. The caveat, however, is that most studies on coral reef fishes have been conducted after 1950. Large herbivore fishes were already decimated in the Western Atlantic by the beginning of the 20th century, due to overfishing (Jackson et al. 2001b). Thus, in the context of shifting baselines, even the earliest modern-era observations lack of a baseline prior to aboriginal and colonial overfishing and ecological extinction.

Nevertheless, visual surveys conducted in 1998 and 1999 by the Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program (Lang 2003), showed that parrotfishes and surgeonfishes were still the most abundant fishes in 22 reefs. Scarids accounted for 31 and 36% of the fish community on shallow reefs ($\leq$5 m depth), and deep reefs (>5 m depth), respectively (Kramer 2003). While carnivorous fish densities averaged 6 fish 100 m^{-2}, parrotfishes had an overall mean of 13.7 fish 100 m^{-2}, followed by surgeonfishes (Acanthuridae), with 11.8 fish 100 m^{-2}. Unlike that of carnivores, herbivore species composition was consistent across the Caribbean, although their densities displayed a high degree of variation. Parrotfishes were most abundant in the eastern and southern Caribbean reefs, ranging from ~7 fish 100 m^{-2} in Belize and Cuba to 36 fish 100 m^{-2} in Venezuela (Kramer et al. 2003). *Scarus iseri*, *Sp. aurofrenatum*, *Sc. taeniopterus*, *Sp. viride*, and *Sc. vetula* displayed the highest densities in decreasing order, averaging 1-4 parrotfishes per 100 m^2 (Table 1.5). Occurrence of larger species, such as *Sc. guacamaia*, *Sc. coelestinus*, and *Sc. coeruleus*, was occasional, but they were more common in the southern Caribbean reefs (Kramer 2003).

Nicholsina usta does not follow the scarid distribution patterns in the Atlantic waters. This species is a seagrass and rubble inhabitant (Table 1.2) reportedly uncommon in the Caribbean reefs (Humann and DeLoach 2002). Although it was among the top 12 most abundant species caught in shrimp trawls in seagrass and hardbottom substrates of Biscayne Bay between 1997 and 2000 (Chapter 2), it only ranked 39th by abundance among the ichthyofauna of seagrass beds in Panama and Gulf of Mexico (Weinstein and Heck Jr. 1979), and it has not been collected in Bermuda since 1929 (Smith-Vaniz et al. 1999). *Nicholsina usta* has also been collected in 18-50 m depth waters off the coasts of Africa, e.g., Guinea (Randall 1983), and Mauritania (Gushchin and Girardin 2000), where it is considered a rare fish. Because of its seagrass association, many fish surveys conducted on coral reefs do not list it, e.g., Lang (2003).

Higher herbivore numbers and biomass in the southern and eastern reefs could be partially explained by factors related to biogeography (e.g., continental vs. insular sites), and environmental conditions (e.g., depth, water temperature seasonality, open ocean swells) (Kramer et al. 2003). Other expected factors, such as coral density and partial mortality indicators, did not show significant effects. The ability of *Sparisoma* and *Scarus* to share food resources (McAfee and Morgan 1996), and to physically overlap their use of space (Overholtzer and Motta 1999), may explain in part the high densities of this family in reef flats and surrounding areas (Table 1.5). That sharing ability could be attributed to differences in buccal musculature (Bellwood and Choat 1990, Bullock and Monod 1997), cephalic osteology (Bellwood and Choat 1990), and teeth morphology (Simoes and Andreucci 1982,1983), resulting in different feeding habits. The sheer number of species, total biomass, total abundances, densities, and frequency of occurrence shows their importance in the tropical reef ecosystem.

Local fishing pressure has an influence on the distribution and relative proportions of feeding guilds (Hay 1984a, Jackson et al. 2001b, Kramer 2003), but predictions and explanations found in the literature are contradictory. Areas with decimated abundances of top predators (e.g., by overfishing), or other grazers (e.g, mass mortality of sea urchin, *Diadema antillarum*), may feature a disproportionate size on the herbivore fish component. For instance, experiments demonstrated that in moderately and lightly fished Caribbean reefs, sea urchin densities are lower, and grazing by herbivorous fishes decreased with depth; the opposite trend was observed in heavily fished reefs (Hay 1984a). On the contrary, Jackson et al. (2001b) suggested that fishing pressure on coral reef and seagrass communities resulted in decreased abundances of grazing taxa, including invertebrates, fish, manatees, and sea turtles.

In Jamaica, scarids dominated the fish community in terms of biomass (53% of the top 8 families, or 0.67 kg 100 m^{-2}), and numbers (17 fish 100 m^{-2}, ranging 3 to 47 fish 100 m^{-2}) in reefs where the top predators were 0.2 – 2.2 fish 100 m^{-2} (Klomp et al. 2003). However, despite that juvenile stages of *Sc. iseri* and *Sp. aurofrenatum* were relatively abundant (10 and 4 fish 100 m^{-2}, respectively), the scarcity of terminal males was notable (Klomp et al. 2003). The authors attributed this condition to either selective fishing of recently transformed larger terminal males, or the lack of females reaching the genetically pre-determined size threshold to change sex. Furthermore, a mean size smaller than other areas of the Caribbean Basin was observed for scarids and for commercially important predatory species, such as groupers, snappers, and grunts. Smaller average size, of course affects the total fish biomass on a reef. Thus, when assessing the condition of a reef fish community, the relative abundances of the guilds may not be a good indicator of the true status.

Relative abundances of Caribbean scarid early stages display high temporal variability, with interannual, seasonal, and lunar cycles overlaying site-specific differences. Although information on abundances of parrotfish eggs was not found in the published literature, their larval stages usually were among the top-ranking families, sometimes with diverse sampling techniques.

Scarids ranked among the top 10 in occurrences and numbers in Caribbean-wide ichthyoplankton surveys in 1972 and 1973 (Richards 1984). The larval stages were abundant both nearshore and offshore, ranging from 11 to >100 larvae 10 m^{-2}, with seasonal variations (Richards 1984). In Barbados, ichthyoplankton assemblage composition was relatively consistent between 1991 and 1992, and parrotfish larvae ranked among the top 5 families captured by light traps, despite a 35% decrease in overall abundance of larval *Sp. viride* from 1991 to 1992 (Sponaugle and Cowen 1996). During 1995-1996, scarid larvae represented 0.33 to 6.04% of the larval fishes sampled with depth-stratified oblique tows, across a neritic-oceanic gradient in Puerto Rican waters (Ramírez-Mella and García-Sais 2003). Their abundances ranged from 0.47 to 3.50 larvae 100 m^{-3}, peaking at the shelf edge and the nearest oceanic contour (13 and 17 Km offshore, respectively). In the Florida Keys, parrotfish was the second most abundant family, representing 14.4% of all larvae collected with nighttime neuston tows, during summer 2000 (Sponaugle et al. 2003).

Concerning smaller scale temporal variability, larval supply of *Sp. viride* displayed lunar cycles, peaking on the 7th (1991) to 10th (1992) day after the full moon (Sponaugle and Cowen 1996). Consistent with these findings, scarid larvae of the Panamanian Caribbean reefs were nearly absent in light traps deployed around new moon, in spring months of 1997-1998 (Wilson 2003). Their absence can be explained by the timing of the sampling with respect to the lunar cycle and the season.

Recruitment cycles, peaks and spatial distributions have not been thoroughly studied in Atlantic parrotfishes. Scarids settle to the reef as 10 mm SL (~11-12.5 mm TL) immature females (Choat and Robertson 2002). Juveniles live on complex bottoms at 4-12 m depth (DeLoach 1999). AGRRA surveys found recruits and juveniles (≤3 cm TL) of *Sp. aurofrenatum*, *Sp. viride* and *Sc. iseri* to be the three most dense and most frequently sighted scarids (Table 1.5) in the Quintana Roo reefs, Mexico, between June and August 1999 (adult phase of the same species also ranked on the top five Caribbean-wide, as discussed above) (González-Salas et al. 2003). Meanwhile, *Sp. radians* and *Sp. atomarium* juveniles were seen only 10% of the times. No other seasons were sampled to assess temporal variability.

1.4 Ecological roles and behavior of parrotfishes in Caribbean reefs as grazers, bioeroders, and prey

Because of their ubiquity and abundance, scarids play multiple ecological roles on coral reefs. They act as a trophic link between producers and predators (Choat 1991), and as major bioeroders (Bellwood 1996a,1996b). It has been suggested that herbivory by fishes is more important than sea urchin grazing in the Caribbean (Hay 1984a). As many as 9 kg of carbonates m^{-2} y^{-1} can be eroded by scarids in ecosystems like the Great Barrier Reef (Kiene 1988), although no annual estimate is available for the Atlantic species. Three feeding modes, namely, browsing, scraping, and excavating (see Table 1.2 for definitions) have been identified for parrotfish, with consequently different ecological, and biosystematic outcomes (Bellwood and Choat 1990, Bellwood 1994, Bullock and Monod 1997, Bernardi et al. 2000).

1.4.1 Herbivory

Scarids feed diurnally (Choat and Robertson 1975, Robins et al. 1986, Claro 1994, Nagelkerken et al. 2000a) on filamentous, encrusting algae growing on the corals, turf (i.e., epilithic algae), sometimes scraping or excavating the coral surface and the coarse sediment (Bellwood and Choat 1990, Bellwood 1994, McAfee and Morgan 1996, Bernardi et al. 2000). Then, the fish grind the turf and encrusting algae with their pharyngeal teeth (Claro 1994). Caribbean parrotfishes are herbivores that include food items other than vegetation, such as sponges and other invertebrates. Macroalgae found in the Caribbean scarid diet include *Halimeda* spp., *Dictyota* spp., and infrequently *Udotea* spp, *Penicillus* spp. (McAfee and Morgan 1996), while manatee seagrass, *Syringodium filiforme*, is a major component in the gut content of *Sc. guacamaia* (DeLoach 1999). The long-heralded importance of turtle seagrass (*Thalassia testudinum*) for the Caribbean seagrass-dwelling scarids (Cervigón 1994, McAfee and Morgan 1996) is under revision. Recent isotope analyses showed that *Cryptotomus, Nicholsina*, and *Sparisoma* spp. feed on epiphytes (filamentous algae), rather than the seagrass blades (Nagelkerken and van der Velde 2004a), although *N. usta* is a bottom feeder with a diet consisting of hermit crabs, sea urchins, and xanthid crabs ranking as the three top food items (Gushchin and Girardin 2000). Other food items include: sponges (Randall 1967, Wulff 1997, Dunlap and Pawlik 1998, DeLoach 1999), thin layers of detritus and diatoms on the bottom, eggs of sergeant major, *Abudefduf saxatilis* (DeLoach 1999), the sand surface, and feces of other reef species (Bellwood 1994). The larger species can take gouging bites from living coral (e.g., *Porites asteroides, P. divaracata, Montastraea* *annularis*) and hydrozoans (e.g., *Millepora alcicornis*) (Gygi 1975, Miller and Hay 1998, DeLoach 1999), or dead coral and associated algae (McAfee and Morgan 1996).

Most parrotfishes eat the same food items, but the proportions of each type of food differ among species (McAfee and Morgan 1996), with some adult parrotfish being more generalist and other specialists. For example, *Sp. aurofrenatum* has a broad diet including seagrasses, and micro- and macroalgae (*Halimeda*, *Udotea*, *Sargassum*) attached to dead coral (McAfee and Morgan 1996), as well as sponges, crabs, brittle stars and sea urchins (DeLoach 1999). *Scarus iseri* bites algae associated with smooth eroded coral, almost exclusively (McAfee and Morgan 1996), while *Sp. viride* feeds on epilithic, crustose, and endolithic algae excavated from coral substrates (van Rooij et al. 1995b, 1996b).

On the other hand, juvenile diets are consistent among most species. *Scarus iseri, Sp. aurofrenatum*, *Sp. chrysopterum*, *Sp. rubripinne*, and *Sp. viride* scrape filamentous microalgae from coral substrates (McAfee and Morgan 1996). Ontogenetic diet shifts are related to habitat shifts, because parrotfishes have been observed to eat mainly the commonest food items in a given habitat (McAfee and Morgan 1996).

There is an ongoing debate regarding corallivory by Caribbean parrotfishes. Depending on the site conditions, scarids have been reported both to not feed on live coral or small coral recruits (Birkeland 1977, Hay 1984a), and to damage juvenile corals (Hay 1984a, Miller and Hay 1998). *Sparisoma viride* and *Sp. aurofrenatum* can consume more than half of transplanted fragments of the coral *Porites divaracata* within two days, commonly bite *P. porites*, and *Siderastrea radians*, but neglect *Manicina* sp. and *Cladocora arbuscula* in the Florida Keys (Miller and Hay 1998). Although high frequency of parrotfish bites on coral heads have been reported in Flower Garden Banks National Marine Sanctuary (Pattengill-Semmens and Gittings 2003), other corallivorous taxa, such as tetraodontiforms (filefish, puffers) may be the actual source of the bites (Jayewardene and Birkeland 2006).

Scarids reach abnormally high grazing intensities in reefs with decimated piscivore abundances (Miller and Hay 1998), supporting the observation of the effects of overfishing on herbivore fish numbers discussed in section 1.3. A measure of grazing intensity can be obtained by the combination of grazing rates (number of bites per unit time, number of forays by unit time), and amount of matter consumed (Bruggemann et al. 1994a, 1994b). Factors influencing grazing rates in Caribbean reefs include abundance and size structure of the grazer's population, time of day, depth, presence of other competitors, herbivorous fish biomass, and reef complexity, but the relative effects of each factor vary among studies, locations and season (Hay 1984a, Lewis 1986, Hay et al. 1989, Bruggemann et al. 1994a, 1994b, 1994c, Schmidt 1997, Miller and Hay 1998, Nagelkerken and van der Velde 2004a, Paddack et al. 2006). In the Florida Keys, the estimated average grazing rates is 43 bites 4 m^{-2} 10 min^{-1} (range 5-101) for 11 scarid species combined (Schmidt 1997), and the proportion of algal production consumed by the herbivore fish guild was lowest in patch reefs (31-51%) and highest in high relief reefs (77-113%) (Paddack et al. 2006).

The role of grazing parrotfishes in defining the community structure of tropical reefs has been studied extensively. In Jamaican reefs, scarids and acanthurids became the most important grazers after the demise of *Diadema* populations (Klomp et al. 2003). Moderate grazing may limit the growth of marine plants in reef ecosystems, thus providing favorable conditions for settlement and growth of algae and invertebrates, especially coral (Ogden and Buckman 1973, Glynn 1990, Miller and Hay 1998). High feeding rates sometimes produces bare zones (halos or Randall zones) surrounding reef patches (Glynn 1990). Heavy grazing could be a contributing factor for low abundance of sessile invertebrates on open reef surfaces, due to direct predation and incidental damage, thus leaving sunlit substrates to be colonized by zooxanthellate corals and plants. Also, herbivory restricts the formation of algal ridges by coralline algae to areas where severe wave action keeps parrotfishes from destroying them (Lewis 1986).

1.4.2 Bioerosion

In tropical reefs, removal of material by living organisms, or bioerosion, is carried out mostly by invertebrates (e.g., sponges, bivalves, sea urchins), and fishes (Bellwood and Wainwright 2002). Scarids act as major bioeroders and sediment producers (Bellwood and Choat 1990, Bellwood and Schultz 1991, Bellwood 1996a,1996b). Their pharyngeal teeth are designed to crush coralline algae, coral fragments, and other food items (Schultz 1958), while their musculature show adaptations to specialized herbivorous regimes (Bullock and Monod 1997). Carbonates are crushed by the surfaces of the toothed lower and upper pharyngeal plates, and then swallowed (Liem and Greenwood 1981). Their pharyngocleithral joint (cf. section 1.1) is designed to smoothen the jaw movement, prevent jamming, and to enhance the biting force.

Scarid bioerosion may modify reef topography by preferential grazing of rugose substrata, reducing the overall rugosity (Bellwood 1994). This habitat modification may be a factor determining microhabitat structure of reefs, as well as their benthic flora and fauna. Parrotfishes have the ability to replace the worn-out coalesced surfaces of their teeth (Simoes and Andreucci 1982,1983), which allows them to cause bioerosion throughout most of their lifespan. It must be noted that only excavators and a few large scrapers remove significant amounts of live coral (Bellwood and Wainwright 2002), which gives them a disproportionate importance as bioeroders. While all the Caribbean *Scarus* spp. are scrapers (Table 1.2), some large species, such as *Sc. guacamaia,* and *Sc. vetula* occasionally produce scars (Bellwood 1994). Reportedly, all *Sparisoma* spp. behave as browsers in seagrass habitats, even the eastern Atlantic species, and turn to an excavating feeding mode when in coral reef habitats (Bernardi et al. 2000).

In areas where wave action is negligible, such as the Western Atlantic reefs, parrotfishes are among the major producers of sand (Fischer 1978). In Barbados, an estimated that 400 ± 50 kg of $CaCO_3$ were annually removed from the solid reef by parrotfishes (Scoffin et al. 1980). Bioerosion rates of up to 7 kg $CaCO_3$ m^{-2} yr^{-1} that declined with depth have been reported for the two most abundant parrotfishes in Bonaire, *Sp. viride* and *Sc. vetula* (Bruggemann et al. 1996). *Sparisoma viride* causes significant bioerosion and new sediment production, while the other species only recycle old sediment (Frydl and Stearn 1978, Bruggemann et al. 1996). Furthermore, this single species is considered a geologically significant agent in the transformation of coral reefs into sediments, since this parrotfish alone may excrete ~1.2 m of uncompacted sediment per 10,000 years in the coral reefs of Bermuda (Gygi 1975).

1.4.3 Scarid role as prey

The trophic role of parrotfishes as prey is scarcely reported in the literature for the Caribbean, especially considering their importance in the transfer of primary production to the higher trophic levels. Small parrotfish species are under predation pressure throughout their life cycle, while the larger species may be most vulnerable at younger developmental stages of their life cycle. Atlantic scarids were found in gut contents of nurse shark, purplemouth moray, barracuda, coney, rock hind, red hind, Nassau grouper, yellowmouth grouper, tiger grouper, yellowfin grouper, mutton snapper, schoolmaster, cubera, and dog snapper in the Virgin Islands (Randall 1967). Parrotfish accounted for 20 to 57% of the diet of bar and yellow jacks in Cuba (Claro 1994). They are also an important food item for marine birds, such as the doubled-crested cormorant in Biscayne Bay, comprising up to 21.9% by weight and 20.5% by number of food samples obtained by regurgitation (Cummings 1987). In fact, *Sp. radians*, a small species, ranked as the 4th most abundant species in the cormorant's diet (5.3% by weight and 5.7% by number), while other *Sparisoma* spp. and *Scarus* spp. were a minor part of their diet. Parrotfish abundance in food samples reflected their availability in the bay waters rather than active selection by the cormorant (Cummings 1987).

Vulnerability of spawners and their products is not well documented, and the determining factors vary with location and spawning strategies. Predation by piscivores on spawning adults of scarids and other reef fishes has rarely been observed in Puerto Rico (Colin and Clavijo 1988), regardless of pair- or group-spawning activity. Mackerels (*Scomberomorus regalis*, and *S. cavalla*), and a lizardfish (*Synodu*s sp.) were observed attacking *Scarus iseri* adults during their spawning rushes in Jamaica (Colin 1978). However, low visibility may decrease the probability of observing predation attempts, and their outcomes. Spawning products are important food source for two types of egg-predators: the "cloud predators", i.e., particulate plankton-feeders that locate a spawn cloud within seconds of its release, and the generalist zooplanktivores that feed in the reefs, including fish eggs (Colin and Bell 1991). Group spawners produce noticeable gamete clouds, so they would bring about higher activity by egg predators than for pair spawners. *Chromis cyanea* and *Clepticus parrae* reportedly feed on freshly spawned eggs of *Sc. iseri* in Jamaica (Colin 1978). On the other hand, surprisingly low overall levels of immediate predation on eggs were observed in Puerto Rico, probably because most planktivores are already well fed by the time of late afternoon spawnings, and despite the large abundances of potential egg predators (e.g., *Ocyurus chrysurus, Melichthys niger, C. parrae, C. cyanea*) present while other reef fishes were spawning (Colin and Clavijo 1988).

1.4.4 Social and circadian behavior

Atlantic parrotfishes display an enormous flexibility in their socio-sexual organization (see section 1.2.4), reflecting a high plasticity for adaptation to local environmental conditions (van Rooij et al. 1996a). The wide range of social behaviors includes loose aggregations or transient small schools, feeding aggregations, small and large mixed interspecific foraging schools (both within and outside family taxon), harems led by territorial TPs, complex social systems with up to three classes, and others. For example, *Sc. iseri* is one of the most sociobiologically versatile scarids (Table 1.3) (Winn and Bardach 1960, Winn et al. 1964, Ogden and Buckman 1973, Colin 1978, Robertson and Warner 1978, van Rooij et al. 1996a, van Rooij et al. 1996b, de-Girolamo et al. 1999, DeLoach 1999).

Interfamily schools vary in size and function (Colin 1978), and require a complex set of communication skills. Small (~dozens) roving bands of *Sc. iseri* mixed with doctorfish (*Acanthurus chirurgus*), blue tang (*A. coeruleus*), goatfishes (Mullidae), hamlets (e.g., *Hypoplectrus puella*, *H. indigo*) remain stable for several months, with clown wrasses (*Halichoeres maculipinna*) occasionally joining the foraging groups (Colin 1978). Large numbers of *Sc. coelestinus* and *A. coeruleus* scraping filamentous algae off reef rocks allow these grazers to overcome the territorialist behavior or damselfishes (Colin 1978, DeLoach 1999). This strategy has also been suggested for the large schools of *Sc. iseri* (Colin 1978).

Scarus iseri displays a unique ethological trait: several individuals may share a territory, thus displaying group territorial behavior. However, group members are not related to each other (i.e., no kin selection), nor are they sharing parental care (Clifton 1989). The adaptive value of such behavior is not based on the usual indirect-reproduction benefit of kin selection, but rather relies on alternative benefits: it allows larger, and/or socially dominant individuals to spend less time in defense and food searching, so they feed faster than solitary fish or roving groups; thus, larger females can mature more rapidly, and the smaller fish can advance faster within the hierarchy (Clifton 1989).

Scarid circadian behaviors show local particularities, but light intensity is the driving factor, rather than time of day (Bruggemann et al. 1994a). As diurnal fishes (Nagelkerken et al. 2000a), they become active about one hour after sunrise in Belize and Bonaire (Lewis 1986, Bruggemann et al. 1994a). However, timing of inactivity varies. In Belize, minimal counts of parrotfishes were reported a couple of hours before sunset (Lewis 1986), while continued feeding after sunset occurred in Bonaire (Bruggemann et al. 1994a). Parrotfishes dedicate 70-90% of their daytime to foraging, and their feeding activity peaks near midday (Bruggemann et al. 1994a). The rest of the daytime is invested in territorial behavior, courtship, spawning, or moving between resting and feeding grounds. Daily migratory behavior of scarids is described in section 1.5 below.

Once in their resting grounds, parrotfishes stay on the bottom at night, leaning against rocks, coral, shells, or hidden under boulders, displaying a quiescent sleep (Bruggemann et al. 1994a, DeLoach 1999), and a marked decrease in respiration rate (Winn 1955). *Scarus iseri*, *Sc. taeniopterus*, and *Sc. vetula* secret a cocoon or transparent, gelatinous sheath by the mouth that surrounds their body completely, extending several centimeters away from the skin (Winn 1955, Winn and Bardach 1960, Ogden and Buckman 1973, van Rooij et al. 1996b, DeLoach 1999). At the mouth, the mucus envelope has a fold with a little flap that moves in and out with the fish's breaths, while the expulsed water exits the sheath by an opening located behind the caudal fin (Winn 1955). The envelope was experimentally induced during daylight under anoxic conditions, darkened tanks (Winn 1955), and blindfolded specimens (Winn and Bardach 1960), separately. It has been suggested that this cocoon disguises the parrotfish's scent from night predators, or protects the fish against silt settling (Winn 1955, DeLoach 1999). This mucous material might be an important food item for some other organisms (e.g., substrate for bacteria). *Scarus guacamaia*, *Sc. coelestinus* and *Sc. coeruleus* and *Sparisoma* have been reported as non-cocooners, while *Cryptotomus roseus* displays the labrid-like behavior of burying in the sand, although might form a coccoon (DeLoach 1999). No data on *Nicholsina* were found regarding its nighttime habits.

1.5 Habitat use, home range, and daily migrations

Relatively little is known about the Atlantic parrotfishes' habitat use, microhabitat distributions, and movement patterns. These are aspects that could optimize management actions, such as the design of marine reserves.

It is apparent that most adult scarids feed, spawn, hold territories, and rest within less than 1 km^2 of area (Table 1.3). Parrotfishes, like many coral-reef dwelling fish, are reluctant to swim over large areas of bare sand. This behavior prevents them from constantly relocating to other areas, which is interpreted as a strong site attachment (Kramer and Chapman 1999). However, juveniles (< 10 cm TL) of *Scarus* spp. and *Sparisoma* spp. occupied a rocky artificial reef within 20 minutes of being constructed on a fishless, sandy substrate (Gratwicke and Speight 2005a). Thus, recently settled or recruiting stages seem more likely to colonize open spaces away from their point of origin.

Scarids may have evolved in seagrass habitats and moved onto the reef environment (Bellwood 1998). There is strong evidence that both social and breeding behaviors of Atlantic parrotfishes are closely tied with seagrass or reef substrate type (Streelman et al. 2002). In the tropical Americas, all six scarid species of the Eastern Pacific live on reefs (either coralline or rocky), compared to the 71% in the Western Atlantic (Robertson 1998); the non-reefal species are found on soft bottom, seagrass, algal beds, and pelagic habitats (Table 1.2). More recently, mangrove and seagrass biotopes have been deemed important nursery grounds or biomass enhancers for some Caribbean scarids. For example, *Sc. guacamaia* juveniles were observed exclusively in the mangroves, and the adults were significantly denser in near-mangrove reefs (Mumby et al. 2004). Also, a 42% greater biomass of *Sc. iseri* occurred in reefs near rich-mangrove areas compared to scarce-mangrove systems suggesting a high dependence of this species on mangrove or seagrass nurseries (Nagelkerken et al. 2002, Mumby et al. 2004). *Sparisoma chrysopterum* was seagrass substrate-dependent but not for mangrove, while the possible dependence of *Sc. coeruleus* on either of these nurseries is yet to be proven (Nagelkerken et al. 2002). Another important consideration is the plasticity of the species to inhabit few or many different biotopes. In Curaçao, *Sc. iseri* can be found in mangroves, seagrass beds, algal beds, channel areas, fossil reef notches and boulders, and coral reef. Conversely, *Sp. radians* was present in mangrove and seagrass, and *Sp. rubripinne* occurred in reef boulders and coral reefs only (Nagelkerken et al. 2000b).

Abiotic and biotic factor interactions, including substrate type (cf. Table 1.2), habitat complexity, predation, and competition reportedly influence abundance of Atlantic parrotfishes. However, studies identifying the environmental variables are consistent only to certain extent, and also show contradictory conclusions. For example, in British Virgin Islands, adult *Sc. vetula*, *Sc. iseri*, *Sc. taeniopterus*, *Sp. rubripinne*, and *Sp. viride* preferred rugose areas on the reef; *Scarus* juveniles and *Sp. aurofrenatum* were found in moderately rugose areas between bay and reef biotopes, and *Sp. radians* was a bay dweller preferring low-rugosity substrates (Gratwicke and Speight 2005a). While positive correlations between adult densities of *Sc. iseri* and substrate rugosity in Belizean reefs confirmed Gratwicke and Speight's findings (Mumby and Wabnitz 2002), *Sp. chrysopterum* and *Sp. rubripinne* did not show a significant correlation with rugosity in Belize. Experimental manipulations in the Bahamas demonstrated that biotic factors can interact with habitat complexity in determining changes of densities of adult *C.*

roseus, *Sp. atomarium*, *Sp. aurofrenatum*, *Sp. chrysopterum*, *Sp. viride*, and *Sc. coeruleus* (Almany 2004). Parrotfish abundance in experimental blocks with predators and competitors increased significantly more in high-complexity reefs than in low-complexity areas. Alternatively, the increase in parrotfish numbers was small when predators and competitors were absent, regardless of the reef complexity.

Other factors and their interactions might be important, but they were not included in the analyses. Unfortunately, no other studies statistically correlating parrotfish distributions to physical factors in Atlantic waters were found in the literature. The biogeographic studies described in section 1.1.2 only partially address the ecology of their movement. Home range and ontogenetic changes in the use of habitat have been studied for few parrotfishes (Ogden and Quinn 1984), while territoriality is better understood for most species (Table 1.3).

A home range consists of a specific area where an animal conducts 95-99% of its usual activities, but it differs from a territory in the lack of defense behavior towards intruders (Kramer and Chapman 1999). Shape and size of parrotfish home ranges are highly variable, but the existence of preferred sites has not been considered. Home ranges of 179-2020 m^2 have been reported for *Sp. cretense* (de-Girolamo et al. 1999). However, foraging ranges and diel shifts in habitat use, both important considerations when estimating home ranges, are poorly understood for most species (Table 1.5). In many cases, feeding grounds are apart from sleeping sites and from spawning grounds some 250-300 m away (cf. Table 1.5 for sources). During daytime, *Sc. iseri* was found on channel and boulder reefs, seagrass, and mangrove, but at night it was scarce or absent in those biotopes (Nagelkerken et al. 2000a). Instead, *Sp. chrysopterum* used boulder and channel reef at all times, mangrove and seagrass during daytime, and notched reefs and algal beds at nighttime only (Nagelkerken et al. 2000a). Parrotfish tend to follow traditional routes to move to and from the nocturnal resting areas to the feeding grounds. Under experimental conditions, the daily migrations of *Sc. coelestinus* and *Sc. guacamaia* between resting caves and feeding grounds were oriented by the sun, and that these fish were able to compensate for the sun's daily movement (Winn et al. 1964). This ability might be the result of a combination between genetically determined sun-orientation behavior, visual cues, and learning directions (Winn et al. 1964). Besides that study conducted in Bermuda, no other work has addressed the guiding mechanisms for parrotfish migrations (Ogden and Quinn 1984).

Ontogenetic shifts of habitat have been observed in *Sc. guacamaia* (Mumby et al. 2004). Juveniles and smaller IPs of this species are found among the prop roots of mangroves along the shores of Biscayne Bay, Florida, but not on the reefs where the larger adults and TPs are present (Pers. Obs.). *Sparisoma chrysopterum* may present a similar life-stage migration from seagrass beds to adjacent reefs (cf. Chapter 2). Habitats of juvenile *Sc. coelestinus* have not been described in the literature.

In summary, habitat use, behavior, and speciation are closely linked in the family Scaridae. Seagrass, mangrove, and reef habitats are fundamental in their ecology and evolution. Ontogenetic and diurnal habitat shifts, niche partitioning, and territoriality influence local distributions of parrotfishes, but specific factors determining the ultimate parrotfish spatial distribution are yet to be elucidated. It is still under debate whether the primitive form of this taxon was a seagrass dweller, and part of the answer lies on the understanding of the biosystematic relationship with the other Labroid groups.

1.6 Growth and aging of scarids

Body growth curves are important in order to establish the timing of events and characteristics of the life cycle of any organism, and growth parameters play a role in fisheries management, including age at first maturity, age at first capture, ontogenetic habitat shifts, longevity, and natural mortality at age. For Atlantic parrotfishes, several population parameter estimates necessary to assess the status of the stocks are unavailable or questionable. Some species are reported to display an astoundingly high adaptive plasticity in terms of population structure, social behavior, and growth parameters, e.g., *Sp. viride* (van Rooij et al. 1996a), and *Sp. cretense* (Lozano and González 1993). Unfortunately, taxonomic issues superimposed on local variability in growth rates, maximum size, and other characteristics only add to the complexity in this family. For instance, *Sc. iseri* has maximum sizes of 17-20 cm in Panama (Ogden and Buckman 1973, Robertson and Warner 1978) and the Florida Keys (I. Clavijo. 2001. Pers. Comm.). These maximum lengths are smaller than those reported in FishBase[11]. A misidentification issue with *Sc. taeniopterus* is a likely explanation, but it also could be due to intraspecific differential growth rates or mortality rates that have not been analyzed.

Growth studies for Atlantic parrotfishes are scarce, partly due to the minimal economic value of these species (Bohnsack et al. 1994, Claro 1994). Relatively little information on growth parameters has been published, and most of the estimates provided in FishBase might be questionable given the large differences in their values. The wide array of techniques applied to determine body growth in scarids make

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[11] http://www.FishBase.org

comparisons difficult. Significant problems involved in the interpretation of the scarid otoliths have been reported by many authors (Lozano and González 1993, Fowler 1995), thus the use of alternative aging approaches. Growth rates for *Sc. coeruleus, Sc. guacamaia, Sc. vetula, Sp. chrysopterum, Sp. rubripinne,* and *Sp. viride* were computed from tag-and-recapture data in the Virgin Islands (Randall 1962), though the study did not provide any von Bertalanffy parameters (Table 1.6). Cleithrum bands outperformed operculum and hyomandibular bone marks as standard to assess growth rates in *Sc. iseri* (Warner and Downs 1977), but the study produced no parameter estimates. Scale studies for *Sp. cretense* in Greece (Petrakis and Papaconstantinou 1990), and length-frequency distributions for this same species in the Canary Islands (Lozano and González 1993), were two alternative approaches due to the unsuccessful attempts to use otoliths (Lozano and González 1993). Both studies rendered comparable estimates of growth coefficient for *Sp. cretense* populations from opposite sides of the Mediterranean, but different maximum lengths, suggesting certain degree of local variability probably accounted for by fishing pressure or adaptive variation.

Despite some difficulties, otolith readings from parrotfish are a valid approach for aging some species. Studies done on Indo-Pacific parrotfishes considered their otolith macrostructure interpretable for annual and daily growth (Lou 1992, Lou and Moltschaniwskyj 1992, Lou 1993, Fowler 1995, Choat et al. 1996). With the exception of aging studies on *Sp. aurofrenatum* (Miranda 1981, Choat and Robertson 2002), *Sp. atomarium*, *Sp. chrysopterum*, *Sp. rubripinne* (Choat and Robertson 2002), and *Sp. viride* (Choat et al. 2003), this literature search found that most of the otolith studies for the Caribbean scarids were unpublished, performed on very few specimens, or lacked validation until the first half of this decade. Unfortunately, vast differences among published parameter estimates of the von Bertalanffy growth model render the estimates unreliable. For example, maximum length estimates, L_∞, of *Sc. iseri* vary 2.5-fold, and K of *Sp. aurofrenatum* is more than three times higher in one source than other (cf. Table 1.6). The sources of that variation might be the methods used to compute the estimates, actual geographic factors or demographic characteristics of the populations.

Geographic and sex-specific variations of growth patterns in parrotfishes have been found by otolith studies (Choat et al. 2003, Munday et al. 2004), but contributing factors remain poorly understood. A comparison of *Sp. viride* otoliths from four Caribbean localities, rendered inconclusive results on whether differences among these populations were related to fishing pressure, latitude or locality (Choat et al. 2003). Indo-Pacific parrotfishes have shown sex-specific growth patterns (Munday et al. 2004), adding to the complex patterns in this taxon.

Lifespan of the Atlantic species is short to medium (3-9 years, Table 1.6), compared to the longevity reported for their Indo-Pacific counterparts and other Atlantic herbivores, such as surgeonfishes (10-37 years) (Choat and Robertson 2002). However, not all species conform to the expected maximum size vs. growth rate patterns in the same manner. While *Sp. atomarium*, a small species, displays a shorter longevity (3 years) with a higher growth coefficient (K), *Sp. chrysopterum* seems to grow much faster through its 4-5 year lifespan, despite its lower K and larger size. Growth coefficient estimates ranging from 0.16 to 1.8, along with maximum lengths of 110-610 mm (TL), indicate widely different growth patterns within Sparisomatinae. Two additional problems are the existence of different reported estimates for life history parameters of some species, and the total absence of data for others. For example, longevity of *Sp. cretense* has been estimated at 5, 8, and 9 years by different authors (cf. Table 1.6), and at the same time, lack of information on the growth curves of the largest Caribbean scarines prevents any further within-family comparison.

In summary, a large variation in growth parameter estimates of Atlantic scarids may have two sources. The first one is the local intraspecific adaptability of growth patterns, which is likely in this family (Choat et al. 2003). The second explanation might be methodological, related to the use of many different approaches to calculate such parameters, or sampling limitations. Once the improvements of otolith techniques minimize the uncertainty of the results, it will be possible to conduct aging studies in different regions of the parrotfish distribution. Then, the occurrence of geographic variation of growth patterns can be assessed, and this important knowledge will be available for the management of this resource.

1.7 Conclusions

This review has detected important information gaps for Atlantic parrotfishes. Despite their widely recognized high abundance and ecological importance in tropical and subtropical reefs, most of the Atlantic species have been given little attention because of their small economic value and a few unsolved taxonomy issues. Each species has a unique combination of feeding habits, bioerosion and grazing effects, habitat use, social behavior, and reproductive strategies. However, species patterns are obscured by the tendency to pool observations on different parrotfishes to overcome taxonomic uncertainties, especially for the younger stages. One of the first steps needed is the resolution of the biosystematic status of life phases, color morphs, and species. This knowledge must be complemented with the understanding of the genetic, phenotypic, ecological, and behavioral variability across their distributional ranges. Preliminary but incomplete descriptions of distinctive characteristics for some juvenile phases are available (Böhlke and Chaplin 1993) but further refinements are yet to be published (D. Jones, unpubl. data; H. Molina-Ureña, unpubl. data). Diagrams of distinguishing features of juvenile stages of Atlantic parrotfish, similar to those of grunts, will be a highly valuable addition in future editions of field guides (Humann and DeLoach 2002).

This review favors the sympatric speciation of parrotfishes by ecological selective forces over the vicariant theory, notwithstanding some reservations. Evidence from genetics, more direct than fossil records, supports the functional morphology conclusions of a clear habitat-use selective pressure. A proposed longer evolutionary history of scarids better fits observations of the development of reef fish assemblages. Four caveats agree with Gasparini et al. (2003)'s critiques regarding the two-clade simplistic view and the ancestral condition of browsing. First, sympatric speciation is uncommon in highly specious taxa (Brooks and McLennan 1991), such as the scarid family. Second, reports of an African population of *N. usta* heavily feeding on mobile invertebrate (crustaceans, echinoderms) besides herbivory (Gushchin and Girardin 2000) may weaken the suggestion that browsing was the primitive form of parrotfish feeding, although whether this is a local adaptation is unknown. Third, while social behavior and certain reproductive characteristics generally follow the reef and seagrass lineages, there are exceptions (cf. sections 1.2.3, 1.2.4). Fourth, ontogenetic habitat shifts observed in

Florida populations include habitats other than seagrass and reefs, such as mangroves and open waters (cf. section 1.5 and Chapter 2).

Therefore, sexual selection is hereby proposed as a second selective force besides ecological segregation. This process is strongly associated with sexually dimorphic species (Brooks and McLennan 1991), and complex social and reproductive behaviors that characterize the scarids (cf. section 1.2.1). Another consideration is that, given the phylogenetic importance of habitat use in this family, this review suggests that habitat degradation, distribution and availability, e.g., fragmentation of reef, seagrass and mangrove habitats, coastal pollution, etc., will have evolutionary consequences that cannot yet be fathomed.

Understanding the importance of ecological and reproductive forces in the phylogenetic history of parrotfishes is fundamental to study the population dynamics of this taxon. Feeding modes are closely related to substrate type, and in combination with social structure and reproductive behavior, drive essential fish habitat requirements. These factors, in turn, must be considered when developing proper sampling designs to address conservation and management issues with an ecosystem-based approach.

Within the context of the shifting baseline syndrome (Pauly 1995), it is important to acknowledge the uncertainties about the original composition and structure of Western Atlantic reef ecosystems prior to fishing. In absence of significant numbers of large herbivores (manatees, and sea turtles), parrotfishes and surgeonfishes (Acanthuridae) became major grazers in Western Atlantic coral reef and seagrass habitats (Jackson et al. 2001b). Thus, the original coral reef community structure was quite different from today, and most of the evolution of the scarids has taken place under those unexploited conditions. The shift in species composition of the herbivore component in Caribbean reefs was especially drastic in the last two decades, after the last remaining abundant grazer of reefal macroalgae, the sea urchin *Diadema antillarum*, suffered mass mortalities (Jackson et al. 2001b). Research on Atlantic parrotfishes started during the second half of the 1900s, as did detailed ecological descriptions of tropical reef ecosystems (Jackson et al. 2001b, Pandolfi et al. 2003). Moreover, this work found that between 1941 and 1965, most parrotfish work dealt with physiology, ethology, and taxonomy. Peer-reviewed literature on reproduction, ecology, and abundance came later, in the 1970s. Given the relatively shorter longevity of Atlantic parrotfish species compared to other herbivorous fishes, those studies only cover 3-5 full generations of the long-lived scarids, and 10-20 of the short-lived species. That is insufficient time to assess the cause-effect relationship between this herbivorous component and the fast changing ecological conditions of the Caribbean reefs. The observed community structure may represent steps in the process of reaching alternate equilibrium states. More exploration in genetics, fossil deposits, and biogeography may provide a long-term evolutionary context.

Nevertheless, the value of the information on relative abundance, size-structure, and spatio-temporal variability of parrotfishes obtained in the last half of the 20th century is undeniable. Although incomplete, it is the closest to an operative baseline we have achieved. Recent developments in field gear and techniques (e.g., SCUBA, visual censuses, stable isotopes, water chemistry), robust multivariate and statistical methods, and computer power provide strong tools to study the forces driving habitat preference, feeding habits, grazing rates, reproductive strategies, and territorial behavior. The better we understand and predict the factors affecting these life strategies of parrotfishes, the better management and protection we can implement for the ecosystem as a whole.

Growth parameter values, and their geographic or ecological variability, are urgently needed for many different applications. Parameter estimates are required in order to obtain age-based stock assessments of parrotfishes for fisheries management. Abundance data lacking the age-size relationship can only provide limited information on the status of the populations. Predicting recovery rates, annual recruitment patterns, or age/size structure shifts after changes of environmental conditions require inputs from growth patterns. It is unknown if scarid abundance patterns and age structure have a cause-effect relationship with changes in macroalgal cover and seagrass die-offs. Grazing intensity is related to abundance and size (therefore, age) of herbivorous species.

Reproductive behavior, age at first sexual maturity, age at sex change, and factors influencing these processes in protogyneous species are fundamental considerations for fisheries management, but still are poorly understood for these taxa. No field data on reproductive strategies were found in the literature for *N. usta*, *Sc. coelestinus*, *Sc. coeruleus*, and *Sc. guacamaia*. As a component of the population dynamics, the reproductive strategies of the largest *Scarus* spp. require attention because despite their relatively low abundances, their trophic dynamics can be significant in certain reefs due to their greater biomass.

The best-known species are *Sp. viride* and *Sc. iseri* in terms of behavior, ecology, abundance patterns, and population dynamics. Both are characterized by their ubiquity rather than large biomass. *Sparisoma cretense* is also well known due to its commercial importance in the Mediterranean fisheries (Petrakis and Papaconstantinou 1990).

Information gaps in growth curves, distribution, ontogenetic patterns, and frequency of occurrence were greatest in *Sc. coelestinus*, *Sc. coeruleus*, and *Sc. guacamaia*, the large but uncommon species. The least studied is *Nicholsina usta*; its ecology and biology are still poorly understood. Aside from lacking commercial value in most Caribbean locations, the large numbers of this parrotfish in some seagrass habitats suggest that *N. usta* plays a major role as grazer in some locations, although this possibility has not been addressed in the literature for unknown reasons.

Three major information gaps on South Florida scarids were selected to address in this dissertation, and relate to essential fish habitat throughout their life cycle, body growth patterns, and effects of fishing and habitat protection on their local demography. Other lines of research needed for such an important taxon in coral reef ecosystems include: relative roles of endocrine activity and social factors in sex change, reproductive cycles and territorial behavior; effects of endocrine disrupting chemicals in population dynamics; otolith ageing of maximum size individuals in different areas of the Caribbean; genetic and ecological connectivity of Caribbean populations; ontogenic migration patterns among adjacent substrate types, and empirical data on fishing effects on local and regional population dynamics.

Table 1.1: Taxonomic classifications of Labroid families and extant parrotfishes (Family Scaridae) found in the literature.

Source	A	B	C, D	E, F	G, H	I, J
Number of families		5	4	6	6	
Subfamilies	Sparisomatinae Scarinae			Sparisomatinae considered paraphyletic. No subfamily division	Sparisomatinae Scarinae	Sparisomatinae (seagrass clade) Scarinae (reef clade)
Number of genera: spp.	9: 80			10: 79 10: 80	9: 83 10: 90	
Comments		*Girella* first step of progressive series that ends with *Scarus*	Girellidae has a different pharyngognathy			*Sparisoma viride:* some features too similar to Scarinae

Sources:

A: Schultz (1958), B: Nelson (1967), C: Liem and Greenwood (1981), D: Kaufman and Liem (1982), E: Bellwood and Schultz (1991), F: Bellwood (1994), G: Nelson (1994), H: Parenti and Randall (2000), I: Bernardi et al. (2000), J: Streelman et al. (2002)

Table 1.2: Scientific names, common names, habitat and feeding modes Atlantic parrotfishes, geographically grouped. Feeding modes *sensu* (Bellwood and Choat 1990, Bellwood 1994): Br=Browser (removes pieces of epilithic algae, fragments of macroalgae and seagrasses with oral jaw teeth, without scraping or scarring the substrate). Sc=Scraper (removes material from the surface of the substrate with a non excavating bite that rarely scars the substrate. It feeds at high rates with no preference for habitat angle). Ex=Excavator (removes pieces of substrate during feeding, leaving distinct grazing scars. It feeds at low rates). Iv=invertivore (feeds mainly on invertebrates)

Substrate types: SG=seagrass beds, AB=algal beds, WB=weedy bottoms, SA=sand, MF=mudflats, CR=coral reefs, MG=mangrove, ES=estuary, RR=rocky reef.

SPECIES	COMMON NAME	OBSERVED HABITATS (SUBSTRATE AND DEPTH)	FEEDING MODE	SOURCE
		WESTERN ATLANTIC SPECIES		
Cryptotomus roseus (COPE, 1871)	Bluelip parrotfish	SG, AB, WB, SA, MF	Br	1, 2, 6
Nicholsina usta (Cuvier & Valenciennes, 1840)	Emerald parrotfish	SG, AB. Depth range shallow to 73 m	Br, Iv (crabs, sea urchins)	1, 2, 3, 6, 14
Scarus coelestinus (Cuvier & Valenciennes, 1840)	Midnight parrotfish	CR (home), SG (foraging)	Sc	1, 2
Scarus coeruleus (Bloch, 1786)	Blue parrotfish	SG, AB, CR	Sc	1, 15
Scarus guacamaia (Cuvier, 1829)	Rainbow parrotfish	MG/ES (juvenile), SG, AB (foraging), CR (adult)	Sc	1, 2, 13, 15
Scarus iseri (Bloch, 1789)	Striped parrotfish	CR (home), SG, AB (foraging) Depth range 1-24 m	Sc	1, 11, 12, 15
Scarus taeniopterus (Desmarest, 1831)	Princess parrotfish	CR	Sc	2
Scarus vetula (Bloch & Schneider, 1801)	Queen parrotfish	CR	Sc	2
Sparisoma atomarium (Poey, 1861)	Greenblotch parrotfish	SG. Depth range 15-75 m, often near drop-offs (35-55 m)	Br	2, 3, 6
Sparisoma aurofrenatum (Cuvier & Valenciennes 1840)	Redband parrotfish	SG, CR, SA, MF	Br, Ex	1, 2, 3, 6, 10, 15
Sparisoma chrysopterum (Bloch & Schneider 1801)	Redtail parrotfish	SG, CR, SA, MF, MGs	Br, Ex	1, 2, 15
Sparisoma radians (Cuvier & Valenciennes, 1840)	Bucktooth parrotfish	SG, MG Depth: shallow water	Br	1, 2, 3, 6, 15
Sparisoma rubripinne (Cuvier & Valenciennes, 1840)	Yellowtail (Redfin) parrotfish	SG, CR Depth: very shallow	Br, Ex	1, 2, 3, 6, 15
Sparisoma viride (Bonnaterre, 1788)	Stoplight parrotfish	CR, MG	Ex	1, 6, 10, 15
Sparisoma griseorubra (Cervigón, 1982)	Gray parrotfish	RR, CR Shallow		7

Table 1.2 continued

SPECIES	COMMON NAME	OBSERVED HABITATS (SUBSTRATE AND DEPTH)	FEEDING MODE	SOURCE
SOUTHWESTERN ATLANTIC SPECIES (BRAZILIAN ENDEMICS)				
Scarus trispinosus *(*Cuvier and Valenciennes, 1840)	Greenbeak parrotfish (bico-verde)	CR, AB, RR, SG Depth range: 1 - 30 m.		8
Scarus zelindae (Moura, Figuereido & Sazima, 2001)	Zelinda's parrotfish			8
Sparisoma amplum (Ranzani, 1842)	Reef parrotfish	CR, AB, RR Depth range: shallow to 30 m.		8
Sparisoma axillare (Steindachner, 1878)	Gray parrotfish	CR, AB, RR, SG Depth range: 1 - 35 m.		8
Sparisoma frondosum (Agassiz,1831)	Agassiz's parrotfish	CR, AB, RR, SG Depth range: 5 - 45 m.		8
Sparisoma tuiupiranga (Gasparini, Joyeux & Floeter, 2003)	Red parrotfish?	RR, AB Depth range: 5 - 20 m.	Sc	9
EASTERN ATLANTIC SPECIES				
Sparisoma cretense (Linnaeus, 1758)	Vieja, Mediterranean parrotfish	RR, SA, AB, SG. Depth range: shallow to 50 m.	Br	4, 5, 6
Sparisoma strigatum (Günther, 1862)	Parrotfish	RR	Br, Sc	6

SOURCES: [1] Opitz (1996), [2] Randall (1983), [3] Robins et al. (1986), [4] Petrakis and Papaconstantinou (1990), [5] Lozano and González (1993), [6] Bernardi et al. (2000), [7] Cervigón (1994), [8] de-Moura et al. (2001), [9] Gasparini et al. (2003), [10] Miller and Hay (1998), [11] Clifton (1989), [12] Humann and DeLoach (2002), [13] Mumby et al. (2004), [14] Gushchin and Girardin (2000), [15] Nagelkerken et al. (2000b)

Table 1.3: Reproductive and behavioral characteristics of the Western Atlantic parrotfish species. Column 2: “Length overlap” between color phases includes duration of the color changing process, and “Protogyny patterns” refer to monandry. Column 3 addresses sexual transformation strategies, where L_x = length at sex change, and F = fecundity estimations. Column 4 describes two components of sexual behavior, “Spawning patterns” and “Harem formation”. Column 5: Territory duration and size (m^2). Column 5: Spawning daily timing. Empty cells indicate information gaps. Species cited in phylogenetic order. See Glossary for definitions.

Notation: color phase: IP=initial phase, TP=terminal phase. Spawning strategy: PS=pair spawning, GS=group spawning, IN=interference, SA=spawning aggregation behavior, LS=lek-like system. Time of spawning: M=morning, A=afternoon, D=dusk

1	2	3	4	5	6
Species	Color phase length overlap (mm) {Protogyny patterns}	Length at sex change (L_x, mm) Fecundity (F)	Spawning modes Harems	Reproductive territory duration and size (m^2)	Time of Spawning
Cryptotomus roseus	Moderate {Monandric}	L_x: 61-64 SL (TP)	PS (TP+♀). No GS	(100s m^2)	A*
Sparisoma atomarium	4 SL (very little) {Monandric}	L_x: ND	PS (TP+♀) No GS Harems: strict	Permanent	A [e]
Sparisoma aurofrenatum	2 SL (very little) {Monandric}	L_x: 119-169 SL (TP)	PS (TP+♀), with IN. No GS [*, a, f]. Harems: strict, small *; size positively correlated to territory size[w]	Permanent (~100 m^2) [w]	A [e, f]
Sparisoma chrysopterum	63 SL (high) {Monandric; not all ♀ change sex}	L_x: 120-194 SL (IP, TP)	PS (TP+♀) No harems.	Temporary (~250, 324, ~500 m^2) [w]	A [e]
Sparisoma cretense	High size overlap [k]	F (# oocites per spawn) = $9.16 \times 10^{-8} * (SL)^{5.0954}$ (u)	Mostly PS. No GS Harems (1TP + 1-4 ♀) [k]	Breeding territories (189-to-587-m^2) [k] Home range: 179-2020 m^2 [k]	D [k]
Sparisoma radians	High {Monandric; not all ♀ change sex}	L_x ~63 SL (IP) ♂F $=8.9 \times 10^6$ sperm [s]	PS (TP+♀), IN, GS. Harems	Permanent [s]	A [e, s]

Table 1.3 continued

Species	Color phase overlap (mm) {Protogyny patterns}	Length at sex change (L_x, mm) Fecundity (F)	Spawning modes Harems	Reproductive territory duration and size (m^2)	Spawning timing
Sparisoma rubripinne	115 SL (very high)[*, a] {Monandric; not all ♀ change sex}	L_x: 143-260 SL (IP, TP)	PS (TP+♀). No GS (Panama)[*] GS (IPs), few PS (Virgin Islands)[a] No harems SA: 50-200 IPs, 46 cm maximum TL (St. John, U.S. Virgin Islands), March, 28 years[a, b, c]	Temporary (330-1400 m^2)[w]	A[a b, e]
*Sparisoma tuiupirang*a				Territorial males (~8 m^2)[h]	
Sparisoma viride	112 SL (very high)[*, p, r]. Transitional: 130-200+ SL ♂, no transitional gonads[*] ~176-180 SL[a] Color changes over 3-5 weeks[r] {Monandric; not all ♀ change sex}	L_x: 110, 199 SL (TP), ~3-week[e] F (# eggs): 10,000 eggs/spawning[v] 5,500 – 68,600 eggs/♀[t]	PS (TP+♀)[*, a], IN[r] Harem: size positively correlated to territory size[w].	Temporary[*] (≥300-529 m^2[p], 240-820 m^2[r], ~100-350 m^2[w]) Foraging ranges: IPs = 102-197 m^2, TPs = 69-360 m^2[r]	M[e, f, r] A[f]
Scarus iseri	Very low[*, q] Color change ~10 days. Transitional color: 140-153 SL a {Diandric (high % 1ary ♂)}	L_x: ~100 SL IP 2ndary ♂. Color changeover and sex change simultaneous.	PS (TP+♀)[*, a, f] GS: small groups IPs[*, a, f] Harem: size positively correlated to territory size[y]. SA: 100- ~500 IPs, 28 cm maximum TL (Jamaica, Puerto Rico), 19 years, summer and winter[b, c]	Territorial groups (TP + several ♀[n], or 1-8 adult ♀ and immature IPs[o]) Territories: 10-12 m^2[n], 2.8-19 m^2[o], 41-120 m^2[y],	A[b]

Table 1.3 continued

Species	Color phase overlap (mm) {Protogyny patterns}	Length at sex change (L_x, mm) Fecundity (F)	Spawning modes Harems	Reproductive territory duration and size (m^2)	Spawning timing
Scarus taeniopterus	Very low {Diandric?}	L_x: 173-200 SL all ♀, 215-265 SL all ♂	PS (TP+♀) m. No GS [*, m] Harems: TP + 3-5 ♀ [l, m]	Permanent (120-500 m^2) [m]	M [e,f,m] Ebb tide [m]
Scarus vetula	24 SL (low) {Diandric (Primary ♂ rare, both IP, TP)}		PS (TP+♀) [*, a], IN [*]. No GS[*, a], LS [x] Harem: small (3-4 ♀)	Permanent	M [e,f,m]

Sources: *, or unless otherwise noted Robertson and Warner (1978) [a] Randall (1963), [b] Colin (1996), [c] Domeier and Colin (1997), [d] Winn and Bardach (1960), [e] DeLoach (1999), [f] Colin and Clavijo (1988), [g] Colin (1978), [h] Gasparini et al. (2003), [i] Petrakis and Papaconstantinou (1990), [j] González and Lozano (1992), [k] de-Girolamo at al. (1999), [l] Winn et al. (1964), [m] Dubin 1981, [n] Ogden and Buckman (1973), [o] Clifton (1989), [p] van Rooij et al. (1996a), [q] Warner and Downs (1977), [r] van Rooij et al. (1996b), [s] Marconato and Shapiro (1996), [t] Koltes (1993), [u] González et al. (1993), [v] van Rooij et al. (1995b), [w] Mumby and Wabnitz (2002), [x] Clavijo (1983).

Table 1.4: Reported spawning months for Atlantic parrtotfishes, by locality.

Symbology: 1=Panama, 2=Venezuela, 3=Jamaica, 4=Puerto Rico, 5=U.S. Virgin Islands, 6=Bermuda, 7=Dry Tortugas (Florida), 8=Mediterranean, 9=Bahamas, *=opposite results on reproductive activity by different studies

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
C. roseus	1	1	1	1	1	1	1	1	1	1	1	1
N. usta	2	2	2	2	2	2	2	2	2	2	2	2
Sp. atomarium		1	1	1	1	1	1	1	1	1	1	1
Sp. aurofrenatum	1, 3, 4	1, 3, 4	1, 3, 4, 5	1, 3, 4, 5	1, 3, 4	1, 3, 4, 5, 6	1, 3, 4, 6	1, 3, 4, 5, 6	1, 3, 4, 6	1, 3, 4	1, 3, 4	1, 3, 4
Sp. cretense						8	8	8	8	8		
Sp. chrysopterum	1	3	1, 3	1	1	1, 6	6	6	3	1	1	
Sp. radians	1	1	1	1	1	1, 6	1, 6, 7	1, 6, 7	1	1	1, 4	1
Sp. rubripinne	1, 3, 5	1, 3, 5	1, 5	1, 5	1, 5	1, 5	1, 5	1, 5	5	5	3, 5	1, 5
Sp. viride	1, 3, 4	1, 3, 4	1, 3, 4	1, 3, 4	1, 3, 4, 5	1, 4*, 6	4, 6	1, 4, 6	1, 4	1, 3, 4	3, 4	3, 4
Sc. coeruleus	3											
Sc. coelestinus						6	6	6				
Sc. guacamaia						6	6	6				
Sc. iseri	1, 3, 4	1, 4, 5, 6	1, 4, 5, 6	1, 3, 5	1, 3	1, 3, 5, 6	1, 3, 6	1, 3, 4*, 5, 6	1, 4	1, 4	1, 4	1
Sc. taeniopterus	3, 4, 9	4, 9	3, 9	4, 9	3, 4, 9	9	9	4, 9	3, 4, 9	3, 4, 9	3, 4	3, 4, 9
Sc. vetula	1, 3, 4		1		3	6	6	5, 6				

Sources: Winn and Bardach (1960), Winn et al. (1964), Robertson and Warner (1978), Dubin (1981), Munro (1983), Colin and Clavijo (1988), Koltes (1993), Cervigón (1994), de-Girolamo et al. (1999).

Table 1.5: Density and habitat shifts of Western Atlantic parrotfishes in coral reefs. Habitat shifts are described as ontogenetic (O) or daily (D) events.

Species	Density Mean (SD, fish 100 m^{-2})	Locality	Habitat shifts: Ontogenetic (O) or Diel (D)
C. roseus	0 - 1.03 (0.26) fish 160 m^{-2} [d]	Brazil	
N. usta			
Sp. atomarium	0.48 [b] (juv) 0.16 (0.06) to 0.72 (0.15) [d*]	Quintana Roo, Mexico	
Sp. aurofrenatum	2.35 [a], 5.28 [b] (juv) 0.3 (0.7) to 3.3 910.5) [c] 4.8 (2.7) [f], 4 (juv) [f] 3.6 [g]	Quintana Roo, Mexico Costa Rica Jamaica Wider Caribbean	D: no diel migrations, sleeping grounds inside their diurnal territories [h]
Sp. axillare	2.10 (0.41) to 6.75 (0.66) fish 160 m^{-2} [d]	Brazil	
Sp. chrysopterum	1.04 [a] 0 - 1.5 (4.7) [c]	Quintana Roo, Mexico Costa Rica	Daytime grounds: boulder and channel areas, less in seagrass and mangrove. At night, rarely observed in any of those habitats [n]
Sp. cretense	0.17 (0.07) ♀, 0.05 (0.02) ♂ 300 m^{-2} [k] Nonterritorial: 2-3 fish 300 m^{-2} [k]	Mediterranean Sea	O: shallow (<8 m depth) for nonterritorial groups only; deep (>11.5 m depth) for territorial groups [k] D: sleeping grounds 5-17 m depth in sheltered sites [k]
Sp. radians	0.76 [b] 0 - 0.86 (0.16) fish 160 m^{-2} [d]	Quintana Roo, Mexico Brazil	

Table 1.5 continued

Species	Density Mean (SD, fish 100 m^{-2})	Locality	Habitat shifts: Ontogenetic (O) or Diel (D)
Sp. rubripinne	1.2 (1.8) to 7.8 (4.4) [c]	Costa Rica	
Sp. viride	1.88 [a], 1.69 [b] (juv) 1.2 (1.4) to 4.8 (5.6) [c] 1.7 (1.2) [f] 2.8 [g]	Quintana Roo, Mexico Costa Rica Jamaica Wider Caribbean	O: Recruits as 1-cm immature ♀, in reef. JP in high relief substrate 4-12 m deep. Maturing ♀ to shallow-water groups or harems [h]
Scarus coelestinus	0 - 0.2 (0.5) [c]	Costa Rica	
Sc. coeruleus			
Sc. guacamaia			O: JP, young IP in shallow areas and mangrove forest [m]. D: sleeping grounds in reef caves [h] shallow feeding grounds.
Sc. iseri	2.96 [a], 3.09 [b] (juv) 1.2 (3.7) to 14.2 (12.2) [c] 6.9 (11.7) [f], 10 (juv) [f] 3.8 [g]	Quintana Roo, Mexico Costa Rica Jamaica Wider Caribbean	D: sleeping grounds in deeper waters, using traditional routes to feeding grounds [h] Feeding and spawning grounds: ≤ 50 m^2 [o], ~300 m apart [j] Daytime grounds: boulder and channel areas, less in seagrass and mangrove. At night, rarely observed in any of those habitats [n]
Sc. taeniopterus	1.01 [a] 0 - 0.2 (0.5) [c] 0.6 (0.6) [f] 3.1 [g]	Quintana Roo, Mexico Costa Rica Jamaica Wider Caribbean	D: sleeping grounds in complex reef structures, ~250 m away from low-profile feeding grounds [h]

Table 1.5 continued

Species	Density Mean (SD, fish 100 m^{-2})	Locality	Habitat shifts: Ontogenetic (O) or Diel (D)
Sc. trispinosus	0.18 (0.06) to 9.72 (1.31) fish 160 m^{-2} [d]	Brazil	
	11.77 [e]	Brazil	
Sc. vetula	1.1 [g]	Wider Caribbean	
	One order of magnitude less abundant than *Sc. taeniopterus* and *Sp. viride* [i]	Puerto Rico	
Sc. zelindae	0 - 0.31 (0.8) fish 160 m^{-2} [d]	Brazil	
	1.48 [e]	Brazil	
Scaridae	2 (1.5) to 25 (13.4) [a]	Quintana Roo, Mexico	
	6.5 (6.5) to 28.5 (17.5) [c]	Costa Rica	
	7.8 (7.2) to 29.7 (12.8) [e]	Jamaica	
	8.1 (6), 2.5 (2) to 17.5 (13.5) [l]	Bahamas	
	Biomass [l] 1.5-3.8 Kg 100 m^{-2}	Bahamas	

Sources: [a] Núñez-Lara et al. (2003); [b] González-Salas et al. (2003), juveniles; [c] Fonseca and Gamboa (2003); [d] Ferreira et al. (2001); [e] Kikuchi et al. (2003); [f] Klomp et al. (2003); [g] Kramer (2003); [h] DeLoach (1999), [i] Colin and Clavijo (1988), [j] Colin (1978), [k] de-Girolamo (1999), [l] Kramer et al. (2003), [m] Mumby et al. (2004), [n] Nagelkerken et al (2000a), [o] Ogden and Buckman (1973)

Table 1.6: Von Bertalanffy growth parameter estimates, and growth rate estimates for Atlantic parrotfish species: growth coefficient (K), infinite length (L_∞), longevity (t_{max}), maximum weight (W_∞), and length at first maturity (L_m). Locality are indicated in the list of sources.

SPECIES	K	L_∞ (mm)	t_{max} (yr)	W_∞ (g)	L_m (S.E. range) (mm)	Monthly growth (mean, range) (mm)	Sample size (n): size range (mm FL)
C. roseus					<20 SL ♀[o]		
N. usta							
Sp. atomarium	1.828[a]	101 SL[a]	3[a]	222[b]	157 (117, 211) TL[c]		
		263 TL[c]			~<30 SL ♀[o]		
Sp. aurofrenatum	0.669[a]	178 SL[a]	7[a]	459.7[b]	150 FL[b]		
	0.2[b]	294 TL[b]			174 (152, 213) TL[c]		
					<90 SL ♀		
Sp. chrysopterum	0.627[a]	258 SL[a]	5[a]		239 (178, 320) FL[c]	12.3 (8.71-19.97)[d]	3: 155-182[d]
	0.782[b]	418 FL[b]	3.6[b]	1432[b]	235 FL ♀[m]		
					140 SL ♀[o]		
Sp. cretense	0.16[e]	389 TL[e]	8[e]	803[e]	213 TL ♀, 233 TL ♂[p]	3.3[e]	330: 148-307[e]
	0.177[f]	612 TL[f]	9[j]		120 TL ♀[q]		548: 175-510[f]
					160 to 170 TL ♀, 210 to 220 TL ♂[e]		
Sp. radians		211 TL[b]		94[b]	174 (152, 213) TL[c]		
					2.61±0.23 cm TL[n]		
Sp. rubripinne	0.811[a]	238 SL[a]	7[a]		160 FL[b]	8.8 (3.13-13.83)[d]	9: 175-266[d]
	0.584[b]	465-505 TL[b]	4.9[b]	2499[b]	129 (96, 173) TL[c]		
					220 SL ♀, 194 SL ♂[l]		
					160 SL ♀, 203-220 SL ♀[o]		
Sp. viride	0.458, 0.559[a]	357, 280 SL[a]	9, 7[a]		160 SL, 180 FL[b]	5.0 (3.53-7.74)[d]	3: 187-236[d]
	0.450, 0.963[b]	267 SL, 290 FL[b]		5748[b]	150 FL ♀[i]		
	0.45-0.82[g]	264-357 SL[g]	7-9[g]		170, 270 SL ♀[k]	2.5 (1.8-3.4)[g]	417: 38-456[g]
					205 FL ♀[m]		
					160-200 SL (♂ IP), 163 SL (♀)[r]		

Table 1.6 continued

SPECIES	K	L_∞ (mm)	t_{max} (yr)	W_∞ (g)	L_m (S.E. range) (mm)	Monthly growth (mean, range) (mm)	Sample size (n): size range (mm FL)
Sc.coelestinus							
Sc. coeruleus						7.1 (1.12-12.56) [d]	14: 188-313 [d]
Sc. iseri	1.235 [a]	117 SL (13.9 TL) [a] 366 TL [b] 90-130 TL (♂ IP) [r] 110-130 SL (♂ IP), 90-100 SL (♀) [r]	8 [a] 6? [h]	814 [b]	155 FL [b] 212 (158-284) TL [c] 135 SL ♂ [l]		
Sc. guacamaia							
Sc. taeniopterus		366 TL [b]		662 [b]	172 TL [b] 212 (158-284) TL [c]		
Sc. vetula					>140 SL ♀, 210-245 SL (♂ IP), 210-220 SL (♀) [r]	13.2 (10.75-18.36) [d]	3: 140-248 [d]

Sources: [a] Central Western Atlantic: Choat and Robertson (2002), [b] Central Western Atlantic: FishBase.org maturity link, [c] Central Western Atlantic: FishBase.org life-history tool, [d] Virgin Islands: Randall (1962), [e] Greece: Petrakis and Papaconstantinou (1990), [f] Canary Islands: Lozano and González (1993), [g] Bahamas: Choat et al. (2003), [h] Panama: Warner and Downs (1977), [i] Bonaire: van Rooij et al. (1996b), [j] Canary Islands: González et al. (1993), [k] Turks & Caicos Islands: Koltes (1993), [l] Virgin Islands: Randall (1963), [m] Puerto Rico: Figuerola et al. (1998), [n] Puerto Rico: Marconato and Shapiro (1996), [o] Panama: Robertson and Warner (1978), [p] Canary Islands: González and Lozano (1992), [q] Greece: de-Girolamo at al. (1999), [r] Bermuda: Winn and Bardach (1960).

Chapter 2: Seasonal and interannual habitat use by South Florida parrotfishes

2.1 Background

The high richness of parrotfishes reflects their importance in South Florida reefs in terms of number of species, total biomass, total abundances, densities, and frequency of occurrence (Chapter 1). However, the information gap analysis performed in the previous section concluded that species-specific information on habitat use, microhabitat distributions, abundance patterns, and temporal variability is limited for most Atlantic taxa.

As part of the approach applied to study South Florida parrotfish populations, the first research priority was species-specific Essential Fish Habitat (EFH, cf. Fig. I.1). Thus, this chapter addresses the shifts in habitat use in Biscayne Bay and the Florida Keys, Florida, that can be inferred from descriptive and assessment methods. It explores the working hypothesis that scarids undertake ontogenetic shifts in habitat use between the bay and reef tract and within each domain, under several alternative life cycle strategies. I expected a spectrum of species-specific relative importance of Biscayne Bay (BB) and the Florida Keys (FK) as main habitats, ranging from nearly exclusive BB dwellers to FK reef populations isolated from Biscayne Bay, with intermediate strategies of demographic connections between both domains, by means of ontogenetic, annual or seasonal migrations in either direction. This research focused on ontogenetic habitat shifts of South Florida scarids.

2.2 Materials and methods

2.2.1 Study areas

The study area comprised two domains: Biscayne Bay, and the Florida reef tract, at the south tip of the Florida Peninsula (Figure 2.1). The Biscayne Bay domain (Figure 2.2) was defined as the area located between Virginia Key and north of Long Arsenicker Key. It covers 386.23 km^2, and is divided into northern and southern portions by the Featherbed Bank that correspond to the central and southern bay *sensu* Lee (1975) and Campos (1985). The main substrate types are seagrass, sand, silt/clay, and hard bottom, with interspersed sponges, octocorals, and mangroves (Ault et al. 1999a, 1999b). During the study, mean bay-wide water temperature, salinity, and dissolved oxygen showed seasonal differences among spring (end of dry season, March and April), summer (wet season, August and September), and fall (beginning of dry season November) (one-way ANOVAs, $P<0.0001$) (Table 2.1). Spatial variation of these three physical parameters showed no significant cross-shelf (longitude as proxy), latitudinal, or depth-wise linear trends. However, ca. 30% of the increase in salinity could be explained by distance from the mainland shore during summer ($Sal = 65.992*(Long) + 5326.9$, $R^2 = 0.296$) and fall ($Sal = 58.032*(Long) + 4688.3$, $R^2 = 0.291$), and a 34% of the temperature decrease was linearly related to latitude during spring ($Temp = -7.9685*(Lat) + 229.16$, $R^2 = 0.345$). These three physical parameters were not linearly correlated to each other.

The Florida reef tract is 6 km wide, and extends ca. 240 km offshore of the Florida Keys. It is characterized by series of banks and channels, with coral reefs on top of 100,000 year-old reefs on the back reef zone and the seaward edge of the platform (Hoffmeister 1974).

Two fishery-independent datasets were used: bottom trawling with shrimp nets within Biscayne Bay and reef fish visual censuses (RVC) by divers on coral reefs in the Florida Keys.

2.2.2 Net trawling

Nighttime net trawls took place during eight cruises between 1996 and 2000, in three different seasons: spring (end of dry season, March and April), summer (wet months, August and September), and fall (beginning of dry season, November). A shrimp boat dragged two 10-mm mesh nets, each with a 3-m wide by 1-m high rectangular mouth, and a bottom roller-beam. A series of 5-cm spaced vertical rods ("fingerbars") covered each net mouth to exclude large objects and debris that might damage the net or obstruct the optimal functioning of the gear. The nets were towed for 200 m, each surveying an average of 600 m^2 per station, and followed a stratified sampling design described in section 2.2.4. The fish data came from the trawl bycatch of a larger project targeting pink shrimp (Diaz 2001), hence the sampling timing and design aimed to maximize estimate precision for the shrimp.

Gear selectivity experiments determined a knife-edge selectivity curve for parrotfishes, where all specimens ≥5 cm TL were collected by the trawl nets and escapement was negligible.

2.2.3 Reef fish Visual Census

Reef fish Visual Census (RVC) surveys in the Florida Keys National Marine Sanctuary (FKNMS) (Figure 2.1) took place from 1997 to 2001, between April and October of each year, using the NOAA R/V Aldo Leopold, and NURC R/V Oak Leaf.

SCUBA divers performed the visual censuses following standardized sampling procedures (Bohnsack and Bannerot 1986). Divers identified, counted, and measured all the fish observed for the first 5 minutes within a 7.5-m radius (177 m^2) cylinder of water. For each species, the minimum, maximum, and modal lengths were recorded based on fork length (in cm). Also recorded was time of day, depth, substrate type, and geographic location in latitude / longitude coordinates.

For the RVC data, gear selectivity considerations referred to the ability of the divers to observe, identify and/or quantify parrotfishes. Thus, a knife-edge selectivity curve was assumed for Florida Keys parrotfishes, by which all specimens ≥4 cm TL were recorded.

2.2.4 Sampling design

Sampling designs for both net trawling and RVCs were based on Stratified Random Sampling (StRS) theory (Chiappone et al. 2002). The StRS approach is more efficient for patchy distributions, as it decreases variance at a given sample size. The goal is to estimate population mean densities ($\overline{D}$), totals ($\hat{Y}$), and proportions (p), both within stratum (i.e., habitat type), and for the whole domain. StRS assumes a finite population, and a homogeneous variance within stratum but not necessarily for the whole study area. Other assumptions are: the domain is explicitly delineated, all sampling units are known and uniquely identified, and selection probability is the same for all units (Cochran 1977). StRS starts by defining the domain (i.e., Biscayne Bay for trawl data, and Reef Tract for RVCs), and the sampling unit (e.g., 600 m^2 trawl area, or a 177 m^2 cylinder for RVC), as well as the strata (based on habitat characteristics as described below).

In this study, habitat type (heretofore *stratum*) classifications were based on previous works headed by Jerald Ault at the Rosenstiel School of Marine and Atmospheric Sciences (RSMAS) Miami, James Bohnsack of the National Marine Fisheries Service (NMFS, NOAA), Miami, and Steven Miller at the National Underwater Research Center (NURC), Key Largo (Lindeman et al. 1998, Ault et al. 1999a, Ault et al. 2001, Chiappone et al. 2002). Stratification designs differed among the domains, reflecting the differences in habitat types. Cross-shelf categories and substrate types were consistently used as criteria in the two domains.

In Biscayne Bay, a simple StRS was implemented, i.e., sample size per stratum was proportional to habitat area, and within-stratum stations (sampling units) were randomly allocated. Three types of substrate, namely seagrass, hardbottom, and barebottom were considered. The seagrass category or submerged aquatic vegetation (SAV, *sensu* Lindeman et al. 1998) comprised grasses and algae, and accounted for 77.3% of the total area of the bay (Table 2.2, Figure 2.2). Surveys in Biscayne Bay were conducted under two different stratified sampling designs. The first design consisted of nine strata (Table 2.2, Figure 2.2), based on a combination of substrate type, depth, and cross-shelf location (Lindeman et al. 1998, Ault et al. 1999a). The largest strata were seagrass basin axis (SBA) and seagrass mainland subtidal (SMS), comprising ~49.7% and ~21% of the total area of the bay, respectively. The second scheme was a 5-stratum composite (Table 2.2, Figure 2.3), under which seagrass deep (SD5), and seagrass shallow (SS5) accounted for 39.6% and 22.5% of the total area, respectively. The 1996 and March 1997 surveys followed the 9-stratum (Table 2.2, Figure 2.2), and the remaining cruises sampled the bay on the 5-stratum scheme (Table 2.2, Figure 2.3). In total, 983 stations were surveyed. Table 2.3 shows sample size allocation per cruise and per stratum, and the corresponding weight assigned to each stratum for the calculations of the stratified design. The categorization and sample allocation was designed for pink shrimp abundances, as part of another research project (Diaz 2001).

For the Florida Keys domain (Figure 2.1), the habitat in each sampling unit was described with criteria defined by coral and fish experts. The major descriptors used in the present study were:

A. Cross-shelf classes: inner shelf, mid-channel, outer shelf, which classified a reef as inshore, mid-channel or fore reef, respectively.
B. Habitat type: high- or low-relief spur and groove and hardbottom, terrace and patch reefs.
C. Station depth and slope (maximum and minimum depth).

In the Florida Keys, the scheme followed a two-stage StRS, where the domain was divided into primary units (reef blocks) of 200 x 200 m (40,000 m^2), and assigned to a habitat type. Within each block, paired secondary units (two divers per station, each a sampling unit) were randomly allocated. A total of 2,511 stations from 814 blocks was surveyed between 1997 and 2001 (Table 2.4). Over time, more area was covered with fewer replicates (i.e., the number of stations nearly doubled while the number of blocks increased four-fold in the 5-year period). The reef tract had six strata following a cross-shelf classification: inshore (including near shore patch reefs), mid-channel patch reefs, offshore patch reefs, shallow forereefs (<6 m depth), mid-depth forereef (6-18 m), and deep forereefs (>18 m). The mid-depth (6-18 m) fore-reef stratum was the most sampled (35% and 39% of stations and blocks, respectively) (Table 2.4). In order to assess alongshore patterns, a secondary classification denoted four regions: Biscayne National Park reefs (BNP), Upper Keys (UK), Middle Keys (MK), and Lower Keys (LK) (cf. Figure 2.1). The latter region accounted for 40% and 37% of the stations and blocks, respectively. The Protection category (unprotected, U, vs. protected, P) was a third classification criterion (Table 2.4).

Sample selection followed Cochran (1977). A number 1 to N was assigned to units of the domain, of which n units per stratum were randomly drawn with a random number generator based on a uniform probability density distribution. The proportional area contributed by each stratum determined the number of samples per stratum. Sample allocation among strata aimed at minimizing within-stratum variance while keeping the smallest sample size possible (Cochran 1977).

2.2.5 Data analysis

Stratum-specific estimates of density (D), total numbers (Y), and variance (S^2) were obtained, and then overall values were computed by incorporating the weighting factor when applicable (see equations on Table 2.5). The adapted coefficient of variation of the mean was selected as a measure of performance, describing how close the estimate was to the aimed level of uncertainty (Table 2.5).

Density and size/lifestage maps using ArcView® provided graphical syntheses of the spatio-temporal variability of these species. Lifestage size ranges were established based on maturity and morphological factors, as well as Principal Component Analysis (described below). The Kruskal-Wallis nonparametric method tested habitat preferences among lifestages (Sprent 1989). Kendall’s Coefficient of Concordance (Tate and Clelland 1959, Sprent 1989, Zar 1999) was used for nonparametric multiple correlations among life stages, because it has a correction factor to account for multiple ties of rankings.

2.2.5.1 Habitat use and ontogenetic shift analyses

This study also addressed habitat selection, defined as the process in which the parrotfishes choose any of the habitat types in each domain (Manly et al. 1993). Level of habitat use (i.e., quantity of habitat type utilized by the fish in a fixed period of time), as a fraction of habitat availability (i.e., quantity accessible to the fish) were considered. Three measures of habitat selection by life stage were applied for each species:

(a) *Probability of use of a habitat unit in stratum h*, $p(\text{use})_h$: proportion of habitat units occupied by at least one fish, where the habitat unit (i.e., average area sampled per station) was 600 m^2 in Biscayne Bay, and 177 m^2 in the Florida Keys domain. Each value of p(use), computed as presence/absence fraction of the sampled stations per stratum per cruise, was considered to represent the whole stratum.

(b) *Per unit amount of use*: comparison of the stratum-specific density against the overall bay density, where densities higher than average indicate higher amount of use of a given habitat. For comparison purposes, all Biscayne Bay cruises were analyzed on a 9-stratum design regardless of the actual sampling design that took place. Density and variance per stratum ($\overline{D}_h, S_h^2$, respectively) and bay-wide ($\overline{D}$, $Var(\overline{D}_h)$, respectively) were computed from equations shown in Table 2.5.

(c) *Relative population amount of use*, p(P) vs. p(A): statistical comparison of population proportion, p(P)= $\hat{Y}_h / \hat{Y}$ (see equations in Table 2.5), against habitat proportion of the total area of the domain, $p(A)=A_h/A$. An intersect of the 95% confidence interval, 95CI, of population proportion with the area proportion is interpreted as p(P)=p(A), i.e., no habitat selection, which indicates a passive use of habitat based on available substrate. When the confidence interval does not intersect the proportion of area there are two alternatives: p(P)>p(A) indicates positive habitat selection, and p(P)<p(A) represents negative selection or avoidance.

Ontogenetic habitat shifts were addressed with different approaches. Firstly, the PCA aided lifestage identification by grouping the size classes that utilized the strata in similar manners. This analysis was run by season or year (Biscayne Bay and Florida Keys, respectively) on a density matrix of length categories (rows) vs. strata (columns), in which only positive (i.e., at least one cell>0) rows and columns were included. The density data were log-transformed (density+C), where C equaled the minimum positive density value of the species in the matrix. The SAS® procedure of PRINCOMP created a *Z* matrix standardized by the mean and standard deviation, *sd*, where $Z_{1i} = (X_{1i} - \overline{X}_1) / sd(X_1)$. Secondly, spatial distribution of length-based lifestages was mapped. Thirdly, the size structure per stratum (based on mode, range, and extreme values of length as obtained from 1-cm or 2-cm size interval histograms) was used to explore patterns of size ranges within and among habitats. The 9-stratum design was used in Biscayne Bay, and the 6-stratum design in the Florida Keys.

Estimates of timeline for lifestage events were calculated from the results obtained in Chapter 3.

2.3 Results

2.3.1 Biscayne Bay parrotfish distributions

2.3.1.1 Species-specific spatial and temporal trends

A total of 34,353 fish of 177 species belonging to 55 families were collected by beam trawls between 1996 and 2000. Among the 11 scarid species found in the samples, the three most abundant were *Nicholsina usta* (Emerald parrotfish), *Sparisoma chrysopterum* (Redtail parrotfish), and *Sp. radians* (Bucktooth parrotfish), ranking 10th, 12th, and 24th by number, respectively (Table 2.6). The remaining parrotfishes included four *Scarus* spp. and four *Sparisoma* spp., and together accounted for 0.22% of the total fish collected in the trawls. No further analyses were performed on these lesser species.

Post-stratification analyses (described in Chapter 5) yielded an acceptable degree of precision for *N. usta* and *Sp. chrysopterum*, under all sampling schemes. Due to the low numbers of *Sp. radians*, this species was removed from several analyses.

Frequencies of occurrence were expressed as number of stations with species *i* present relative to the total number of stations sampled per cruise. The values ranged 20-40% for *S. chrysopterum*, 15-30% for *N. usta* (except in spring 2000 when its frequency reached ~43%), and 1-15% for *S. radians* (Figure 2.4). The three species were more frequent during summer and fall, and showed the lowest occurrences in spring, although some trends were reversed for the fall 1999-spring 2000 campaigns. *Nicholsina usta* showed an increasing trend in the 1996-2000 period, *Sp. chrysopterum* was relatively stable, and *Sp. radians* frequencies declined to nearly zero. Interannual variability overlaying seasonal patterns may have obscured the trends.

Overall and spatially-explicit density estimates are presented in Table 2.7 and Figure 2.5, respectively. The three parrotfishes were more abundant in summer and fall than in spring, matching the seasonal patterns of their frequency of occurrence. Spatially, their densities were higher close to Safety Valve, and consistently zero at two sites on the mainland side: (a) the outlet of canal C-100, between Coral Gables and Black Point, near the Cutler Ridge Plant; and (b) Mowry canal outlet, between Black Point and Turkey Point (Figure 2.5).

Nicholsina usta densities progressively increased from low (0.1-0.3 fish 1000 m^{-2}) in spring, to moderate (0.4-0.6) in summer, to highest (0.8-1.0) in November. The numbers peaked near Safety Valve during the wet months. *Sparisoma chrysopterum* showed moderate bay-wide densities (0.3-0.6 fish 1000 m^{-2}), with no seasonal trends (Table 2.7). However, localized abundances were higher in summer and fall in two "hot spots": Boca Chita Key, and the basin axis of the northern half of the Bay (Figure 2.5b). *Sparisoma radians* was the least abundant of the three parrotfishes (Table 2.7, Figure 2.5c), with densities usually < 0.3 fish 1000 m^{-2}. It was largely absent from the south part of the bay throughout the year, and more concentrated on the ocean side, nearby Safety Valve. A few specimens also were found in the southern bay, occasionally close to the mainland areas during summer.

2.3.1.2 Lifestage designations in Biscayne Bay

A synthesis of several sources was the basis for assigning a life stage to each of the size classes. The data comprised a summary of size-frequency distribution histograms, color phase observations, PCA outcomes, and available literature on the life history of each species. Timeline for lifestages was computed from the results in Chapter

3. PCA provided a multivariate approach to detect life phase progression, by plotting 1-cm size intervals with respect to fish density at each habitat type. The first two principal components (Eigenvalues) consistently accounted for ~60-80% of the variation of the three parrotfishes regardless of season (Table 2.8), suggesting moderate to high association of body length with habitat. In order to describe the ontogeny in biologically meaningful steps, lifestage names were based on developmental criteria (e.g., juvenile, JP; subadult/immature, SP), and color phase categories (e.g., initial phase, IP; terminal phase, TP) (Table 2.8). Although the names are standardized for all parrotfishes analyzed, the corresponding size ranges were adapted to the biology and maximum size of each species.

Nicholsina usta showed a habitat change at ~11-13 cm TL (Figure 2.6a), coinciding with phase color changes from IP to TP. The PCA outcome (Table 2.8) supported the designation of three life stages, namely, JP, IP, and TP. *Sparisoma chrysopterum*'s life cycle was divided into four lifestages, three of which (JP, SP, and IP) were observed in the PCA plot (Figure 2.6b). The end of its subadult stage is associated with the shape change of its caudal fin; the elongation of the external caudal rays of the truncate tail starts at ~9 cm TL (~5 mo. old), and by 11-12 cm size (~6.5 mo. old) changes to a well-defined concave shape. IPs ≤20 cm were at sex-changing ages but sexually immature, while those 21- 30 cm TL (1-2 yrs. old) were considered a subgroup of sexually maturing IPs (see explanation below). However, fish > 22 cm TL (≥1.2 y old) were absent in the trawl samples. Thus the second stage of IP and the TP of this parrotfish were not represented in the bay domain (Table 2.8), but they occurred in the Florida Keys. These life stage designations were supported by observations on color phases, reported size of sex change, changes in caudal fin shape, and visual inspection of gonad maturity (H. Molina-Ureña, unpubl. data). A limitation to the interpretation of the data is that *Sp. chrysopterum* has a large size overlap of color phases, and combined with the presence of gonochorist females, may confound the use of color phase as descriptor of gender.

PCA provided no defined patterns of habitat shifts for *Sp. radians* because low occurrences and different groupings among seasons obscured patterns of ontogenetic shifts. However, three life stages were assigned (JP <5 cm, IP 5-10 cm, TP>10 cm TL) to *Sp. radians*, using the same principles of color phase and reported maturity schedules applied in the two cases above.

Regardless of the PCA outcome, all parrotfishes ≤5 cm TL were considered to be JPs, mostly under the operational criterion of catchability. Selectivity and/or catchability factors may result in specimens <5 cm being less vulnerable to capture or net retention.

Proportions by lifestages and spatio-temporal distributions are shown in Table 2.9 and Figure 2.7. For *N. usta*, IPs represented >60-85% in spring, occurring mainly in the northern bay (Figure 2.7a). TP proportions increased in summer and fall to 50-70%, the largest specimens appearing during November. Juveniles (3-5%) were found in all seasons, usually near Safety Valve and Bear Cut.

Table 2.9 shows that *Sp chrysopterum* subadults (SP, 5-11 cm TL, 2.5-6 mo. old) usually represented >60% of the specimens collected, while the IPs ranged from ~20% (spring) to ~35% (fall). Juveniles (≤2 mo. old) occurred at all seasons, accounting for 4-12% in spring and summer, but <3% in fall. TPs were <3% during the study period. This parrotfish was more restricted to the northern half of the bay (Figure 2.7b). The high summer densities near Boca Chita Key (Figure 2.5b) were comprised by SPs, and the second hot spot along the deep mid-axis of the bay consisted mainly of JPs and SPs. The magnitude of the secondary juvenile hot spot might be underestimated, as suggested by the knife-edge gear selectivity curves. SPs largely outnumbered IPs in November (Table 2.9), and concentrated near Safety Valve, while juveniles were spread across the shelf in spring, and restricted to the seagrass/barebottom interface during summer (Figure 2.7b). All lifestages were represented in the bay in every survey, except spring and summer 1996 when TPs were absent (Table 2.9). *Sparisoma radians* occurred in very low densities. IPs almost always accounted for more than half of the fish collected, except in November 1999 when >80% were TPs. Despite the low numbers, a few adult specimens were found in low-salinity areas (Figure 2.7c) during the rainy months. Juveniles were absent to rare in the summer and fall, but present in spring.

2.3.1.3 Habitat use and ontogenetic shifts

Three measures of habitat use and selection were applied to each parrotfish as a whole and by life stage. A first step analyzed overall species patterns, and a second step targeted life stages when enough data were available.

Measure 1: probability of use

Probability of use by lifestage, p(Use-stage), is displayed in Table 2.10 to Table 2.12. Juveniles of *N. usta* were restricted to seagrass axis and leeward strata, captured at all seasons during 1997 almost exclusively, but with low probabilities ≤ 0.10 (Table 2.10). IPs were major users of SBA and SLS (15 to 44%) except in spring, when they had 17-25% probabilities to use hardbottom (HMS). IP use of barebottom ranged from 0 to 56% with no apparent seasonal trends. TPs used seagrass and barebottom strata more consistently than the other habitats. Seagrass p(Use) was higher during fall than spring and summer (Table 2.10). For all stages combined (p(Use-sp), not shown), *N. usta* consistently showed ≥30% occurrence probabilities in seagrass (basin axis and leeward subtidal, SBA, SLS) and barebottom axis (BBA), regardless of time of year. The highest means were for BBA and SLS (0.53±0.27 SD and 0.52±0.26, respectively). On hardbottom (HMS, HBA, HLS) it was present only in the spring.

Juveniles of *Sp. chrysopterum* were infrequent, but concentrated along the basin axis, seagrass and barebottom. Subadults expanded to all seagrass strata year-round (Table 2.11). IPs and TPs consistently used more the seagrass habitats, with summer of 1997 showing peaks of probability of use by any parrotfish (>0.7). Overall probability of seagrass usage was >35% cross-shelf, but slightly lower on the mainland side (p(Use-sp), not shown). The maximum mean probabilities were 0.43±0.10 and 0.41±0.25 SD for SBA and SLS, respectively. It was absent to rare on hardbottom during fall, but had moderate probabilities ~0.2-0.4 in spring.

Sparisoma radians displayed low probabilities of use bay-wide (≤50%), with an overall mean p(Use)=0.28±0.25, thus the analysis by lifestage was not pursued. This parrotfish used mostly seagrass leeward (SLS), and showed lower probabilities on SBA, BBA, and BLS (Table 2.12). The highest occurrences were observed in fall (0.43±0.09). It was virtually absent from hardbottom except during fall (Table 2.12).

Measure 2: per-unit amount of use

This second measure, PUA, is one of several complementary perspectives addressing size-specific density patterns of the parrotfishes, and is expressed here as deviations from the bay-wide mean density. The per-unit amount of use by lifestage (PUA-stage) is depicted in Figure 2.8 to Figure 2.10 and relative occurrence of length modes, minima and maxima per stratum are shown in Table 2.13. In general, rather than sharp habitat shifts, parrotfishes seemed to expand their habitat range as they grew.

Nicholsina usta expanded from seagrass onto hardbottom, as detailed below. JPs (3-5 cm TL) were abundant to common on SBA and BBA, as were the young IPs (5-7, 8-10 cm) (Table 2.13, Figure 2.8a). At 10-12 cm mode, IPs became occasional in HBA and HMS, while still abundant on seagrass (Table 2.13, Figure 2.8b). Higher densities of larger fish (modes>17 cm) occurred during fall leeward, on seagrass and barebottom (Figure 2.8c, Table 2.13). This species had high PUA-sp (not shown), i.e., above-mean densities, on seagrass axis (SBA) in all seasons, on seagrass leeward (SLS), and barebottom axis (BBA) strata in summer and fall. This parrotfish was scarce to absent on hardbottom (HMS, HBA, HLS), and barebottom shallow (BLS, BMS).

The earliest stages of *Sp. chrysopterum* occupied depths > 2 m along the northern basis axis of Biscayne Bay, on barebottom and seagrass substrates, concentrating on the northeastern sector of the bay throughout its life cycle. Juveniles attained their highest densities on BBA (Figure 2.9a). While still dense on barebottom, JPs and early SPs (minimum 4-6 cm, mode 6-8 cm) also dominated in SBA and SLS in summer and fall (Figure 2.9b), whereas the 9-10 cm mode characterized SLS, SMS, and BBA (Table 2.13). IPs were more dense on SLS, SBA, and BBA (Figure 2.9c). The rare largest specimens (TPs) were collected nearly exclusively on barebottom (Figure 2.9d), but this may reflect a catchability issue rather than habitat use. With all lifestages pooled, PUA-sp (not shown) suggested that *Sp. chrysopterum* used least the mainland shallow areas, and it consistently occurred at or above mean density on seagrass (SLS, SBA), and barebottom axis (BBA). *Sparisoma radians* was abundant to common on seagrass axis and leeward, especially the 4-6 cm and 6-8 cm TL, and occasional on barebottom axis and leeward (Table 2.13, Figure 2.10). They were rare to absent along the mainland side of the bay (Figure 2.10, Table 2.13).

Nonparametric test results supported the PUA results (Table 2.14). *Nicholsina usta* showed no significant differences in rankings of stratum-specific densities among the three lifestages, either when considering all habitats included (i.e., multiple ties effects, Kruskal-Wallis nonparametric test $\chi^2=5.66$, $0.05<P_{all}<0.10$), or comparing only those strata where this parrotfish was present (Kruskal-Wallis $\chi^2=0.80$, $P_{positive}>0.75$). Furthermore, the three lifestages of *N. usta* displayed significantly correlated rankings of densities among habitats (nonparametric Kendall's Concordance Coefficient, W=0.62, $0.01<P<0.05$), confirming the lack of sharp ontogenetic shifts. Stratum density rankings did not differ significantly among JP, SP, IP and TP of *Sp. chrysopterum*, with all habitats considered (Kruskal-Wallis $\chi^2=6.92$, $0.05<P_{all\ habitats}<0.10$, Table 2.14), which suggested no habitat shifts. However, there were significant differences among the four lifestages (Kruskal-Wallis $\chi^2=9.49$, $P_{positive}<0.025$, Table 2.14) when only positive strata were compared. The high correlation among habitat-specific densities of all lifestages of *Sp. chrysopterum* (Kendall's Concordance Coefficient, W=0.74, $P<0.001$) confirmed the lack of significant shifts of habitat use of *Sp. chrysopterum* within Biscayne Bay. The contradictory result of Kruskal-Wallis on positive habitats might be due to overall lower abundances, and the fact that significant occupation of hardbottom substrates by this parrotfish was restricted to subadults and in spring only, thereby affecting the outcome of the positive-only tests. *Sparisoma radians* was uncommon in the trawl surveys, which may have caused nonparametric tests to fail detecting habitat trends (Table 2.14: Kruskal-Wallis $P_{\text{all habitats}}>0.50$ and $P_{\text{positive}}>0.50$; Kendall's Concordance Coefficient, $P>0.20$).

Measure 3: relative population amount of use

Figure 2.11 displays the third measure of habitat selection, p(P) | p(A) for the species as a whole. The p(P) | p(A) estimates by lifestage results are not shown. Juvenile *N. usta* had an affinity for SBA in spring, and SLS in fall 1997; otherwise, they were non-selective when present. IPs and TPs showed positive selection of SBA. SLS was selected by IPs, and occupied non-selectively by TPs. Avoidance of all mainland habitats (SMS, HMS, and BMS) was inferred for both lifestages. With all lifestages combined, *N. usta* had a significant preference for seagrass deep (SBA) year round, and leeward (SLS) in summer and fall, but avoided SMS and HBA (Figure 2.11a). There was no selection for hardbottom (HMS, HLS) and barebottom (BMS, BBA, BLS) substrates.

Sparisoma chrysopterum showed a pattern of affinity for SBA and SLS, avoidance for SMS (Figure 2.11b), and passive selection for hardbottom and barebottom, except for a positive trend for BBA in spring and fall. When present, JPs usually selected basin axis seagrass and barebottom, with no defined seasonal patterns. SPs and IPs avoided all mainland strata; they selected SBA and SLS, and occupied BBA, HBA, and BLS proportionally to each stratum's availability. The scarce collections of TPs seemed to avoid the mainland strata as well. Similarly, *Sp. radians* selectively used SBA and SLS, but avoided mainland habitats (Figure 2.11c). Otherwise, it showed no habitat selection.

2.3.2 Florida Keys parrotfish distributions

2.3.2.1 Species-specific spatial and temporal trends

A total of 39,522 parrotfishes was recorded in the Florida Keys with the RVC technique, from May to October, between 1997 and 2001. The four most abundant parrotfishes in the samples were *Sc. iseri* (Striped parrotfish), *Sp. aurofrenatum* (Redband parrotfish), *Sp. viride* (Stoplight parrotfish), and *Sp. chrysopterum* (Redtail parrotfish) (Table 2.15). None of the samples in this data set included *N. usta*, the most abundant parrotfish in Biscayne Bay.

The reef tract frequency of occurrence for the top four species did not show significant interannual variations. Aside from a decreased occurrence of *Sp. viride* in 1999, all population frequencies were relatively stable (Figure 2.12) throughout the study. Both *Sc. iseri* and *Sp. aurofrenatum* were present in ~75-88% of the stations sampled, *Sp. viride* was observed in 56-81%, and *Sp. chrysopterum* in 20-30%.

Annual density estimates of each parrotfish varied little throughout the 5-year study (Table 2.16). Mean densities ranged between 5.7 and 8.5 fish per 177 m^2 plot for *Sc. iseri*; 2.8 and 4.5 fish per station for *Sp. aurofrenatum*; and 1.1 to 1.7 individuals for *Sp. viride*. *Sp. chrysopterum* was scarce, averaging <1 fish per station, but densities were doubled in 1999 and 2000 compared to other years. The coefficients of variation were 5-25% for the 3 top species and 16-35% for *Sp. chrysopterum* in all years.

2.3.2.2 Lifestage designation in the Florida Keys

Principal Component Analysis (PCA) showed life phase shifts of parrotfishes in the Florida Keys. The first two principal components (Eigenvalues) consistently accounted for ~75-95% of the variation of the top three parrotfishes regardless of year

(Table 2.17), suggesting a strong association of body length and habitat. The exception was *Sp. chrysopterum*, for which the two Eigenvalues only explained 60-73% of its variation among habitats, but reaching 74-87% with the third component.

Lifestage names follow same criteria as in section 2.3.1.2. Four major developmental stages were determined for each parrotfish (Table 2.17). From the PCA results, the juvenile phase (JP) of the four species was comprised by individuals <4 cm TL (Table 2.17), either reflecting similarities of habitat use, or the ability of the divers to observe, identify and/or quantify these specimens (cf. section 2.2.3). Thus, the JP category is based on ecological and operational considerations.

For *Sc. iseri,* the 3 categories besides JP were denominated initial phase female (IPF, ≤11 cm TL), initial phase male (IPM, 12-16 cm TL) -during which sex and color transformations may take place (cf. Table 1.3)-, and Terminal Phase (TP, ≥17 cm TL). This grouping showed moderate to high consistency among years (PCA plots not shown), and the patterns were distinct despite their complex social behavior (see Table 1.3). However, contrary to previous literature reports, *Sc. iseri* specimens collected in this study showed an extended size overlap between color phases (cf. Figure 3.1a), a drawback when using length as proxy for lifestage. *Sparisoma aurofrenatum* also had four stages: JP<4 cm, subadult (SP, 4-10 cm), initial phase (IP, 11-18 cm, matching reported sex change size range, cf. Table 1.3), and TP (≥19 cm TL) (Table 2.17).

In the case of *Sp. viride*, the lifestages were more difficult to establish. The 2000 and 2001 Principal Component graphs, PC2 vs. PC1 lacked discernable patterns (PCA plots not shown); thus, additional plots with PC3 had to be analyzed. However, despite the inclusion of the PC3 axis, the clustering by size was variable. Even under these circumstances, the SPs (4-11 cm TL) and larger TPs (≥25 cm) seemed to form clusters; the intermediate sizes were denoted as a single lifestage IP, pooling two possible subgroups: the true IP encompassing 12-17 cm, when some individuals can undergo prematurational sex transformation (cf. section 1.2.3), and the maturing transitional fish (18-24 cm). The fourth lifestage consisted of the juveniles.

PCA plots of lifestage designation in *Sp. chrysopterum* were similar in Biscayne Bay and the Florida Keys. JP, SP and immature IP were described above (cf. Table 2.8). Thus, the Keys IP included a younger sex-changing sub-stage (12-20 cm, 6.5-13 mo. old), also present in the bay (cf. section 2.3.1.2). In the Florida Keys, older phases of *Sp. chrysopterum* were present, and included an older, sexually maturing IP sub-stage (21-30 cm, 1.2-2 yrs. old), and the Terminal Phase (TP, ≥31 cm, ≥2.13 yrs. old).

Interannual variability of lifestage proportions of Florida Keys parrotfishes is shown in Table 2.18. *Sc. iseri* showed no major interannual differences in lifestage structure. IP-Females represented >81-88% (Table 2.18), and JPs accounted for 4-15%. IP-Males were scarce, while TP proportions remained below 1%. *Sparisoma aurofrenatum* SPs usually represented 46-60% of the specimens collected, closely followed by the IPs (~28 to 38%). Juveniles accounted for 3-6%. TPs were 6-12% in the study period Table 2.18). Despite the lack of major year-to-year fluctuations, proportions of the younger stages increased in 2000 and 2001. *Sparisoma viride*, on the other hand, was represented by ~34-37% SPs and ~35-42%IPs, while JPs ranged 2.4-4.5% (Table 2.18). Unlike the previous parrotfishes, TPs were well represented in the population (20-25%). IPs of *Sp. chrysopterum* accounted for >74% of the fish counted. The strong signature of the 2001 TP cohort (14% at ages ≥3 y) could be tracked back to the 1999 IPs

(98% at ages 0.5 to 2 y), the 1997 SP (25% at ages 2.5 to 5 months) (Table 2.18), and the summer 1996 JP cohort (12%) in Biscayne Bay (Table 2.9). Juveniles were absent or rarely seen in the Florida Keys.

2.3.2.3 Habitat use and ontogenetic shifts

Measure 1: probability of use

The first measure of habitat selection displayed relatively low interannual variability for the four parrotfishes studied (Table 2.19). Bearing in mind that >80% of observed *Sc. iseri* were IP-Females, this species consistently showed use of a wide range of habitats in the Florida reef tract. Its p(Use) was usually >75% in the 6 strata, and varied little from year to year, but least frequent on inshore and fore reefs shallow and mid-depth (Table 2.19). Its presence was evenly distributed across the four regions (Biscayne National Park, and Upper, Middle and Lower Keys, cf. Figure 2.1), with mean p(Use) 0.77-0.88 (Table 2.20a). *Sparisoma aurofrenatum*, mainly SPs and IPs, occurred at 80-100% of the stations, except on inshore patches, where p(Use) = 0.26-0.51 (Table 2.19b). Alongshore, its occurrence showed a small decreasing trend from BNP to the Lower Keys (Table 2.20b).

Sparisoma viride occurred mostly from midchannel to shallow forereefs, and was less common in deeper forereef strata. Inshore and mid-depth forereefs showed greater interannual fluctuations (e.g., 30-71% on inshore patches) than in other strata and other species (Table 2.19c). Region-wise, this parrotfish occurred more frequently in the two northern regions (mean >80%) than in the southern ones (mean ~60%) (Table 2.20c). This species showed higher interannual variability in the Middle Keys.

Sparisoma chrysopterum (mostly IPs) averaged p(Use) values comparable to those in Biscayne Bay, but much lower than that of the preceding parrotfishes in the Keys (Table 2.19d). This parrotfish occupied each stratum in the Florida Keys with similar probabilities, except for low occurrence on deep forereef (>18 m depth). Average p(Use) values suggested a moderately even distribution among the BNP, Upper and Middle Keys (0.27-0.30), and lower frequencies in the Lower Keys (Table 2.20d).

Measure 2: per-unit amount of use

The second measure, (PUA-sp), is shown by lifestage and protection status in Figure 2.13 to Figure 2.16 as anomalies from the Keys-wide mean density. Size-frequency histogram results synthesized in Table 2.21 complements the PUA analysis. For *Sc. iseri*, all lifestages were observed in all strata (Table 2.21), but the peaks occurred at progressively larger size categories from onshore towards offshore sites. The smaller *Sc. iseri* (JPs and IP-females) were denser on inshore, mid-channel and offshore reefs, regardless of protection status (Figure 2.13a,b); the main modes were 4-6, 5-7 and 9-10 cm TL (Table 2.21). However, there were two pulses of juvenile abundance, the first on shallow forereefs (1997), and the second inshore (2001). These younger stages were absent to rare in deep forereefs. While still present in onshore areas, IP-males spread towards the forereefs (Figure 2.13c), with secondary modes at 15-18 cm TL (Table 2.21). TPs were usually absent inshore and dense in forereefs (Figure 2.13d). The largest specimens (>20 cm TL) occurred on offshore and fore reefs only (Table 2.21). These findings could be interpreted as product of a progressive spatial expansion as the fish grows, from onshore waters to forereefs.

Sparisoma aurofrenatum also displayed an inshore-offshore ontogenetic pattern. JPs and SPs had low densities on inshore patches (mode 5-7 cm TL). As they grew old, subadults increased their density in midchannel (7-8 cm mode), and offshore (10-12 cm mode) (Table 2.21). IPs were more abundant in offshore and shallow to mid-depth fore reefs (Figure 2.14c). TPs progressed to be most dense in shallow forereefs where a secondary mode at 15 cm TL was consistently observed (Table 2.21).

All size categories of *Sp. viride* were present in all strata. Trends were not as obvious as in the other parrotfishes, but some patterns related to density and modal distributions suggested ontogenetic progressions. Average densities of JPs and very young SPs occurred inshore, comprising the major mode in unprotected sites (4-6 cm TL). Their abundance increased in midchannel and offshore strata (modes 4-6 cm), and displayed a peak in fore reefs in 2001 (mode 5-6 cm) (Figure 2.15a, Table 2.21). SPs (6-10 cm TL) were common cross shelf (Figure 2.15b, Table 2.21). IPs displayed a progressive increase in their densities towards the intermediate habitats, with secondary modes at 15 and 18-20 cm size intervals (Figure 2.15c, Table 2.21). The absence of TPs inshore and in midchannel combined with the higher-than-average densities in fore reef strata could be interpreted as ontogenetic progression from nearshore to offshore habitats.

Sparisoma chrysopterum JPs were nearly absent in the Florida Keys, and the most common minimum length observed was 4 cm TL (Table 2.21). SPs were rare inshore – except in protected reefs during 1997 and 1998-, but they were more dense in shallow fore reef than elsewhere (Figure 2.16a). Contrary to a size progression towards the outer reefs, *Sp. chrysopterum* IPs -comprising ≥75% of the population-, reverted the trend and were more dense in midchannel and offshore strata (Figure 2.16b), where size frequency peaked at 15-18 cm TL (Table 2.21). Unlike IPs, the TP densities followed the usual pattern of higher outer densities, i.e., offshore, and all fore reef strata (Figure 2.16c), where the predominant size classes were 17-20 and 24-25 cm TL (Table 2.21).

Measure 3: relative population amount of us.

A summary of the results by lifestage of p(P) | p(A) is shown in Table 2.22. *Scarus iseri* displayed non selective use the different habitat types across the shelf. However, the IP-females positively selected inshore, mid-channel, and offshore patches, whether or not protected; IPFs occupied the shallow fore reefs more proportionally to area availability, but avoided the deeper fore reef habitats. IP-males had a more variable pattern, tending to positively use the fore reefs more than the onshore regions. The TPs had a clear pattern of selection for the fore reefs and avoidance of the onshore areas (Table 2.22). This provided evidence of an ontogenetic shift from nearshore to offshore strata.

Sparisoma aurofrenatum had non selective occupancy of the available habitat types at older stages, but they avoided inshore patches throughout the whole life cycle (Table 2.22). Juveniles preferred intermediate strata, and selected negatively the fore reefs >6 m deep. Presence of subadults was proportional to the availability of the habitat in protected areas, but the IPs were absent at inshore and midchannel reefs and showed affinity for the offshore strata. TPs, instead, tended to concentrate in fore reefs >6 m depth (Table 2.22).

Sparisoma viride had a complex pattern of habitat use, which is also reflected in the PCA results described in section 2.3.2.1. All lifestages tended to occupy protected areas non selectively. JPs and SPs preferred most of the unprotected strata except the fore reefs >6 m depth. IPs and TPs avoided the onshore and deep fore reef strata, and positively selected the intermediate reefs (offshore and shallow fore reefs).

Sparisoma chrysopterum had too few JPs to elucidate any trends. Protected areas across the shelf and fore reefs >6 m depth were either used proportionally to their area or avoided altogether by the remaining lifestages. In the non-protected sites, the subadults selected the intermediate strata, IPs occupied the inner reefs, and the TPs restricted themselves to 6 to ≥18 m depth fore reefs. Their absence from protected areas might be associated with their preference for rubble substrates (H. Molina-Ureña, pers. obs.), which may not be common at sites that had been targeted for protection.

2.4 Discussion

This study is unique because it provided medium and large scale analyses of temporal and spatial patterns of habitat use by South Florida parrotfishes. It compared ontogenetic habitat shifts within and among a seagrass embayment and an adjacent coral reef. In Biscayne Bay, the results demonstrated the importance of seagrass beds as settlement, recruitment, and nursery areas for parrotfish; seasonal movements were also detected. In the Florida Keys, there was evidence of ontogenetic cross-shelf shifts from inshore to offshore habitats, and annual variability of abundance and distribution of fish. By following the only species with significant presence in both sampling domains, the results suggested a role of Biscayne Bay as source of juveniles and subadults of *Sp. chrysopterum* to the Florida reef tract.

2.4.1 Biscayne Bay

The bay domain of this study comprised the central and south Biscayne Bay (Lee 1975). The strong cross-shelf zoning defined by seasonal hydrographic features was reflected on the parrotfish distributions.

With more sophisticated approaches, I revisited and enhanced the sampling effort of a previous work by Campos (1985), who had surveyed Biscayne Bay during 1982 with a roller frame trawl net (Table 2.6). Little has changed in the relative abundance of *N. usta, Sp. chrysopterum* and *Sp. radians* (Table 2.6), even 20+ years after the fish trap ban, and despite the continuous removal as bycatch by the shrimp fisheries. On the other hand, in nearby Florida Bay, Sogard et al. (1987) only found two unidentified juvenile *Sparisoma* sp. from seagrass beds. The large difference between results in Florida Bay (Sogard et al. 1987) and Biscayne Bay (Campos 1985) could be due to differences in sampling methodologies (1-m^2 throw-traps vs. roller beam trawls), and station depths (<0.5 m in Florida Bay vs. >1 m in Biscayne Bay).

***Nicholsina usta* (Emerald parrotfish).** The results indicated that this parrotfish has its own reproductive population in Biscayne Bay, possibly using open waters during part of its life cycle, but with very little exchange with the Florida Keys reefs. Previous studies support these findings. *Nicholsina usta* is considered a seagrass dweller (Yáñez-Arancibia et al. 1993, Streelman et al. 2002), although with variable abundance rankings in coastal localities. It is also reported to inhabit offshore waters in the western (Robins et al. 1986) and eastern sides of the Atlantic, living at 18-50 m depth off Guinea and Mauritania coasts (Randall 1983, Gushchin and Girardin 2000). It ranged from virtually absent in Bermuda since 1929 (Smith-Vaniz et al. 1999), to low relative abundances in seagrass beds of Panama (Weinstein and Heck Jr. 1979) and Belize (Sedberry and Carter 1993), to the top six fish species in embayments of Guatemala (Arrivillaga and Baltz 1999) and Southern Gulf of Mexico (Yáñez-Arancibia et al. 1993). However, gears used in these works, including the present study, were size-selective towards smaller fish, thus the fate of the older individuals >20 cm TL is unknown. In order to clarify whether the bay acts as nursery grounds for open water populations of *N. usta*, or constitutes a lifelong habitat, trawl samples from ocean waters 20-100 m depth should be obtained off the South Florida coast.

A progressive expansion onto nearby substrates associated with growth was observed, but no sharp ontogenetic within-bay habitat shifts were detected. *Nicholsina usta* was mostly represented by IP individuals concentrating in the north bay. Adults were denser and more frequently collected in seagrass, showed no selection for hardbottom and barebottom, and avoided mainland habitats. Ontogenetic trends observed in this work supported previous findings, in which younger *N. usta* (< 7 cm SL) were reported in 30% of seagrass samples in a Guatemalan bay, but were absent on barebottom (Arrivillaga and Baltz 1999).

Salinity may influence this species' seasonality patterns. Near Safety Valve, an oceanographically dynamic area with high salinity (ranging 30-38, this study) and tidal currents reaching 0.5-0.8 m s^{-1} (Sengupta et al. 1980), IPs had the highest localized densities in summer. The absence of *N. usta* in two spots on the mainland side coincided with high freshwater input and low water circulation (cf. Figure 2.2a, Figure 2.5a). However, one of those sites had barebottom and seagrass substrates, and was too shallow (< 1m) for a thorough sampling effort with the roller beam trawls. Similarly, *N. usta* was a dominant fish species in hypersaline seagrasses of Terminos Lagoon (Yáñez-Arancibia et al. 1993), an embayment with a net inflow from the Gulf of Mexico by strong tidal currents, and ranging from to in June. Yáñez-Arancibia et al. (1993) reported the lowest catches of *N. usta* during summer (salinity ~37) and highest in October-February (salinity ~30), and suggested that adult fishes of several species entered the lagoon aided by the tidal inflow, and used seagrass habitats close to the inlet as area of transit. Biscayne Bay could play a similar role for this scarid.

Abundances of *N. usta* displayed seasonal trends. The lower densities occurred in spring, increased progressively in summer, and peaked in fall. This work agreed with Campos (1985)'s preliminary observations that *N. usta* remains in Biscayne Bay mostly during the wet, warm months (summer, fall), and a considerable portion of the population leaves the bay in winter and spring. Furthermore, my results also indicated that these emigrating fish do not go to the adjacent reef habitats of the Florida reef tract, although IPs and TPs have been found on seagrass beds of Florida Bay in September and October otter trawls (Florida Marine Research Institute, unpubl. data).

Fish returned to Biscayne Bay by the beginning of summer, especially the larger individuals (cf. Figure 2.8). The year-round presence of juveniles in areas where bay and ocean waters are largely exchanged every tidal cycle (Wang et al. 2003) suggested a prolonged influx of new recruits into the bay, likely reflecting a protracted spawning activity (Cervigón 1994). The actual spawning grounds of *N. usta* have not been determined. Although Cervigón (1994) cited a year-round reproductive season in Venezuela, no published studies to date have identified eggs or larvae of this species. However, a few inferences can be made from the results of this research. Firstly, increased presence of larger fish in the bay during November may be interpreted as influx of maturing adults to spawn and feed during the colder months. Secondly, concentration of juveniles on seagrass near Safety Valve indicated possible settlement to seagrass beds from either local or ocean-water spawned products. Thirdly, their total absence in the visual census data suggested *N. usta* did not use the Florida Keys reefs at any stage of their life cycle, although the bulk of its bay population occurs towards the south within Biscayne National Park (BNP). Lack of information regarding *N. usta*'s age/size at first maturity did not allow inferences about reproduction-related changes in habitat use. Yet, the outcome of this study supported the dual use by this parrotfish of seagrass habitats and ocean waters, rather than coral reefs. Mangroves may not be important for this parrotfish (Yáñez-Arancibia et al. 1993, Newman and Gruber 2002).

***Sparisoma chrysopterum* (Redtail parrotfish).** Indirect evidence suggested a degree of connectivity between *Sp. chrysopterum* populations in Biscayne Bay and the Florida reef tract, i.e., seagrass beds and reefs are important components of the life cycle. My results also demonstrated that it has a close association with seagrass habitats >2 m deep, while avoiding substrates near the mainland. At about 6 weeks of age, this parrotfish may settle selectively on barebottom and seagrass along the mid-axis of Biscayne Bay all year. As the individuals grow, they actively prefer seagrass and non-selectively occupy bare- and hardbottom. All lifestages avoided mainland strata, probably due to freshwater input. This parrotfish was common in the northern bay, where the freshwater input during the rainy season is lower than in the south (Wang et al. 2003). Among the four life phases (JPs, SPs, IPs, and TPs), subadults of 5-9 cm TL (2.5-3.5 months old) accounted for >60% of the population. Younger stages were more abundant in the northern half, while adults more frequently occupied the southern area. Proportion of JPs increased in spring and summer, and localized densities of SPs peaked in summer and fall. JPs, SPs, and IPs showed preference for seagrass and barebottom deep strata, while TPs were there in proportion to area availability. No evidence of seasonal emigration pulses was detected for *Sp. chrysopterum*.

Reproductive activity is thought to occur year-round except in December in the Western Atlantic (cf. Table 1.4). Elsewhere, spawning was reported in January-May and October-November in Panama, and in June-August in Bermuda (Winn and Bardach 1960, Robertson and Warner 1978). Results of the present study suggest a protracted spawning season between March and October in Biscayne Bay, peaking after the end of summer, given that the 1.5-month old settling juveniles occurred more frequently in November. Because female size at maturity was reported to be ~25 cm TL in Puerto Rico (Wilson 2003), nearly all individuals collected in the Biscayne Bay trawl surveys might be sexually immature. Gear catchability limitations did not allow determination of whether spawning take place inside the bay.

Connectivity with the Florida reef tract for populations of *Sp. chrysopterum* is yet to be determined. This study suggested that Biscayne Bay may export IPs to the reefs. The lack of >23 cm TL specimens in the trawl surveys is likely due to gear avoidance, since larger individuals occasionally are seen in the bay (C. Faunce, University of Miami, 2004, pers. comm.; H. Molina-Ureña, pers. obs.).

***Sparisoma radians* (Bucktooth parrotfish).** Despite low numbers in the trawl surveys, this study suggested that the bay population of *Sp. radians* has little exchange with the Florida Keys. Characterized by small body size, epibenthic habits on seagrass substrates, permanent territorialism, and schooling behavior (cf. Chapter 1), *Sp. radians* displays traits that could significantly affect its catchability and selectivity. However, it is likely that the whole life cycle of this parrotfish may take place within the bay. Other studies found that this parrotfish preferred low rugosity and sandy substrates (Gratwicke and Speight 2005b), or were exclusively found in seagrass and mangrove habitats but not on coral reefs (Nagelkerken et al. 2000b). There might be latitudinal differences in fish assemblages of seagrass beds. In a comparative study between Panama (9° N), Marco Island (20° N), and Apalachee Bay (30° N), on the gulf coast of Florida, Weinstein and Heck Jr. (1979) used an otter trawl with 1.9 cm mesh at all localities. While parrotfishes were infrequent in the west Florida trawls, as also found in the present study and Campos (1985), *Sp. radians* ranked first of all species collected in Panamanian seagrass habitats.

In this study, the adult phases showed higher tolerance of low salinities than the other two parrotfishes. Although no life stages were clearly designated, some general size-related patterns were considered. *Sparisoma radians* preferred the central axis and leeward subtidal seagrass strata, where JPs and IPs had above-mean densities. It avoided all mainland strata, and occupied the remaining strata proportionally to their area availability. Reproductive seasons may vary among geographic locations. Considered to have year-round reproductive activity in Panama (Robertson and Warner 1978), it is a summer spawner in Dry Tortugas and Bermuda (Winn and Bardach 1960, Munro 1983). In Biscayne Bay, JPs were absent in summer and most frequent in spring, suggesting that *Sp. radians* may have a reproductive peak during winter. Its size at first maturity (L_m) has been computed in FishBase (from Froese and Binohlan 2000) as 12.9 cm TL, but Marconato and Shapiro (1996) reported spawning females as small as 2.61±0.23 cm TL.

2.4.2 Florida Keys

In the Florida Keys domain, *Sc. iseri*, *Sp. aurofrenatum*, and *Sp. viride* were the most numerous parrotfishes, and were also among the top five parrotfishes on reefs of Belize (Mumby and Wabnitz 2002), and the Western Atlantic (Kramer 2003). Comparing the three studies, two *Sparisoma* (*Sp. chrysopterum* and *Sp. rubripinne*) were the other most abundant parrotfishes in the Keys (this work) and Belize (Mumby and Wabnitz 2002), whereas in the Western Atlantic (Kramer 2003), two *Scarus* (*Sc. taeniopterus* and *Sc. vetula*) rounded the top five. This difference might be due to the AGRRA bias toward deep (>5 m), and probably more structurally complex sites. This was inferred from the AGRRA sampling ratio of 5:1 of deep:shallow samples, and the finding of a positive correlation of *Sc. taeniopterus* and *Sc. vetula* with live coral cover reported by Kramer (2003).

***Scarus iseri* (Striped parrotfish).** Results suggested that the population of *Sc. iseri* from the reef tract had little exchange with Biscayne Bay. It was a ubiquitous species that displayed ontogenetic shifts from inshore to offshore in the Florida Keys. However, it ranked low among Biscayne Bay trawl collections. Along the Florida reef tract, younger stages had more affinity to the three onshore habitats, non-selectively used shallow fore reefs, and avoided deep forereefs. IP males occurred in all habitats, usually preferring <6 to 18 m deep forereefs but avoiding deeper strata. Large males > 20 cm TL occupied offshore and forereefs almost exclusively. Previous works classified *Sc. iseri* among reef-dwelling fish that prefer or correlate with rugose substrates (Mumby and Wabnitz 2002, Gratwicke and Speight 2005a). Alternatively, others stressed the importance of non-reefal habitats where rugosity is not a factor, e.g., seagrass and mangrove (Nagelkerken et al. 2000b, Newman and Gruber 2002, Mumby et al. 2004).

Although it is the most abundant parrotfish in the Western Atlantic, *Sc. iseri* was not among the 43 species of juveniles and adults colonizing an experimental artificial reef, in the Bahamas (Almany 2004). Two possible explanations are (a) the location of the artificial reefs on sand substrate prevented the arrival of this parrotfish, which probably avoids sand flats, and (b) the artificial reef did not provide sufficient resources to support a *Sc. iseri* population. Nevertheless, my results suggested that the success of this species relies partially on generalized habitat requirements, which explains why it is found in a diverse range of habitat types (Nagelkerken et al. 2000b). Thus, *Sc. iseri*'s plasticity may allow for local adaptations of this parrotfish.

No regional patterns in abundance were observed among BNP, upper, middle and lower Keys. While a small species (≤ 20 cm TL), this parrotfish had four recognizable life stages, if which initial phase female accounted for ≥80-88% of the population. *Scarus iseri* was the most abundant parrotfish in the Florida Keys as well as the Western Atlantic (Kramer 2003). Its abundance and frequency of occurrence did not display interannual trends, except for the juvenile pulses observed in 1997 and 1999.

***Sparisoma aurofrenatum* (Redband parrotfish).** This study suggested great similarity of life strategies between *Sp. aurofrenatum* and *Sc. iseri*. In the Florida Keys, *Sp. aurofrenatum* was observed at 80-90% of the stations, but its density was nearly half that of the previous species. It was rare in the Biscayne Bay surveys, suggesting low catchability or avoidance of bay habitats. A separation between habitat types agrees with two previous studies elsewhere, but disagrees with others. Nagelkerken et al. (2002)

reported this scarid in highest density on coral reefs and absent in mangroves, but present at low densities in a channel connecting a bay and the open sea and in seagrass beds in Curaçao. Conversely, in British Virgin Islands, this species was part of fish assemblages in areas between bays and reefs, and on moderately rugose substratum, but was not a reef-dweller (Gratwicke and Speight 2005a).

In the present study, *Sp. aurofrenatum* displayed a cross-shelf ontogenetic pattern, even though this population was concentrated on mid-shelf habitats. Two pre-reproductive categories, namely juveniles and subadults, accounted for 50-60% of the population. As they grew older, the initially low numbers of JPs, which preferred inshore patches and avoided deep forereefs, progressively became SPs, expanding to a non selective occupancy of mid-channel and offshore patches. IPs avoided inshore and midchannel, and tended to prefer offshore, shallow, and mid-depth forereefs. Meanwhile, occupancy of shallow forereefs by TPs was sometimes selective. These ontogenetic shifts may partially explain the contradictory findings among different studies, because the lifestage accounting for the largest proportion of the population has the greatest influence on overall distribution patterns. Furthermore, microhabitat differences and biological interactions were experimentally detected in the Bahamas, where abundance changes of *Sp. aurofrenatum* and other parrotfishes were affected by higher levels of reef complexity and the presence of predators and competitors (Almany 2004). In the present study, frequency of occurrence of *Sp. aurofrenatum* was similar across the four regions, but there was a slight progressive decrease from BNP to the Lower Keys.

***Sparisoma viride* (Stoplight parrotfish).** As the most studied parrotfish of the wide Caribbean basin, the ecology, behavior, reproductive biology, and population dynamics of *Sp. viride* are known in more detail than the other scarids (cf. Chapter 1 tables). While considered a coral reef dweller preferring rugose substrates over mangrove and seagrass (Nagelkerken et al. 2000b, Gratwicke and Speight 2005b), this scarid is also influenced by local interactions between habitat complexity, predation, and competition (van Rooij and Videler 1997, Almany 2004). My results were consistent with these observations, and suggested that the reef population of *Sp. viride* has little connection with the Biscayne Bay population. Lifestage designation was difficult for this species, and its ontogenetic patterns were not well defined, due to three probable causes: (1) the wide size overlap among different color and sex phases (van Rooij et al. 1996a, 1996b) obscuring the lengths of phase change; (2) the complex social structure of this parrotfish that renders schools of fish with variable body sizes; and (3) the species' plasticity to adapt to very localized conditions (Robertson and Warner 1978, Koltes 1993, van Rooij et al. 1996b).

Sparisoma viride was rare in Biscayne Bay, but it was the third most frequently observed parrotfish in the nearby Florida Keys (~50 – 81% of samples). It tended to concentrate on mid-shelf habitats (midchannel to shallow forereefs), but its abundance was highly variable among years, perhaps associated with high recruitment pulses in 1997 and 2001. The Florida Keys population was mostly represented by subadult and initial phase (≤ 24 cm TL, 70-75% of total *Sp. viride* observed), and TPs were abundant (20-25%). However, an onshore-towards-offshore general trend could be inferred, as well as an affinity for fished areas (unprotected reefs). On mid-shelf reefs, the smaller modes dominated; JPs and SPs preferred unprotected reefs, but occupied protected areas of those strata when available. Conversely, TPs were absent inshore and in midchannel, but selected unprotected reefs of offshore and forereef strata, while non-selectively using sites under protection. This scarid is frequent along the Keys, with a trend of higher probability of use in BNP and upper Keys (~80%), and slightly lower use in middle and lower Keys (~60%). Interannual variability showed a drop in frequency of occurrence in 1999, which was not observed in the other parrotfishes. A large recruitment peak might have occurred in 2001.

***Sparisoma chrysopterum* (Redtail parrotfish).** The general life cycle of *Sp. chrysopterum* illustrated the Biscayne Bay and the Florida reef tract connectivity. Based on the results from both domains, I hypothesize that part of the population emigrates from Biscayne Bay towards nearby reefs, while the other remains. After juveniles settle along the deep bare substrate of the north bay, their tail morphology changes from truncated to concave at ~3.5 months old, and they begin expanding onto seagrass beds on the ocean side of the bay, near Safety Valve. Because the spawning is protracted, emigration towards the reef tract may be on daily or lunar cycles, but not in obvious seasonal pulses. Thus, the bay population maintains relatively stable densities through time. Interannual variability of abundance may be due to mortality cycles rather than to migratory or low recruitment pulses. *Sparisoma chrysopterum* stays in the bay through most of its subadult stage, and the largest habitat shift occurs when a portion of the larger SPs, ≥5 months old, move out to the reef tract to start their reef dwelling life as sex-changing IPs. Migration may take place through Safety Valve, the ocean opening of north Biscayne Bay, instead of through Florida Bay via Long Arsenicker Key. The progression of immigrating SPs and IPs onto the reef tract is from offshore towards onshore, which explains why the ontogenetic pattern seems reversed. As the fish ages becoming a TP, the forereefs become its preferred habitat.

Spawning may occur year-round, within Biscayne Bay or on reefs in the BNP and Upper Keys regions. *Sparisoma chrysopterum* is monandric but not all females change sex; although TPs pair-spawn, this species does not form harems, nor holds permanent territories (Robertson and Warner 1978). Even though presence of TPs inside the bay is yet to be confirmed, TPs may pair spawn in temporary territories on the forereef. In that case, the settling grounds of the resulting larvae are unknown, since juveniles are virtually absent from the reef tract. It is unknown whether changes of tail shape or sex transformation prompt the emigration from the bay, and what proportion of the gonochorist females stays in the bay or leaves. Bay-reef connectivity of *Sp. chrysopterum* populations is yet to be proven with direct evidence, e.g., tagging studies.

In conclusion, essential habitat use by South Florida parrotfishes is represented by three major types of strategies, with varying degrees of relative importance of seagrass and reef habitats. (1) Use of bay seagrass as main habitat and negligible demographic exchange with nearby reefs, either with an early-stage bay habitat and open water adult life (e.g., *N. usta*), or a bay-bound life cycle (e.g., *Sp. radians*). (2) Use of bay seagrass as nursery grounds and source of older life stages for the adjacent reef tract habitats (e.g., *Sp. chrysopterum*). (3) Reef dwelling in the Florida Keys, with little connectivity to Biscayne Bay, displaying an ontogenetic expansion from onshore to offshore areas under two subtypes of cross-shelf patterns: a well defined affinity for onshore and mid-shelf reefs (e.g., *Sc. iseri* and *Sp. aurofrenatum*), or a weak ontogenetic trend characterized by highly ubiquitous, coexisting lifestages with an apparent expansion from mid-shelf non-territorial distribution to forereef TP territories (e.g., *Sp. viride*).

2.4.3 Methodological considerations

Shortfalls of bay survey data refer mostly to the gear selectivity and sample allocation. It is unknown if the absence of larger specimens in the samples is due to either size selectivity or the fish actually leaving the domain. Time of day and stratum classification may affect collection of these diurnal species. A new stratified sampling design customized for parrotfishes of Biscayne Bay is proposed in Chapter 5.

Table 2.1: Mean, standard deviation (SD) and ranges of temperature, salinity, and dissolved oxygen in Biscayne Bay, 1996-2000.

PERIOD		TEMPERATURE (C)		SALINITY		DISSOLVED OXYGEN (mg L^{-1})	
	n	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
Spring:							
April 1996	117	25.2 (1.7)	{22.3, 27.8}	36.8 (1.3)	{32.0, 40.0}	7.5 (0.9)	{6.0, 9.8}
March 1997	122	25.7 (0.4)	{24.8, 27.0}	34.9 (3.5)	{20.3, 37.7}	6.7 (0.6)	{4.3, 8.3}
March 2000	0	N/A		N/A		N/A	
Summer:							
August 1996	93	29.8 (1.2)	{28.2, 31.8}	34.9 (2.2)	{23.7, 38.0}	6.0 (0.4)	{5.0, 6.7}
September 1997	151	29.0 (0.6)	{27.4, 30.1}	29.1 (5.1)	{15.7, 35.1}	5.6 (1.0)	{3.9, 7.9}
Fall:							
November 1996	150	23.90 (2.21)	{19.9, 27.1}	30.80 (4.4)	{11.3, 36.9}	6.9 (0.6)	{5.0, 9.0}
November 1997	120	23.02 (0.23)	{22.0, 24.8}	33.78 (2.9)	{26.5, 38.0}	6.3 (0.6)	{5.5, 8.0}
November 1999	41	23.38 (0.23)	{22.9, 23.9}	27.94 (1.9)	{21.6, 30.9}	N/A	

Table 2.2: Alternative sampling designs applied to the parrotfish database, Biscayne Bay, 1996-2000. Sources: Lindeman et al. (1998), Ault et al. (1999a), Diaz (2001).

Code name and number	Stratum name	Depth (m)	Equivalency to other designs	General location	Total area (Km^2)
9-stratum design					
SMS (1)	Seagrass mainland subtidal	1-2	shallow	west shore, north and south of the bay	81.2
SBA (2)	Seagrass basin axis	>2	deep	central longitudinal axis, north and south of bay	192
SLS (3)	Seagrass leeward subtidal	1-2	shallow	east shore, north and south of bay	25.3
HMS (4)	Hardbottom mainland subtidal	1-2	shallow	west shore, south half of the bay	31.5
HBA (5)	Hardbottom basin axis	>2	deep	central longitudinal axis, south half of bay	21.7
HLS (6)	Hardbottom leeward subtidal	1-2	shallow	east shore, south half of bay	8.4
BMS (7)	Barebottom mainland subtidal	1-2	shallow	west shore, north half of the bay	1.2
BBA (8)	Barebottom basin axis	>2	deep	central longitudinal axis, north half of bay	19.1
BLS (9)	Barebottom leeward subtidal	1-2	shallow	east shore, north half of bay	5.8
5-stratum design					
SS5	Seagrass shallow	1-2	SMS, SLS	mostly west shore, north and south of the bay	87.1
SD5	Seagrass deep	>2	SBA	central longitudinal axis, north and south of the bay	153
HB5	Hardbottom	>1	HMS, HBA, HLS	central longitudinal axis, south of the bay	51.1
BB5	Barebottom	>1	BMS, BBA, BLS	central longitudinal axis, north of bay	15.9
HS5	High salinity	1-2		east shore, north and south of the bay	79.2
3-stratum design					
SG3	Seagrass	>1	SMS, SBA, SLS, SS5, SD5		298.5
HB3	Hardbottom	>1	HMS, HBA, HLS, HB5		61.6
BB3	Barebottom	>1	BMS, BBA, BLS, BB5, BB3		26.2

Table 2.3: Sampling effort in Biscayne Bay with bottom beam trawls between 1996 and 2000. Number of stations per stratum (n), and weight (w) assigned as explained in Table 2.5, and recalculated each cruise from the actual mean size of the sample unit.

Stratum acronyms as in Table 2.2

	TOTAL	1996 Apr		1996 Aug		1996 Nov		1997 Mar		1997 Sep		1997 Nov		1999 Nov		2000 Mar	
TOTAL	**983**	**118**		**93**		**150**		**122**		**151**		**120**		**119**		**110**	
Stratum		**n**	**w**	**n**	**w**	**n**	**w**	**n**	**w**	**n**	**w**	**n**	**w**	**n**	**w**	**n**	**w**
SMS	**280**	27	0.21	18	0.21	32	0.21	43	0.21	57	0.21	34	0.21	31	0.22	38	0.22
SBA	**431**	47	0.51	25	0.50	74	0.49	52	0.50	64	0.50	53	0.50	64	0.50	52	0.52
SLS	**67**	10	0.07	15	0.06	9	0.07	7	0.07	8	0.07	11	0.07	6	0.07	1	0.07
HMS	**53**	6	0.08	6	0.08	11	0.08	5	0.08	4	0.08	8	0.09	9	0.09	4	0.09
HBA	**59**	9	0.06	7	0.05	10	0.06	5	0.06	8	0.06	3	0.06	5	0.06	12	0.06
HLS	**14**	3	0.02	3	0.02	3	0.02	1	0.02	1	0.02	2	0.02	1	0.02	0	0.00
BMS	**5**	0	0.00	2	<0.01	1	<0.01	1	<0.01	0	<0.01	1	<0.01	0	0.00	0	0.00
BBA	**52**	12	0.05	9	0.05	8	0.05	5	0.05	4	0.05	8	0.05	3	0.04	3	0.06
BLS	**22**	4	0.01	8	0.02	2	0.02	3	0.02	5	0.02	0	0.00	0	0.00	0	0.00

Table 2.4: Sampling effort in Florida Keys with Reef fish Visual Census (RVC): number of stations (number of reef blocks) sampled between 1997 and 2001, in Unprotected (U) and Protected (P) areas.

		TOTAL	1997	1998	1999	2000	2001
TOTAL		**2,511 (814)**	404 (68)	462 (78)	438 (159)	487 (215)	720 (294)
Stratum							
Inshore (IN)	U	**196 (55)**	25 (4)	32 (5)	10 (5)	30 (13)	16 (8)
	P		26 (4)	29 (4)	4 (2)	16 (6)	8 (4)
Mid-channel (MCH)	U	**339 (119)**	37 (6)	79 (13)	34 (17)	34 (16)	99 (50)
	P		14 (2)	12 (2)	4 (2)	14 (5)	12 (6)
Offshore (OFF)	U	**360 (115)**	36 (6)	36 (6)	18 (7)	84 (39)	54 (20)
	P		31 (5)	30 (5)	17 (6)	30 (11)	24 (10)
Fore-reef shallow (FORE-Sh)	U	**711 (187)**	48 (9)	73 (12)	30 (12)	16 (7)	161 (49)
	P		90 (15)	110 (17)	37 (14)	42 (20)	104 (32)
Fore-reef mid-depth (FORE-Md)	U	**868 (317)**	50 (8)	31 (6)	189 (64)	144 (63)	134 (61)
	P		47 (9)	30 (8)	95 (30)	65 (28)	83 (40)
Fore-reef deep (FORE-Dp)	U	**37 (21)**	0 (0)	0 (0)	0 (0)	12 (7)	25 (14)
	P		0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Region							
Biscayne Park		**345 (113)**	79 (13)	79 (14)	37 (10)	68 (35)	82 (41)
Upper Keys		**532 (182)**	69 (13)	105 (20)	48 (21)	100 (50)	210 (78)
Middle Keys		**618 (219)**	90 (15)	72 (14)	161 (58)	115 (58)	180 (74)
Lower Keys		**1,016 (300)**	166 (27)	206 (30)	192 (70)	204 (72)	248 (101)

Table 2.5: Stratified random sampling and habitat selection equations. Sources: Cochran (1977), Ault (1999a), Manly et al. (1993).

VARIABLE DESCRIPTION	UNITS	EQUATION	NOTATION
Number of total possible samples within a stratum	Number	$N_h = \frac{A_h}{U_h}$	A_h=total area of stratum h U_h=sample unit area
Weighting factor for stratum h	Fraction	$W_h = \frac{N_h}{N}$	N = total number of possible samples in the whole domain
Mean density per stratum	Fish 1000 m^{-2}	$\overline{D}_h = \frac{1}{\mathrm{n_h}} \sum_h D_j$	D_j= density per sampling unit, e.g., fish m^{-2} n_h= number of samples taken within stratum h
Overall mean density	Fish 1000 m^{-2}	$\overline{D} = \sum_h W_h \overline{D}_h$	
Sample variance per stratum		$S_h^2 = \frac{1}{(\mathrm{n_h} - 1)} \sum_h (D_j - \overline{D})^2$	
Variance of mean per stratum		$Var(\overline{D}_h) = \frac{S_h^2}{(\mathrm{n_h})} \frac{[(N_h - n_h)]}{N_h}$	
Overall variance around the mean density		$Var(\overline{D}) = \sum \frac{W_h^2 S_h^2}{n_h} - \sum_h \frac{W_h S_h^2}{N}$	
Standard error of the stratum mean	Fish 1000 m^{-2}	$SE(\overline{D}_h) = \sqrt{Var(\overline{D}_h)}$	
Total numbers of fish per stratum	Numbers of fish	$\hat{Y}_h = A_h \overline{D}_h$	
Overall numbers of fish in the domain	Numbers of fish	$\hat{Y} = \sum_h \hat{Y}_h$	
Variance of numbers of fish per stratum		$Var(\hat{Y}_h) = \frac{A_h^2 S_h^2}{n_h} * \frac{(N_h - n_h)}{N_h}$	
Overall variance of numbers of fish		$Var(\hat{Y}) = \sum [Var(\hat{Y}_h)]$	
Standard error of the numbers of fish per stratum	Numbers of fish	$SE(\hat{Y}_h) = \sqrt{Var(\hat{Y}_h)}$	
Overall standard error		$SE(\hat{Y}) = \sqrt{Var(\hat{Y})}$	
95% Confidence Intervals	Numbers of fish	$\hat{Y} \pm t_{(0.05)2-tailed,n-1} SE(\hat{Y})$	
Coefficient of variation of the mean	Percentage	$CV(\overline{D}) = \frac{SE(\overline{D})}{\overline{D}} * 100$	

Table 2.5 continued

VARIABLE DESCRIPTION	UNITS	EQUATION	NOTATION
Probability of use of a habitat unit in stratum h	Fraction	$p(\text{Use})_h = n_i / n_h$	n_i = number of stations where species i was present
Per unit amount of use in stratum h	Fish 1000 m^{-2}	$PUA_h = \overline{D}_h - \overline{D}$	$\overline{D}_h$ = mean density per stratum $\overline{D}$ = overall mean density
Relative population amount of use	Fraction of population and area	$p(P) = \hat{Y}_h / \hat{Y} \pm 95CI$ vs. $p(A) = A_h / A$	$p(P)=p(A)$: passive use $p(P)>p(A)$: affinity $p(P)<p(A)$: avoidance

Table 2.6: Parrotfish abundance data, species richness, and sampling effort from roller beam trawls in 1996-2000 (this study) vs. 1982-1983 (Campos 1985), Biscayne Bay, Florida.

	This study			Campos (1985)		
Species or Sampling descriptor	Number collected	rank	percent of top 24 spp	Number collected	rank	percent of top 20 spp
Nicholsina usta	596	12	1.84	713	9	2.43
Sparisoma chrysopterum	630	10	1.95	300	16	1.02
Sparisoma radians	129	24	0.40	238	18	0.81
Scarus iseri	24	53	negligible			
Sparisoma rubripinne	22	55	negligible			
Sparisoma atomarium	12	68	negligible			
Sparisoma viride	6	84	negligible			
Scarus coelestinus	3	107	negligible			
Scarus guacamaia	3	107	negligible			
Scarus taeniopterus	3	107	negligible			
Sparisoma aurofrenatum	1	169	negligible			
Total species (families) collected	177 (55)			160 (52)		
Proportion of total number by 20 top species	92.4%			91.4%		
Total number of stations	983 with 2 replicas each = 1966			22 with 6 replicas each = 132		
Mean surface area per trawl per net	627.03 ± 65.23 m^2			700.7 m^2		
Total area sampled	123.3 Has			9.25 Has		
Study period {sampling stratification design}	1996: April, August, November {9-stratum} 1997: March {9-stratum}, September, and November {5-stratum} 1999: November {5-stratum} 2000: March {5-stratum}			April 1982 – March 1983 (no October 1982) {No stratified design}		

Table 2.7: Number of stations surveyed per cruise (n), overall mean density ($\overline{D}$ **),** standard error of the mean SE($\overline{D}$),and relative coefficient of variation (CV) of three parrotfishes in Biscayne Bay, 1996-2000. The cruises are grouped by season: spring (April and March), summer (August and September), and fall (November). Values correspond to the actual sampling design applied for each cruise (* is 9-stratum, # is 5-stratum).

SPECIES		*Nicholsina usta*			*Sparisoma chrysopterum*			*Sparisoma radians*		
CRUISE	n	$\overline{D}$ (fish 1000 m^{-2})	SE ($\overline{D}$) (fish 1000 m^{-2})	CV (%)	$\overline{D}$ (fish 1000 m^{-2})	SE ($\overline{D}$) (fish 1000 m^{-2})	CV (%)	$\overline{D}$ (fish 1000 m^{-2})	SE ($\overline{D}$) (fish 1000 m^{-2})	CV (%)
April 1996	118*	0.113	0.029	25.44	0.498	0.074	14.93	0.031	0.014	45.50
March 1997	122*	0.272	0.066	24.42	0.326	0.055	16.96	0.063	0.022	34.46
March 2000	$110^{\#}$	0.949	0.253	26.60	0.594	0.096	16.18	0.009	0.009	99.99
August 1996	93*	0.411	0.129	31.36	0.546	0.135	24.67	0.138	0.049	35.52
September 1997	$151^{\#}$	0.582	0.092	15.85	0.432	0.073	16.96	0.274	0.073	26.70
November 1996	150*	0.781	0.183	21.54	0.597	0.082	13.71	0.124	0.034	27.70
November 1997	$120^{\#}$	1.008	0.248	24.64	1.206	0.208	17.25	0.351	0.077	22.07
November 1999	$119^{\#}$	1.101	0.203	18.42	0.413	0.079	19.18	0.043	0.022	49.89

Table 2.8: Life stages of parrotfishes and PCA results, Biscayne Bay. Lifestages are defined by size range (cm, TL). Age estimate {months or years} is provided when available. The last two columns show the first 2-3 Eigenvalues and the corresponding proportion of observed variation. See text for lifestage description; age estimates from Chapter 3.

SPECIES AND # STAGES	LIFESTAGE: SIZE RANGE {AGE}	SEASON	EIGENVALUES (1^{ST}, 2^{ND}, 3^{RD})	PROPORTION OF VARIATION (%)
N. usta	Juvenile (JP): <5 cm	Spring	2.46	35.14
			1.78	25.43
			1.35	19.35
	Initial Phase (IP):	Summer	2.86	40.88
3 stages	5-12 cm		1.44	20.61
			1.02	14.64
	Terminal Phase (TP): ≥13 cm	Fall	2.00	33.29
			1.69	28.21
			1.14	19.06
Sp. chrysopterum	JP: <5 cm {≤2.5 mo.}	Spring	2.75	39.33
			1.42	20.23
	SP: 5-11 cm {2.5-5 mo.}		1.10	15.71
		Summer	2.26	56.58
			1.14	28.47
4 stages	IP: 12-20 cm {6-11 mo.}	Fall	3.13	62.53
			0.89	17.83
	IP-Mat: ≥21 cm {>11 mo}			
Sp. radians		Spring	3.52	58.69
	(JP: <5 cm)		1.32	22.05
arbitrarily chosen stages		Summer	1.78	35.67
	(IP: 5-10 cm)		1.38	27.66
		Fall	1.61	32.23
	(TP: >10 cm)		1.38	27.64
			0.99	19.91

Table 2.9: Life stage proportions (based on total length) in *Nicholsina usta*, *Sparisoma chrysopterum*, and *Sp. radians* collections with roller beam trawl samples, Biscayne Bay, 1996-2000.

Nicholsina usta		Phase proportion (%)			
CRUISE	n	Terminal (≥13 cm)	Initial (5-12 cm)	Subadult	Juvenile (<5 cm)
April 1996	71	10.2	86.8	N/A	3.0
March 1997	43	36.4	61.1	N/A	2.5
March 2000	63	18.2	81.8	N/A	0
August 1996	66	56.1	43.9	N/A	0
September 1997	69	37.8	57.7	N/A	4.6
November 1996	110	52.6	47.4	N/A	0
November 1997	134	28.5	66.8	N/A	4.7
November 1999	64	69.3	30.7	N/A	0

Sp. chrysopterum		Phase proportion (%)			
CRUISE	n	Initial-Mat (>20 cm)	Initial (12-20 cm)	Subadult (5-11 cm)	Juvenile (<5 cm)
April 1996	22	0	18.8	75.5	5.7
March 1997	36	3.3	16.8	69.7	10.3
March 2000	85	1.2	46.7	49.2	2.9
August 1996	43	0	7.3	80.8	11.9
September 1997	93	1.3	28.6	66.0	4.0
November 1996	138	1.7	18.4	78.1	1.8
November 1997	109	2.0	34.6	62.3	1.1
November 1999	152	0.8	35.4	61.3	2.5

Sp. radians		Phase proportion (%)			
CRUISE	n	Terminal (≥20 cm)	Initial (10-20 cm)	Subadult (5-<10 cm)	Juvenile (<5 cm)
April 1996	6	31.3	50.0	N/A	18.7
March 1997	9	0.0	86.7	N/A	13.3
March 2000	1	0.0	0.0	N/A	100.0
August 1996	13	40.8	59.2	N/A	0.0
September 1997	41	54.5	47.5	N/A	0.0
November 1996	21	43.4	56.6	N/A	0.0
November 1997	40	35.7	54.7	N/A	9.6
November 1999	6	82.9	17.1	N/A	0.0

Table 2.10: Probability of use of each habitat type by lifestage, p(Use-stage), of *Nicholsina usta*, Biscayne Bay, 1996-2000. Stratum acronyms as in Table 2.2

Cruise	SPRING			SUMMER		FALL		
	Juvenile	Phase						
Habitat	April 1996	March 1997	March 2000	August 1996	September 1997	November 1996	November 1997	November 1999
SMS	0	0	0	0	0	0	0	0
SBA	0.02	0.02	0	0	0.01	0	0.05	0
SLS	0	0	0	0	0.09	0	0.06	0
HMS	0	0	0	0	0	0	0	0
HBA	0	0	0	0	0	0	0	0
HLS	0	0	0	0	0	0	0	0
BMS	0	0	0	0	0	0	0	0
BBA	0	0	0	0	0	0	0.11	0
BLS	0.20	0	0	0	0	0	0	0
	Initial	Phase						
SMS	0.05	0.05	0	0.05	0.04	0.09	0.03	0
SBA	0.21	0.29	0.44	0.15	0.23	0.26	0.25	0.14
SLS	0.03	0	0	0.39	0.36	0.22	0.44	0.38
HMS	0.02	0.20	0.25	0.17	0	0	0	0
HBA	0.04	0	0.17	0.14	0	0	0	0
HLS	0	0	0	0	0	0	0	0
BMS	0	0	0	0	0	0	0	0
BBA	0.04	0	0.33	0.25	0	0.22	0.56	0
BLS	0.01	0.33	0	0.13	0.40	0	0	0
	Terminal	Phase						
SMS	0	0.05	0	0.16	0.04	0.19	0.06	0
SBA	0.08	0.14	0.18	0.22	0.19	0.35	0.24	0.30
SLS	0	0.14	0	0.17	0.27	0.22	0.25	0.38
HMS	0	0.20	0	0	0	0	0	0
HBA	0	0	0	0	0.13	0.20	0	0
HLS	0	0	0	0	0	0	0	0
BMS	0	0	0	0	0	0	0	0
BBA	0.08	0.20	0	0.25	0.25	0.11	0.11	0.33
BLS	0	0	0	0.25	0	0.50	0	0

Table 2.11: Probability of use of each habitat type by lifestage, p(Use-stage), of *Sparisoma chrysopterum,* Biscayne Bay, 1996-2000. Stratum acronyms as in Table 2.2

Cruise	SPRING			SUMMER		FALL		
	Juvenile	Phase						
Habitat	April 1996	March 1997	March 2000	August 1996	September 1997	November 1996	November 1997	November 1999
SMS	0	0.02	0	0	0	0	0	0
SBA	0	0.04	0.02	0	0.03	0.02	0	0.01
SLS	0	0	0	0	0	0	0	0
HMS	0	0	0	0	0	0	0	0
HBA	0	0	0	0	0	0	0	0
HLS	0	0	0	0	0	0	0	0
BMS	0	0	0	0	0	0	0	0
BBA	0.08	0	0.33	0.30	0.17	0	0.08	0.17
BLS	0	0	0	0.11	0	0	0	0
	Subadult	Phase						
SMS	0	0	0.08	0.11	0.05	0	0	0.16
SBA	0.09	0.19	0.34	0.26	0.26	0.33	0.14	0.24
SLS	0.20	0.14	0	0.47	0.45	0.50	0.27	0.33
HMS	0	0	0	0	0	0	0	0
HBA	0.30	0.20	0.17	0	0	0	0	0
HLS	0.33	0	0	0	0	0	0	0
BMS	0	0	0	0	0	0	0	0
BBA	0.31	0.20	0.33	0.10	0.33	0.22	0.33	0.33
BLS	0	0	0	0.22	0.40	0.33	0	0

Table 2.11 continued

Cruise	SPRING			SUMMER		FALL		
	Initial	Phase						
Habitat	April 1996	March 1997	March 2000	August 1996	September 1997	November 1996	November 1997	November 1999
SMS	0	0	0.18	0	0.10	0	0.03	0
SBA	0	0.07	0.22	0.07	0.18	0.16	0.22	0.24
SLS	0.10	0	1.00	0	0.27	0.20	0.23	0.33
HMS	0	0.20	0.00	0	0	0	0	0
HBA	0.10	0	0.17	0	0	0	0	0
HLS	0	0	0	0	0	0	0	0
BMS	0	0	0	0	0	0	0	0
BBA	0.15	0	0.33	0	0	0.11	0.42	0.17
BLS	0	0	0	0	0	0	0	0
	Terminal	Phase						
SMS	0	0	0	0	0.71	0	0	0
SBA	0	0.02	0	0	0.68	0.01	0.02	0
SLS	0	0	0	0	0.78	0	0.07	0
HMS	0	0	0	0	0	0	0	0
HBA	0	0	0.08	0	0	0	0	0
HLS	0	0	0	0	0	0	0	0
BMS	0	0	0	0	0	0	0	0
BBA	0	0	0	0	0	0	0	0.17
BLS	0	0	0	0	0	0.33	0	0

Table 2.12: Probability of use, p(Use-sp), of each habitat type for *Sparisoma radians*, Biscayne Bay, 1996-2000. Stratum acronyms as in Table 2.2

Cruise	SPRING			SUMMER		FALL		
Habitat	April 1996	March 1997	March 2000	August 1996	September 1997	November 1996	November 1997	November 1999
SMS	0	0.02	0	0.11	0.02	0	0	0
SBA	0.04	0.08	0.02	0.20	0.19	0.12	0.13	0.03
SLS	0	0.29	0	0	0.63	0.33	0.45	0.50
HMS	0	0	0	0	0	0	0	0
HBA	0.11	0	0	0	0	0.10	0	0
HLS	0	0	0	0	0	0	0.50	0
BMS	0	0	0	0	0	0	0	0
BBA	0.17	0	0	0.11	0.25	0	0.50	0
BLS	0.25	0.33	0	0.13	0.20	0.50	0	0

Table 2.13: Length (TL, cm) modes, minima, and maxima per stratum for parrotfishes of Biscayne Bay, 1996-2000.
Abundance categories: ***abundant***= present in all cruises, bi- to multimodal distributions; ***common***= present in 4 (multimodal) to 7 (bimodal) cruises; ***occasional***= present in 3 (multimodal) to 5 (bimodal) cruises; ***rare***=1-2 cruises, very few specimens/cruise; ***absent***=none. Stratum symbology: see Table 2.2 for acronyms. <, >, = indicate ranking of occurrence
Mode symbology: the most representative mode for a given stratum is in bold (dominant stratum) or underlined (secondary stratum).

SPECIES	ABUNDANCE	STRATUM CATEGORY	MODES (cm TL)	MINIMA / MAXIMA (cm TL)
N. usta	Abundant to common	Basin axis (**SBA>BBA**)	**8-9,** 9-10, 13-14, 17-19	3-5 / 20
		Seagrass (**SLS>SMS**)	**9-10,** 13-14, 16	5-7 and 9-11 / 17-18
	Occasional	Hardbottom (**HBA>HMS**)	7-8, **10-12**	7-9 / 18
		BLS	12-13	5 / 20
	Rare to absent	BMS	1 cruise, 3 specimens	-
		HLS	none	-
Sp. chrysopterum	Abundant to common	Seagrass (**SBA**>SLS>SMS)	**6-8,** 9-10, 14-15	4-6 / 15 (20 on SBA)
		BBA	4-5, 6-7, **9-10**	4-5 / 12-14
	Occasional	BLS	**6-8**	4-5 / 9
		HBA	**6-8**, 16-17	5-6 / 22
	Rare to absent	Hardbottom (HLS>HMS)	1 cruise each	-
		BMS	none	-
Sp. radians	Abundant to common	Seagrass (**SBA>SLS**)	**6-8**, 10-11	4-6 / 14-16
	Occasional	Barebottom (**BLS>BBA**)	**7**, 10	5-7 / 12-13
	Rare	Hardbottom (HBA=HLS)	1 cruise each	
	Absent	Mainland subtidal (HMS=BMS)	none	

Table 2.14: Kruskal-Wallis nonparametric test ($\chi 2$) and Kendall’s Concordance Coefficient (W) values for habitat distribution of parrotfish lifestages (based on mean density per stratum), Biscayne Bay, 1996-2000. Chi-square ($\chi^2{}_{\text{calc}}$) and W_{calc} are adjusted for the ties occurring among some ranks. N=total number of observations, m=number of habitats, α=0.05, k=number of lifestages.

		Kruskal-Wallis: ALL HABITATS SAMPLED		
SPECIES	N (m)	χ^2_{calc}	χ^2_{Tab} (α, k-1)	P-value
N. usta	24 (8)	5.66	5.99	$0.05<P<0.10$
Sp. chrysopterum	32 (8)	6.92	7.81	$0.05<P<0.10$
Sp. radians	24 (8)	1.85	5.99	$0.5<P<0.75$
		Kruskal-Wallis: POSITIVE HABITATS ONLY		
	N (m)	χ^2_{calc}	χ^2_{Tab} (α, k-1)	P-value
N. usta	17 (3 to 7)	0.80	5.99	$0.75<P<0.90$
Sp. chrysopterum	24 (4 to 7)	9.49	7.81	$0.001<P<0.025$
Sp. radians	16 (5 to 6)	2.33	5.99	$P>0.50$
		Kendall’s Concordance Coefficient: ALL HABITAT TYPES		
	(m)	W_{calc}	W_{Tab} (α, k-1, n)	P-value
N. usta	(8)	0.62	0.60	$0.01<P<0.05$
Sp. chrysopterum	(8)	0.74	0.46	$P<0.001$
Sp. radians	(8)	0.30	0.60	$P>0.20$

Table 2.15: Comparison of parrotfish abundances and rankings in the Florida Keys, Florida (RVC) vs. Western Atlantic (AGGRA). RVC = reef fish visual census in two-stage stratified random design, 1997-2001 (this study). AGGRA = Atlantic and Gulf Rapid Reef Assessment 1997-2000 (Kramer 2003).

	RVC This study		AGRRA Kramer (2003)	
	Number observed	Rank among Scaridae	Density observed (# fish 100 m^{-2})	Rank among Scaridae
C. roseus	377	10		
N. usta	0	-		
Sc. coelestinus	436	9		
Sc. coeruleus	365	11		
Sc. guacamaia	349	12		
Sc. iseri (Sc. croicensis)	19,225	1	3.8	1
Sc. taeniopterus	787	7	3.1	3
Sc. vetula	772	8	2.8	5
Sp. atomarium	1,121	6		
Sp. aurofrenatum	8,820	2	3.6	2
Sp. chrysopterum	1,651	4		
Sp. radians	102	13		
Sp. rubripinne	1,279	5		
Sp. viride	4,151	3	1.1	4

Table 2.16: Number of stations surveyed per year (n), overall mean density ($\overline{D}$), standard error of the mean SE($\overline{D}$), and relative coefficient of variation (CV) of the four most abundant parrotfishes, in reef fish visual census (RVC) samples, Florida Keys, 1997-2001.

SPECIES		*Sc. iseri*			*Sp. aurofrenatum*		
YEAR	n	$\overline{D}$ (fish 177 m^2)	SE ($\overline{D}$)	CV (%)	$\overline{D}$ (fish 177 m^2)	SE ($\overline{D}$)	CV (%)
1997	404	5.693	0.913	16.04	4.546	0.454	9.98
1998	462	7.861	0.935	11.90	4.110	0.889	21.63
1999	438	6.203	0.487	7.85	2.823	0.210	7.42
2000	487	8.508	0.822	9.66	3.647	0.271	7.42
2001	720	7.474	0.460	6.16	3.222	0.171	5.31

SPECIES		*Sp. viride*			*Sp. chrysopterum*		
YEAR	n	$\overline{D}$ (fish 177 m^2)	SE ($\overline{D}$)	CV (%)	$\overline{D}$ (fish 177 m^2)	SE ($\overline{D}$)	CV (%)
1997	404	1.749	0.273	15.60	0.547	0.150	27.37
1998	462	1.124	0.279	24.82	0.426	0.151	35.51
1999	438	1.199	0.139	11.58	0.938	0.276	29.37
2000	487	1.321	0.136	10.33	0.959	0.170	17.75
2001	720	1.117	0.076	6.76	0.492	0.081	16.45

Table 2.17: Summary of the Principal Component Analysis (PCA) results for the ontogenetic habitat shift in parrotfishes of Florida Keys, per species and year. When appropriate, lifestages are defined by the size range (cm, TL), and an age estimate {months or years} is provided when available. See text for lifestage description; age estimates come from models developed in Chapter 3.

SPECIES AND # STAGES	LIFESTAGE: SIZE RANGE {AGE}	YEAR	EIGENVALUES	PROPORTION OF VARIATION (%)
Sc. iseri	Juvenile (JP): <4 cm {<5 mo.}	1997	4.39	87.82
	Initial Phase -Female (IPF):	1998	4.63	92.63
4 stages	4-11 cm {5-14.4 mo.}	1999	4.55	90.95
	Initial Phase -Male (IPM): 12-16 cm {1.4-2.4 y}	2000	4.06 0.70	79.34 11.64
	Terminal Phase (TP): ≥17 cm {2.6-7 y}	2001	5.25 0.49	87.47 8.24
Sp. aurofrenatum	JP: <4 cm {<2.4 mo}	1997	3.84 0.58	76.78 11.56
	Subadult (SP): 4-10 cm {2.4-7.2 mo}	1998	3.77 0.64	75.40 12.85
4 stages	Initial Phase (IP): 11-18 cm	1999	3.31 0.85	66.18 16.90
	{8.4 mo-1.5 y}	2000	4.41 0.60	73.49 10.04
	Terminal Phase (TP): ≥19 cm {≥1.6-7 y}	2001	4.42 3.74	73.66 11.27

Table 2.17 continued

SPECIES AND # STAGES	LIFESTAGE: SIZE RANGE {AGE}	YEAR	EIGENVALUES	PROPORTION OF VARIATION (%)
Sp. viride	JP: <4 cm	1997	3.83	76.68
	{≤2.5 months}		0.58	11.56
		1998	3.46	69.25
	SP: 4-11 cm		0.69	13.89
4 stages	{2.5-6 mo.}	1999	3.09	61.76
			0.84	16.88
	IP: 12-24 cm	2000	3.32	55.43
	{6-13 mo.}		1.10	18.34
			0.61	10.10
	TP: ≥25 cm	2001	3.54	59.02
	{≥1.2-10 y}		1.13	18.81
			0.69	11.52
Sp. chrysopterum		1997	2.07	41.52
	JP: <5 cm		1.10	22.06
	{≤2.5 mo.}		0.70	14.04
		1998	2.25	44.91
	SP: 5-11 cm		0.96	19.27
	{2.5-5 mo.}		0.88	17.66
4 stages		1999	2.72	54.39
	IP: 12-30 cm		0.96	19.12
	{6 mo-1.6 y}		0.69	13.88
		2000	2.49	41.54
	TP: ≥31 cm		1.14	18.94
	{1.8-5 y}		0.92	15.28
		2001	2.57	42.85
			1.09	18.16
			0.80	13.34

Table 2.18: Life stage proportions (based on total length) of *Scarus iseri*, *Sparisoma aurofrenatum*, *Sp. viride,* and *Sp. chrysopterum* records in reef fish visual censuses (RVC), Florida Keys, 1997-2001.

Sc. iseri		Phase proportion (%)			
CRUISE	n	Terminal (>17 cm)	Initial Male (12-16 cm)	Initial Female (4-11 cm)	Juvenile (<4 cm)
1997	2,948	0.2	2.6	81.8	15.3
1998	3,843	0.9	6.7	88.2	4.2
1999	2,402	0.7	5.9	84.7	8.7
2000	4,205	0.6	3.7	85.4	10.3
2001	5,828	0.2	3.7	88.2	7.8

Sp. aurofrenatum		Phase proportion (%)			
CRUISE	n	Terminal (>19 cm)	Initial (11-18 cm)	Subadult (4-10 cm)	Juvenile (<4 cm)
1997	1,503	12.4	38.5	46.1	3.0
1998	1,363	9.0	35.6	52.3	3.1
1999	1,226	6.3	34.5	53.7	5.4
2000	1,731	6.0	27.8	60.1	6.1
2001	2,997	6.4	27.7	60.5	5.4

Sp. viride		Phase proportion (%)			
CRUISE	n	Terminal (>25 cm)	Initial (12-24 cm)	Subadult (4-11 cm)	Juvenile (<4 cm)
1997	902	20.8	38.3	37.1	3.9
1998	713	21.4	41.9	34.3	2.4
1999	461	22.2	40.7	33.9	3.2
2000	748	25.0	34.7	36.3	4.0
2001	1,327	21.5	38.8	35.2	4.5

Sp. chrysopterum		Phase proportion (%)			
CRUISE	n	Terminal (≥31 cm)	Initial (12-30 cm)	Subadult (5-11 cm)	Juvenile (<5 cm)
1997	290	0.9	74.3	24.5	0.4
1998	170	2.9	87.5	9.6	0.0
1999	239	0.6	97.6	1.2	0.0
2000	498	5.7	84.8	8.4	1.2
2001	453	14.4	80.4	5.2	0.0

Table 2.19: Probability of use of each habitat type for parrotfishes, Florida Keys, 1997-2001. (a) *Scarus iseri*, (b) *Sparisoma aurofrenatum* (c) *Sp. viride*, (d) *Sp. chrysopterum.*

(a) *Sc. iseri*

Habitat/Year	1997	1998	1999	2000	2001	Mean±SD
Inshore	0.88	0.80	0.71	0.61	0.71	0.74±0.10
Midchannel	0.92	0.98	0.95	0.89	0.97	0.94±0.04
Offshore	0.91	0.91	0.97	0.83	0.96	0.92±0.06
Shallow fore reef	0.82	0.80	0.94	0.81	0.74	0.82±0.07
Mid-depth fore reef	0.73	0.85	0.77	0.77	0.74	0.77±0.05
Deep fore reef	N/A	N/A	N/A	0.92	0.88	0.90±0.03

(b) *Sp. aurofrenatum*

Habitat/Year	1997	1998	1999	2000	2001	Mean±SD
Inshore	0.51	0.26	0.36	0.33	0.29	0.35±0.10
Midchannel	0.92	0.84	0.82	0.85	0.80	0.85±0.05
Offshore	0.94	0.92	0.97	0.84	0.91	0.92±0.05
Shallow fore reef	0.90	0.81	0.88	0.90	0.81	0.86±0.05
Mid-depth fore reef	0.98	1.00	0.88	0.83	0.86	0.91±0.08
Deep fore reef	N/A	N/A	N/A	0.83	0.96	0.90±0.09

(c) *Sp. viride*

Habitat/Year	1997	1998	1999	2000	2001	Mean±SD
Inshore	0.71	0.49	0.57	0.30	0.54	0.52±0.15
Midchannel	0.86	0.71	0.87	0.77	0.79	0.80±0.07
Offshore	0.76	0.65	0.80	0.67	0.73	0.72±0.06
Shallow fore reef	0.86	0.85	0.75	0.83	0.69	0.80±0.07
Mid-depth fore reef	0.78	0.54	0.44	0.55	0.50	0.56±0.13
Deep fore reef	N/A	N/A	N/A	0.25	0.28	0.27±0.02

(d) *Sp. chrysopterum*

Habitat/Year	1997	1998	1999	2000	2001	Mean±SD
Inshore	0.39	0.23	0.36	0.17	0.29	0.29±0.09
Midchannel	0.35	0.11	0.37	0.31	0.26	0.28±0.10
Offshore	0.13	0.12	0.20	0.33	0.29	0.21±0.09
Shallow fore reef	0.28	0.28	0.25	0.43	0.20	0.29±0.09
Mid-depth fore reef	0.26	0.26	0.17	0.29	0.19	0.23±0.05
Deep fore reef	N/A	N/A	N/A	0.17	0.12	0.15±0.04

Table 2.20: Probability of use in each region for parrotfishes, Biscayne National Park and Florida Keys, 1997-2001.

(a) *Sc. iseri*

Habitat/Year	1997	1998	1999	2000	2001	Mean±SD
Biscayne National Park	0.71	0.90	0.78	0.85	0.89	0.83±0.08
Upper Keys	0.96	0.95	0.88	0.78	0.84	0.88±0.08
Middle Keys	0.77	0.85	0.71	0.76	0.75	0.77±0.05
Lower Keys	0.88	0.80	0.93	0.81	0.78	0.84±0.06

(b) *Sp. aurofrenatum*

Habitat/Year	1997	1998	1999	2000	2001	Mean±SD
Biscayne National Park	0.91	0.97	0.95	0.91	0.87	0.92±0.04
Upper Keys	0.97	0.89	0.79	0.89	0.88	0.88±0.06
Middle Keys	0.96	0.82	0.92	0.84	0.78	0.86±0.07
Lower Keys	0.78	0.65	0.82	0.69	0.79	0.75±0.07

(c) *Sp. viride*

Habitat/Year	1997	1998	1999	2000	2001	Mean±SD
Biscayne National Park	0.81	0.85	0.84	0.69	0.78	0.79±0.06
Upper Keys	0.99	0.83	0.90	0.75	0.74	0.84±0.11
Middle Keys	0.83	0.60	0.43	0.52	0.48	0.57±0.16
Lower Keys	0.72	0.63	0.53	0.54	0.61	0.61±0.08

(d) *Sp. chrysopterum*

Habitat/Year	1997	1998	1999	2000	2001	Mean±SD
Biscayne National Park	0.33	0.22	0.16	0.41	0.22	0.27±0.10
Upper Keys	0.22	0.13	0.48	0.39	0.26	0.30±0.14
Middle Keys	0.26	0.26	0.25	0.41	0.22	0.28±0.07
Lower Keys	0.28	0.24	0.10	0.17	0.17	0.19±0.07

Table 2.21: length (TL, cm) modes, minima, and maxima per stratum for parrotfishes of Florida Keys, 1997-2001. Stratum symbology: see Table 2.2 for acronyms. The highest length mode for a given stratum is underlined.

SPECIES	ZONE	STRATUM CATEGORY	MODES (cm TL)	MINIMA TO MAXIMA
Sc. iseri	Onshore	IN-U / IN-P	4-6, 12-14 / 4-6, 10-11, 14-15	2 to 15 / 1 to 15
		MCH-U / MCH-P	5-7, 9-10, 13 / 5-7, 10, 13-15	1 to 15 / 2 to 20
	Offshore	OFF-U / OFF-P	4-6, 10-12 / 5-6, 8-10	2 to 18 / 1 to 20
		FORE-Sh-U / FORE-Sh-P	4-6, 10, 15-17 / 5-7, 12-13	2 to 20 / 1 to 20
	Forereefs	FORE-Md-U / FORE-Md-P	5-6, 8, 10, 13-15 / 5-6, 9-10, 14-15	2 to 20 / 2 to 20
		FORE-Dp-U / FORE-Dp-P	5-7, 12-13, 16-18 / ND	3 to 20 / ND
Sp. aurofrenatum	Onshore	IN-U / IN-P	5-7, 10-12, 15-16 / 4-6, 16	3 to 25 / 3 to 18
		MCH-U / MCH-P	4-6, 7-8, 10, 14-15 / 6-8, 14-15	2 to 27 / 2 to 28
	Offshore	OFF-U / OFF-P	4-6, 10-12 / 5-7, 11-12, 14-15	3 to 27 / 2 to 28
		FORE-Sh-U / FORE-Sh-P	4-5, 8-9, 14-15 / 6-8, 10, 15	2 to 28 / 2 to 28
	Forereefs	FORE-Md-U / FORE-Md-P	5-6, 10, 15 / 5-6, 10, 15	2 to 28 / 2 to 28
		FORE-Dp-U / FORE-Dp-P	7-8 / ND	3 to 26 / ND

Table 2.21 continued:

SPECIES	ZONE	STRATUM CATEGORY	MODES (cm TL)	MINIMA TO MAXIMA
Sp. viride	Onshore	IN-U / IN-P	4-6, 10 / 4-8, 15-16	2 to 33 / 3 to 40
		MCH-U / MCH-P	5-6, 12 / 5, 17-18, 20	2 to 40 / 3 to 35
	Offshore	OFF-U / OFF-P	4-6, 12-14, 25, 30 / 5-6, 10, 12, 15	3 to 40 / 3 to 35
		FORE-Sh-U / FORE-Sh-P	4-5, 15, 18-20, 30 / 3-5, 20-21, 30	2 to 45 / 1 to 45
	Forereefs	FORE-Md-U / FORE-Md-P	5-6, 20, 30 / 4-5, 20, 30	2 to 60 / 2 to 60
		FORE-Dp-U / FORE-Dp-P	25-27 / ND	16 to 36 / ND
Sp. chrysopterum	Onshore	IN-U / IN-P	11-12, 14-15, 20 / 12-13, 15, 18	4 to 36 / 4 to 30
		MCH-U / MCH-P	5-6, 16-18, 22 / 25	3 to 40 / 7 to 39
	Offshore	OFF-U / OFF-P	13-15, 25 / 27-28, 35	2 to 44 / 14 to 28
		FORE-Sh-U / FORE-Sh-P	17-20, 25-27 / 12-15, 17-20, 25	4 to 35 / 6 to 40
	Forereefs	FORE-Md-U / FORE-Md-P	16-18, 25, 35-36 / 13, 20, 25	4 to 37 / 10 to 42
		FORE-Dp-U / FORE-Dp-P	24-25 / ND	25 to 35 / ND

Table 2.22: Summary of habitat selection by parrotfishes in the Florida Keys, 1997-2001, based on the measure of relative population amount of use. The categories negative selection (-), positive selection (+), and passive selection (=) are explained in the text. See Table 2.17 for lifestage definitions.
* indicates a general trend associated with high variability among years.

SPECIES (lifestage)	PROTECTION STATUS	STRATUM					
		INSHORE	MID CHANNEL	OFFSHORE	FORE REEF SHALLOW	FORE REEF MID–DEPTH	FORE REEF DEEP
Sc. iseri (JP)	Unprotected	=*	+	=*	–	=	–
	Protected	–	=	–	=	=	ND
Sc. iseri (IPF)	Unprotected	+	+	+	=*	–	–
	Protected	=	+ *	= to +	=*	–	ND
Sc. iseri (IPM)	Unprotected	–	–	=*	+	–	+ and –
	Protected	=	+ *	–	–	=	ND
Sc. iseri (TP)	Unprotected	–	–	–	–	+	+
	Protected	–	–	–	=	=*	ND
Sp. aurofrenatum (JP)	Unprotected	–	+	=	+	–	–
	Protected	–	–	–	= to +	=*	ND
Sp. aurofrenatum (SP)	Unprotected	–	=*	+	–	+	–
	Protected	–	=*	+	=	=	ND
Sp. aurofrenatum (IP)	Unprotected	–	–	+	= to +	+	–
	Protected	–	= to –	=*	+	=*	ND
Sp. aurofrenatum (TP)	Unprotected	–	= to –	=*	= to –	= to +	+ and –
	Protected	–	– to =	– to =	=*	=*	ND

Table 2.22 continued:

SPECIES (lifestage)	PROTECTION STATUS	STRATUM					
		INSHORE	MID CHANNEL	OFFSHORE	FORE REEF SHALLOW	FORE REEF MID–DEPTH	FORE REEF DEEP
Sp. viride (JP)	Unprotected	+	=*	+	+	=*	–
	Protected	–	–	=	=*	=*	ND
Sp. viride (SP)	Unprotected	+	+	+	+	– *	–
	Protected	=*	+ *	=*	=*	– to =	ND
Sp. viride (IP)	Unprotected	–	–	+	+	=*	–
	Protected	– to =	– to =	=*	=*	–	ND
Sp. viride (TP)	Unprotected	–	–	+	+	+	– to no
	Protected	–	–	=*	=*	+	ND
Sp. chrysopterum (SP)	Unprotected	–	+	+	+	–	–
	Protected	–	–	–	+	–	ND
Sp. chrysopterum (IP)	Unprotected	=	= to +	=*	–	–	–
	Protected	=*	–	– to =	=*	=*	ND
Sp. chrysopterum (TP)	Unprotected	–	–	–	– and +	+	–
	Protected	–	–	–	=*	– to =	ND

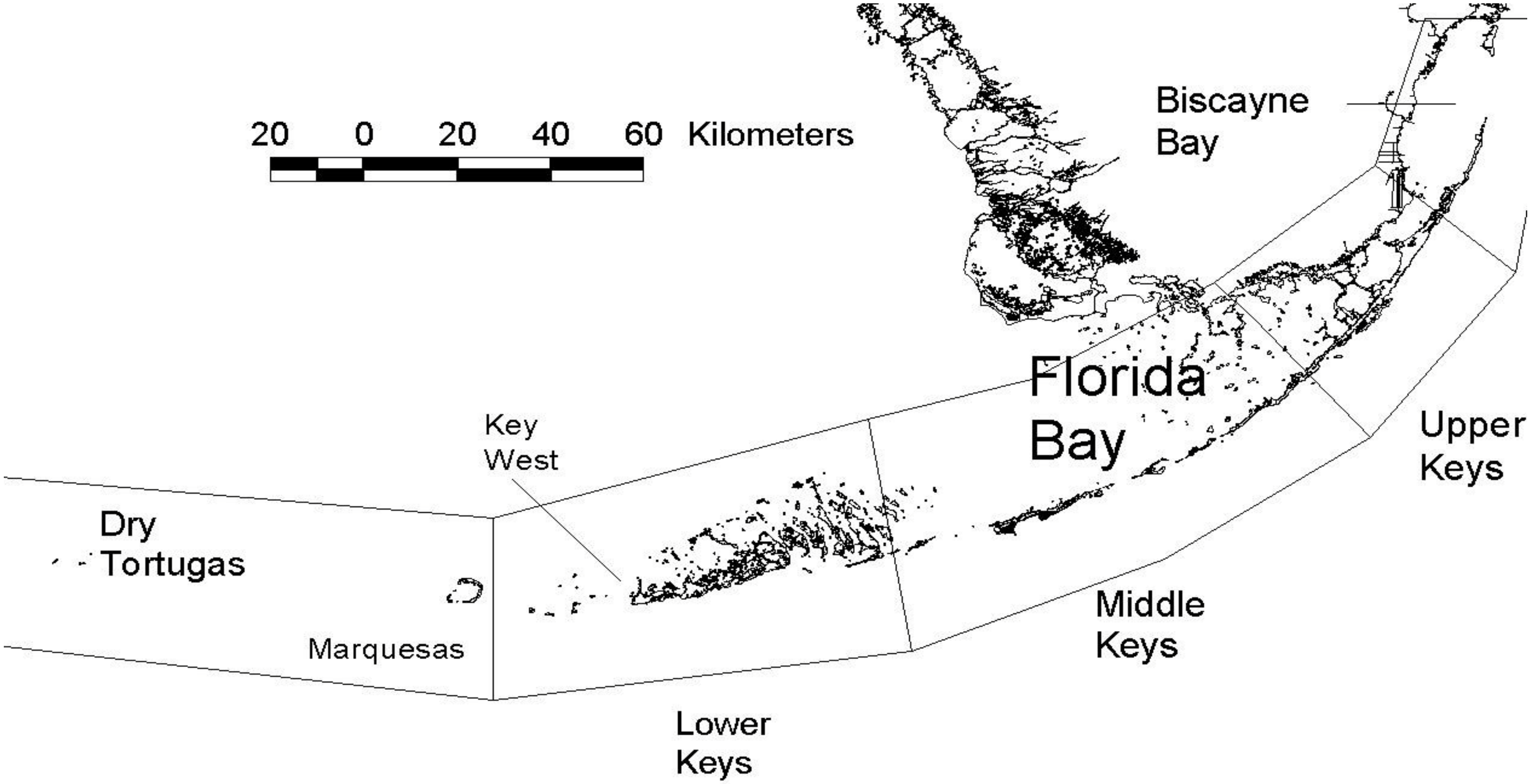


Figure 2.1: Domains of the study area, Biscayne Bay, and Florida reef tract (with Upper, Middle, and Lower Keys regions).

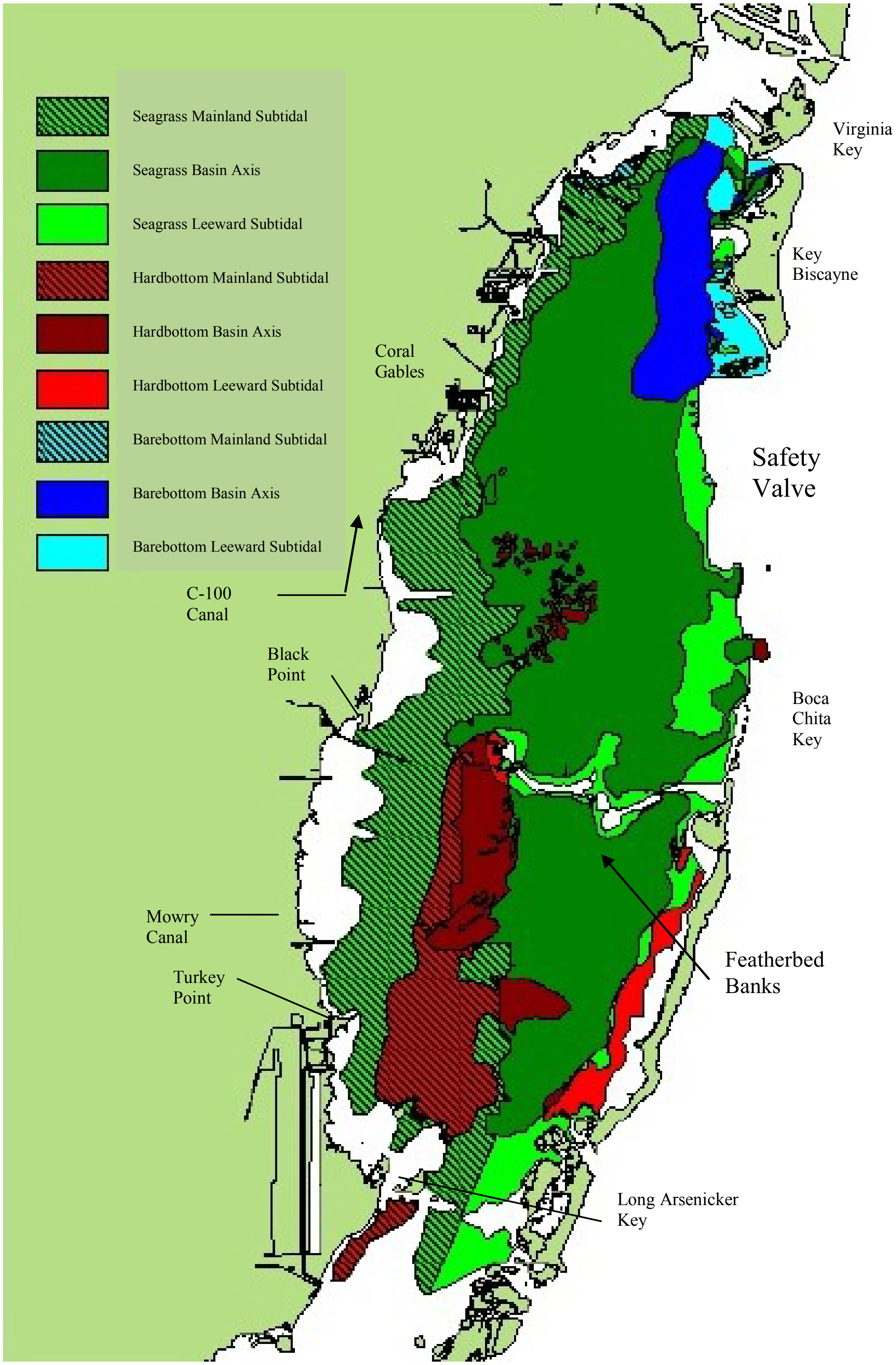


Figure 2.2: Biscayne Bay 9-stratum distribution of habitat types. Sources: Ault et al. (1999b), Diaz (2001), Wang et al. (2003).

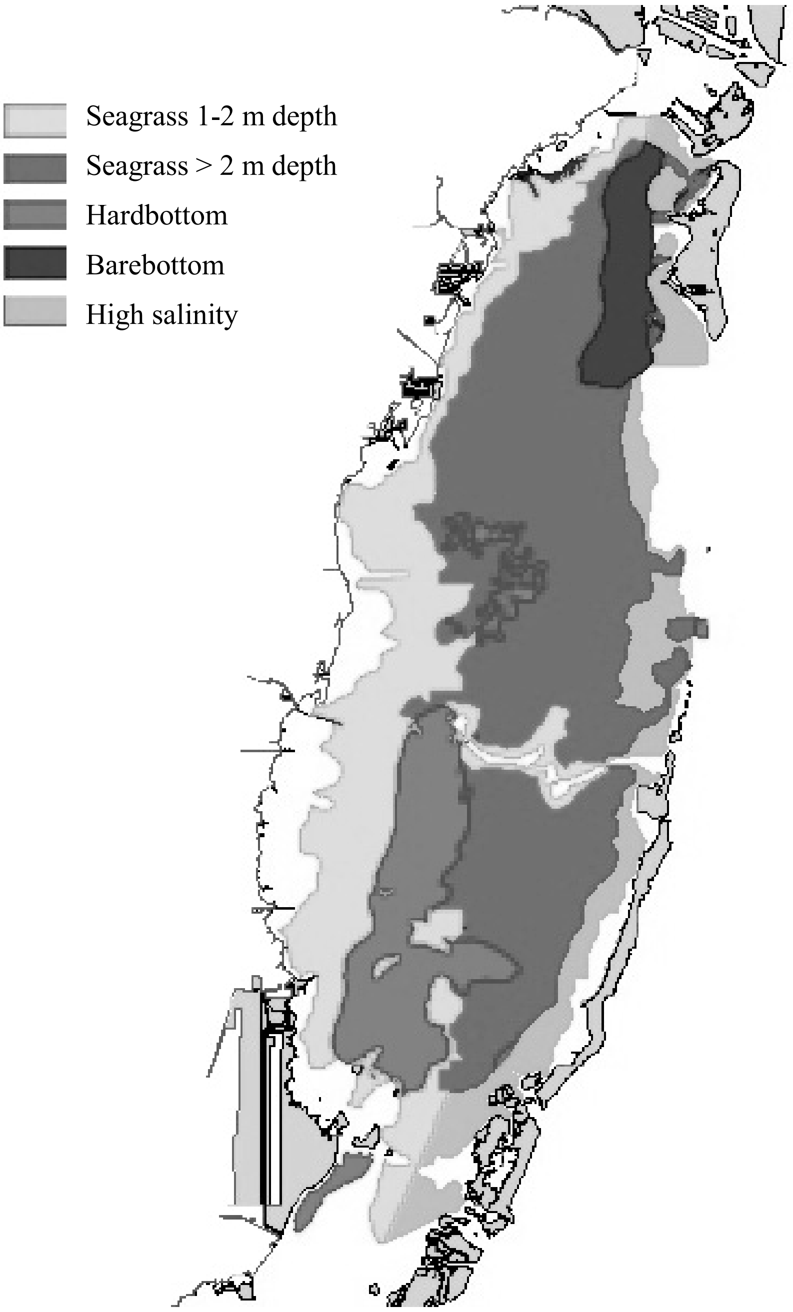


Figure 2.3: Biscayne Bay 5-stratum distribution of habitat types. Sources: Ault et al. (1999b), Diaz (2001), Wang et al. (2003).

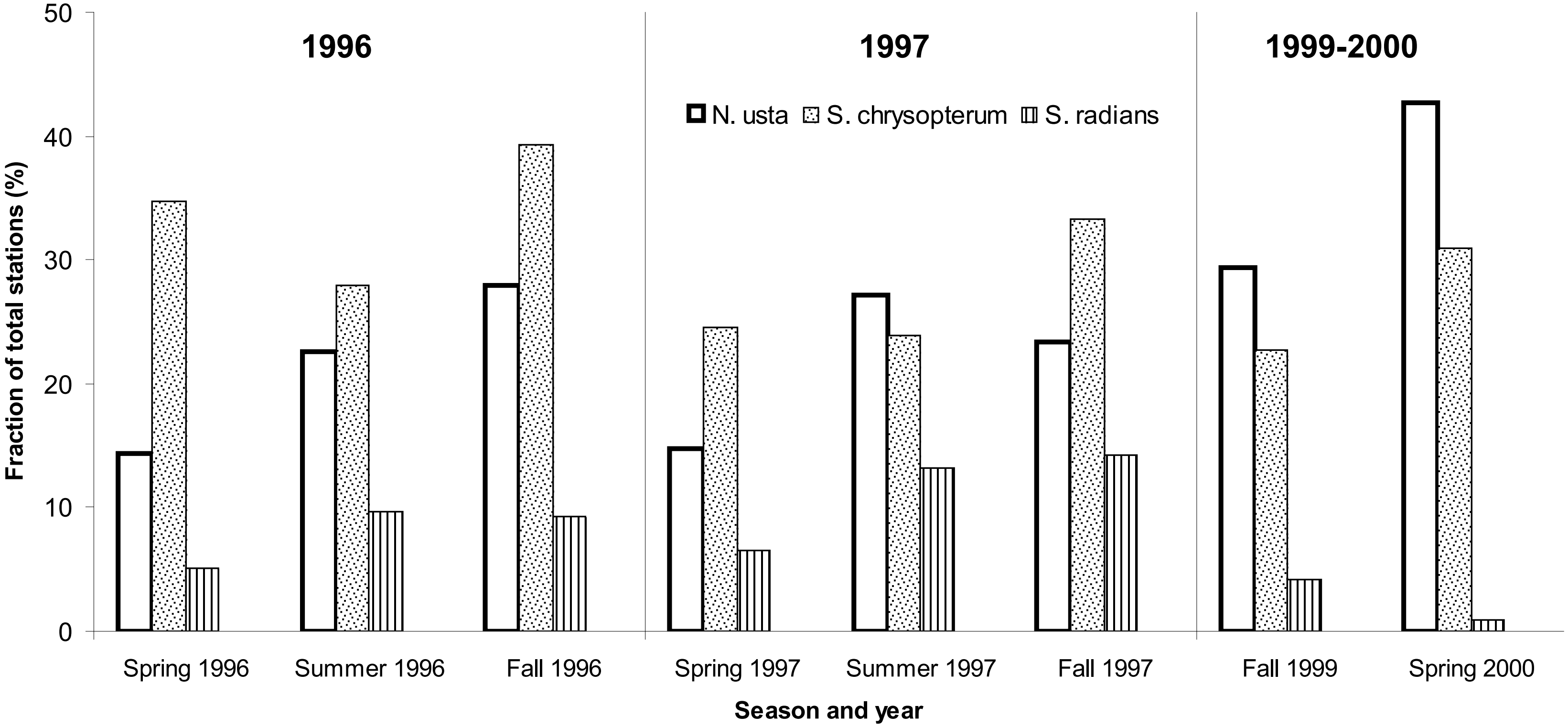


Figure 2.4: Frequency of occurrence of three parrotfishes in trawl collections, Biscayne Bay, 1996-2000. The scale of the X axis is not continuous.

(a)

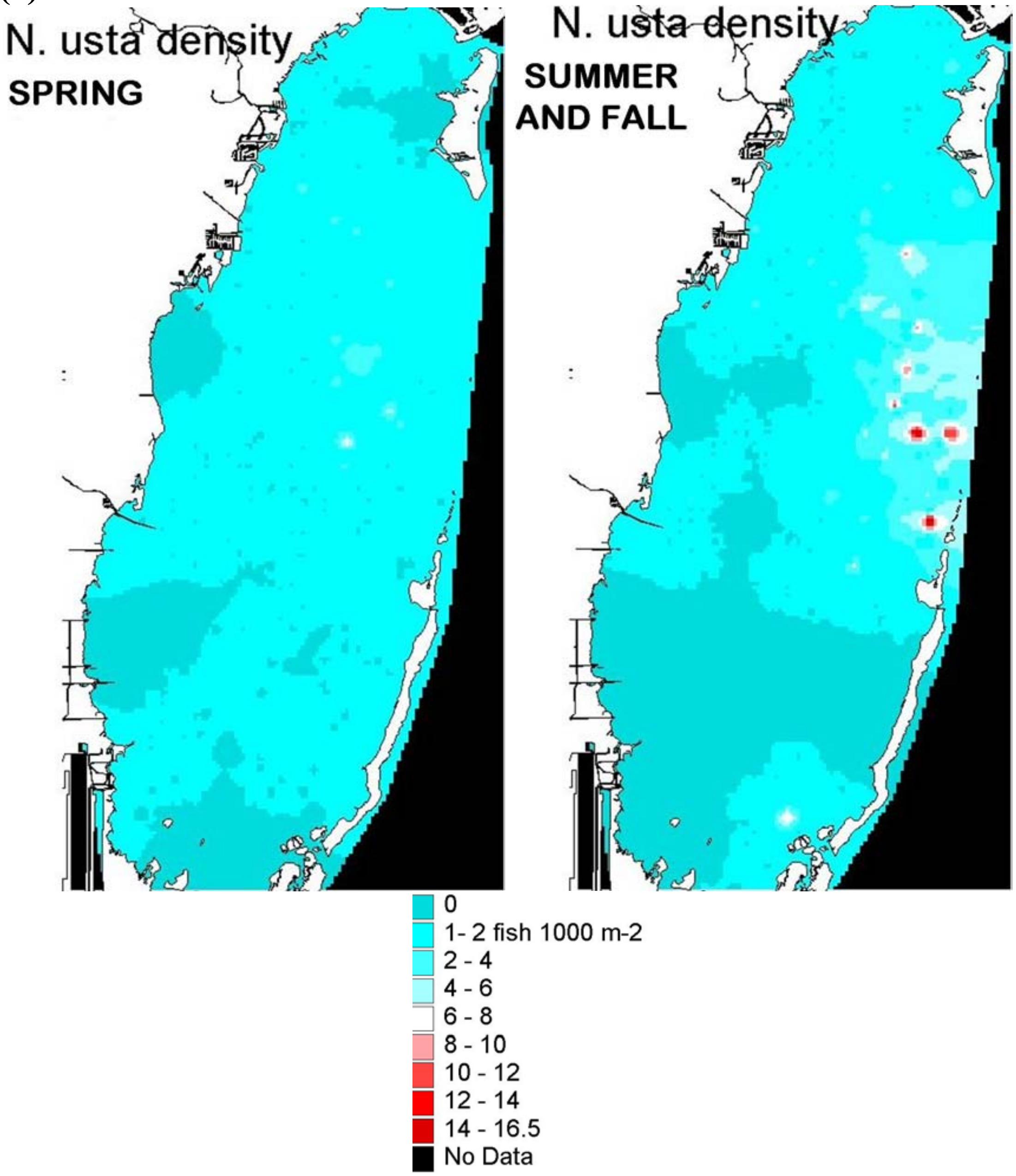


Figure 2.5: Seasonal distribution by density (fish 1000 m^{-2}) of (a) *Nicholsina usta*, (b) *Sparisoma chrysopterum*, and (c) *Sparisoma radians* in Biscayne Bay. The points are a composite of the cruises conducted between 1996 and 2000. SPRING= 3 cruises, SUMMER and FALL = 5 cruises.

(b)

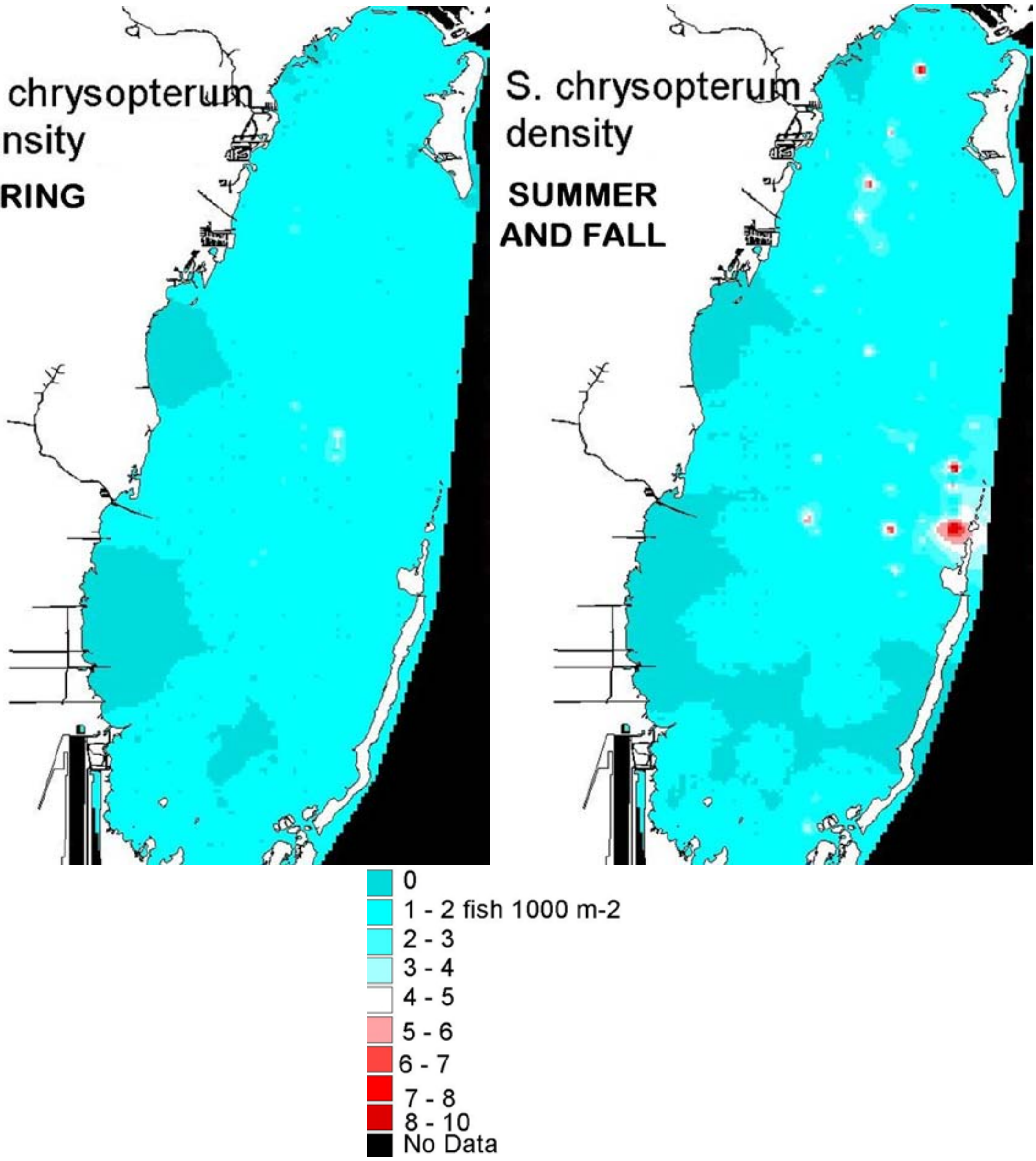


Figure 2.5 continued

(c)

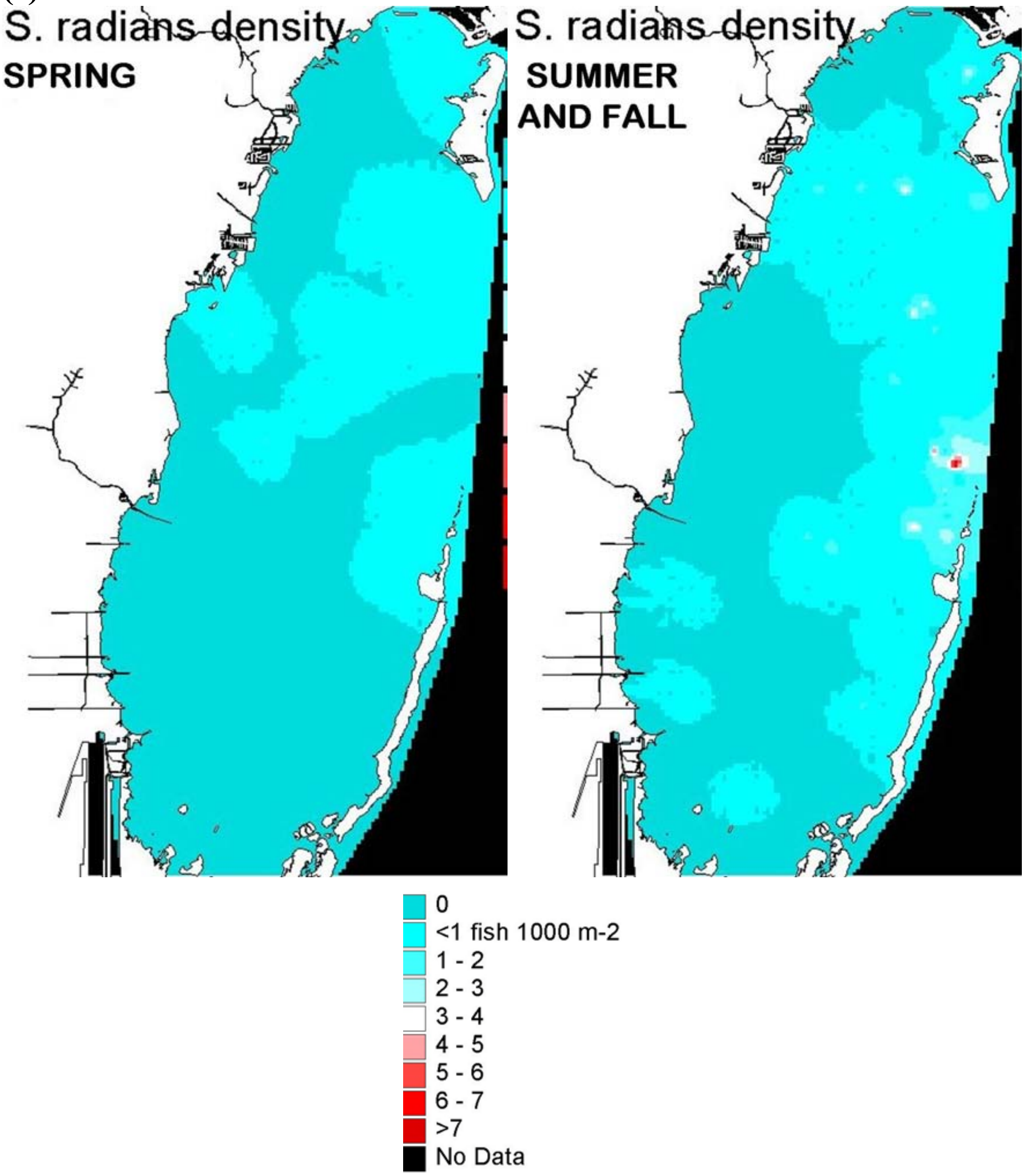


Figure 2.5 continued

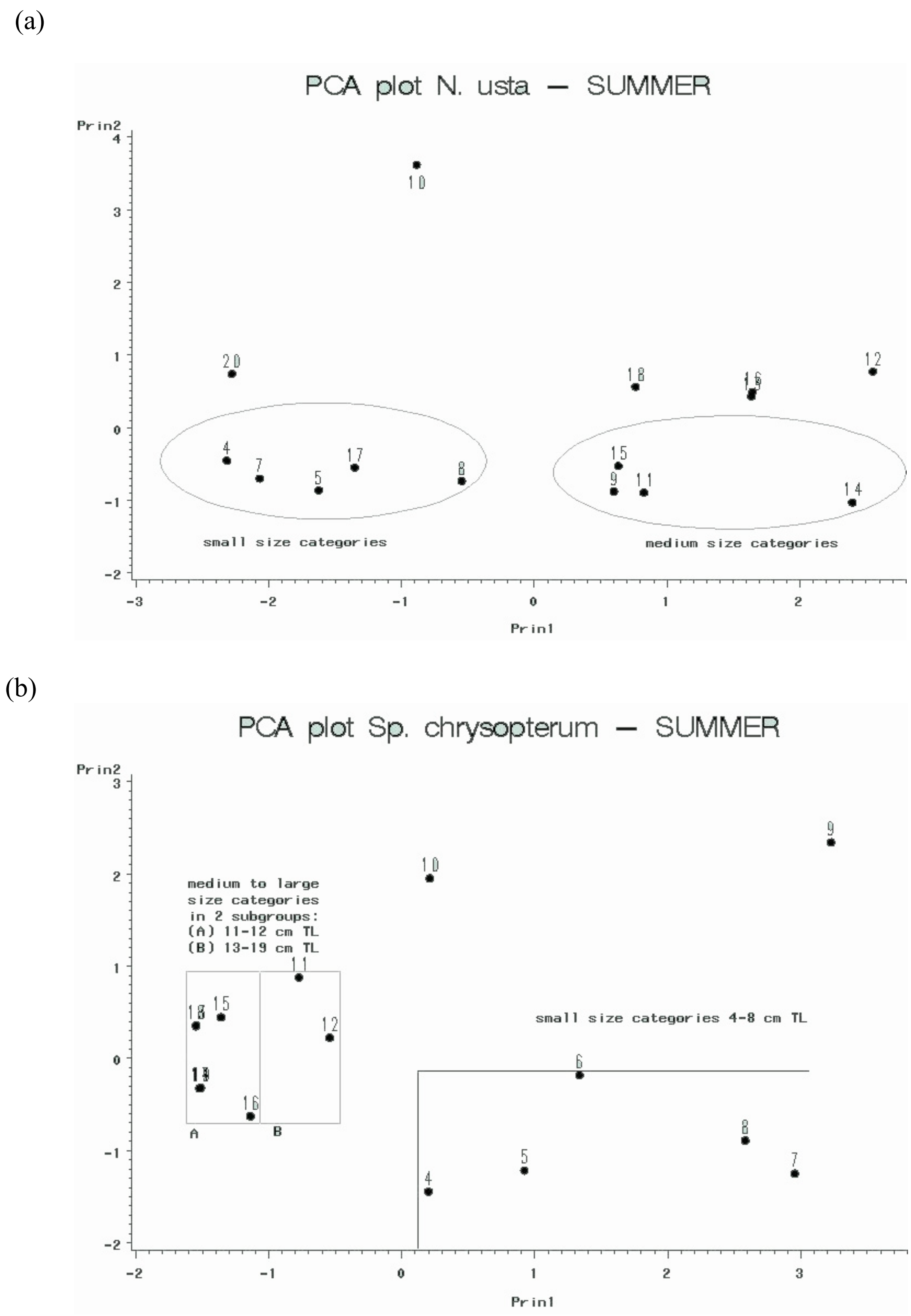


Figure 2.6: Principal Component Analysis results on size category grouping based on habitat shifts per parrotfish species, Biscayne Bay, 1996-2000. (a) *Nicholsina usta* in summer, (b) *Sparisoma chrysopterum* in summer. The plots show Principal Component 2 (PC2) against Principal Component 1 (PC1).

(a)

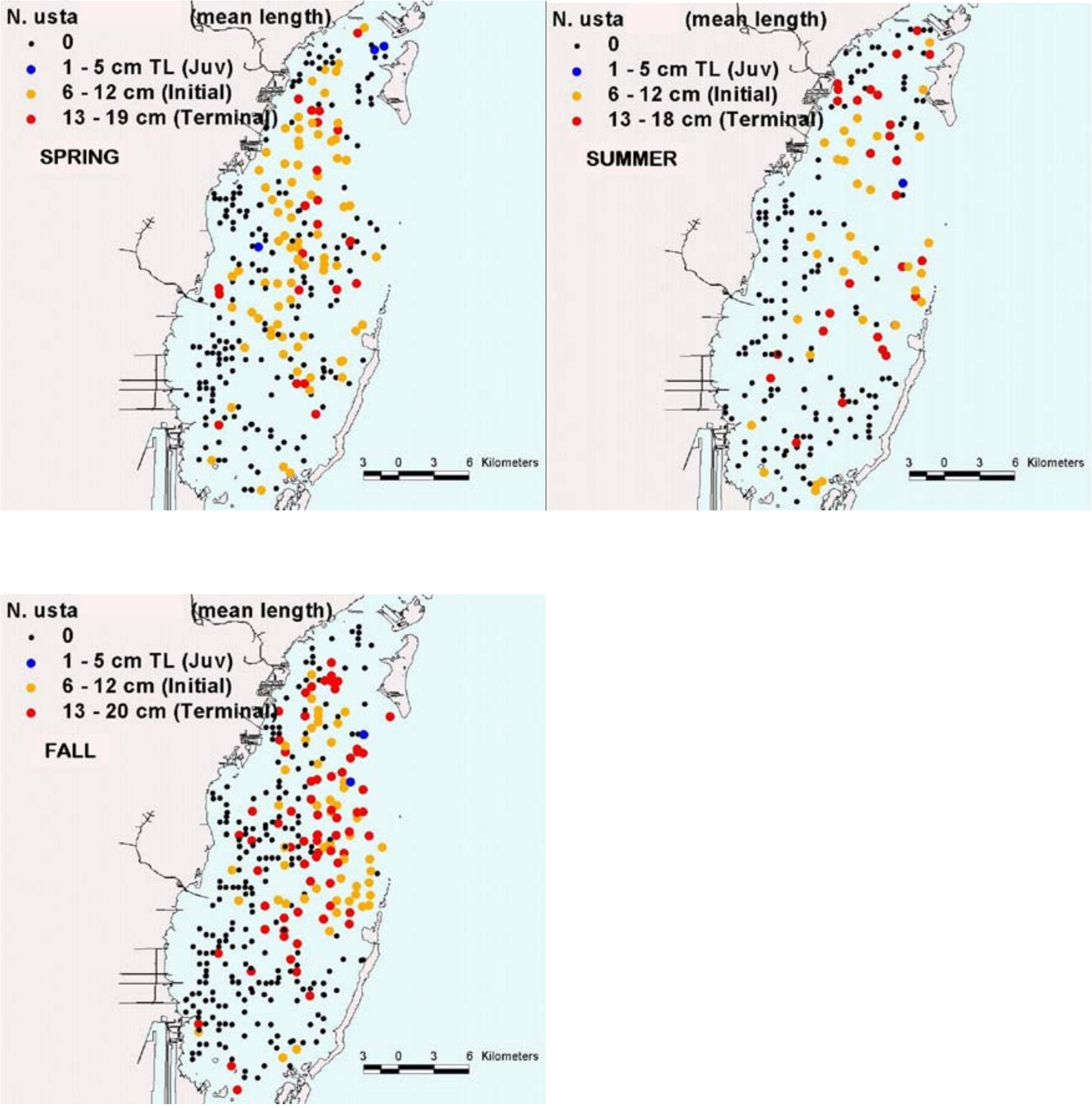


Figure 2.7: Seasonal distribution by size (TL, cm) and lifestage (juvenile, immature/subadult, initial phase, terminal phase) of (a) *Nicholsina usta*, (b) *Sp. chrysopterum*, and (c) *Sp. radians* in Biscayne Bay. The points are a composite of the cruises conducted between 1996 and 2000. Upper panels = spring and summer months; lower panels = fall months.

(b)

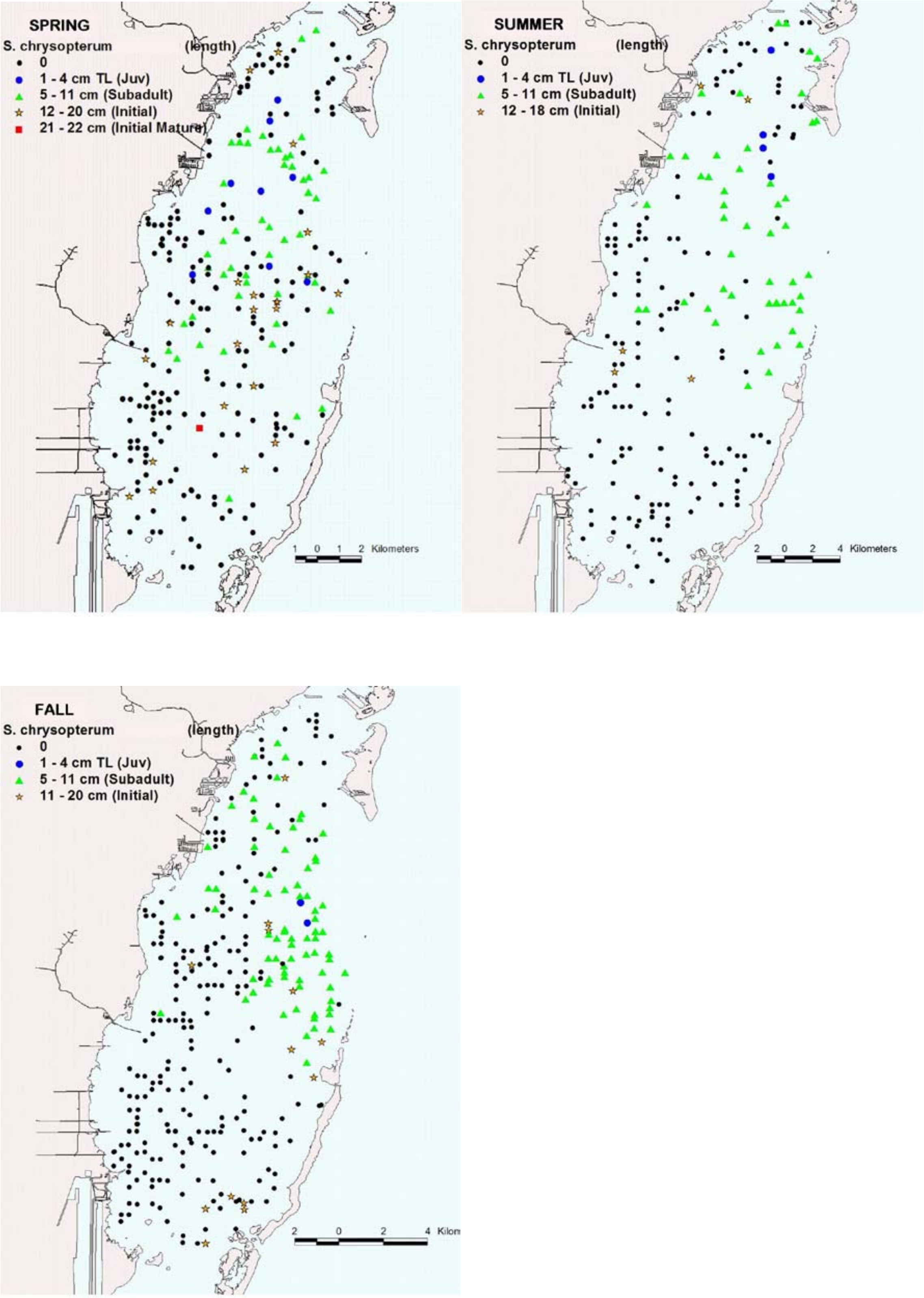


Figure 2.7 continued

(c)

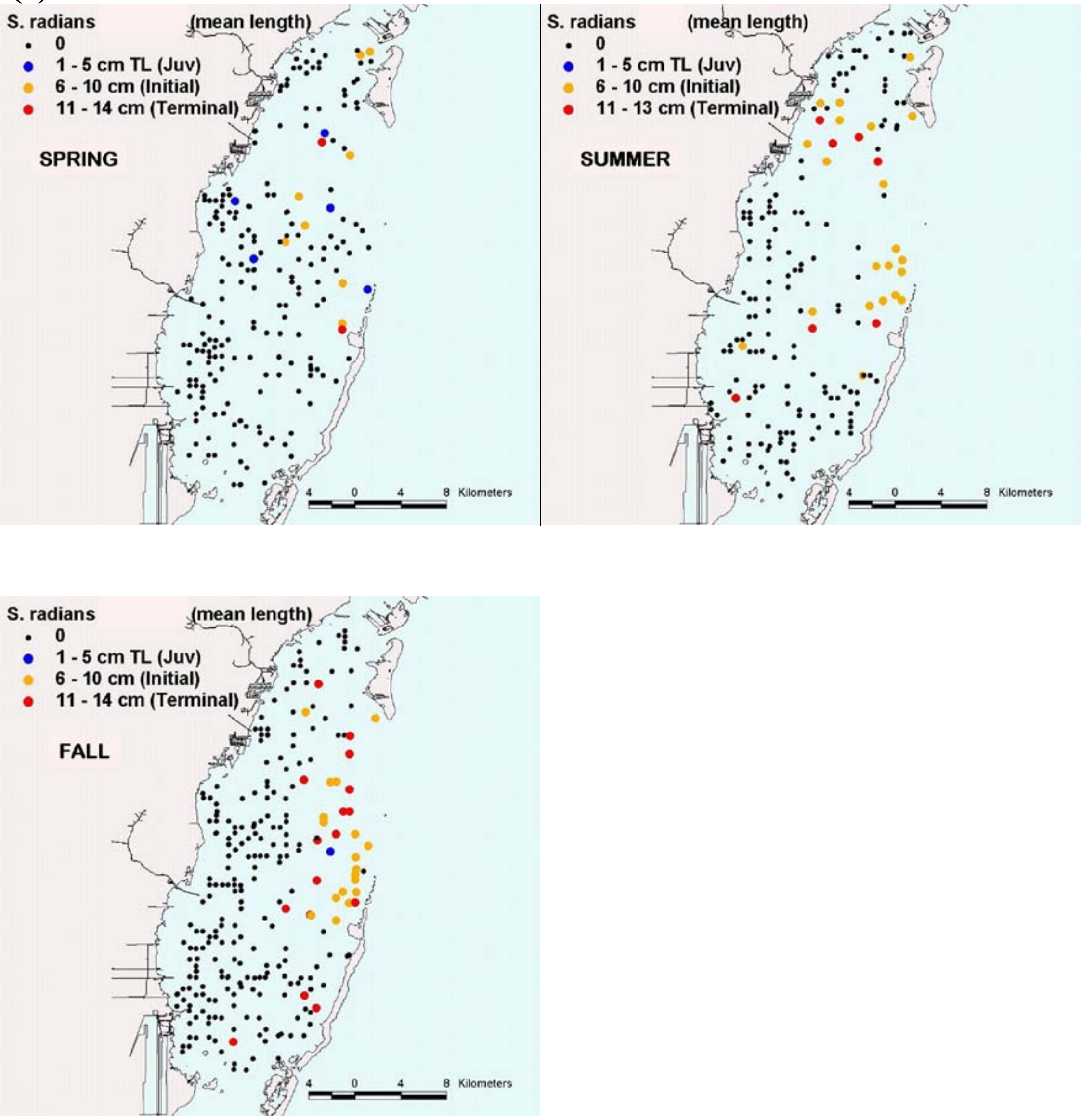


Figure 2.7 continued

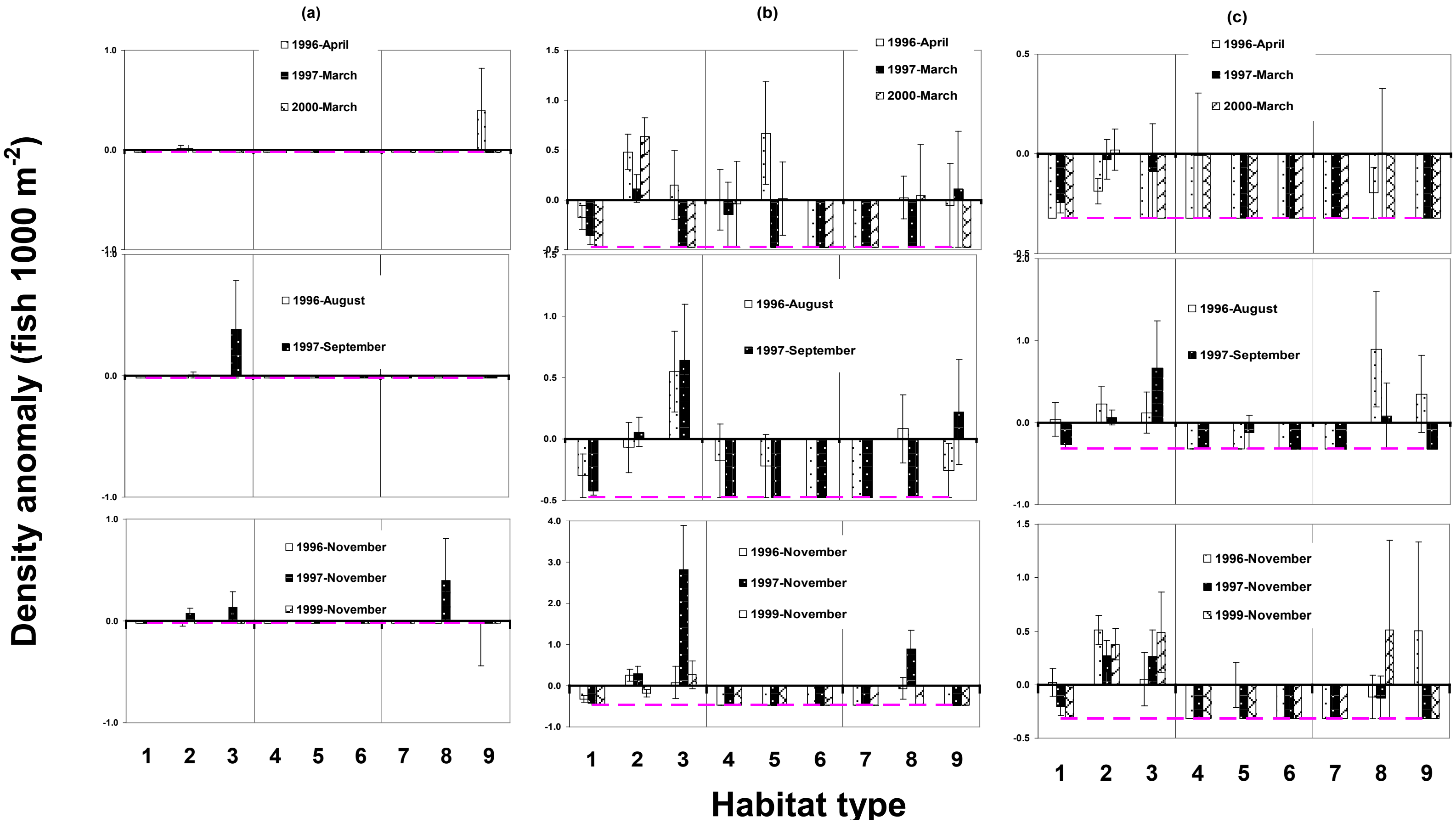


Figure 2.8: Per-unit amount of use by lifestage (PUA-stage) of *Nicholsina usta*, expressed as stratum deviations from the bay-wide lifestage mean density in Biscayne Bay, 1996-2000. (a) Juvenile phase (JP), (b) Initial phase (IP), and (c) Terminal phase (TP). Global mean density is set to zero. Error bars represent the standard error of the stratum mean density. Hatched horizontal line indicates the values where parrotfish were absent. Upper panel=spring cruises; middle panel=summer cruises; bottom panel=fall cruises. Stratum symbology: see Table 2.2 for habitat code number, and text for life stage definitions.

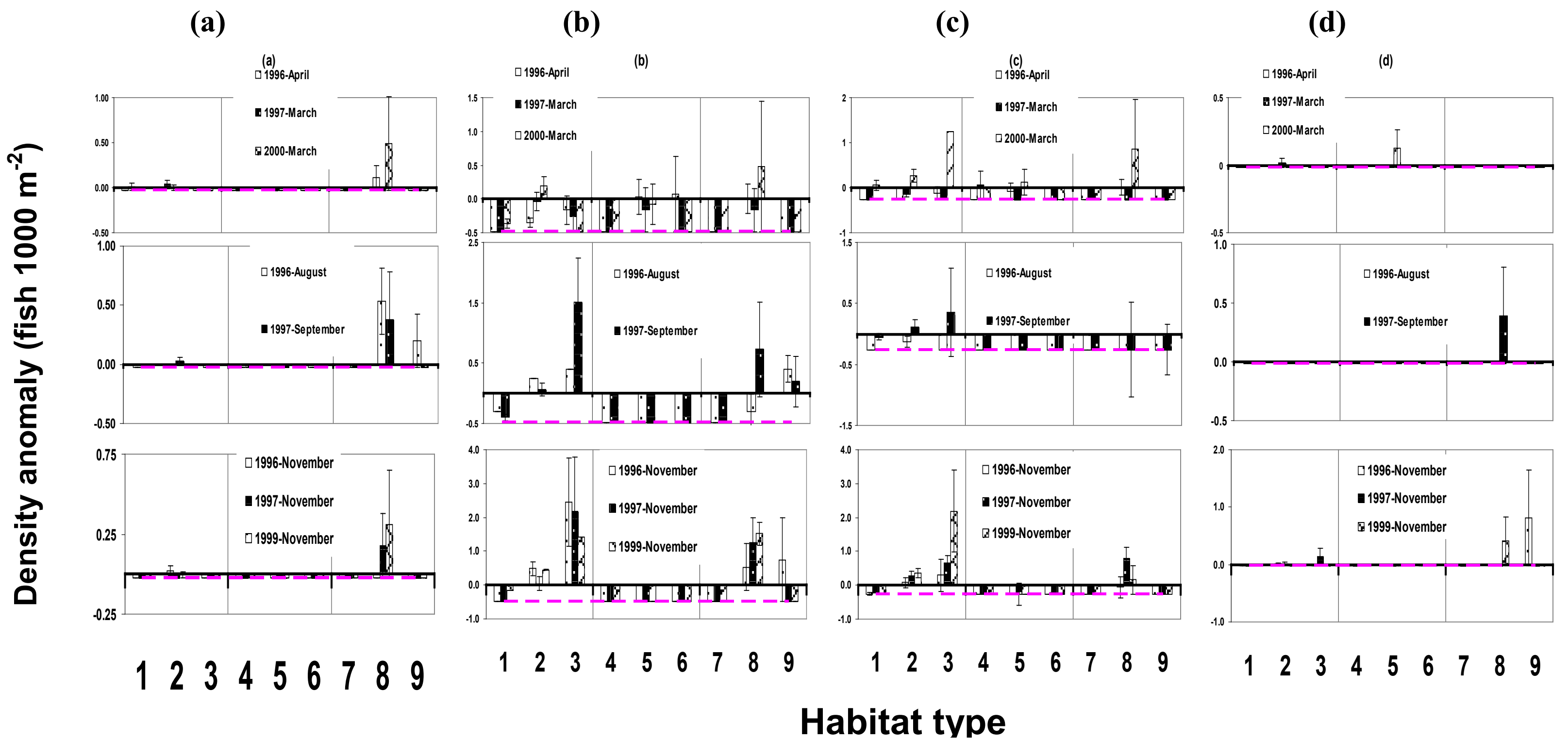


Figure 2.9: Per-unit amount of use by lifestage (PUA-stage) of *Sparisoma chrysopterum*, expressed as stratum deviations from the bay-wide mean density in Biscayne Bay, 1996-2000. (a) Juvenile (JP), (b) Subadult phase (SP), (c) Initial phase (IP), and (d) Terminal phase (TP). Upper panels: spring cruises; medium panels: summer cruises; lower panels: fall cruises. Symbology: same as in Figure 2.8.

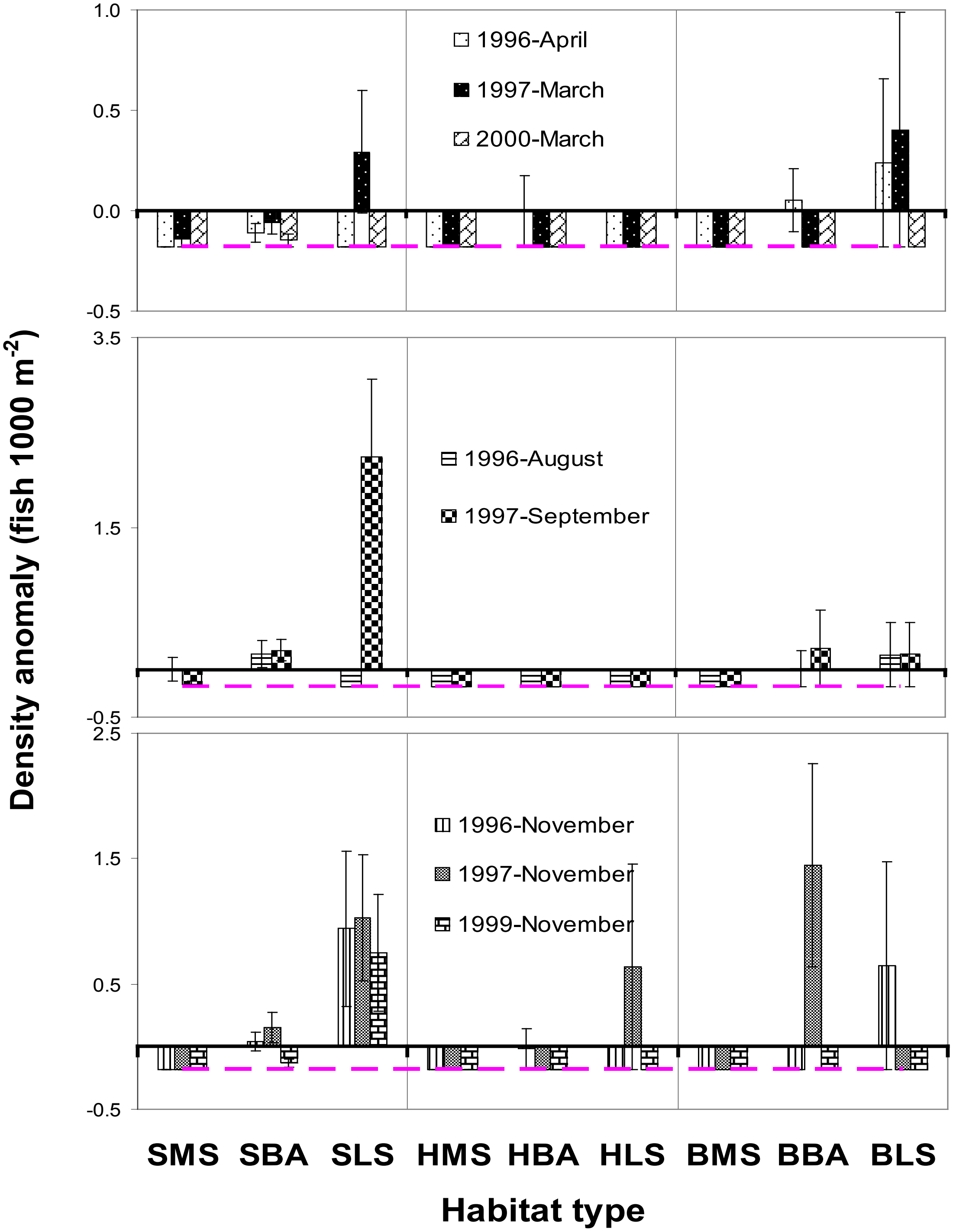


Figure 2.10: Per-unit amount of use (PUA-sp) of *Sparisoma radians*, expressed as stratum deviations from the bay-wide mean density in Biscayne Bay, 1996-2000. All lifestages were pooled (see text for explanation). Symbology: same as in Figure 2.8.

(a) *N. usta*

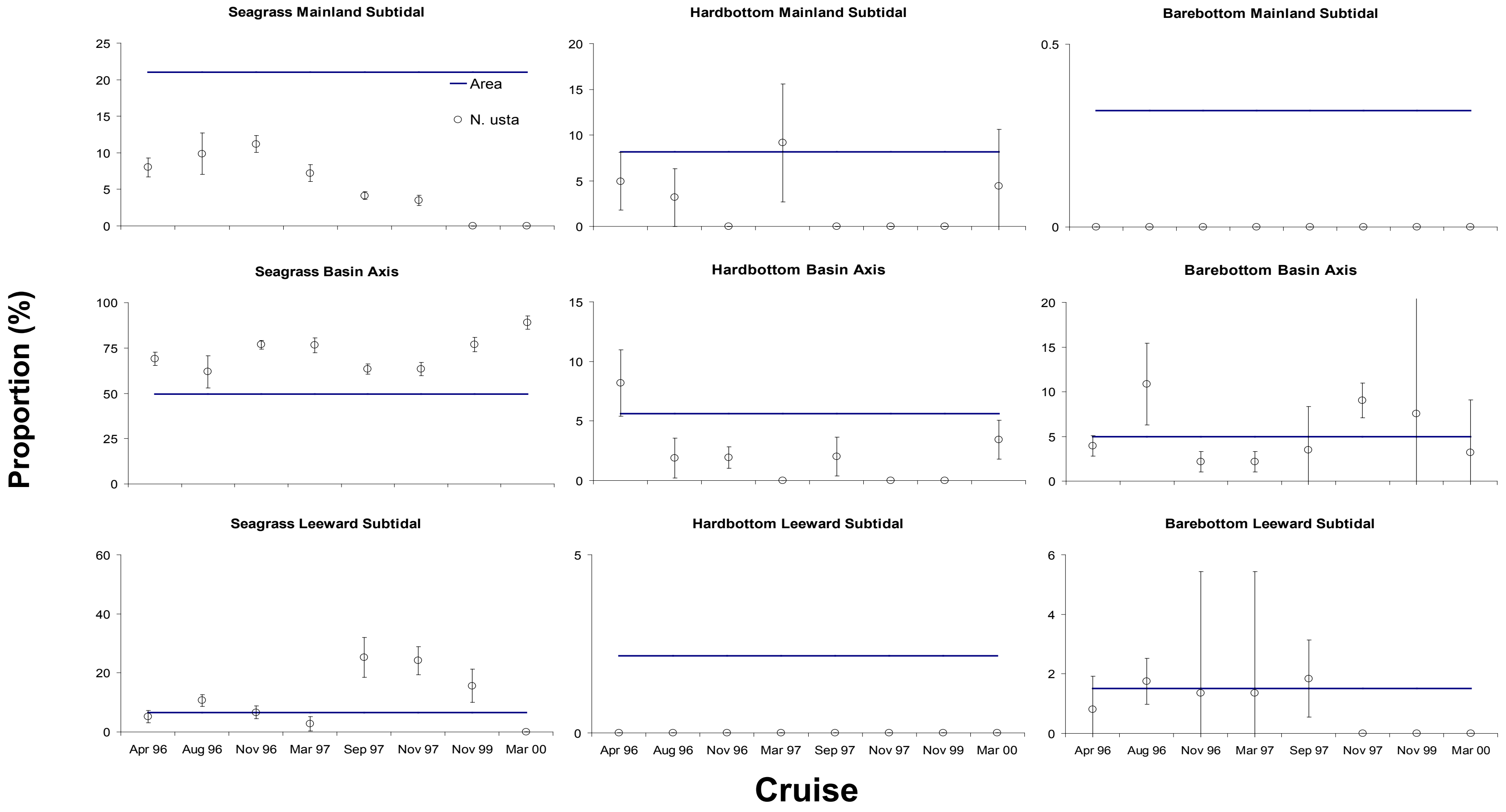


Figure 2.11: Population proportions, p(P), with their 95% confidence intervals of (a) *Nicholsina usta*, (b) *Sparisoma chrysopterum*, and (c) *Sp. radians*. The horizontal line represents stratum proportion by area, p(A), in Biscayne Bay, 1996-2000. Significant differences occur when the confidence intervals do not intersect the horizontal line, p(A).

(b) *Sp. chrysopterum*

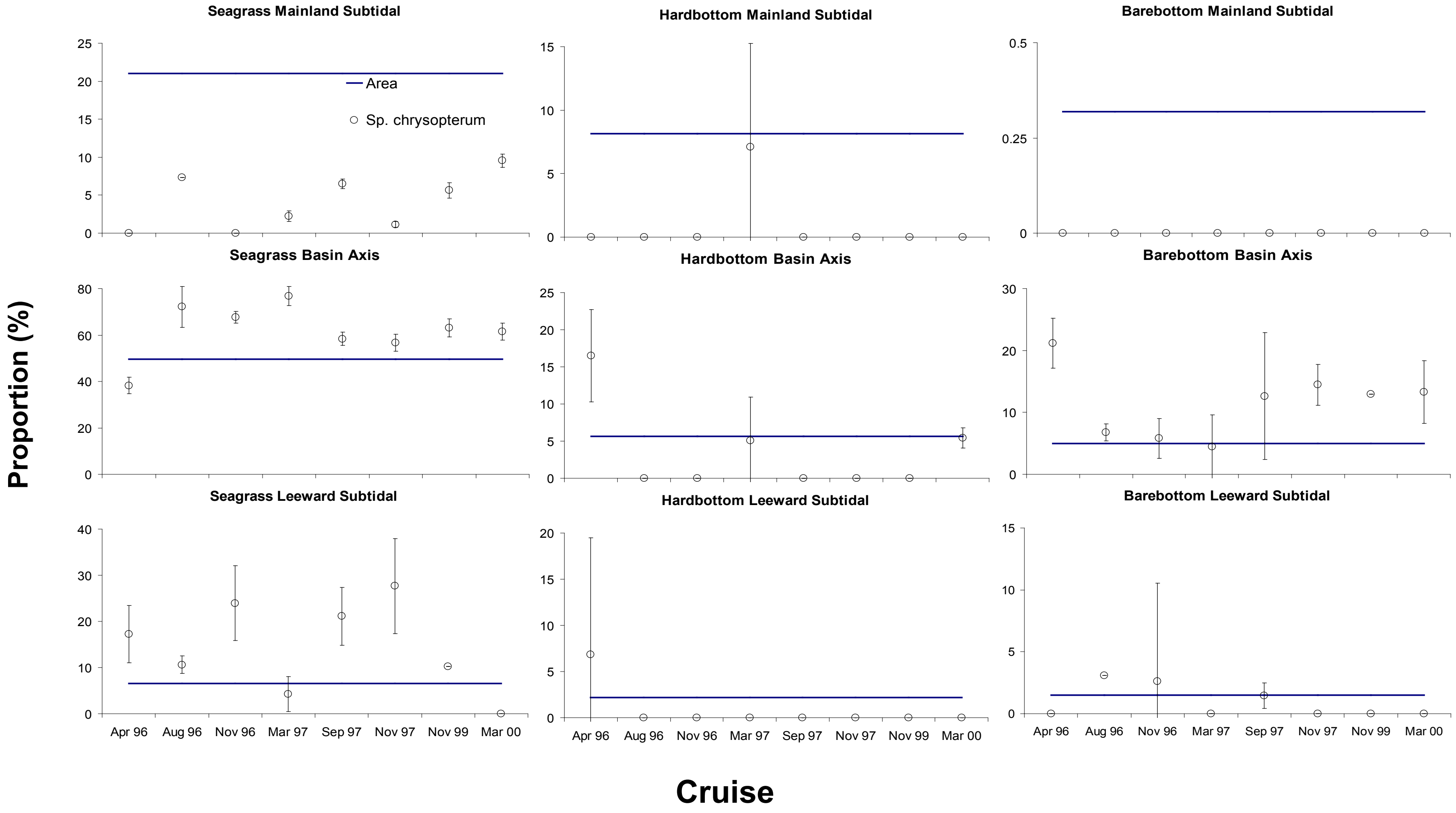


Figure 2.11 Continued

(c) *Sp. radians*

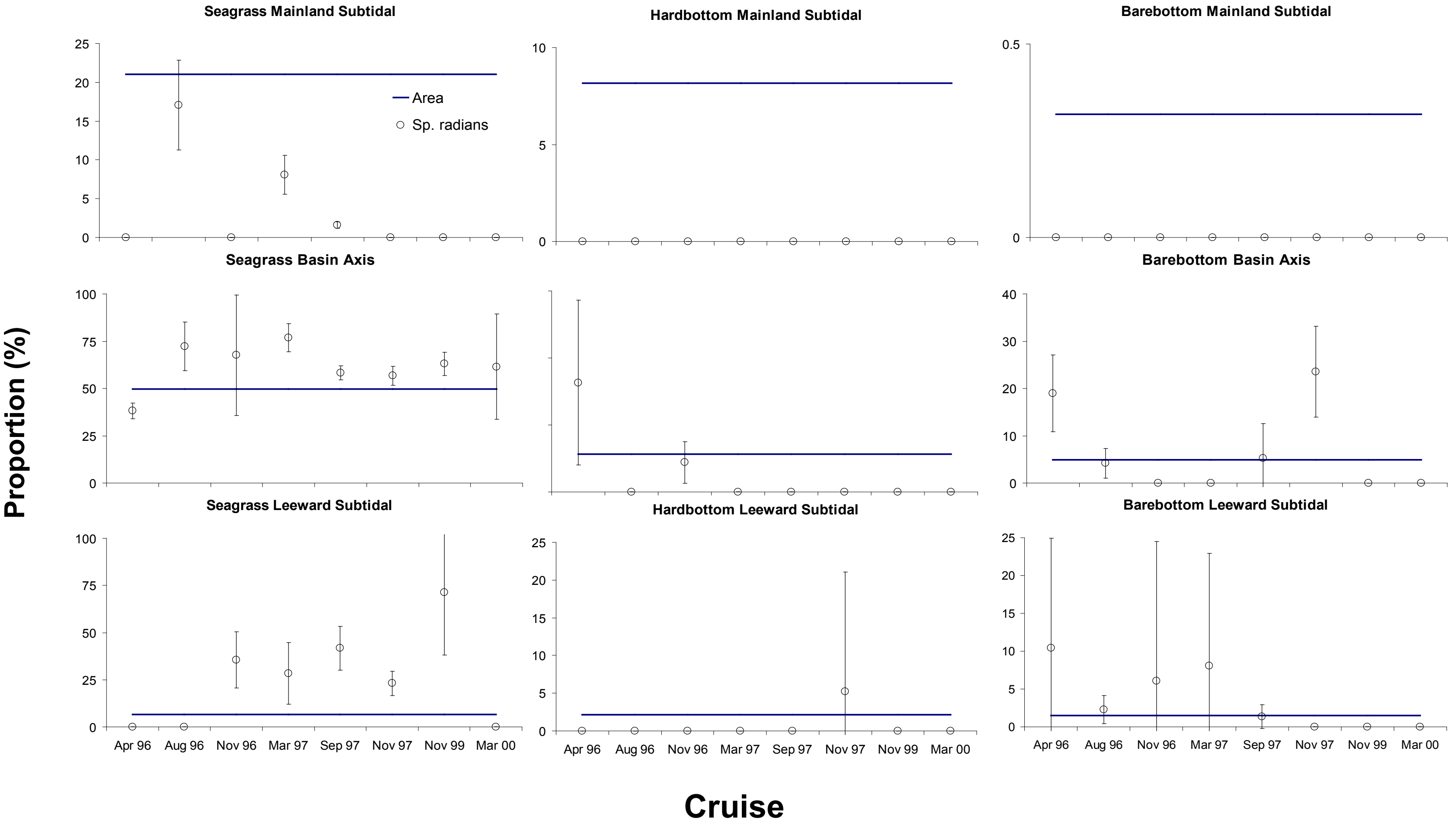


Figure 2.11 Continued

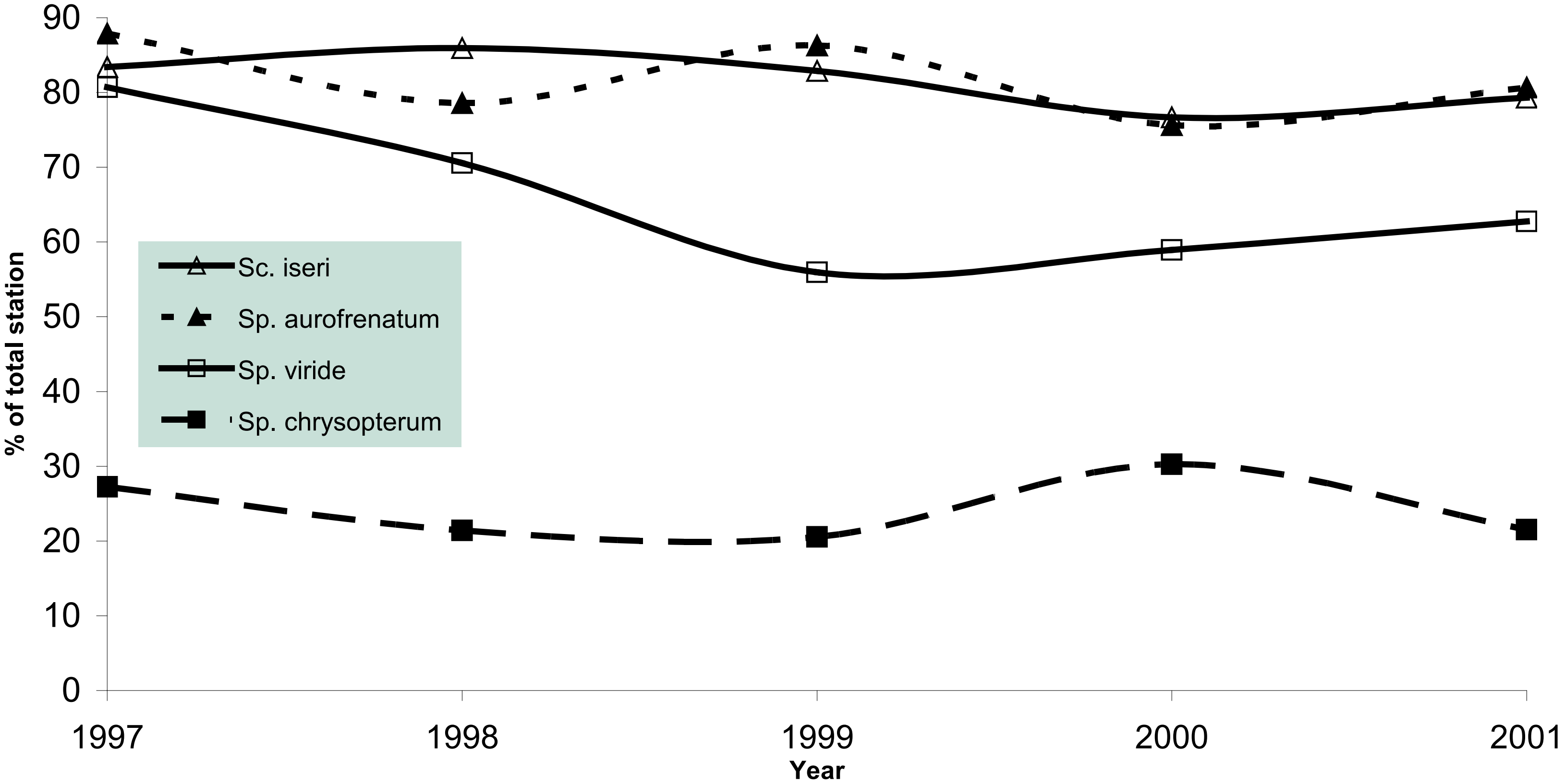


Figure 2.12: Frequency of occurrence of four parrotfishes in visual censuses, Florida Keys, 1997-2001.

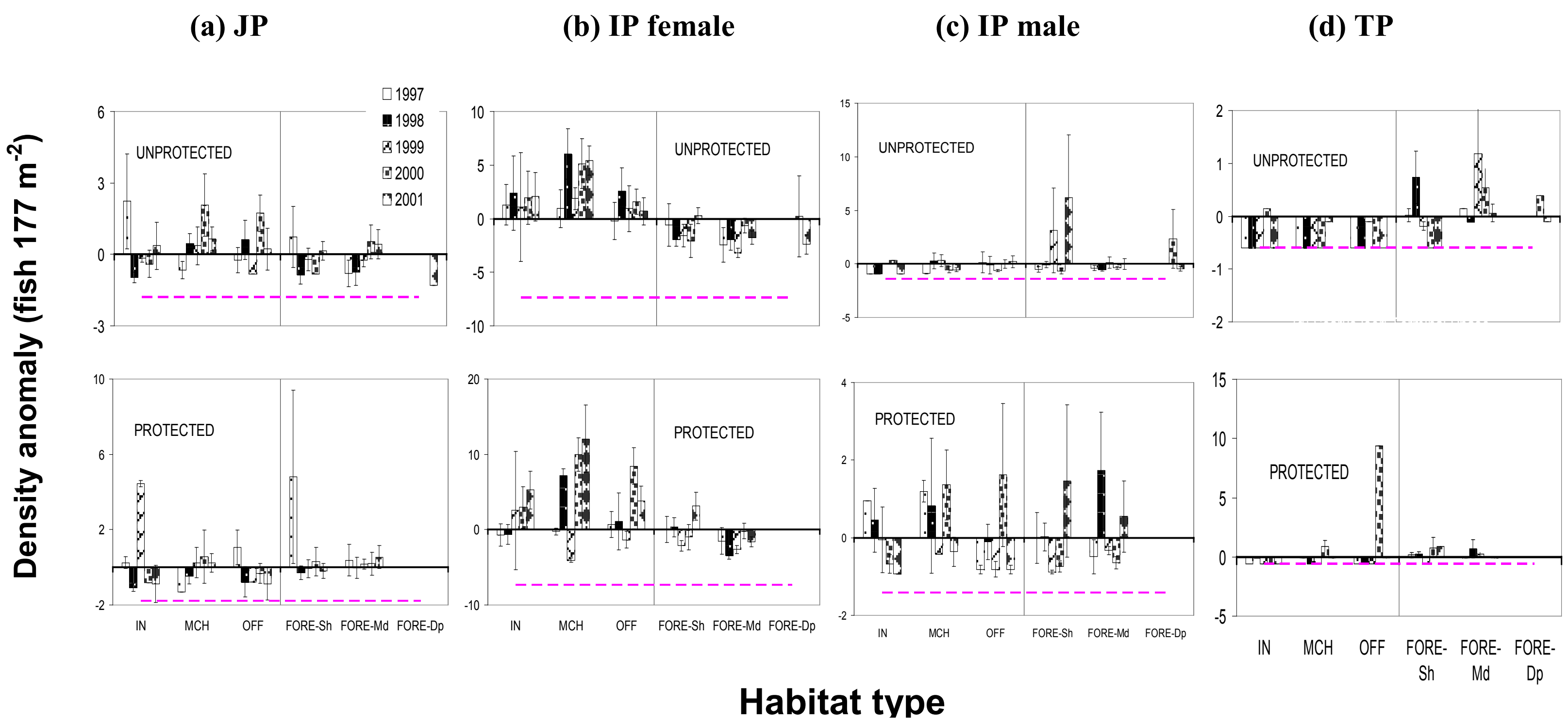


Figure 2.13: Per-unit amount of use by lifestage (PUA-stage) of *Scarus iseri*, expressed as stratum deviations from the Keys-wide mean density in the Florida Keys, 1997-2001. (a) Juvenile (JP), (b) Initial phase female (IPF), (c) Initial phase male (IPM), and (d) Terminal phase (TP). Note Y axes are at different scales.

Upper panel: habitats in unprotected areas; lower panel: protected areas (MPAs). Global mean density is set to zero. Error bars represent the standard error of the stratum mean density. The hatched horizontal line indicates parrotfish were absent. Symbology: IN: inshore; MCH: mid-channel; OFF: offshore; FORE SH: forereef shallow; FORE MD: forereef mid-deep; FORE DP: forereef deep. See text for life stage definitions.

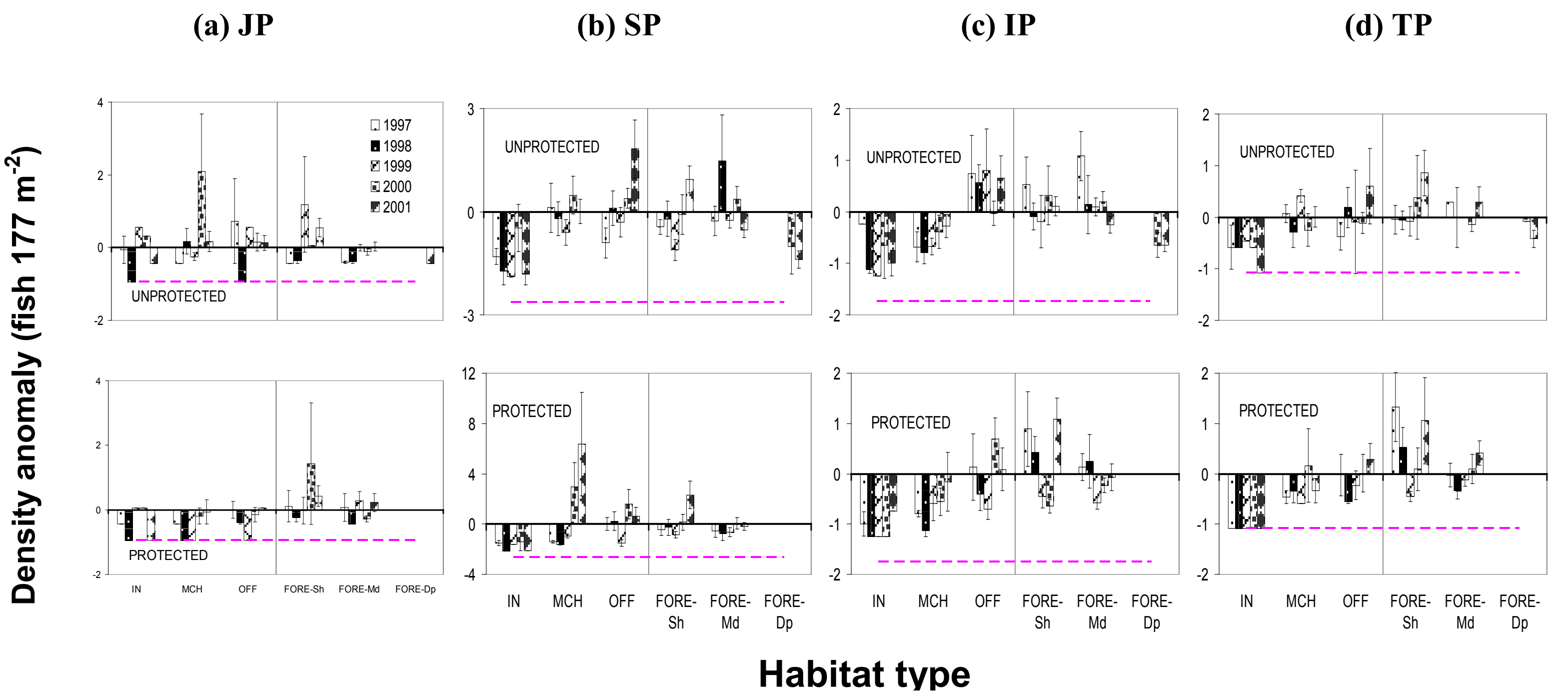


Figure 2.14: Per-unit amount of use by lifestage (PUA-stage) of *Sparisoma aurofrenatum*, expressed as stratum deviations from the Keys-wide lifestage mean density in the Florida Keys, 1997-2001. (a) Juvenile (JP), (b) Subadult phase (SP), (c) Initial phase (IP), and (d) Terminal phase (TP). Symbology: same as Figure 2.13.

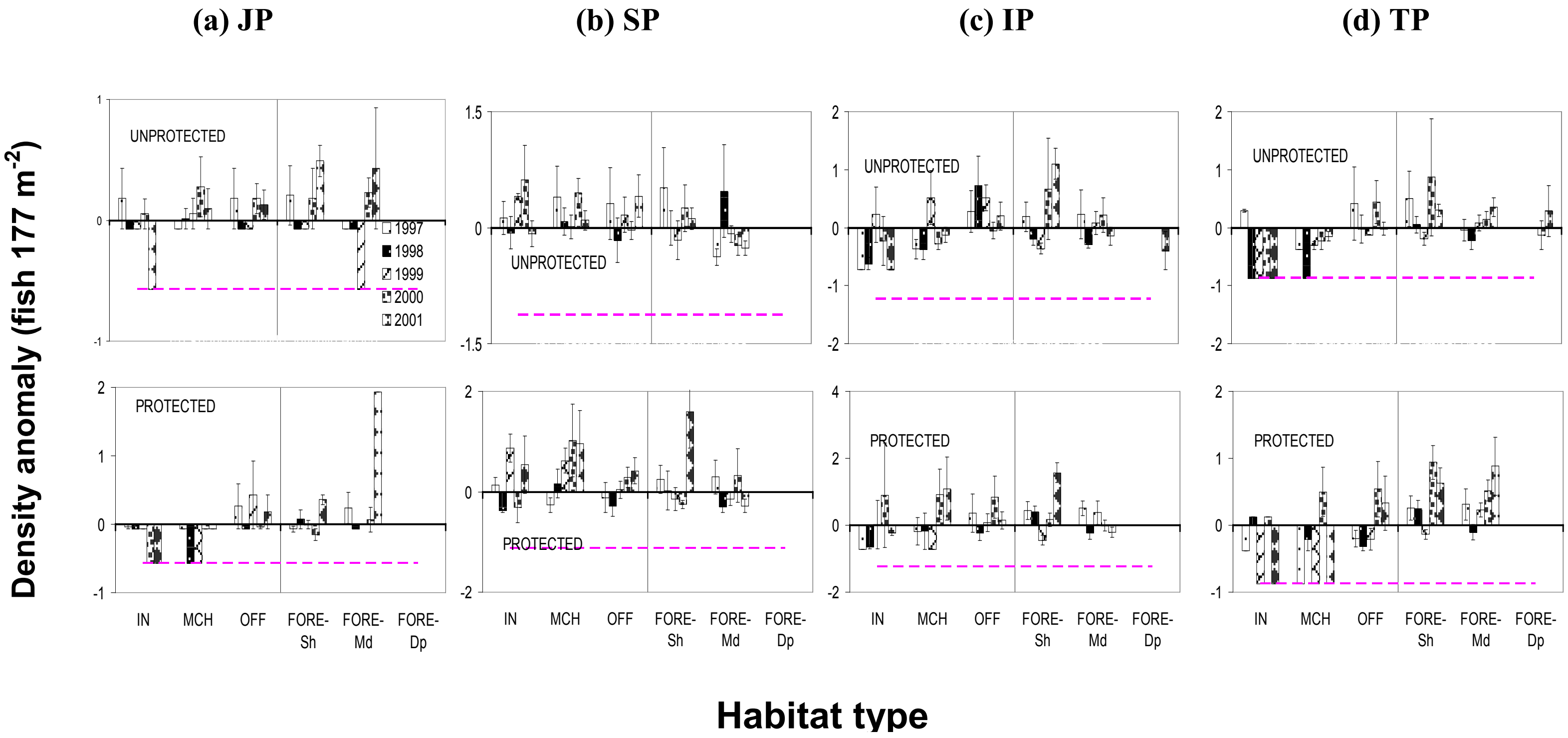
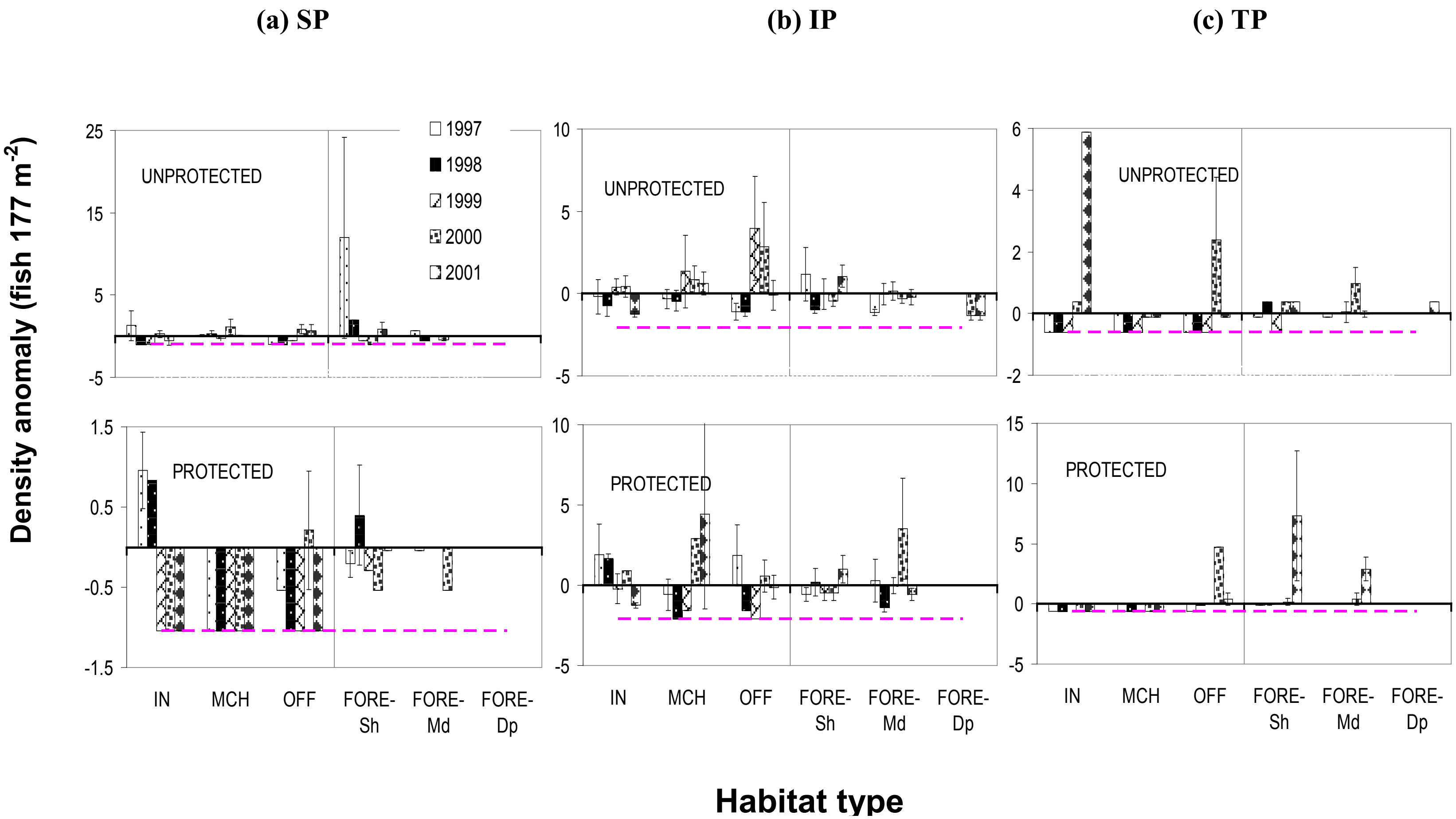


Figure 2.15: Per-unit amount of use by lifestage (PUA-stage) of *Sparisoma viride*, expressed as stratum deviations from the Keys-wide lifestage mean density in the Florida Keys, 1997-2001. (a) Juvenile (JP), (b) Subadult phase (SP), (c) Initial phase (IP), and (d) Terminal phase (TP). Symbology: same as Figure 2.13.


(a) SP

(b) IP

(c) TP

Figure 2.16: Per-unit amount of use by lifestage (PUA-stage) of *Sparisoma chrysopterum*, expressed as stratum deviations from the Keys-wide lifestage mean density in the Florida Keys, 1997-2001. (a) Subadult phase (SP), (b) Initial phase (IP), and (c) Terminal phase (TP). Upper panel: habitats in unprotected areas; lower panel: protected areas (MPAs).
Global mean density is set to zero. Error bars represent the standard error of the stratum mean density. The hatched horizontal line indicates parrotfish were absent. Symbology: same as Figure 2.13.

Chapter 3: Body growth, morphometrics, and life history of South Florida parrotfishes

3.1 Background

As discussed in Chapter 1, several population parameter estimates necessary to assess the status of the stocks of Atlantic parrotfishes are unavailable or questionable. Growth studies for Atlantic parrotfishes are scarce, partly due to the minimal economic value of these species (Bohnsack et al. 1994, Claro 1994). Unfortunately, large differences among published parameter estimates of the von Bertalanffy growth model render the estimates unreliable. Sources of that variation might include methods used to compute the estimates, local factors, or demographic characteristics of the populations.

Chapter 3 evaluates, computes, interprets and summarizes life history parameter estimates related to growth, life phase, and reproductive characteristics of *Scarus iseri*, *Sparisoma aurofrenatum*, *Sp. chrysopterum*, and *Sp. viride*, the most abundant South Florida parrotfishes, as well as other minor species. The present chapter addresses a major goal established as a priority by the information gap analysis (Figure I.1). It aims at providing a timeline to better understand ontogenetic habitat shifts, and the timing of important life history events. This section also provides isometry tests and length-to-weight relationships for biomass estimations of abundance and growth. This information will be used as input for the population modeling (Chapter 4) and to establish the mean age of habitat shifts in the different domains of this study.

3.2 Materials and methods

3.2.1 Fieldwork

The collection efforts targeted specimens of *Sc. iseri* and *Sp. chrysopterum*, and secondarily other minor species (e.g., *N. usta*, *Sp. radians*) at selected sites of Biscayne Bay and the Upper Keys (cf. Figure 2.1). In Biscayne Bay, the individuals were collected by bottom roller-beam trawl nets as described in section 2.2.1.1, in November 1999 and March 2000. In the Florida Keys domain, the sites included Little Grecian, Sand Island, Pickles, Three Sisters, Horseshoe, Admiral Reef, as well as seagrass patches on the Florida Bay side of Key Largo. The Upper Keys specimens were collected at different times of year between 2000 and 2002, by three means: (1) the larger individuals of *Sp. chrysopterum* were pole-speared, (2) the smaller fish (e.g., *Sc. iseri*) were herded into a standing 1.2 m high x 1.8 m long set net of 0.64 cm stretched mesh size, and (3) small and medium-sized specimens were obtained from otter trawl samples on seagrass during a Florida Marine Research Institute (FMRI) survey, courtesy of James Colvocoresses and colleagues.

Collected specimens were classified by color phase and size into four categories: juvenile (JP), subadult (SP), initial phase (IP), and terminal phase (TP) as described in section 2.3.2.3. Three measures of body length, total length (TL), fork length (FL), and standard length (SL) to the nearest mm were taken for each individual. Additionally, total wet weight was obtained from all the speared and netted individuals while fresh, except the ones captured in Biscayne Bay. All specimens retained were frozen and labeled for later analysis.

Observed maximum length was obtained from Reef Fish Visual Census (RVC) databases, as displayed in Table 2.21 (cf. Chapter 2).

3.2.2 Morphometrics

The length-to-weight relationship was computed as a nonlinear regression model (Can et al. 2002):

$$W = aL^{b} \tag{3.1}$$

where: W=fresh body weight in grams; L=total length in cm; a='condition factor' or regression parameter β_0; b = measure of curvature, or regression parameter β_1

In this equation, the value of b bears biological meaning for fish species, because isometric growth is assumed to occur when $b = 3$. Isometry implies that body length, width, and depth change proportionally to one another as the individual grows, i.e., maintains its body shape, thus rendering the fish's weight proportional to the cube of the length (Choat and Robertson 2002). Assumption of isometry simplifies many calculations, from growth curves to yield-per-recruit analyses. Allometric growth is denoted positive or negative when $b > 3$ or $b < 3$, respectively (Quinn and Deriso 1999). Isometry was tested with the method of 95% confidence interval (95CI) (Can et al. 2002).

Length-to-weight (L-W) and length-to-length (L-L) equations were developed for each lifestage of the parrotfishes when there were enough data. Analyses of Covariance (ANCOVA) determined whether a single equation was applicable for the whole species, or each lifestage had unique morphometrics.

3.2.3 Growth and other life history parameter estimations

Published length-at-age curves from otolith data (e.g., Choat and Robertson 2002, Choat et al. 2003, Paddack 2005) follow the von Bertalanffy (VB) function for body growth:

$$L_t = L_\infty\left(1 - e^{-K(t-t_0)}\right) \qquad (3.2)$$

where: L(t)=length at time t; L_∞=horizontally asymptotic maximum mean length, also known as ultimate length; K=Brody growth parameter (curvature parameter governing the speed at which the curve approaches L_∞); t_o=location parameter indicating the x-intercept of the curve (hypothetical age at which mean length equals zero).

However, maximum length estimates reported by Choat and Robertson (2002), Choat et al. (2003), and Paddack (2005) were 23 – 30% shorter than the values observed in this work (cf. Tables 1.7 vs. 2.21), which would potentially bias estimation of mortality and other fisheries parameters. Thus, a numerical approach was used to find point estimates of K ($\hat{K}$), life span (t_λ), maximum length (L_λ), and ultimate length (L_∞), that fitted local growth patterns better.

Firstly, the maximum size (expressed as SL, in mm) observed in any of the datasets was used as L_λ, and a published t_λ estimate was used as initial input. Then, $\hat{K}$ was computed by having two forms of Equation 3.2 analytically and simultaneously solved between two constraints (cf. Rothschild et al. 1994), namely: (a) length is zero at age zero, i.e., at $t_0 = 0$ then $L_0 = 0$; and (b) the mean length of the oldest age (L_λ) occurs at the maximum age or life span of the stock, i.e., $L_t = L_\lambda$ at $t = \lambda$, such that (note that observed maximum length was used as proxy for L_λ):

$$\hat{K} = \frac{1}{(t_\lambda - t_0)} \ln\left[\frac{L_\infty - L_0}{L_\infty - L_\lambda}\right] \qquad (3.3)$$

(Terms are the same as in Equation 3.2).

Growth parameter estimates of South Florida populations of *Sc. iseri*, *Sp. aurofrenatum*, *Sp. chrysopterum*, and *Sp. viride* were adapted from otolith-based von Bertalanffy Growth Functions (Choat and Robertson 2002, Choat et al. 2003, Paddack 2005), by numerically combining those parameter estimates with observed data from the Reef fish Visual Censuses (RVC) as initial inputs. The process started with an initial rough estimate of $\hat{K}$ (Equation 3.3) obtained from literature estimates. Observed L_λ values were fixed or set with very small variations, while L_∞ estimates were adjusted as necessary with 0.5-cm steps. $\hat{K}$ was fine-tuned numerically by changing alternatively t_λ, L_λ and L_∞ on an Excel® spreadsheet for ≥ 40 iterations, until the resulting curve matched the otolith-based VB predicted curve as much as possible, while still reaching the larger sizes observed in the field. The constraints used in this numerical procedure were: (a) the growth curve of younger stages must follow a pattern as close as possible to that obtained by the literature parameter estimates; (b) life span, t_λ, may differ by only ≤ 2 years from the published model in the short longevity scenario; (c) age is expressed as integers, with no fractions of years; (d) maximum length, L_λ, equals the largest observed length in the Reef fish Visual Censuses (RVC) database of the i^{th} species (cf. Table 2.20).

For each species, the deterministic VB function that best fitted the constraints was chosen to estimate other life parameters. In order to incorporate stochastic effects and compare my simulated results to published otolith-based functions, Monte Carlo simulation techniques were applied under three scenarios regarding the statistical distribution of $\hat{K}$. Each treatment consisted of 1000 iterations of a probability density function (normal, gamma, and exponential) assumed for $\hat{K}$. A random variation up to 10% of the mean value was applied to normal distributions of L_∞. A uniformly distributed t_o was assumed, with the minimum given by Choat and Robertson (2002) and Paddack (2005), and the maximum at 0.0 set by the constraint on Equation 3.3. Selection of the growth model and distribution assumption was based on the combination of several criteria: predicted mean values of maximum age and length, width of simulated 80th percentile confidence intervals (80CI), and similarity to otolith-based growth functions.

Given the information gap on Atlantic parrotfish population dynamics, the application of invariant relationships under the framework of dimensionless theory (Charnov and Berrigan 1990, Jensen 1997, Williams and Shertzer 2003) was a useful alternative to calculate other life history parameters. This approach has been used and tested in other cases related to fishery management (e.g., Williams and Shertzer 2003). Once a set of growth parameter estimates was chosen for a species, the invariants approach provided a means to predict unknown estimates based on constants of proportionality among growth and mortality parameters (e.g., Jensen 1997, Allsop and West 2003b) that hold across a wide range of taxa. These equations, of which Beverton and Holt (B&H) invariants form part (Jensen 1997, Williams and Shertzer 2003), relate life span, maximum size (both length- and weight-wise), growth coefficients, size/age at first maturity, and instantaneous rate of mortality across a wide array of fish orders (cf. Table 3.1). Alternative proportionalities assuming indeterminate growth models were not considered here. Length at first maturity was obtained from the empirical proportion for unsexed data obtained from 467 populations belonging to 88 families of 27 different orders (Froese and Binohlan 2000). Estimates of length and age at sex transformation of these sequential hermaphrodites could be obtained from invariants (Allsop and West 2003b). ‘Sex transformation’ was defined in the present work to occur when at least 50% of the individuals were males (hence, $L_x = L_{50}$ = length at sex change). This L_{50} definition holds better with the invariant theory, and has more robust statistical background behind it. Those proportionalities will be called the Allsop and West (A&W) invariants heretofore. Despite some controversy regarding the underlying assumptions of the A&W sex change theory (cf. Allsop and West 2003a, Buston et al. 2004), invariant theory was used to obtain rough estimations of expected size and age at sex change, in order to provide a more complete picture of the species population dynamics. Three different assumptions were used to explore alternative scenarios: (a) L_x equals a species-specific value L_{50}/L_λ from field data by Robertson and Warner (1978); (b) A&W length-based invariant, where L_x occurs at 79% of L_λ; and (c) A&W age-based invariant, where t_x is located 2.5 times the age at first maturity, t_m.

Note that Atlantic parrotfish-specific observed L_x/L_λ ratios, ranging from 0.56 to 0.81 (Robertson and Warner 1978, Allsop and West 2003b), were used to obtain a third estimate of L_x.

Because length was the size measure recorded in all the samples, the computation of the corresponding age at a given mean size was done by solving the VB model for age *t* (Ault et al. 1998):

$$t = \frac{-\ln\left[\frac{L_{\infty} - L_{(t)}}{L_{\infty}}\right]}{K} + t_0 \qquad (3.4)$$

(Terms are the same as in Eq. 3.2 above). A limitation of this approach is that by solving for any of the terms on the right side of Eq. 3.2, the error structure of the original data would be changed. However, because the data used are simulated, they will have their own error structure.

3.3 Results

3.3.1 Color phase and body size

Besides the known Initial (IP) and Terminal (TP) color phases of the Western Atlantic parrotfishes (Allsop and West 2003b), some particularities were found in this work, that may aid scarid identification underwater. Although IP pattern of most species was characterized by dull or cryptic colors, *Sp. chrysopterum* always had a distinctive 2-3 cm diameter white spot on the dorsal side of the caudal peduncle. IPs also displayed a well developed ability for sudden changes, either to mottled patterns when escaping from potential predators (e.g., *Sp. aurofrenatum*; red-and-white in *Sp. chrysopterum*), or fading to gray while in their regular grazing behavior (e.g., *Sc. iseri*, *Sp. chrysopterum*). A coloration pattern of IP *Sp. chrysopterum* not reported before was occasionally found in ~20-cm TL grazing specimens of the upper Keys, presenting red-and-white longitudinal stripes on the sides of the body that did not change during the escape. None of the TP colorations changed as defensive mechanism, but regional variation was observed in *Sc.*

iseri TPs, because their typically yellow wide stripe of upper & middle Keys was orange in the lower Keys and Dry Tortugas.

Size ranges of IP and TP color phases overlapped extensively in *Sc. iseri* and *Sp. chrysopterum* (Table 3.2, Figure 3.1). *Sc. iseri* TPs were as small as 7.5 cm TL, and IPs as large as 14.1 cm TL, while *Sp. chrysopterum* had both IPs and TPs >21 cm TL. No TP of *N. usta* was recorded at TL ≤ 19 cm.

3.3.2 Morphometrics and isometry

Length variation explained ≥98% of the weight variation in *Sc. iseri*, *Sp. chrysopterum, N. usta*, and *Sp. radians* throughout their life cycles (Table 3.2). Slope estimates, *b*, were not significantly different among lifestages (ANCOVA, $F_{b\ Sc.\ ise} = 1.33$, $P>0.05$; $F_{b\ Sp.\ chr} = 2.13$, $P>0.05$). Intercept estimates, *a*, did not differ significantly among lifestages either (ANCOVA, $F_{a\ Sc.\ ise} = 0.37$, $P>0.05$; $F_{a\ Sp.\ chr} = 2.97$, $P>0.05$). The 95% confidence intervals (95CI) of the parameter *b* for the pooled regression equation indicated that both *Sc. iseri* and *Sp. chrysopterum* displayed an overall isometric growth (Table 3.2), since their 95CI included the value of 3.0.

The underlying assumption of isometric growth in the life history proportionalities proposed by Jensen (1997), Allsop and West (2003b), and Williams and Shertzer (2003), was practically fulfilled in most of the Western Atlantic parrotfishes. Species-pooled isometry tested by 95% confidence intervals (95CI) showed that only *N. usta* and *Sp. radians* were significantly positively allometric (Table 3.2). However, the CI lower limits of all these cases had $b \leq 3.2$, suggesting a very small deviation from isometry.

High (>94%) R^2 values were also obtained for the length-to-length equations of *Sc. iseri* and *Sp. chrysopterum*. TL-to-SL regression parameters did not differ significantly among lifestages for either species (ANCOVA, $F_{b\ Sc.\ ise} = 1.96$, $P>0.05$; $F_{b\ Sp.\ chr} = 2.26$, $P>0.05$; $F_{a\ Sc.\ ise} = 1.00$, $P>0.05$; $F_{a\ Sp.\ chr} = 1.54$, $P>0.05$) (Table 3.2), so a single equation can describe the species.

In the TL-to-FL curves of *Sp. chrysopterum*, the slopes did not differ significantly among lifestages (ANCOVA, $F_b = 2.02$, $P>0.05$), but the intercepts did ($F_a = 17.80$, $P<0.001$). Thus, TL to FL conversions could not be pooled into a single equation for the whole species. Specimens ≤9-cm TL have a truncated tail. At larger sizes, the external caudal rays begin to elongate and change the shape to a concave or emarginated tail, which may explain the difference of intercepts.

3.3.3 Growth parameter estimates

Two alternative outcomes of the model iterations were chosen for each parrotfish, each referred to as "short life span" (low t_λ) or "long life span" (high t_λ) model (Table 3.3). In the case of *Sp. viride*, Model A was developed by using Choat et al. (2003)'s Bahamas VB Model estimates for initial parameters and constraints, while Model B was adapted from Paddack (2005)'s Upper Keys Overall Model (Table 3.3). The resulting deterministic length-at-age curves are shown in Figure 3.2.

For the four parrotfishes, estimated longevities ranged from 5 to 10 years under the short-lifespan assumption, and 8 to 12 if a longer lifespan was assumed. Either way, those estimates were shorter than those for Indo-Pacific scarids (Choat and Robertson 2002). $\hat{K}$ values differed little between the low and high t_λ models for each species (Table 3.3). Under the short-lifespan assumption, steepness of growth curves decreased in the following order: *Sp. aurofrenatum*, *Sp. chrysopterum*, *Sc. iseri*, and *Sp. viride*. Those trends were less defined when assuming long-lived conditions.

Figure 3.3 displays the length-at-age outcome of Monte Carlo simulations for short and long lifespan, with normal probability distributions assumed for $\hat{K}$, and input parameters from Table 3.4. Under the normality assumption, this study's 80CI contained Choat and Roberston (2002)'s predicted sizes for the first 2 and 4 years of age of *Sc. iseri* and *Sp. viride*, respectively, but only age 1 for *Sp. aurofrenatum* and *Sp. chrysopterum* (Figure 3.3). High-t_λ model's 80CI included more otolith-derived data points than the shorter lifespan alternative. The gamma and exponential distributions (not shown) yielded expected means more similar to those of published models, but their 80CI were too wide to be informative, thus these scenarios were discarded.

Life history parameter estimates were derived from the VB model and other invariant proportions for each species under short (Table 3.5) and long (Table 3.6) lifespan conditions. Figure 3.4 shows that, regardless of longevity, t_m and W_m were located near the inflexion point, as expected from the bioenergetics calculations. Age at first maturity ranged from ca. 1.5 y.o. (*Sp. aurofrenatum* and *Sp. chrysopterum*), to ca. age 2 and > 2.5 (*Sc. iseri* and *Sp. viride*, respectively).

Table 3.3 displays the growth parameter estimates selected to compute other life history parameters. For consistency purposes, the use of TL was preferred when possible, using the conversion equations from Table 3.2.

Figure 3.4 compares size at first maturity against estimates of size at sex change from three different sources: (1) R&W proportion reported in Panamanian parrotfishes by Robertson and Warner (1978); (2) A&W length invariant proportion, $0.79L_\infty$; and (3)

A&W age invariant proportion, $2.5t_m$, the latter two proposed by Allsop and West (2003b), in simulated weight-at-age curves. R&W size-at-sex change estimates occurred at ages 1.5-3 of all species, within a few months of reaching sexual maturity. *Sc. iseri* was the only species in which sex change apparently preceded maturity.

Different criteria (i.e., either age-based or length-based proportions) on size-at-age sex change gave a wide range of estimates for L_x, W_x, and t_x, as shown in Table 3.5 and Table 3.6. The A&W age-derived ($2.5*t_m$) and length-derived invariants ($0.79*L_\lambda$) appeared to overestimate the size and age of sex transformation, and rendered very different values. Because in the Florida Keys, mature individuals were found at sizes smaller than predicted by these invariants (H. Molina-Ureña, pers. obs.; Figure 3.4), the A&W L_x and W_x estimates were discarded in further analyses. On the contrary, the parrotfish species-specific R&W proportion yielded L_x estimates more compatible with observed characteristics (H. Molina-Ureña, pers. obs.).

3.4 Discussion

This chapter makes three basic points concerning the growth patterns of South Florida scarids. Firstly, although coloration is a complex characteristic whose relationships to length, age, and growth are yet to be understood, color phase does not affect isometry of the parrotfishes. Secondly, it was possible to develop a deterministic model with an added stochastic component to simulate size-at-age estimates that matched observed demographic characteristics of each species. Thirdly, in absence of observed data, life history dimensionless theory can be a useful tool to estimate demographic parameters, as long as its limitations are well understood.

3.4.1 Color phase, morphology, and growth patterns

South Florida scarids display a wide variety of coloration strategies, associated mainly with socio-sexual roles (long lasting) or escape mechanisms (instantly changing). The TP color-acquisition process is driven by hormonal changes acting independently from those controlling sex transformation, and it is associated with social structure rather than to sex identities, as Cardwell and Liley (1991a, 1991b) demonstrated in *Sp. viride*. Effects of endocrine disruptors in coastal waters, such as PCBs, PAHs, DDT, etc. are expected, but are yet to be formally addressed (see Chapter 1). On the other hand, the physiological mechanisms enabling sudden mottled or faded colorations as escaping strategies have not been studied.

The blue coloration, while common in TPs of *Scarus* spp. and *Sparisoma* spp., is rare in most animals (Robertson and Warner 1978, Koltes 1993, de Girolamo et al. 1999), and it is probably given by the combined effect of melanophores and guanophores instead of a blue pigment (Goodrich and Biesinger 1953). Once an individual acquires the TP coloration, it loses the ability to use color change as defense mechanism. Chromatophore shapes are genus-specific and distinguish *Scarus* from *Sparisoma* (Goodrich and Hedenburg 1941).

The extensive size overlaps between color phases described by Robertson and Warner (1978) were corroborated in this study. Differential age structures and growth rates between color phases of the same species have also been demonstrated in this family of fishes (e.g., Munday et al. 2004, Paddack 2005). These issues of length and age overlap between color phases depict a complex population structure where relationships among the three characteristics do not follow straightforward patterns. Secondary gonochorism (an outcome of prematurational sex transformation, cf. Choat et al. 2003) in Sparisomatinae and diandry in Atlantic scarines (Robertson and Warner 1978) are probable biological sources of this complexity.

The isometric nature of the parrotfish growth patterns allowed further inferences from invariant theory with respect to important life history parameters, such as L_m, and L_x. As for the change of tail shape in *Sp. chrysopterum*, the onset of the caudal fin ray elongation coincided with the size at transition from subadult to initial phase. Although the biological significance of shape change for this parrotfish is not fully understood, the results in Chapter 2 suggested the possibility of an adaptation for an ontogenetic migration from bay seagrass substrates towards surrounding reef habitats. The switch from truncate to emarginated tails may bring about decreased friction while keeping an effective acceleration and maneuverability, an optimal combination to move moderate distances at moderate speeds associated with more range of movement.

3.4.2 Simulated growth parameter estimates

None of the otolith-based growth models published to date account for the larger maximum sizes (L_λ) of parrotfish found in the Florida Keys. L_λ reported in this work were up to 54% longer than those found in the literature (Choat and Robertson 2002, Choat et al. 2003, Paddack 2005). Two factors may explain this difference. First, this research demonstrated a cross-shelf trend, where larger individuals could be found in deep forereefs, located farther offshore (cf. Table 2.21), while otolith analyses were likely conducted on specimens collected from onshore areas. Second, the extremely low frequencies of the largest specimens could be easily missed in sampling sizes < 500, whereas this study recorded at least 1500 individuals of each scarid in the Florida Keys alone (cf. Chapters 2 and 4).

This discrepancy alone justified the need to obtain growth models of South Florida populations explaining the observed data. Considering Choat et al. (2003)'s findings of positive latitudinal effects on maximum size, the similar latitudes of Lee Stocking Island (Bahamas) and South Florida do not account for the differences reported in maximum size.

In absence of well defined latitudinal trends in longevity of Atlantic scarids (e.g., (Choat et al. 2003), the high-t_λ model parameter estimates with normally distributed K were considered the best in each of the four species, although it provided higher life expectancy than predicted by otolith studies elsewhere in the Western Atlantic (Choat and Robertson 2002, Choat et al. 2003). For *Sp. viride*, Model A was preferred over Model B because the former predicted values closer to the published parameters for at least the first four years of age. Despite the smaller size of *Sc. iseri*, its high-t_λ model was deemed more suitable because it reflected the longer life span reported for many of the Western Atlantic and Indo-Pacific *Scarus* spp. (Choat and Robertson 2002).

The parameter estimates proposed herein retain the very important feature of fast growth at early ages, a strategy found in scarids around the world (Choat and Robertson 2002) as a probable adaptation to counteract high predation rates on the young. According to the 80CI lower limits of models parameterized in this work, South Florida mid-sized species might be 10-16 cm TL at age 1, while *Sp. viride* could reach at least 18 cm TL. A 1-y.o. *Sc. iseri*, being a small species, was expected to be ≥ 6-7 cm TL.

Within-species longevity variability is more complex than expected in scarids. For example, no latitudinal gradients in maximum age were detected by Choat et al. (2003), but cross shelf differences have been reported, with opposite trends, in the Florida Keys (Paddack 2005) and the Great Barrier Reef (Gust et al. 2002). Cross shelf differences in rates of growth may result as a composite of many factors, from intra- and interspecific social interactions to food or habitat availability and quality, water temperature, natural or fishing mortality, color phase proportions, migration of larger specimens to forereefs, etc. (e.g., Warner and Downs 1977, van Rooij et al. 1995b, Gust et al. 2002, Munday et al. 2004, Paddack 2005). Models simulated in this work do not consider cross-shelf effects because there is a high probability of gene flow (Geertjes et al. 2004), thus they provide Keys-wide overall body growth curves only. The "high-t_λ" models matched more otolith-predicted length-at-age points than the low-t_λ did.

Otolith data show a tendency in Indo-Pacific and Atlantic scarids for an apparent strongly determinant growth in which the fish reach the maximum size early in their life, and stay at that size for the rest of their lifespan (Choat and Robertson 2002). In heavily fished areas, this pattern could reflect juvenescence by fishing pressure (Ault et al. 1998) rather than the normal demography of the species. Fishing usually targets the larger specimens, leaving the smaller individuals of older year classes to represent the age class in the collections for otolith studies. Thus, the maximum size and the mean length of the population can be reduced by fishing activity (Ault et al. 1998). This could explain the L_λ differences between the Florida Keys scarids and those recorded elsewhere. However, Paddack (2005) did not record *Sp. viride* specimens >40 cm TL in the Upper Keys. Her L_λ matched this work's reported maxima from nearshore habitats (cf. Table 2.20), but was far smaller than those fish found at 12-18 m depth forereef stratum. Besides, given the relatively short life span of 5 to 12 years, the 25 year fish trap ban in South Florida may have allowed 2 to 5 generations for recovery from any previous exploitation effects on their population dynamics. It must be noted that relative abundances of parrotfishes in shrimp trawls have not varied between 1982 and 2000 (Chapter 2), which supports the idea that considering the South Florida parrotfish populations as unexploited to lightly exploited stocks is a sound assumption.

Choat and Robertson (2002) suggested geographic region (i.e., West Atlantic vs. Indo-Pacific), phylogeny (e.g., *Sparisoma* vs. *Scarus*), and maximum size influenced scarid longevity. Those authors found Indo-Pacific parrotfishes lived longer than their Western Atlantic congeners; *Scarus* lived longer than *Sparisoma* spp. of similar size, and larger species had longer lifespan than smaller scarids. While my results supported the role of regional and phylogenetic factors, variance of maximum length accounted for only ≤25% of the increase in longevity in this study.

3.4.3 Life history invariants and growth

In most cases, L_m invariant-derived estimates are comparable to observed data converted to TL across the Caribbean (cf. Table 1.7, Chapter 1). *Scarus iseri*'s standard error (SE) range of L_m (9.4 to 17 cm) included the 16-cm in the Virgin Islands (Randall 1963). L_m of *Sp. chrysopterum* (SE range 12.3 to 22) was below that of 25 cm in Puerto Rico (van Rooij et al. 1996b). *Sp. viride*'s point mean L_m estimate is higher than the observed 16 cm from Bonaire (Koltes 1993), 23 cm in Puerto Rico (Figuerola et al. 1998), and the 21-33 cm in Turk & Caicos Islands (Koltes 1993, van Rooij et al. 1996b). However, its SE range (25.5 to 46 cm) is wide enough to include the two latter reports.

The ratio L_m/L_∞ held relatively constant for field observations from Caribbean localities. Size at maturity of *Sp. aurofrenatum* was 51% of its ultimate length. For the larger species, *Sp. viride* reported L_m (Koltes 1993, van Rooij et al. 1996b) represented 43-45% of L_∞ estimated by Choat and Robertson (2002). L_m empirically computed (Froese and Binohlan 2000) was located near the inflexion point of the weight-at-age curve, and thus was consistent with expected values.

Sex change occurs within 4 months before (*Sc. iseri*) or 3-10 months after (*Sparisoma* spp.) the time of first maturity. *Sc. iseri*, the only diandric[12] parrotfish in this study, is also the only one with predicted $L_x < L_m$ (Figure 3.4). The presence of two types of males (primary and secondary) may shift the L_{50} towards younger ages in this species. *Sp. aurofrenatum*, the only monandrous species whose all females undergo sex transformation, followed a pattern much closer to the 79% A&W invariant predictions, changing sex nearly a year after first maturity.

Based on dimensionless life history theory, the asymptotic length (L_∞) and growth coefficient (K) from the von Bertalanffy growth equation can provide a rough approximation on expected length at maturity, instantaneous natural mortality rate (Jensen 1997, Williams and Shertzer 2003), and life span (Charnov and Berrigan 1990). Maximum length (L_λ) is useful to estimate age and size of sex change for scarids and other sequential hermaphrodite fishes (Allsop and West 2003b). There are several limitations, however. Mortality in protogynous or polychromatic species cannot be assessed by lifestage, sex, or color phase, due to the impossibility of distinguishing between mortality and stage change (Gust et al. 2002). While the B&H dimensionless proportions have not been disproved, the A&W sex change invariants are subject to

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[12] Some males present are transformed from females (secondary males), and others were primary males.

debate because of the overwhelming evidence of the role of social interactions as trigger of sex transformation, among other factors (Allsop and West 2003a, Buston et al. 2004). Also, parameter estimates for Caribbean parrotfishes found in the literature have a high degree of uncertainty due to the wide range of values found for any given species (Chapter 1), thus complicating the attempts to address the population dynamics of an already complex family of reef fishes.

Regarding the A&W sex change invariants, these results suggested that this theory holds better for species in which all individuals undergo transformation. Diandry, sex reversal of transformed fish, or cases in which not all individuals change sex, may not follow the predicted proportions. Another application of these proportionalities could be as a way to cross-check for parameter estimates. For example, age at maturity (t_m) is closely related to age at inflection point in the von Bertalanffy weight-at-age growth equation (cf. Table 3.1), which in turn can be validated with the combination of the weight-length curves obtained in this study and the growth parameters from the literature.

An obvious limitation to the simulation modeling approach is that reported maximum length and life span of each species may have latitudinal, cross-shelf, insular, local, sex or life phase variations. However, the specific factors driving those differences within the scarid family are poorly understood. Thus, a single growth curve per species was applied in subsequent analyses, assuming they are the best representation available of the actual growth patterns of each parrotfish.

3.5 Recommendations

It is hereby recommended to describe Labroid taxa (scarids and labrids) by species and color phase in visual censuses (RVC). Extensive overlap between IP and TP lengths *per se* made it very challenging to use body length as a proxy for lifestage as defined in this work. However, the combined information of color phase, body length, and habitat use provided a robust indicator of life changes (see Chapter 2) that allowed a better understanding of the population dynamics of this taxon.

Another recommendation is developing numerical growth models for local characteristics of scarids, as a useful alternative when no other source of information is available. When applied, it must be considered that the similar-early-growth constraint is based on the assumption that the younger stages of scarids will show similar growth patterns regardless of latitudinal, cross-shelf, or local differences. This assumption was derived from the von Bertalanffy size-at-age otolith based curves developed by Choat and Robertson (2002), who demonstrated similar growth patterns of year classes 1 to 3 among Panamanian populations of five *Sparisoma* spp., and between mid shelf and outer shelf populations of *Sc. frenatus* in the Great Barrier Reef.

Table 3.1: Life history invariants equations, following: {a} Williams and Shertzer (2003), {b} Jensen (1997), {c} Froese and Binohlan (2000), {d} Allsop and West (2003b), {e} Choat and Robertson (2002).

B&H= Beverton & Holt invariants from the von Bertalanffy model

VARIABLE NAME	EQUATION	NOTATION	{SOURCE}/ COMMENT
Weight at age	$W_t = W_\infty (1 - e^{-K(t-t_0)})^3$	W_∞=asymptotic weight K=growth parameter for weight	{a}
Inflection point of VB growth equation for weight	$W_t = 0.296W_\infty$	W_t = weight at time t	{a} Assumed to coincide with age at first maturity
Age at first maturity	$L_m = 10^{(0.8979 * \log L_\infty - 0.0782)}$		{c}
1st B&H invariant (VB model)	$Mt_m = 1.65$		{a, b} Range: 1.54-3.33 $\cong 2.2$ in {a}
2nd B&H invariant (VB model)	$\frac{M}{\mathrm{K}} = 1.5$	M = natural mortality rate, K = Brody growth parameter	{a, b} = 1.6 for 175 spp. (Pauly 1980)
3rd B&H invariant (VB model)	$\frac{L(t_m)}{L_\infty} = 0.66$		{a, b} = 0.4-0.8 in Charnov 1993 cited in {a}
Length at age t (indeterminant growth model)	$L_t = at^b$	a, b = parameters b = 0.5964 (n = 19 spp.)	{a} Alternative 2 of growth model
Length at sex change	$L_x = 0.79L_\lambda$	L_λ = observed maximum length	{d}
Age at sex change	$t_x = 2.5t_m$		{d}
Atlantic parrotfish growth curve intercept	$L_{(t_0)} = L_r$		{e} = 10 mm SL = 1-1.25 cm TL

Table 3.2: Length –weight, and length-length relationships for South Florida parrotfish populations.

W=weight, TL=total length, FL= fork length, SL=standard length.

α and β are parameters in the equation $W = \alpha*(TL)^{\beta}$. The growth is isometric when the 95% confidence interval (95CI) of the β estimate contains the value 3.0.

β_o and β_1 are parameters in the equation $SL = \beta_o + \beta_1*TL$

Parameters for *Sp. aurofrenatum* and *Sp. viride* were calculated from unpublished data generously provided by Paddack, M (2004).

Species	*Sc. iseri*	*Sp. aurofrenatum*	*Sp. chrysopterum*	*Sp. viride*	*N. usta*	*Sp. radians*
n	82	7	105	53	42	12
Size range (TL)	2.0, 14.3	4.6, 22.4	5.9, 35.1	4.3, 39.8	5.5, 19.2	4.1, 15.8
W-TL:						
R^2	0.980	0.993	0.997	0.990	0.990	0.998
α	0.0126	0.0128	0.0152	0.0226	0.0069	0.0122
β	3.1426	3.0857	3.0274	2.9298	3.3046	3.1414
95CI(β) Lower, Upper	2.946, 3.340	N/A	2.970, 3.085	N/A	3.222, 3.387	3.083, 3.200
Isometry	Yes	N/A	Yes	N/A	No	No
SL-TL						
β_o	-0.0273	+0.4179	-0.2932	+1.0818	-0.0445	+0.0928
β_1	0.8411	0.7882	0.7916	0.749	0.8037	0.7894
R^2	0.940	0.997	0.990	0.994	0.995	0.998

Table 3.3: Von Bertalanffy parameter estimates for South Florida parrotfishes computed with numerical approaches. "Low t_λ" and "High t_λ" are alternate models with short and long life span, respectively. (A) and (B) indicate parameter estimations for *Sp. viride* based on Choat et al. (2003) and Paddack (2005), respectively. L_∞: TL and SL in cm. Initial input parameters are shown in the bottom panel for comparison purposes. ND: no data available. Asterisks indicate the more suitable model parameters for each species.

Parameter estimates	*Sc. iseri*	*Sp. aurofrenatum*	*Sp. chrysopterum*	*Sp. viride*	
Short (low) t_λ				(A)	(B)
$\hat{K}$	0.5303	0.7020	0.6808	0.3242	0.4321
t_o	0	0.0	0.0	0.0	0.0
L_∞: TL (SL)	20.5 (17.2)	27.7 (25.5)	45.5 (35.7)	62.5 (47.9)	62.0 (47.6)
L_λ: TL (SL)	20.0 (16.8)	27.5 (25.4)	44.0 (34.5)	60.0 (46.1)	60.0 (46.1)
t_λ	7	7	5	10	8
Long (high) t_λ	*	*	*	(A)*	(B)
$\hat{K}$	0.4418	0.5638	0.6244	0.3445	0.4016
t_o	0.0	0	0	0	0
L_∞: TL (SL)	21.0 (17.6)	28.1 (25.9)	44.3 (34.5)	61.0 (46.8)	60.5 (46.4)
L_λ: TL (SL)	20.0 (16.8)	28.0 (25.8)	44.0 (34.8)	60.0 (46.1)	60.0 (46.1)
t_λ	12	10	8	12	12
Published Models	Choat and Robertson (2002)	Choat and Robertson (2002)	Choat and Robertson (2002)	Choat et al. (2003)	Paddack (2005)
$\hat{K}$	1.235	1.163	1.176	0.4580	0.8400
t_o	-0.05	-0.04	-0.04	-0.06	-0.06
L_∞: TL (SL)	13.8 (11.7)	18.2 (17.1)	26.3 (23.8)	47.2 (35.7)	33.5 (26.9)
L_λ: TL (SL)	ND	25.5 (23.4)	34.7 (27.8)	49.0 (37.9)	39.0 (30.3)
t_λ	8	7	5	9	8

Table 3.4: Input values and assumed distributions for the MonteCarlo simulations on von Bertalanffy growth functions of South Florida parrotfishes, under three assumed $\hat{K}$ distributions: normal (N), gamma (Γ), and exponential (Expo) under two longevity assumptions: (a) short and (b) long. L_∞ = SL, cm

(a) SHORT LONGEVITY

Short longevity	*Sc. iseri*	*Sp. aurofrenatum*	*Sp. chrysopterum*	*Sp. viride*	
Parameter estimates				(A)	(B)
t_o~Uniform (range)	-0.05 – 0.0	-0.04 – 0.0	-0.04 – 0.0	-0.06 – 0.0	-0.06 – 0.0
$L_\infty \sim N(\mu, \sigma)$	(17.2, 1.72)	(25.5, 2.55)	(35.7, 3.57)	(47.9, 4.8)	(47.6, 4.8)
$\hat{K}$	0.5303	0.7020	0.6808	0.3242	0.4321
		$\hat{K}$ ~NORMAL			
$N(\mu, \sigma)$	(0.5303, 0.05)	(0.7020, 0.07)	(0.6808, 0.069	(0.3242, 0.03)	(0.4321, 0.043)
		$\hat{K}$ ~GAMMA			
$\Gamma(\alpha, \beta)$	(2, 0.2652)	(2, 0.3501)	(2, 0.3404)	(2, 0.1621)	(2, 0.2160)
		$\hat{K}$ ~EXPONENTIAL			
Expo(β)	(1, 0.5303)	(1, 0.702)	(1, 0.6808)	(1, 0.3242)	(1, 0.4321)

(b) SHORT LONGEVITY

Long longevity	*Sc. iseri*	*Sp. aurofrenatum*	*Sp. chrysopterum*	*Sp. viride*	
Parameter estimates				(A)	(B)
t_o~Uniform (range)	-0.05 – 0.0	-0.04 – 0.0	-0.04 – 0.0	-0.06 – 0.0	-0.06 – 0.0
$L_\infty \sim N(\mu, \sigma)$	(16.9, 1.69)	(25.9, 2.59)	(34.8, 3.48)	(47.9, 4.8)	(46.8, 4.7)
$\hat{K}$	0.2536	0.5638	0.6244	0.3242	0.3445
		$\hat{K}$ ~NORMAL			
$N(\mu, \sigma)$	(0.4418, 0.04)	(0.5638, 0.06)	(0.6244, 0.069	(0.3242, 0.03)	(0.3445, 0.034)
		$\hat{K}$ ~GAMMA			
$\Gamma(\alpha, \beta)$	(2, 0.2209)	(2, 0.2819)	(2, 0.3122)	(2, 0.1621)	(2, 0.1723)
		$\hat{K}$ ~EXPONENTIAL			
Expo(β)	(1, 0. 4418)	(1, 0.5638)	(1, 0. 6244)	(1, 0.3242)	(1, 0.3445)

Table 3.5: Life history parameter estimates as predicted by simulations and invariant theory, under the assumption of short lifespan. Input values are given in Table 3.4: longevity (t_{max} in years), ultimate length and weight (L_∞, W_∞), maximum observed length and weight (L_λ, W_λ), size and age at recruitment (L_r, t_r in months) size and age at first maturity (L_m, t_m in months), size and age at first capture (L_c, t_c in months), size and age at sex change (L_x, t_x in years), natural mortality (M). Length: TL (SL), mm. Weight: (g)

* computed from observed L_{50}/L_λ: [a] (Robertson and Warner 1978)
** computed from 0.79 L_λ invariant (Allsop and West 2003b) (cf. Table 3.1)
*** computed from $2.5t_{mat}$ invariant (Allsop and West 2003b) (cf. Table 3.1)
† assuming 5% survivorship until maximum age ($M = -\ln(0.05)/t_{max}$) (Alagaraga 1984)

Parameter type	Estimator	*Sc. iseri*	*Sp. aurofrenatum*	*Sp. chrysopterum*	*Sp. viride*
Maxima observed	t_{max}	7	7	5	10
	L_∞	205 (172)	277 (255)	455 (357)	625 (479)
	W_∞	97	410	1590	4076
	L_λ	200 (168)	275 (254)	440 (345)	600 (461)
	W_λ	155	405	1436	3662
Recruitment	L_r	12.5 (10)	12.5 (10)	12.5 (10)	12.5 (10)
	t_r	1.4	0.7	0.5	0.8
Sexual maturity	L_m	128 (108)	167 (153)	257 (207)	345 (270)
	W_m	38	74	284	721
	t_m	22	16	15	31
First capture	L_c	40 (33)	40 (33)	150 (118)	150 (123)
	W_c	1	0.6	55	63
	t_c	4.9	2.4	7.1	11
Sex change	L_x *	112 (94) [a]	204 (187) [a]	290 (229)	378 (294)
	W_x *	25	146	406	946
	L_x **	158 (133)	221 (203)	363 (287)	474 (366)
	W_x **	74	192	805	1836
	L_x ***	187 (157)	271 (229)	395 (316)	542 (418)
	W_x ***	124	388	1034	2718
	t_x *	1.5 [a]	1.9 [a]	1.5 [a]	2.9 [a]
	t_x **	2.8	2.3	2.4	4.5
	t_x ***	4.6	3.3	3.2	6.4
Natural mortality	M †	0.43	0.43	0.60	0.30

Table 3.6: Life history parameter estimates as predicted by simulations and invariant theory, under the assumption of long lifespan. Input values are given in Table 3.4. Symbology and units: same as in Table 3.5.

Parameter type	Estimator	*Sc. iseri*	*Sp. aurofrenatum*	*Sp. chrysopterum*	*Sp. viride*
Maxima observed	t_{max}	12	10	8	12
	L_∞	210 (176)	281 (259)	443 (348)	610 (468)
	W_∞	104	432	1466	3802
	L_λ	200 (168)	280 (258)	440 (345)	600 (461)
	W_λ	155	426	1436	3634
Recruitment	L_r	12.5 (10)	12.5 (10)	12.5 (10)	12.5 (10)
	t_r	1.6	0.8	0.6	0.8
Sexual maturity	L_m	130 (110)	170 (155)	251 (202)	337 (264)
	W_m	40	77	263	676
	t_m	26.5	19.5	16.7	29
First capture	L_c	40 (33)	40 (33)	150 (118)	150 (123)
	W_c	1	0.6	55	63
	t_c	5.7	2.9	8	10.6
Sex change	L_x *	112 (94) [a]	204 (187) [a]	290 (229)	378 (294)
	W_x *	25	146	406	946
	L_x **	158 (133)	221 (203)	363 (287)	474 (366)
	W_x **	74	192	805	1836
	L_x ***	191 (161)	276 (233)	385 (308)	530 (409)
	W_x ***	133	408	956	2544
	t_x *	1.7 [a]	2.3 [a]	1.7 [a]	2.9 [a]
	t_x **	3.2	2.7	2.8	4.4
	t_x ***	5.5	4.1	3.5	6.0
Natural mortality	M [†]	0.25	0.30	0.37	0.25

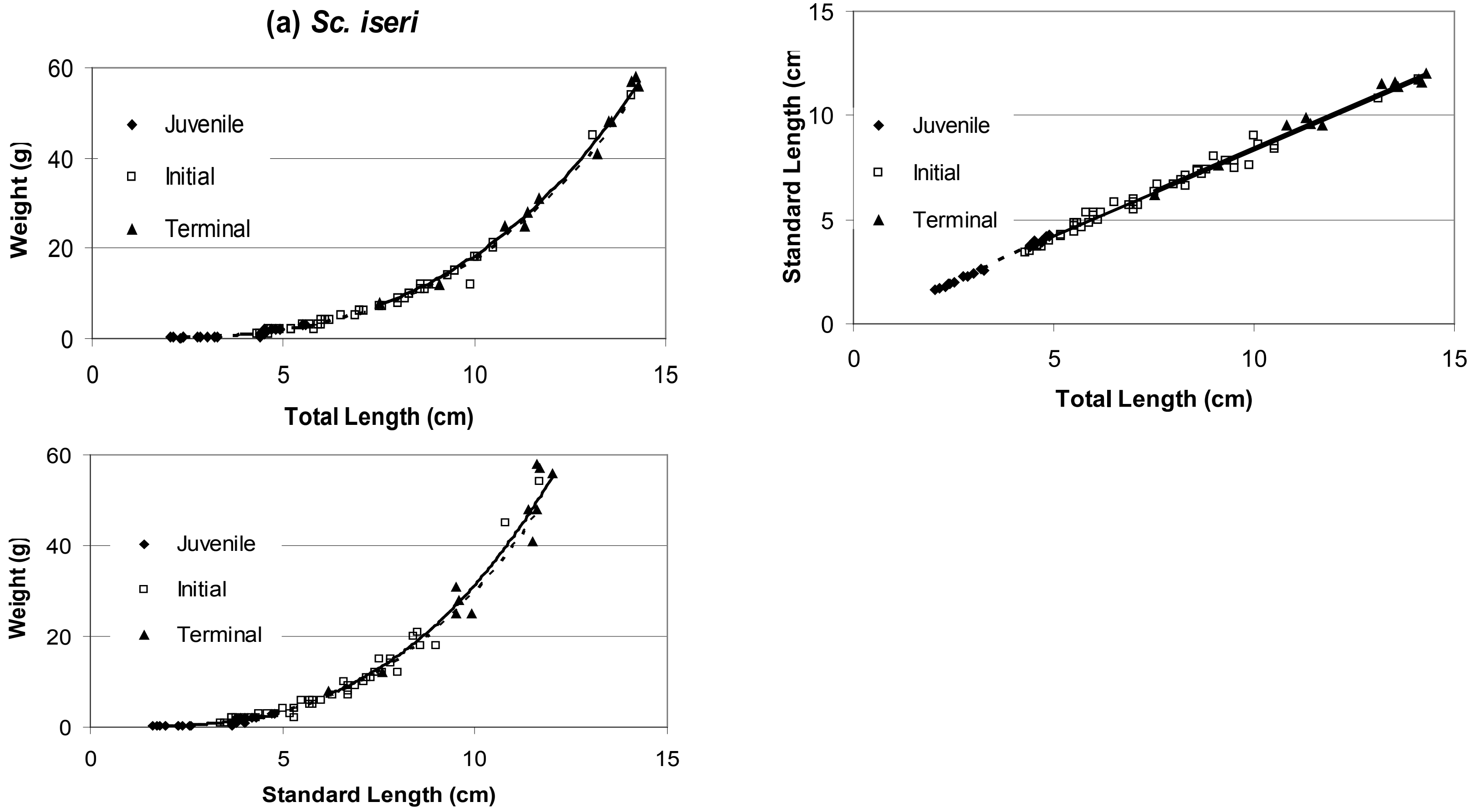

Figure 3.1: Weight-to-length and length-to-length relationships for (a) *Scarus iseri,* and (b) *Sparisoma chrysopterum* by lifestage. Left panels represent weight vs. total and standard lengths. Dashed line: Initial Phase regression line. Solid line: Terminal Phase regression line. Regression parameters are taken from Table 3.2. Right panels show standard or fork lengths vs. total length.

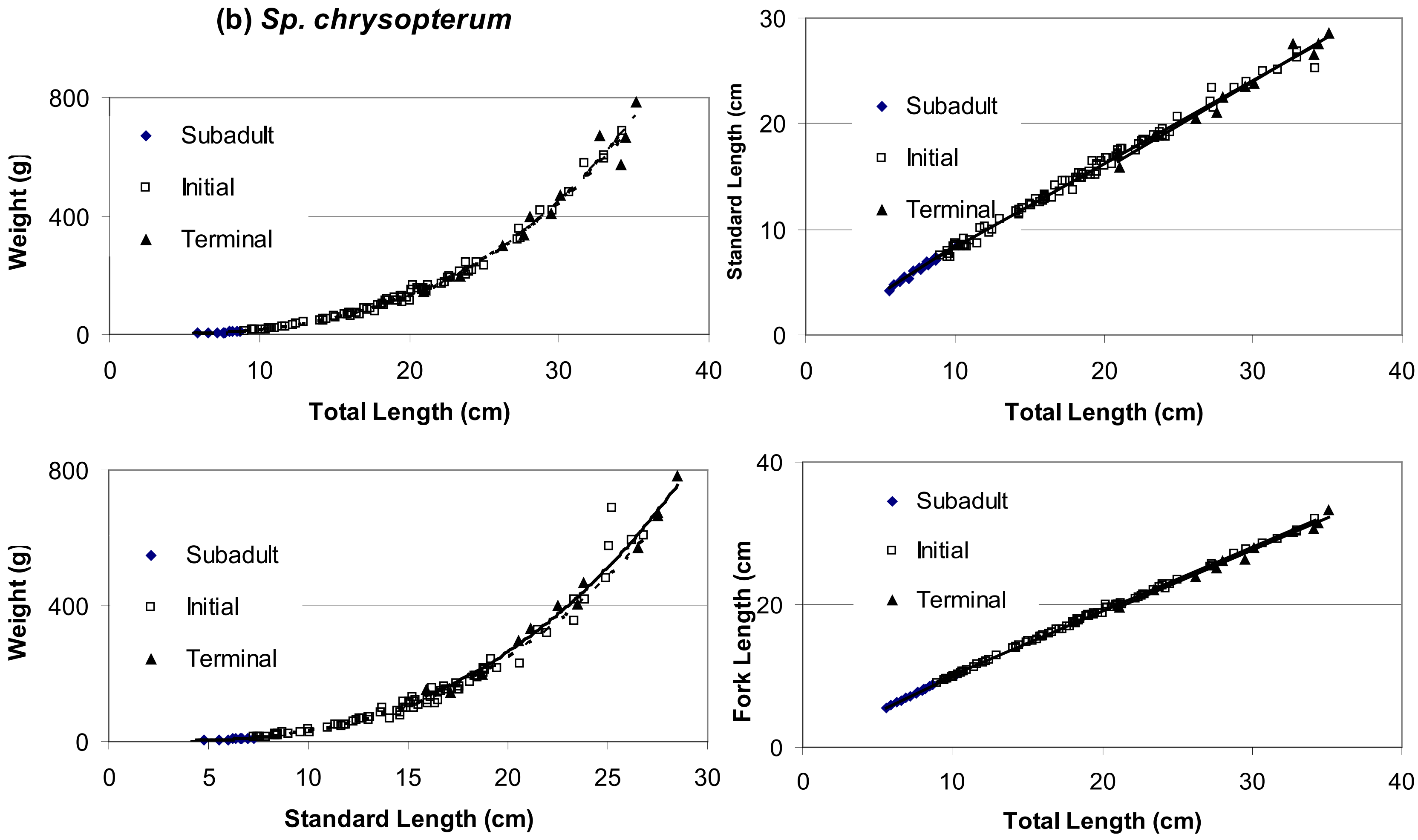

Figure 3.1continued

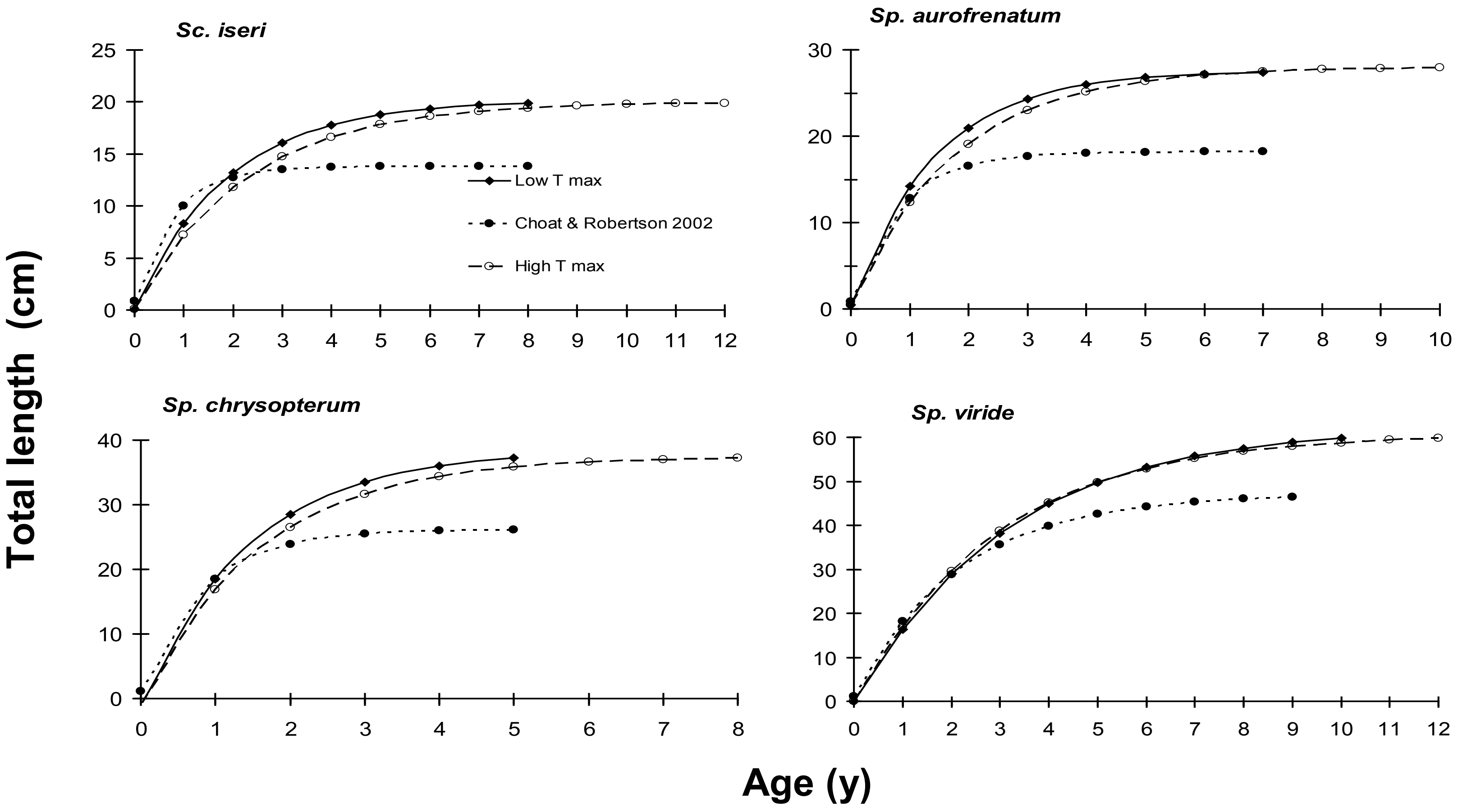

Figure 3.2: Deterministic length-at-age models of *Sc. iseri*, *Sp. aurofrenatum*, *Sp. chrysopterum*, and *Sp. viride* adapted numerically from (Choat and Robertson 2002, Choat et al. 2003). “Low T max” model represents the outcome of the short lifespan alternative. “High T max” model represents the outcome of the longer lifespan.

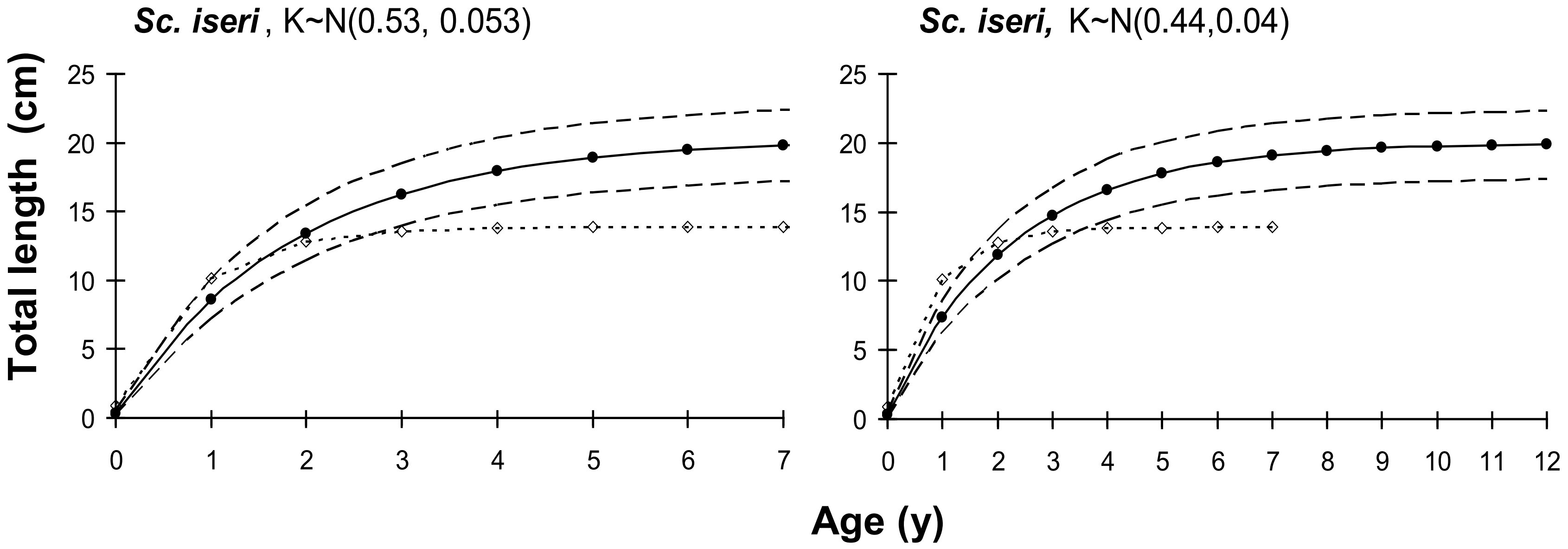

Figure 3.3: Expected mean (black circles) and 80th percentile confidence intervals (hatched lines) of selected length-at-age models of South Florida parrotfishes, under normally distributed $\hat{K}$ assumption, N(μ,σ). Left panels show short lifespan scenario. Right panels show long lifespan scenario. Otolith-based models (open diamonds) are shown as reference. *Sparisoma viride* shows alternative models based on Choat and Robertson (2002) and Paddack (2005) on top and bottom panels, respectively. Note the axis scales vary among species.

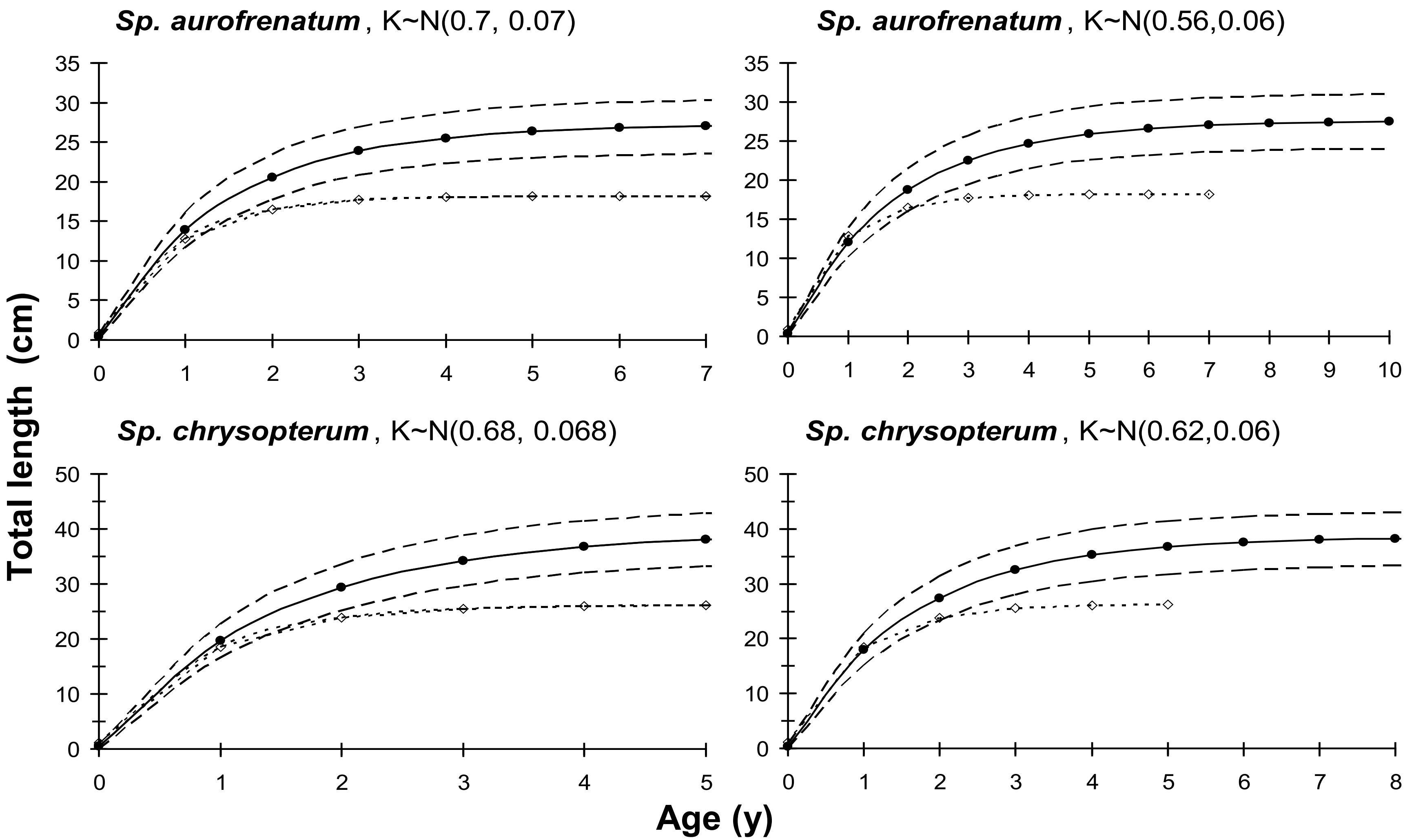

Figure 3.3 continued

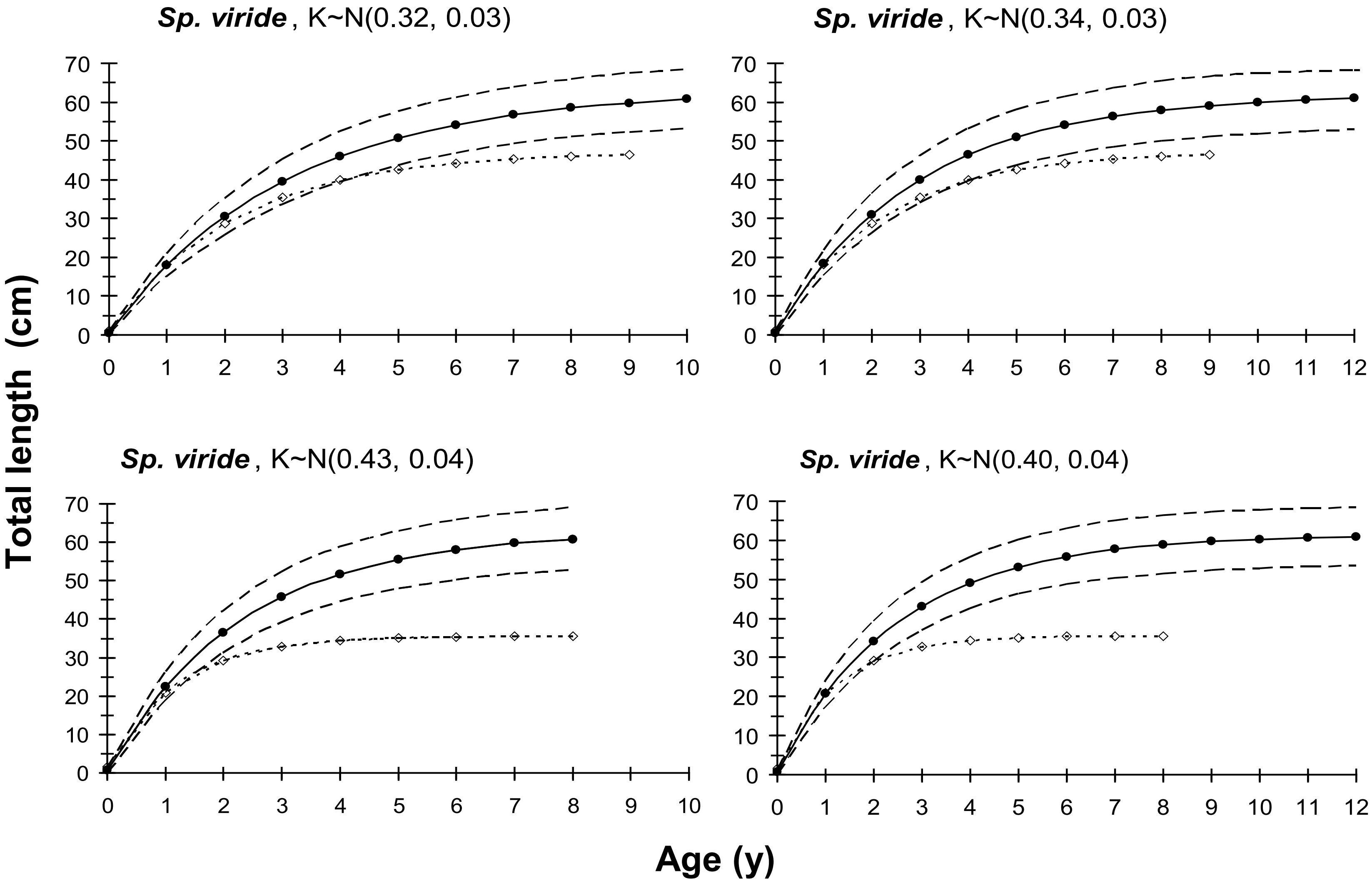

Figure 3.3 continued

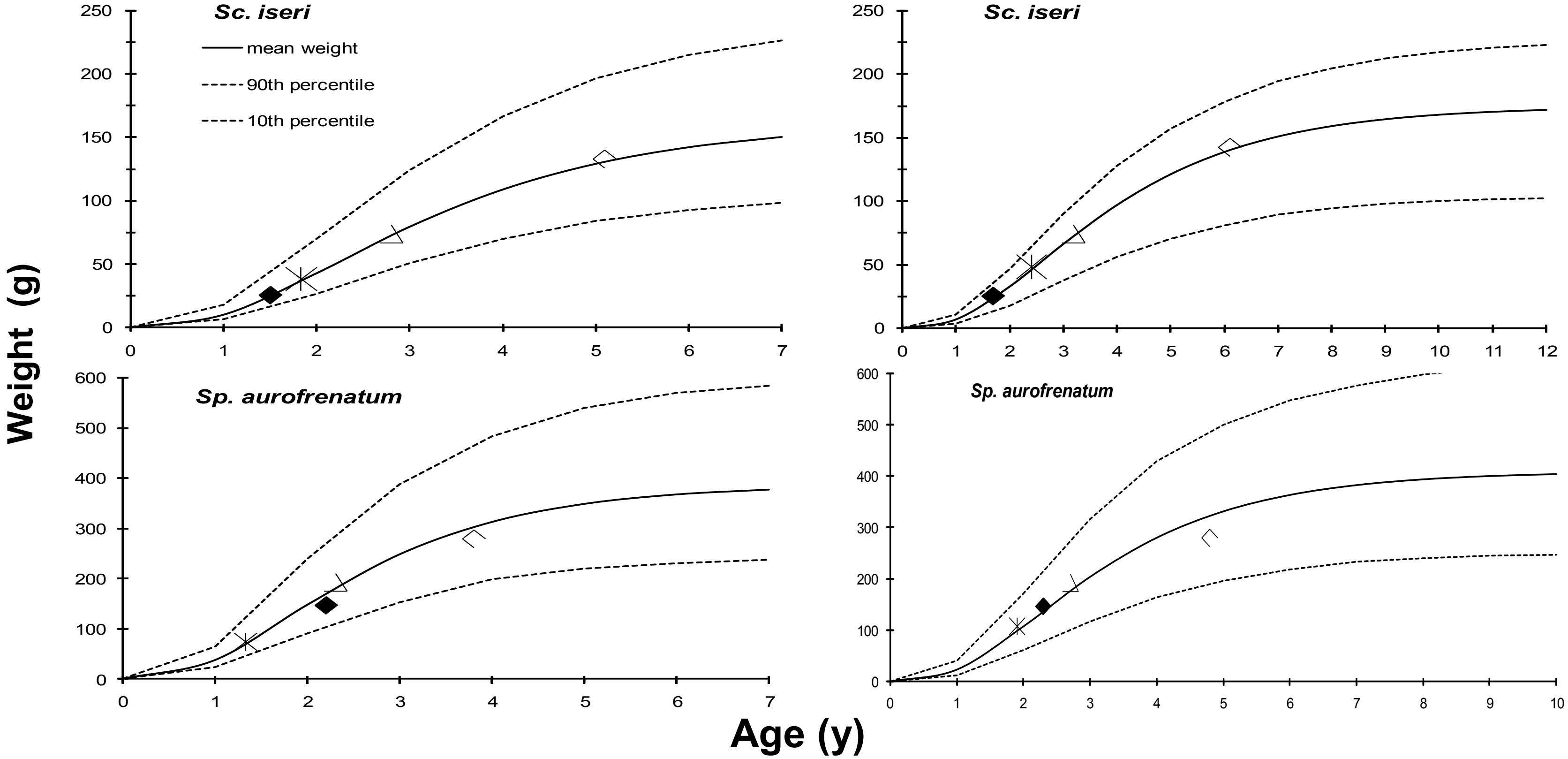

Figure 3.4: Comparison of size at first maturity (W_m) and size at age estimates of sex change (W_x) against expected mean (solid line) with 80th percentile confidence intervals (hatched lines) of weight-at-age models of South Florida parrotfishes. Simulations are based on normally distributed $\hat{K}$ and L_∞, $N(\mu,\sigma)$. Left panels: short lifespan scenario. Right panels: long lifespan alternative.

Symbology: (Ж)= size at first maturity; ♦= empirical size at sex change from Robertson and Warner (1978)'s observed L_x/L_λ proportion; ◊= aged-based size at sex change from A&W's $2.5{*}t_\lambda$ age proportion (Allsop and West 2003b); Δ= length-based size at sex change from A&W's $0.79{*}L_\lambda$ length proportion (Allsop and West 2003b). Note the axis scales vary among species.

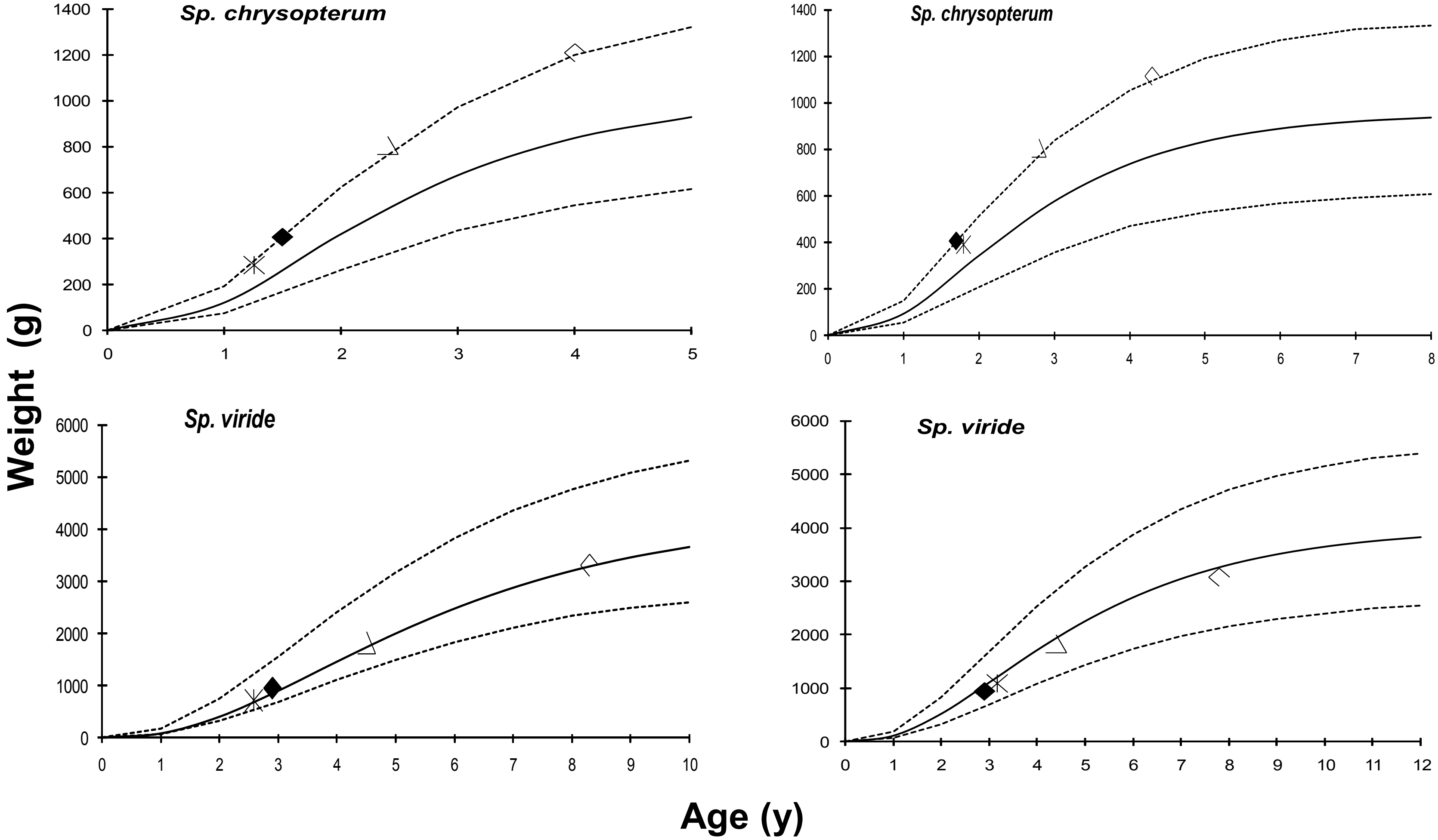

Figure 3.4: continued

Chapter 4: Population dynamics parameters and demographic modeling

4.1 Background

The Western Central Atlantic (FAO Area 31) is reportedly undergoing the transition from predatory-species fisheries to low-trophic level fishing, as a consequence of targeting secondary species due to drastic declines in the more valuable fishes (Pauly et al. 1998). This trend of fishing down from high quality carnivores to less valuable herbivores or planktivores, also known as "serial fishing", involves the targeting of relatively unexploited, thus not very studied, species. In the context of the precautionary principle in fisheries management, it is necessary to identify those species vulnerable to exploitation before their populations start showing effects of overfishing. However, because most stock assessment methods rely on landings and catch information, the management actions usually are remedial rather than preventive. Different approaches have been applied to predict vulnerability to fishing, such as using phylogenetics and life history (e.g., Jennings et al. 1998), modeling actual and virtual populations under a wide arrange of scenarios (e.g., Jensen 1991, Chen et al. 1998), and developing length-based estimators when age data are not available (e.g., Ault et al. 1998, 2005, 2008).

Atlantic scarids are exploited for consumption (marketed fresh and salted), ornamental trade, or are caught incidentally (Table 4.1) to varying degrees. In the Caribbean basin, their commercial value was relatively low ten years ago (Cervigón et al. 1993, Claro 1994b), although some areas showed high fishing pressure on these species since the early seventies (Munro 1983) to the point that Jamaican scarid populations are considered currently overfished (Klomp et al. 2003, Kramer 2003). South Florida is at the opposite end of this spectrum, and parrotfish catches were considered incidental in the 1960s and 1970s (Welch 1965, Joyce Jr. and Beaumariage 1975, Sutherland and Harper 1983, Taylor and McMichael Jr. 1983). Even though scarid commercial exploitation has been considered negligible in the Florida Keys for the past 25 years (Bohnsack et al. 1994, Ault et al. 1998), there is ornamental trade and bycatch in the lobster fishery. Fisheries status of endemic parrotfishes in Venezuela and Brazil is unknown.

Regarding the ornamental industry, *Cryptotomus* and *Nicholsina* do not have any value. *Scarus iseri* and *Sc. taeniopterus*, whose appearances are very similar, are the most traded or collected parrotfishes for aquarium markets (GMAD)[13]. Both species represent the only scarids with major ornamental trade (notwithstanding the usual taxonomic misidentifications between both species). The main exporters of live Western Atlantic scarids are the Caribbean island nations, Florida, and Cuba. The main importers are the United States, France, Germany, United Kingdom, Netherlands, and Japan, all of whom are also the major receptors of all aquatic ornamental trade (FAO 2000). Nevertheless, ornamental parrotfish catches reportedly extracted from Florida waters are very low (Figure 4.1). A trip ticket system established by the FWRI reported a grand total of 43,593 parrotfishes collected between 1990 and 1998 as ornamentals in the state's coastal waters (S. Larkin, FWRI, 2000, unpubl. data), averaging 4,844 parrotfish annually (Figure 4.1). While ornamental trade might be a source of mortality for *Sc. iseri*, other parrotfishes, such as *Sparisoma aurofrenatum* and *Sp. viride*, can be considered minor ornamental species.

With respect to bycatch, Matthews and Donahue (1997) found low numbers of parrotfish caught in lobster traps (1-3 fish/100 traps). Considering a total of ~704,000

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[13] http://www.unep-wcmc.org/marine/GMAD/

lobster traps in the Florida Keys region (T.R. Matthews, unpubl. data), ~8,600 parrotfishes would be caught per year, 3,000 of which would be *Sp. chrysopterum* (as calculated from Matthews' unpublished data), suggesting that the current lobster fishery bycatch for most of the scarids could be considered negligible. Unreported captures as ornamentals in lobster traps can take place, but cannot be quantified (T.R. Matthews, Florida Marine Research Institute, 2001, pers. comm.).

Within this complex fishery status of parrotfishes in the Western Atlantic reefs, South Florida populations present an extraordinary opportunity for the holistic approach to fisheries management, and to compare simulated to observed data as a tool to assess the current status and predict potential effects of fishing and management actions. This chapter addresses the dynamics and fisheries parameters for the four most abundant scarids of the Florida Keys: *Sc. iseri*, *Sp. aurofrenatum*, *Sp. chrysopterum*, and *Sp. viride*. By simulating different scenarios of increasing fishing pressure under alternative longevity and natural mortality assumptions, a better understanding of their potential vulnerability and response capability can be achieved. Pertinent management recommendations are provided based on the understanding acquired with these analyses.

4.2 Materials and methods

An iterative process simulating potential exploitation levels was performed as indicated in Figure 4.2. In the first and second steps, field length distributions were used to adjust published von Bertalanffy (VB) growth models to local population characteristics, as described in Chapter 3 (cf. section 3.2.3).

Observed data was obtained by Reef fish Visual Census (RVC) surveys in the Florida Keys National Marine Sanctuary, FKNMS (cf. Figure 2.1) from 1997 to 2001, between April and October of each year, under a stratified random sampling design. The stratification scheme and sampling unit characteristics are described in section 2.2.1.2. Cross-shelf and region classes were pooled by year. In order to consider effects of protection status, no-take areas were considered separately from unprotected sites when they differed statistically. This analysis excluded deep fore reefs (>18 m) because this stratum was sampled in 2000 and 2001 only, with no representation of protected reefs.

Estimates of overall numbers of each species in the Florida Keys domain were obtained from estimates of mean density per stratum (Chapter 2) and the area covered by stratum *h*, following the equation:

$$\hat{Y} = \sum_{h} \hat{Y}_h \qquad \text{Equation 4.1}$$

Where:

$\hat{Y}_h$ = total number of fish per stratum (cf. Table 2.5)

Morphometric functions, e.g., length-length (L-L) and weight-length (W-L), developed in Chapter 3 (cf. Table 3.2), were required to (a) standardize length units from published growth curves (Standard Length, SL) and field data (Fork and Total Length, FL, TL, respectively), and (b) provide biomass estimates. Field data comparisons included minimum, maximum, and mode length intervals, and main size range. The *main size range* descriptor was defined here by the lower and upper limits of the distribution containing ≥85% of the population, to avoid influence of extreme values.

Total mortality rate (Z) has two additive components, natural (M) and fishing (F) mortality rates, such that:

$$Z = M + F \qquad \text{Equation 4.2}$$

In order to address potential effects of increased fishing pressure (cf. third step in Figure 4.2), five levels of fishing mortality (F) were set at 0, 0.1, 0.5, 1.0, and F=M. Originally, fishery biologists considered the latter as a proxy for maximum sustainable fishing rate (F_{MSY}=M). The current trend is to use it as the upper bound of allowed fishing mortality when limited data do not allow a reliable estimation of F (Williams and Shertzer 2003). Outputs of two models, Reef Ecosystem Exploited Fisheries Simulator (REEFS)[14] and LBAR (Ault et al. 1996), were used to simulate different levels of exploitation (Steps 4 and 5, Figure 4.2), based on the life history parameters estimated in Chapter 3. REEFS is an object-oriented model developed by Jerald S. Ault (University of Miami), to explain the response of coral reef fish stocks based on their population dynamics. This program allows for assumptions applying to tropical reef fish population-dynamic processes, such as a quasicontinuous growth, protracted spawning and recruitment, and population dynamics based on competition (Ault et al. 1998). The LBAR algorithm (Ault et al. 1996) is designed to compute the annual instantaneous rate of total mortality in year t, Z_t, from the average length of the exploited stock obtained from REEFS. The fundamental equations of both models are shown in Table 4.2, and the input values under short and long lifespan scenarios are listed in Table 4.3 and Table 4.4, respectively. The endpoints chosen for comparative analyses of simulation scenarios and between observed and simulated data were instantaneous rate of total mortality (Z),

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[14] Ault, J.S. 1998. Tropical coral reef fishery resource decision dynamics. Unpubl. manuscript.

annual mortality rate as a percentage of the population (A), mean length of the exploited phase ($\overline{L}$), shape of size frequency distribution, amount and location of modal size intervals, and relative abundance of larger individuals (Figure 4.2).

Input values for REEFS and LBAR were obtained from simulations based on field data and literature (cf. Table 3.5, Table 4.2), modified to account for observed length distributions. Two possible longevities were assumed for each species, adjusted to observed maximum lengths (cf. input values in Table 4.3 and Table 4.4): (a) short lifespan, equal to otolith-estimated maximum age (±1 year) (Choat and Robertson 2002, Choat et al. 2003); (b) long lifespan, calculated as the proportional increase in longevity to the difference between otolith-derived maximum lengths (Choat and Robertson 2002, Choat et al. 2003) and the values recorded in the present study. The long-life scenario was aimed at exploring an alternative that might account for the larger specimens observed, while keeping growth rates comparable to those described in the literature. Thus, if L_λ in this study was 40% larger than that obtained via otolith analyses, then the lifespan was arbitrarily assumed to be approximately 40% longer than the otolith-estimated t_λ.

Given the information gap on life history parameters of Atlantic parrotfishes, the application of invariant relationships under the framework of dimensionless theory was a useful alternative. The inputs required were: von Bertalanffy growth parameters (K, t_o), survivorship or natural mortality ($M_{a,t}$), maturity and reproduction schedules (t_m, L_m), longevity (t_λ), maximum and ultimate size (L_λ, L_∞, W_∞), age/size at first capture (t_c, L_c), and weight-to-length relationships (Table 4.3). L_c was assumed 15 cm TL for the larger species, *Sp. chrysopterum* and *Sp. viride* (fish trap median length data, Ferry and Kohler

1987). For the smaller species, *Sc. iseri* and *Sp. aurofrenatum*, assumed L_c was 4 cm TL, i.e., minimum observable size by the divers conducting visual censuses; these species showed ornamental trade activity (Figure 4.1). Other assumptions of the simulation process were: recruitment to the population is periodic and trigonometrically distributed as unimodal with 12 annual time-steps, with no interannual pulses; fishing occurs throughout the year; selectivity pattern is constant through time. All simulations were run on standard length; outcomes were converted to total length for comparison purposes.

Because mortality in protogynous or polychromatic species cannot be assessed by lifestage, sex, or color phase, due to the impossibility of distinguishing between mortality and stage change (Gust et al. 2002, Paddack 2005), a single overall instantaneous mortality rate was computed for each species. In order to test moderate and high natural mortalities, two estimates of natural mortality ($\hat{M}$) were computed (Table 4.2, App. Table A.1): the 5% survivorship to maximum age assumption, S5 (Alagaraga 1984), and the second Beverton & Holt (B&H), invariant M =1.5K (Jensen 1996).

Comparisons between simulated and observed length distributions were used to determine the most realistic combination of growth functions, exploitation levels, lifespan estimates and natural mortality rates that may account for the population length structures found in the field.

4.3 Results

During the study period, the combined numbers of the top four most abundant parrotfishes in the Florida Keys domain averaged nearly 33.6 x 10^6 individuals at any time (Table 4.5). *Scarus iseri*, the most ubiquitous and numerous scarid in the Florida

Keys (cf. Chapter 2), accounted for approximately 56% of the overall quantity (ranging 46 to 61% between 1997 and 2001). Relative abundances of *Sp. aurofrenatum*, *Sp. viride*, and *Sp. chrysopterum* followed, with ca. 28, 10, and 5%, respectively (Table 4.5).

Annual observed length frequency distributions are shown in Figure 4.3. No significant fluctuations of minimum, maximum, mode, and main size range over time were detected within each species. Size structures of *Sc. iseri, Sp. aurofrenatum*, and *Sp. viride* did not differ significantly between protected and unprotected reefs (χ^2 $P>0.10$). However, distributions of *Sp. chrysopterum* varied with protection status (χ^2 $P<0.01$), thus its data were not pooled.

Scarus iseri frequencies peaked at 5-6 cm TL in a unimodal distribution (Figure 4.3a). *Sparisoma aurofrenatum* displayed multiple modes at 5-6, 8, 10, 15, and 20 cm TL (Figure 4.3b). Multimodal distribution of *Sp. viride* peaked at 5, 15 cm (occasionally), 20, 25, and 30 cm (Figure 4.3c), and the upper limit of its size range increased from 30 to 35 cm after 1999. Although length ranges of *Sp. chrysopterum* were similar regardless of protection status, its minima were smaller in unprotected sites (2-4 cm) compared to those in protected reefs (4-10 cm). Modal lengths of this parrotfish were more variable than in the other species; the 13-16, 20, and 25 cm intervals peaked more frequently in unprotected reefs, while the 12-13 and 25 occurred occasionally in protected sites (Figure 4.3d).

Expected length frequency distributions were obtained under different combinations of exploitation rates and life history demographics with simulations by REEFS and LBAR algorithms. Figure 4.4 shows the resulting simulated distributions from sizes greater than length at first capture (L_c), under increasing levels of fishing mortality, F, based on two different longevities.

When comparing predicted modal intervals, distribution shape, relative frequency of the larger size classes, and the mean length against the observed size structure, the scenarios assuming short- longevity with low natural mortality and F=M scored more similarities to the observed data in each species (Figure 4.3, Figure 4.4, Figure 4.5, and Table 4.6). Alternatively, the high-M assumption combined with F values ~0.1 (App. Figure A.1) produced size structures resembling field observations, but required extremely high natural mortality rates.

REEFS simulated a 4.6 cm TL peak for *Sc. iseri*, matching the observed 5-6 cm mode (Figure 4.4a). The short lifespan (t_λ=7) with F=M=0.43 assumptions better explained the observed data. Simulated length frequency distributions of *Sp. aurofrenatum* resembled observed data only moderately. The 15, 19-20, and 25-cm expected peaks in the long lifespan scenarios matched observed modes; the assumptions t_λ=10 with M=0.5 performed better to account for the actual distributions (Figure 4.4b). *Sparisoma viride* long lifespan simulations predicted modes at 15.6, 22.6, 26.6, and 29.2-cm. Notwithstanding a missing 22-23 cm peak, the expected values agreed with 15, 25 and 30-cm modes (Figure 4.4c). In this species, the F=M=0.25 and 12-year lifespan assumptions provided a moderate resemblance to the overall actual distribution. Size structures of *Sp. chrysopterum* predicted by the short longevity scenario peaked at 25.4 and 29.1 cm TL, the former matching the 25-cm mode observed in both unprotected and protected reefs (Figure 4.4d). This parrotfish did not show a close agreement between observed and any predicted size structure; the 25 and 30 cm modes were better depicted by the t_λ=5 and F=M=0.6 scenario, although that model overestimated the relative abundances of larger individuals.

The simulation outcomes indicated that total mortality rates, Z, ranged 0.25-1.6 (*Sc. iseri*), 0.3-1.7 (*Sp. aurofrenatum*), 0.25-1.4 (*Sp. viride*), and 0.4-1.8 (*Sp. chrysopterum*) at increasing fishing mortality (Table 4.5). The models that performed better with respect to observed data are indicated by asterisks in Table 4.5, and suggested that South Florida populations of parrotfishes may be undergoing annual removal ranging from 39% in *Sp. viride* to 73% in *Sp. chrysopterum* with fishing mortality rates between 0.25 and 0.5.

REEFS model predicted shape changes in the size distribution curve with increasing fishing pressure (Figure 4.6), suggesting a progressive normalizing trend associated with the removal of larger specimens, as fishing pressure increased on the exploited phase. Observed maximum sizes of the four species studied would be eliminated at fishing mortalities ≥ 1.0.

Observed population average length ($\overline{L}$) of the four species was lower than expected under the short- and long-life contrasts (Figure 4.5). Thus, a short t_λ-high M scenario was also simulated for each species (App. Table A.1), in order to consider possible local adaptations on mortality and longevity suggested in other studies (Chapter 1). The high-M values, derived from the B&H invariant (Table 4.2), were nearly twice as high as the lifespan-estimated M (cf. App. Table A.1). Under these circumstances, high-M simulations with $0.1 \leq F \leq 0.5$ performed better at accounting for the observed size distributions and mean lengths of all species (App. Table A.2, Figure A.1). However, under this scenario, the age composition would be dominated by much younger individuals.

In general, those outcomes suggested that 64-75% of the individuals were removed from the population annually, mostly due to natural mortality. Relative frequencies of the larger individuals in the population were also affected by natural mortality and increased fishing pressure (App. Table A.2). Furthermore, when compared with predicted estimates given by REEFS algorithms, the mean length indicator rendered similar conclusions to those of size frequency analyses (App. Figure A.1): the high-M simulations better fitted the dynamics of the four species, and fishing mortality estimates from 0.1 (*Sc. iseri, Sp. chrysopterum*) to 0.5 (*Sp. aurofrenatum*). However, these simulations overestimated mean length of *Sp. viride* (Figure 4.4).

4.4 Discussion

Three major findings resulted from this work. Firstly, protection status in the Florida Keys did not have an effect on observed population size structure, maximum size, or mean length of parrotfishes. Secondly, reported ornamental and lobster trap bycatch captures of Florida parrotfishes, totaling ~13,600 annually combined, were confirmed to be negligible (< 0.05%), compared to the estimated overall ~36.8 x 10^6 scarids in the Florida Keys alone (Table 4.5). The third finding apparently contradicts the previous one. Simulation results indicated that the current status of Florida Keys parrotfishes appears to be lightly to moderately exploited with short longevity (t_λ=7 and F=M=0.43 for the smaller species, *Sc. iseri* and *Sp. aurofrenatum*; t_λ=10 with F=M=0.3 for *Sp. viride*; and t_λ=5 with F=M=0.6 for *Sp. chrysopterum*). The alternative explanation would be a higher natural mortality that can not be extrapolated from a von Bertalanffy model of growth curve.

4.4.1 Effects of habitat protection

Contrary to what has been suggested in other studies (e.g., Mumby et al. 2006), this work found no evidence of hypothesized depleting effects of population enhancement of predatory species on scarids, caused by implementation of marine protected areas. Trophic cascades in Caribbean coral reefs predicted by Mumby et al. (2006) were not observed in the Florida Keys parrotfish populations in terms of abundance (Table 4.5), even seven years after the first protection was implemented (National Marine Sanctuary, cf. Figure 5.2). Variation in recruit density showed no trends during the study period (cf. App. Figure A.2). Several factors can explain this difference. It is possible that Mumby et al.'s (2006) model assumption that large groupers (e.g., *Epinephelus striatus*, *Mycteroperca tigris*), barracudas (Sphyraenidae), jacks (Carangidae) and large snappers (*Lutjanus* spp.) were major predators of parrotfishes, does not hold. Investigations quantifying predation pressure on Western Atlantic parrotfishes are scarce in the literature (cf. Chapter 1). Also, factors other than predation may drive natural mortality in parrotfishes, as discussed in detail below.

Significant differences in size structure of *Sp. chrysopterum* between protected and unprotected reefs can be explained by the preference of this species on seagrass, hard bottom, and rubble substrates (H. Molina-Ureña, pers. obs.), especially during its early developmental stages (Chapter 2). Those low rugosity habitats tend to be more common outside of no-take areas of the Florida Keys. The other three parrotfishes are associated with structurally more complex bottoms at all life stages (Chapters 1 and 2).

Simulated mean lengths from REEFS and LBAR algorithms overestimated the observed values. This difference can be explained by several sources of variation. The rapid growth of scarids at early stages, confirmed by otolith data (Choat and Robertson 2002), will produce greater proportions of large individuals by accumulation. This effect is shown on both observed and simulated length frequency distributions to varying degrees, although simulation outputs show continuous, higher frequencies of larger size intervals. The gaps in the survey data could be related to the census measuring system (minimum, maximum and mean size, instead of individual length observations), as well as the small bin size (1 cm).

On the other hand, the extremely low frequencies of the largest size classes (< 0.5%), suggested that those specimens could be easily missed in sample sizes < 500. The uniquely large scale of this research allowed recording sample sizes > 1500 for each of the four scarids considered here (Table 2.15). This fact may mark a great difference with otolith studies, especially concerning the detection of the maximum observed length (L_λ).

Despite the mismatch between simulated and survey $\overline{L}$ estimates, there are well defined patterns. Firstly, the short-life scenario rendered more accurate estimates than the long-lifespan option. Secondly, as F increased, $\overline{L}$ estimates approached the observed values, while the difference between model outputs decreased. Thirdly, although F=1 gave the most accurate $\overline{L}$ estimates, this scenario was not realistic because it did not explain the observed larger-sized modes.

4.4.2 Empirical fishing mortality in South Florida parrotfishes

Fishing mortality estimates, usually ≤ M, indicated a light to moderate exploitation rate of parrotfishes, regardless of the life history attributes (e.g., longevity, natural mortality). Empirical data, however, suggested that F levels were negligible for the most abundant scarids in the Florida Keys. Ornamental trade might be a source of fishing mortality for *Sc. iseri*, *Sc. taeniopterus* (both highest ranking scarids in Florida ornamental industry), *Sp. aurofrenatum* and *Sp. viride* (minor ornamental species). A trip ticket system established by the FWRI reported a grand total of 43,593 parrotfishes collected between 1990 and 1998 as ornamentals in the state's coastal waters (S. Larkin, 2000, FWRI, unpubl. data), averaging 4,844 fish annually. Thus, less than 0.15% of any of the ornamental scarids were captured by this industry (cf. Table 4.5).

Sparisoma chrysopterum is not reported in this activity (Figure 4.1), but was the top parrotfish in the lobster trap fishery bycatch (Matthews and Donahue 1997), with ca. 3,000 specimens annually (as calculated from Matthews' unpublished data), which represented 0.15% of the mean population size in the Florida Keys (cf. Table 4.5).

While allowing a 27-54% annual survivorship on the four species, levels of local trade and bycatch apparently have no changing effect on their populations. The density and occurrence of *Sc. iseri* were similar to those found in many other Caribbean localities (Chapter 2, Kramer 2003). Its maximum size in the South Florida habitats was comparable to that of Panama from over three decades ago (Ogden and Buckman 1973), although there is no historical information on maximum size before the 1970s.

4.4.3 Simulated mortality in South Florida parrotfishes

Estimates of fishing mortality rates (F) were higher than expected, given the empirical evidence of negligible removal by ornamental trade and bycatch. Also, scarid natural mortalities (M) estimated from lifespan (cf. Table 4.2) were larger than estimates for Caribbean groupers and snappers (0.1-0.3), but closer to those of grunts (0.3-0.5)

(Ault et al. 1998, 2008). Parrotfish lifespan (5-12 years) and its derived natural mortality estimates appeared unrelated to genus, maximum size, abundance, and assumed age at first catch. Longevity estimates were comparable to those of Caribbean grunts (Ault et al. 1998, 2008).

Several explanations for the mismatch between empirical and simulated data can come forward. Firstly, it has been suggested that body growth rates, longevity, mean size, and population density of scarids show important local variations (e.g., Clifton 1995, Gust et al. 2002, Paddack 2005). These differences are likely phenotypic in nature, since allozyme electrophoresis and randomly amplified polymorphic DNA (RAPD) analyses have demonstrated high level of migration among Caribbean subpopulations, e.g., *Sp. viride* (Geertjes et al. 2004). This, in turn, supports the assumption of open cross-shelf subpopulations of Florida Keys parrotfishes. Alternatively, ontogenetic progression from onshore to offshore reefs could partially explain the reports of cross-shelf differential longevities of parrotfishes (Paddack 2005), while simulation assumptions pool all this information under single M, F estimates. A third mechanism could be that the B&H-derived, high-$\hat{M}$ assumption (cf. Table 4.2, and App. Figure A.1) may help explain the reportedly shorter lifespan of *Sp. viride* onshore (Paddack 2005).

Sparisoma viride is a unique case, because no particular simulation accounted for the observed patterns. Estimated annual survival rates of 54% seemed sufficient to maintain high frequencies of occurrence (70-80% sampled stations) of this parrotfish in mid-shelf reefs (cf. Table 2.19c). Meanwhile, neither FWRI reported catches of this minor ornamental species (cf. Figure 4.1b) or projected lobster fishery bycatch (Matthews and Donahue 1997) were high enough to justify the F=0.3 concluded from the simulations. The simulated vs. observed data mismatch might be explained by this parrotfish's astounding phenotypic plasticity of its population dynamics, social behavior, and reproductive strategies (van Rooij et al. 1996a, Paddack 2005), because local adaptations may render highly different dynamics among subpopulations. Thus, cross-shelf or regional patterns may have been obscured by pooling this parrotfish across all strata in the simulations. However, assuming high genetic flow among strata allows precautionary predictions for management purposes. Underestimation of natural mortality could be another factor partially explaining the mismatch.

Hypothetical situations of fishing pressure on these parrotfishes predicted a decrease in mean length associated with the change of shape of the size distribution curve, with a greater impact at high natural mortalities. The use of this endpoint, in combination with observed size distribution patterns and proportion of larger sizes, provides a more robust picture of the actual status of the species. A limitation of the model is that the $\overline{L}$ -based mortality estimator of an exploited population can be positively biased if recruitment shows an increasing trend (Ault et al. 2005), as it may currently happen with other reef fish of the Florida Keys, after the implementation of no-take marine reserves (Ault et al. 2006). Conversely, this estimator is unbiased under constant annual recruitment (Ehrhardt and Ault 1992), which is the case for the scarids (cf. Chapter 5).

Parrotfishes have been commercially unexploited (or lightly exploited) for over 25 years (Sutherland and Harper 1983, Taylor and McMichael Jr. 1983). No great effect on their occurrence or their abundance from a marine reserve has been observed (e.g., Ault et al. 2006), thus stochastic recruitment variation might be the major pattern.

Fortunately, $\overline{L}$-based mortality estimator is relatively insensitive to recruitment trends (Ault et al. 2005), and the outcome hereby presented should not have been affected significantly. Predictions of negative effects of increased predation in protected areas were not supported by the observed data, probably due to their relatively high $\hat{M}$ values.

Limitations of this approach for non-target species include the lack of estimates-at-age or habitat-related M and F. Simulations were based on a single species-wide set of life history parameters and growth curve, disregarding any potential cross-shelf or alongshore differences. The reason is that due to the lack of otolith data matching the observed maximum sizes, the growth parameter estimations had to be simulated. By using the largest observed size of each scarid that would render the corresponding longest lifespan, the outputs from REEFS and LBAR would be more conservative because it would treat them as long-lived species, thought to be more vulnerable to fishing pressure (Coleman et al. 2000).

Geographic variation in commercial importance of parrotfishes across the Mediterranean, Caribbean Sea, and Atlantic Ocean, may partially and qualitatively reflect local pressure on this resource. With serial fishing reportedly occurring in the Western Central Atlantic (Pauly et al. 1998), parrotfishes are not exempt from that trend. In the ornamental industry, scarids are sold online by distributors across the United States, despite being considered “high maintenance” or “difficult care level” species by the sellers themselves (cf. aquarium websites, e.g., Marine Depot Live[15], eTropicals.com[16]).

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[15] MarineDepotLive, 1300 East Gene Autry Way, Anaheim, CA 92805-6717 (http://marinedepotlive.com).

[16] eTropicals.com, 2253 Air Park Road P.O. Box 100 Rhinelander, WI 54501 (http://www.etropicals.com/default.htm).

These fish do not live long in captivity. They die either from starvation or from terminal stress triggered by confinement (Fenner 1998), usually within 6-8 months after purchase (F.M. Greco, private aquarist. 2001, pers. comm.), or after collection from the wild (H. Molina-Ureña, pers. obs.). Furthermore, a list of marine fish unsuitable for captivity recently proposed by Reefs UK[17] included 6 Caribbean *Scarus* spp., and 5 *Sparisoma* spp. The reason for their unsuitability was mostly due to diet deficiencies that are difficult to surmount (F.M. Greco, private aquarist. 2001, pers. comm.).

Unfortunately, fisheries statistics and ornamental trade data are insufficient, incomplete, sometimes unreliable, and often unspecific. As a consequence, the socioeconomic and ecological impact of parrotfish fisheries is likely grossly underestimated. The Global Marine Aquarium Database is a valuable tool that will become indispensable as the data quality of the sources improve. A better effort must be made by international and government agencies to record and share data on recreational, incidental, and subsistence fishing of reef fishes. Difficulty in maintaining Atlantic parrotfishes in captivity also makes them unsuitable for commercial aquaculture. But their gregarious behavior, their ability to share resources, and their relatively fast growth rates are good features of a cultivable species. This area has not been explored scientifically or empirically, and could be an alternative to fishing.

From a heuristic point of view, the trend of reaching a constant maximum length at an early age found in scarids from diverse locations (Choat and Robertson 2002) may cause the overestimation of fishing mortality at the expense of underestimating natural mortality rates (M). Alternatively, given the population and fisheries-associated

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[17] Reefs UK http://www.reefsuk.org, link to Captive Breeding articles, link to Unsuitable Marine Fish For Captivity.

dynamics of these parrotfishes, a number of factors other than fishing and higher predation rates may also have additive or synergistic roles. Conditions such as coastal pollution, habitat loss, parasites (H. Molina-Ureña, pers. obs.) or substrate-related availability of quality food (cf. Chapters 1 and 2) may influence natural mortality. For example, sequential hermaphrodites, e.g., parrotfishes and groupers, can be susceptible to chronic exposure to endocrine disrupting chemicals (EDCs), which can display estrogen-mimicking (e.g., DDT[18], some PCBs[19], some PAHs[20]), antiestrogenic (e.g., dioxins), and antiandrogenic (e.g., DDE[21]) effects (IEH 1999). Despite that their effects on fish fauna are still poorly understood, ECDs could be affecting marine fishes more than expected (Matthiessen 2003), and their presence in Florida coastal waters has been reported (Grabe and Barron 2004, Poor et al. 2004). On the other hand, habitat loss in coastal waters might have a serious long-term effect on scarid populations, given the potentially critical role of habitat use in the evolutionary history of this family (cf. Chapter 1).

The REEFS and LBAR simulations resulted invaluable approaches to improve the understanding of parrotfish population dynamics, and can be very useful for managers. Even under assumptions based on simulated data, these algorithms helped explain observed size structure, and provided reliable information on different scenarios. The use of short vs. long lifespan, and moderate vs. high natural mortality alternatives may improve the understanding of fishing and marine reserve effects on non-target species. Coupling it with comparative analyses of multiple attributes of output distributions (e.g., modal intervals, overall distribution shape, mean length, frequency of larger size classes)

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[18] Dichloro-diphenyl-trichloro-ethane
[19] Polychlorinated biphenyls
[20] Polycyclic aromatic hydrocarbons
[21] Dichloro-diphenyl-dichloro-ethylene

between observed and expected values, enables an assessment of current exploitation and could help detect effects of environmental factors.

Table 4.1: Fisheries activity and status of Atlantic parrotfishes. Maximum size is given as the largest length reported Atlantic-wide.

SPECIES	MAXIMUM [COMMON] SIZE (cm, Kg)	Mean total length (SE) (cm) Locality	FISHING GEAR [a, l]	TARGET (T) OR INCIDENTAL (I) FISHERY [a]	COMMERCIAL IMPORTANCE (RELATIVE ABUNDANCE)
C. roseus	13 [10] [b]		Fine mesh beach net	I	Negligible due to small average size [a]
N. usta	29 [18] [b]		Beach net, trap	I	Only large specimens marketed [a]. Growing acceptance in Venezuela [a]
Sp. atomarium	Very small [b]			I	None [a, d]
Sp. aurofrenatum	28 [20] [b]	13.1 (1.6) Jamaica [c]	Mainly trap	I Artisanal	Least important of genus (small average size) [a] Ornamental [k]
Sp. chrysopterum	45 [25] [b]		Mainly trap	I Artisanal	Little (Cuba) [d]
Sp. cretense	61 [i]	15 Greece [h]	Canary Is.: traps, nets, fixed gill nets, hook and line	Italy: I [f] Canary Is.: I & T [g] Greece: I [h] Artisanal [g]	Italy: negligible [f] Greece: little (< 2% total weight of commercial landings) [h]
Sp. radians	20 [15] [b]		Beach net	I	Minor (small average size) [a]
Sp. rubripinne	45 [30] [b]		Mainly beach net, also trap	T	High (relatively large size and abundance) [a]
Sp. viride	64 [38] [b]	13.1 (2.8) Jamaica[c]	Mainly trap	I Artisanal	High (relatively large size and abundance) [a] Ornamental [k]
Sp. griseorubra	N/A			I	None. Endemic to Venezuela [a]

Table 4.1 continued

SPECIES	MAXIMUM [COMMON] SIZE (cm, Kg)	Mean total length (SE) (cm) Locality	FISHING GEAR [a, l]	TARGET (T) OR INCIDENTAL (I) FISHERY [a]	COMMERCIAL IMPORTANCE (RELATIVE ABUNDANCE)
Sc. coelestinus	76 , 7 Kg [50] [b]		Large-mouthed trap	I	Little (Cuba) [d] Marketed fresh and salted [a] Ornamental [k]
Sc. coeruleus	90, most ≤60 [40][b]		Large-mouthed trap	I	Marketed fresh and salted [a] Ornamental [k]
Sc. iseri	27 [18] [b] 20 [j]	11.7 (1.8) Jamaica[c]	Large-mouthed trap, beach net	I	Little, regularly marketed in some locations [a] Ornamental [k]
Sc. guacamaia	120 [70] [b]		Large-mouthed trap, trammel net (occasional)	T	Little (Cuba) [d] Local dish “empanadas” [a]
Sc. taeniopterus	33 [22] [b]	12.4 (2.8) Jamaica[c]	Trap, beach net	I Artisanal	Ornamental [k]
Sc. vetula	60 [30] [b]		Mainly trap	I Artisanal	Ornamental [k]

Sources: [a] Cervigón et al. (1993), [b] Robertson and Warner (1978), [c] Klomp et al. (2003), [d] Claro (1994a), [e] DeLoach (1999), [f] de Girolamo (1999), [g] González and Lozano (1992), [h] Petrakis and Papaconstantinou (1990), [i] Lozano and González (1993), [j] Ogden and Buckman (1973), [k] GMAD (Global Marine Aquarium Database, http://www.unep-wcmc.org/marine/GMAD), [l] Cervigón (1994).

Table 4.2: Reef Ecosystem Exploited Fisheries Simulator (REEFS) and LBAR equations, based on von Bertalanffy (VB) growth model. Sources: Ricker (1975), Alagaraga (1984), Ehrhardt and Ault (1992), Ault (1998, 2005, 2008).

VARIABLE	EQUATION	NOTATION	COMMENT
Average length in the exploitable phase of the stock	$\overline{L}(t) = \dfrac{F(t) \times \int_{t_c}^{t_\lambda} N(a,t) \times L(a,t)da}{F(t)\int_{t_c}^{t_\lambda} N(a,t)da}$	F(t)= instantaneous fishing mortality rate at time *t* N(a,t)= abundance of age class *a* L(a,t)= length of age class *a*	t_c=minimum age at first capture t_λ= oldest age in the stock = longevity
Average number of fish by age over time (1)	$dN_{(a,t)} = \dfrac{\partial N(a,t)}{\partial a} da + \dfrac{\partial N(a,t)}{\partial t} dt$	∂N/∂a = contribution to the change in $N_{(a,t)}$ as a result of individuals ageing	da/dt = 1 for a>0 and t>0, since age a gets 1 unit older with each time unit t increase
Unbiased estimate of Z	$\left[\dfrac{L_\infty - L_\lambda}{L_\infty - L_c}\right]^{\frac{Z(t)}{K}} = \dfrac{Z(L_c - \overline{L}) + K(L_\infty - \overline{L})}{Z(L_\lambda - \overline{L}) + K(L_\infty - \overline{L})}$	L_∞, K = von Bertalanffy model parameters L_c = length at first capture	
Average number of fish by age over time (2)	$dN_{(a,t)} = -Z(a,t) \times N(a,t)dt$	Z(a,t)= total instantaneous mortality rate of age class *a* at time t	
Mean number at a given length for the entire population structure	$\overline{N}(L) = \int_{t_\tau}^{t_\lambda} R_{(\tau-a)} S_{(a)} \Theta_{(a)} P_{(L\|a)} da$	$R_{(\tau-a)}$= recruitment lagged back to cohort birth date $S_{(a)}$= survivorship to age a $\Theta_{(a)}$= sex ratio at age a $P_{(L\|a)}$= the conditional probability of a fish being of length L at age a, whose probability distribution of length and age is assumed as bivariate normal.	t_τ= time of recruitment t_λ= reported maximum age in the stock = duration of one generation
Natural mortality rate	$\hat{M} = \dfrac{-\ln[S(t_\lambda)]}{t_\lambda}$, $\hat{M} = 1.5K$	$S(t_\lambda)$= fraction of the initial cohort surviving at age t_λ from recruitment t_τ	
Annual rate of total mortality	$A = 1\text{-}S = 1\text{-}e^{-Z}$	S=rate of survival	

Table 4.3: Input values of life history parameter estimates for short lifespan assumption, as predicted by simulations and invariant theory: longevity (t_{max}), weight-length parameters (α, β), ultimate length and weight (L_∞, W_∞), von Bertalanffy model curvature coefficient (K), maximum observed length and weight (L_λ, W_λ), size and age at recruitment (L_r, t_r) size and age at first maturity (L_m, t_m), size and age at first capture (L_c, t_c), natural mortality estimates from 5% survivorship (M). Length: (mm) TL (SL). Weight: (g)

Parameter estimates	*Sc. iseri*	*Sp. aurofrenatum*	*Sp. viride*	*Sp. chrysopterum*
t_{max} (y)	7	7	10	5
Weight – Length				
α	0.0126	0.0162	0.0226	0.0152
β	3.1426	3.2321	2.9298	3.0274
K	0.5303	0.7020	0.3242	0.6808
L_∞	205 (172)	277 (255)	625 (479)	455 (357)
W_∞	97	410	4076	1590
L_λ	200 (168)	275 (254)	60.0 (46.1)	440 (345)
W_λ	155	405	3662	1436
L_r	12.5 (10)	12.5 (10)	12.5 (10)	12.5 (10)
t_r (months)	1.4	0.7	0.8	0.5
L_m	135 (114)	184 (168)	406 (316)	294 (236)
W_m	45	102	1170	422
t_m (months)	24.4	18.4	40	19
L_c	40 (33)	40 (33)	150 (123)	150 (118)
W_c	1	0.6	63	55
t_c (months)	4.9	2.4	11	7.1
M (y^{-1})	0.4280	0. 4280	0. 2996	0. 5991

Table 4.4: Input values of life history parameter estimates for long lifespan assumption, as predicted by simulations and invariant theory. Symbology and units: same as in Table 4.3.

Parameter estimates	*Sc. iseri*	*Sp. aurofrenatum*	*Sp. viride*	*Sp. chrysopterum*
t_{max} (y)	12	10	12	8
Weight – Length				
α	0.0126	0.0128	0.0226	0.0152
β	3.1426	3.0857	2.9298	3.0274
K	0.4418	0.7020	0.3242	0.6808
L_∞	210 (176)	281 (259)	610 (468)	443 (348)
W_∞	104	432	3802	1466
L_λ	200 (168)	280 (258)	600 (461)	440 (345)
W_λ	155	426	3634	1436
L_r	12.5 (10)	12.5 (10)	12.5 (10)	12.5 (10)
t_r (months)	1.6	0.8	0.8	0.6
L_m	138 (116)	187 (171)	397 (309)	286 (230)
W_m	48	107	1090	388
t_m (months)	29	23	38	21
L_c	40 (33)	40 (33)	150 (123)	150 (118)
W_c	1	0.6	63	55
t_c (months)	5.7	2.9	10.6	8
M (y^{-1})	0.2496	0. 2996	0. 2496	0.3745

Table 4.5: Estimated overall numbers of four parrotfish populations in the Florida Keys, 1997-2001.

Year	*Scarus iseri*	*Sparisoma aurofrenatum*	*Sparisoma viride*	*Sparisoma chrysopterum*	TOTAL
1997	16,010,601	12,001,701	4,889,034	1,566,551	34,469,884
1998	22,158,504	10,745,433	3,153,233	1,077,429	37,136,597
1999	17,595,052	7,474,146	3,463,910	2,697,292	31,232,399
2000	25,876,824	11,086,161	4,002,439	2,898,277	43,865,701
2001	22,725,368	9,781,796	3,385,844	1,492,752	37,387,761
Mean	20,873,270	10,217,847	3,778,892	1,946,460	36,818,468

Table 4.6: Annual total mortality predicted by simulations with REEFS and LBAR algorithms (Ault et al. 1996, Ault 1998, Ault et al. 1998) at increasing levels of fishing mortality (F), under two longevity (t_λ) scenarios. Total instantaneous mortality is given as a rate (Z, y^{-1}) and as fraction of the population (A, %), cf. Ricker (1975). Asterisks indicate the models that fitted better the observed size frequency distributions in each species.

Species	*Sc. iseri*				*Sp. aurofrenatum*			
t_λ	7		12		7		10	
M	0.43		0.25		0.43		0.30	
Parameter estimate	Z	A	Z	A	Z	A	Z	A
At F=0.0	0.45	36	0.25	22	0.48	38	0.32	27
At F=0.1	0.56	43	0.35	30	0.59	45	0.42	34
At F=0.5	-	-	0.75	53	-	-	0.85	57
At F=1.0	1.55	79	1.25	71	1.72	82	1.41	76
At F=M	0.91*	60	0.50	39	0.98*	62	0.63	47

Species	*Sp. viride*				*Sp. chrysopterum*			
t_λ	10		12		5		8	
M	0.30		0.25		0.60		0.37	
Parameter estimate	Z	A	Z	A	Z	A	Z	A
At F=0.0	0.31	27	0.25	22	0.64	47	0.39	32
At F=0.1	0.41	34	0.35	30	0.75	53	0.50	39
At F=0.5	0.84	57	0.75	53	-	-	0.93	61
At F=1.0	1.39	75	1.25	71	1.76	83	1.50	78
At F=M	0.62*	46	0.50	39	1.30*	73	0.80	55

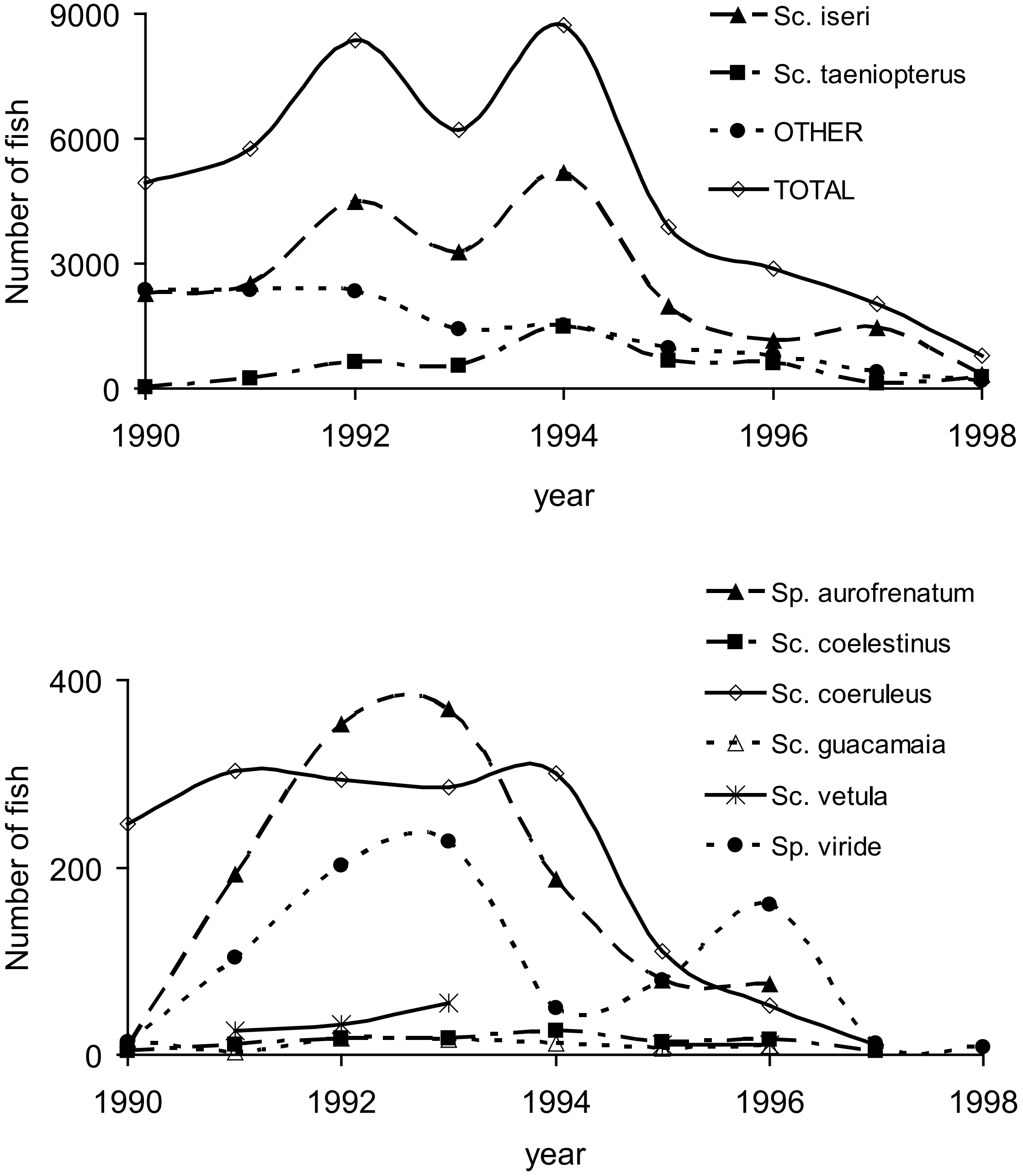


Figure 4.1: Ornamental catches of parrotfish in Florida, 1990-1998, calculated from Florida Wildlife Research Institute (FWRI) database (courtesy of Sherry Larkin). Upper panel: major ornamentals. Lower panel: minor ornamentals.

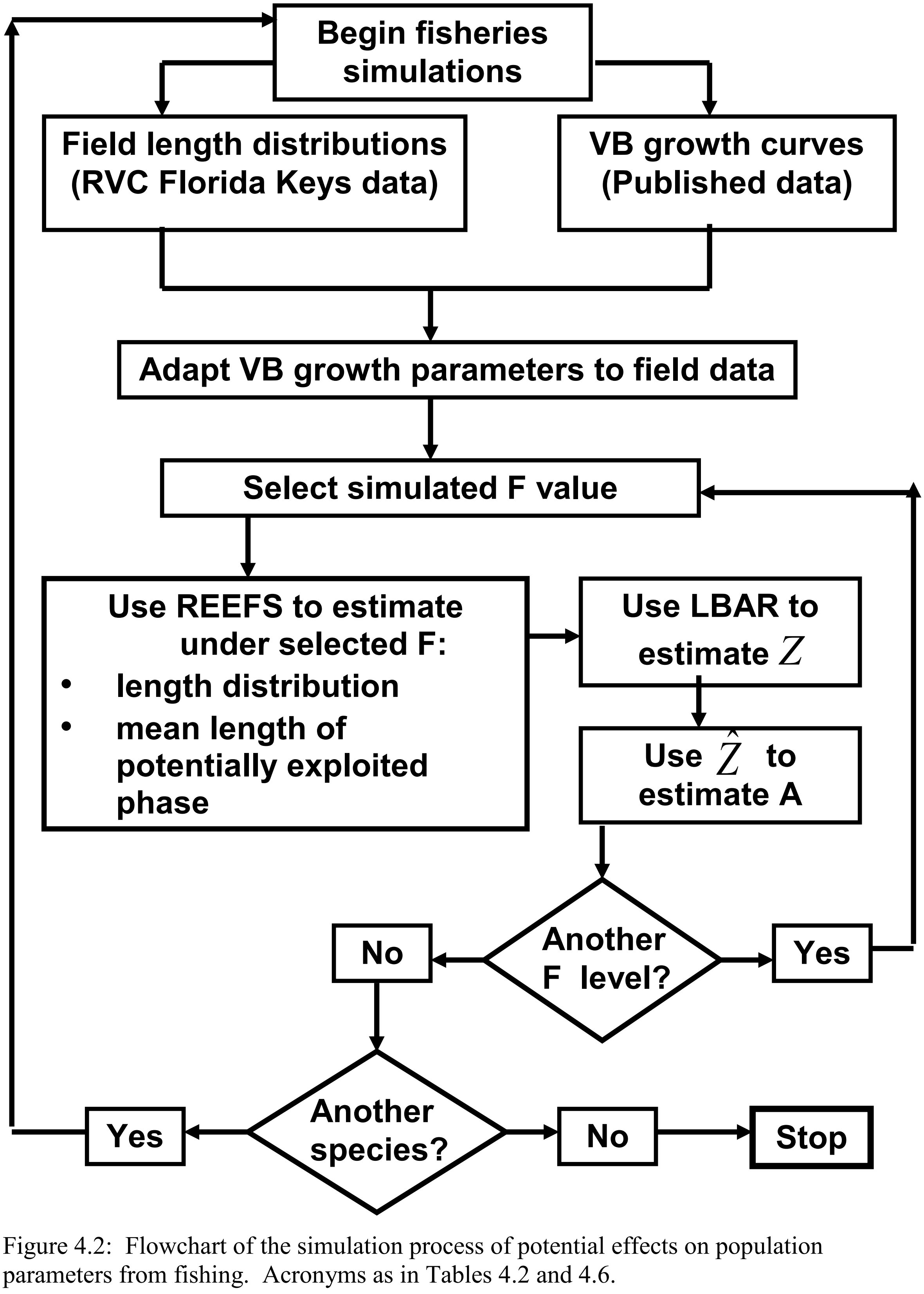


Figure 4.2: Flowchart of the simulation process of potential effects on population parameters from fishing. Acronyms as in Tables 4.2 and 4.6.

(a) *Sc. iseri*

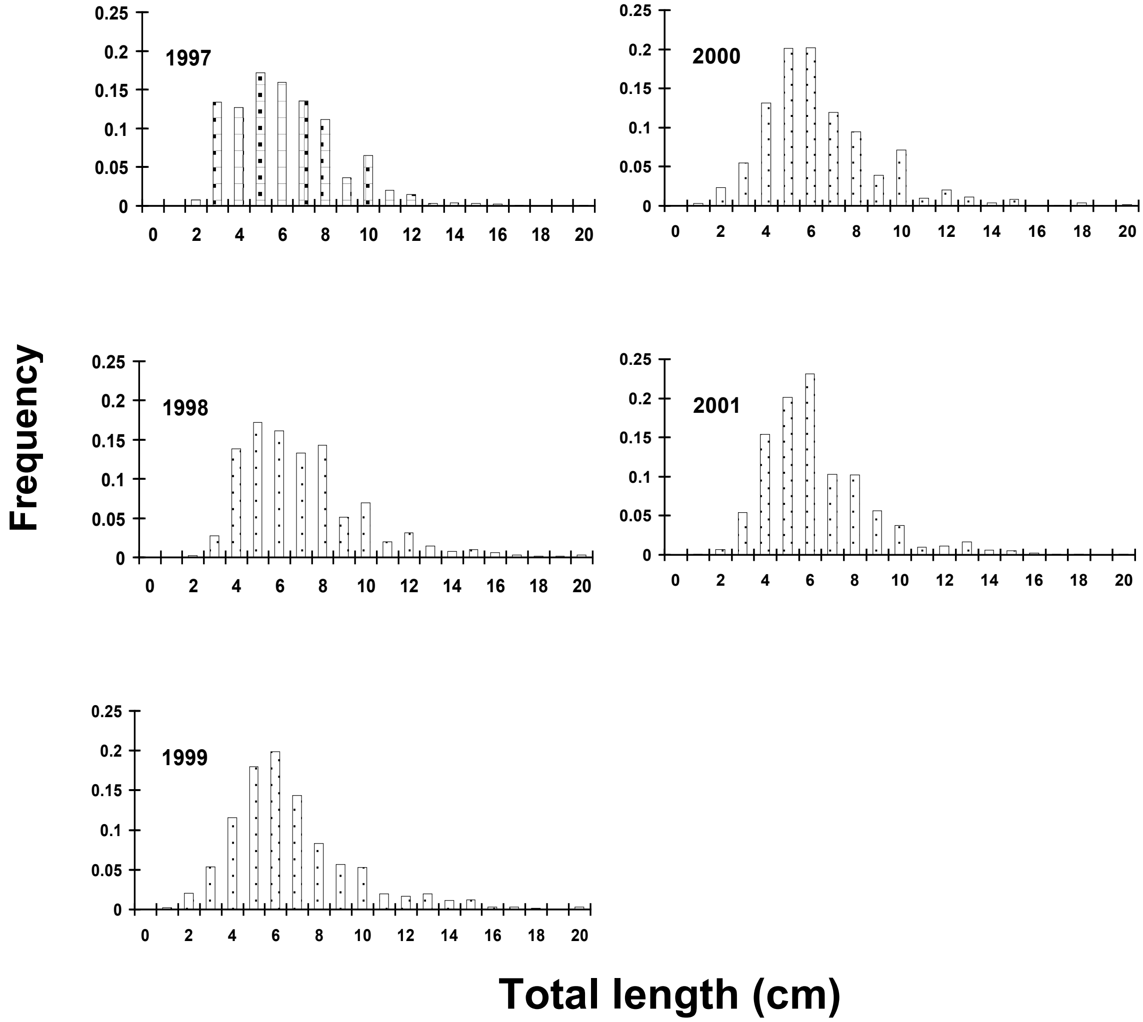


Figure 4.3: Observed length frequency distributions of Florida Keys parrotfishes from Reef Fish Visual Censuses (RVC), 1997-2001.

(b) *Sp. aurofrenatum*

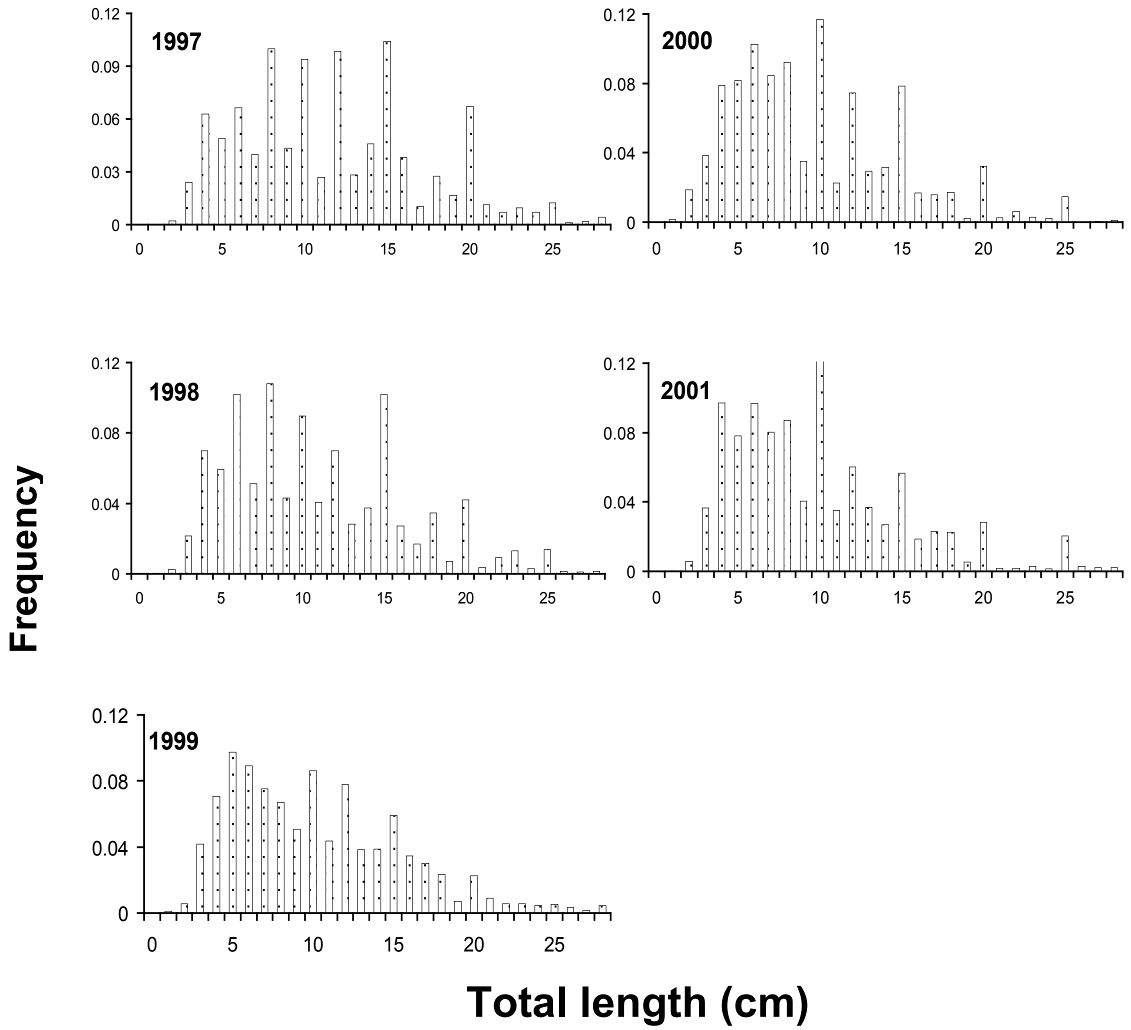


Figure 4.3 continued

(c) *Sp. viride*

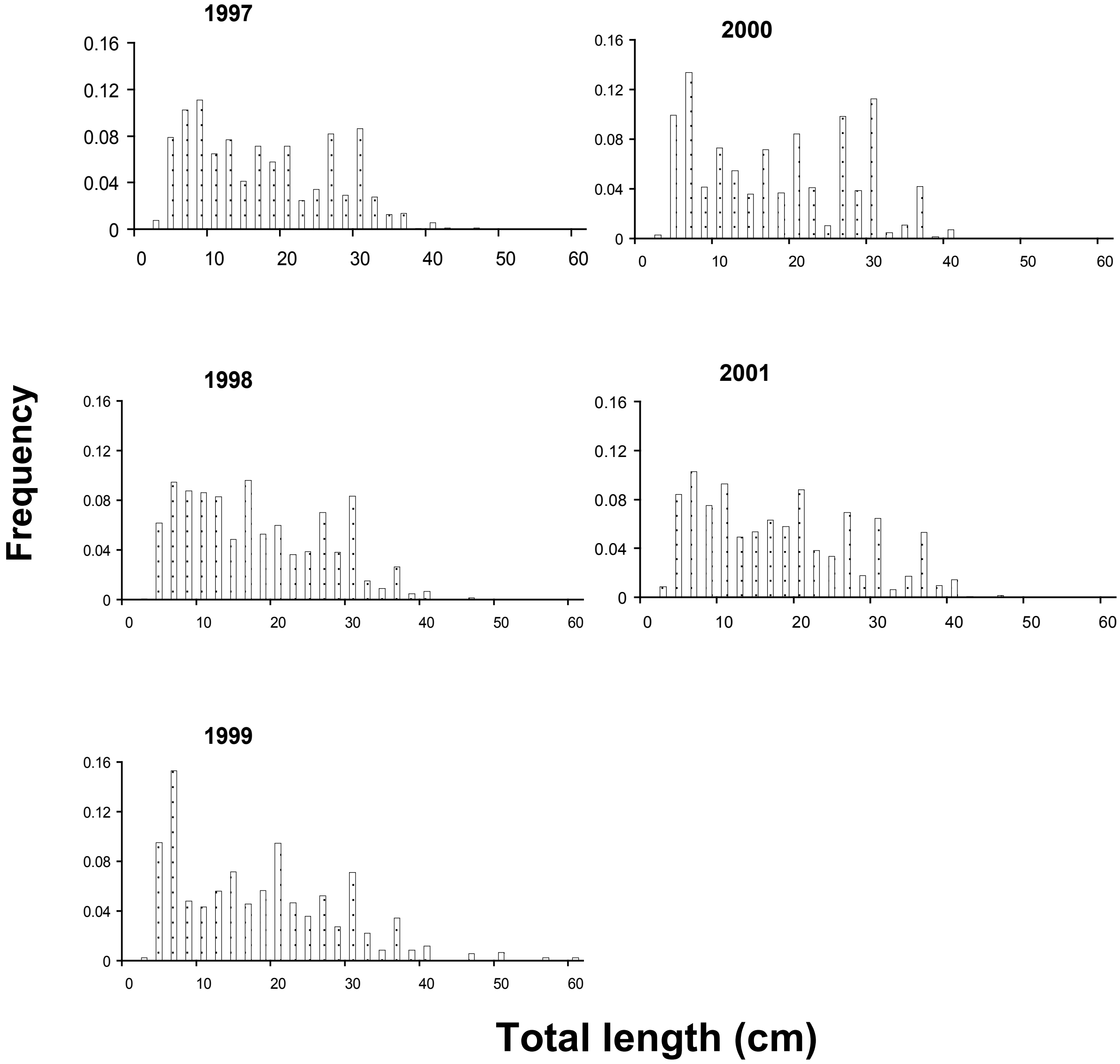


Figure 4.3 continued

(d) *Sp. chrysopterum*

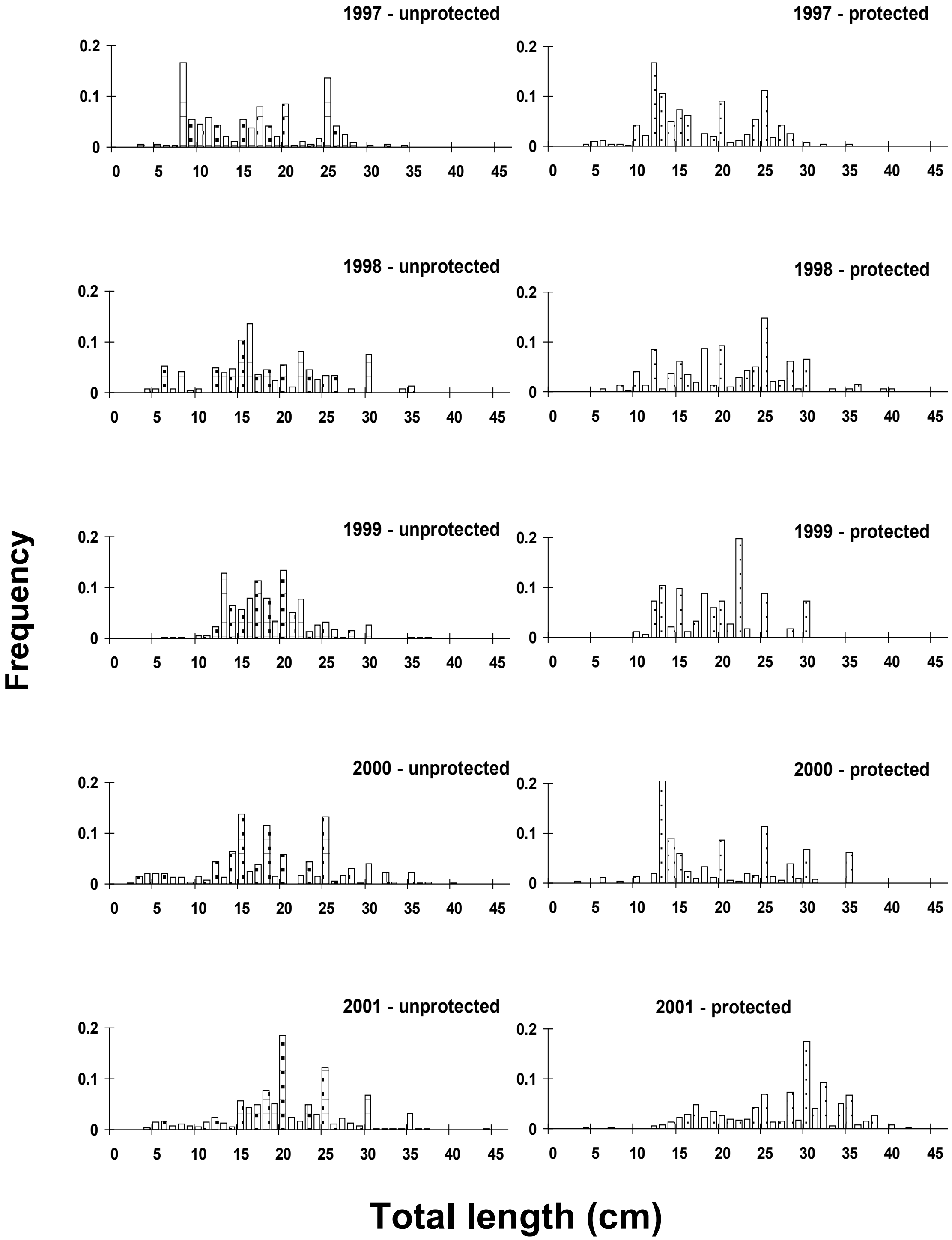


Figure 4.3 continued

(a) Sc. iseri. Left panel t_λ=7, M=0.43. Right panel t_λ=12, M=0.25

SHORT LIFESPAN LONG LIFESPAN

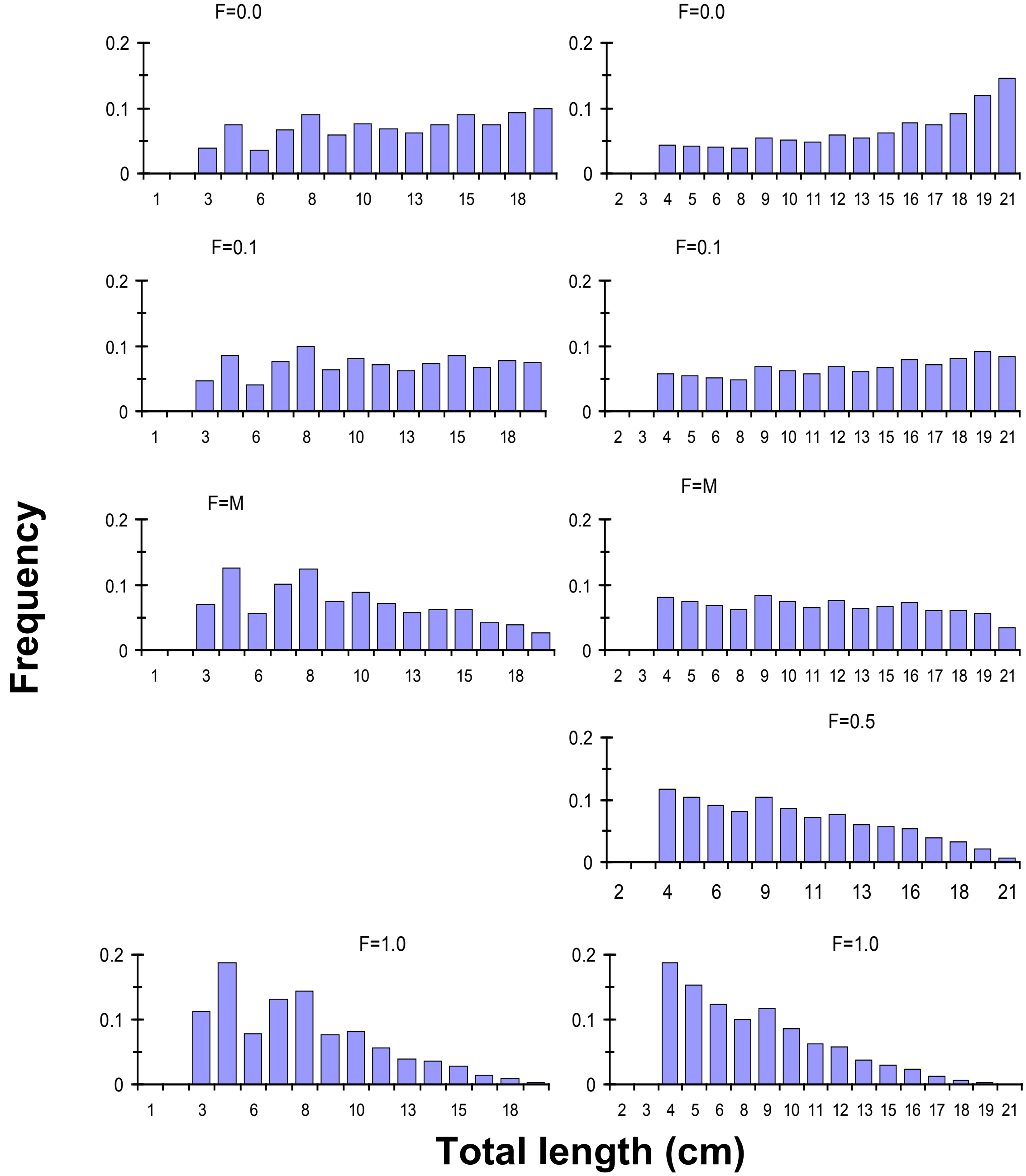


Figure 4.4: Predicted length distribution histograms from REEFS and LBAR models for four populations of Florida Keys parrotfishes. Left panel represents simulations assuming short longevity. Right panel represents long longevity. Original standard length outputs were converted to TL units for comparison purposes only.

(b) *Sp. aurofrenatum.* Left panel $t_\lambda=7$, M=0.43. Right panel $t_\lambda=10$, M=0.30

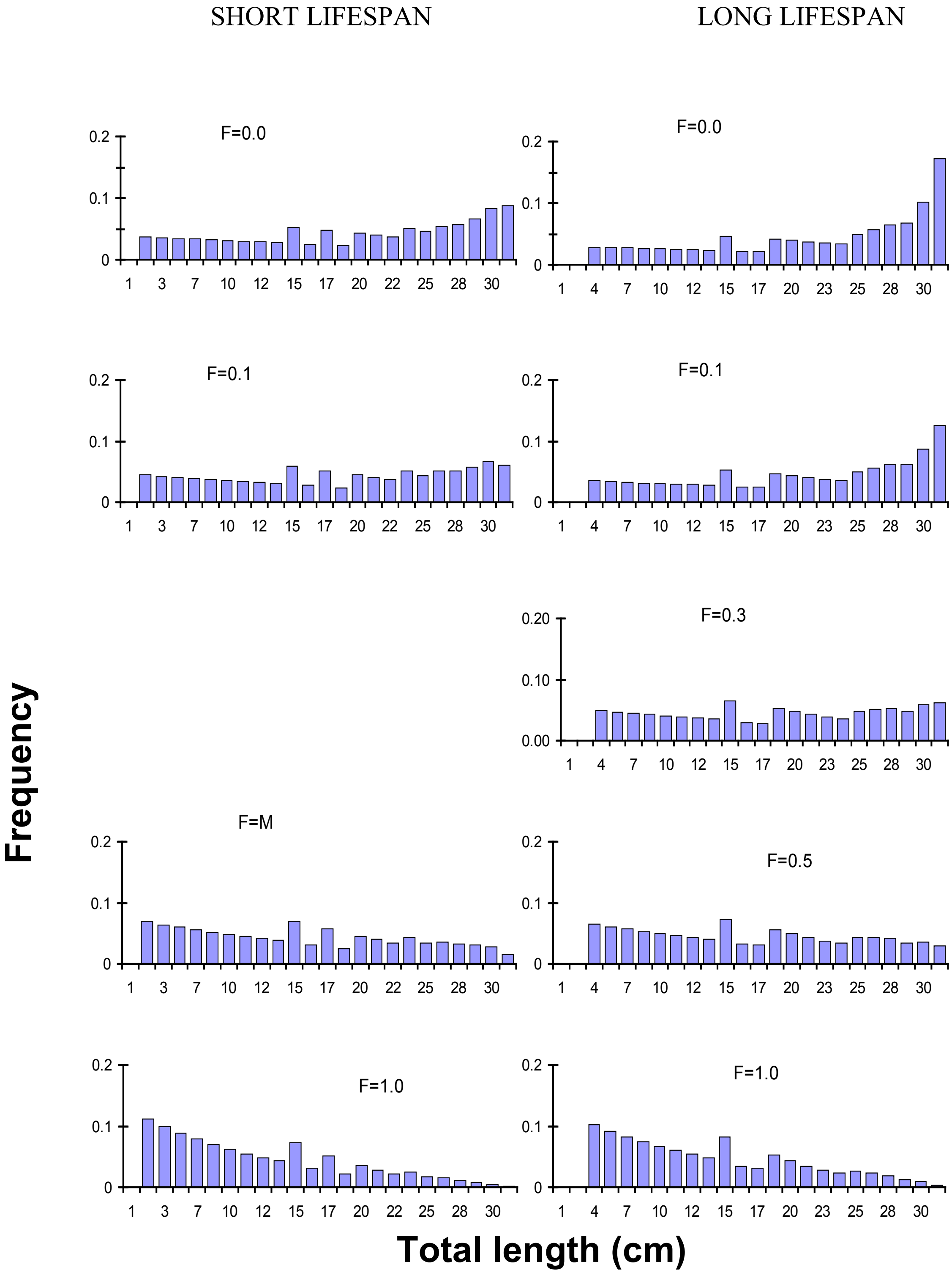


Figure 4.4 continued

(c) *Sp. viride.* Left panel t_λ=10, M=0.30. Right panel t_λ=12, M=0.25. Only size intervals equal or greater than size at first capture (L_c = 15 cm TL) are displayed.

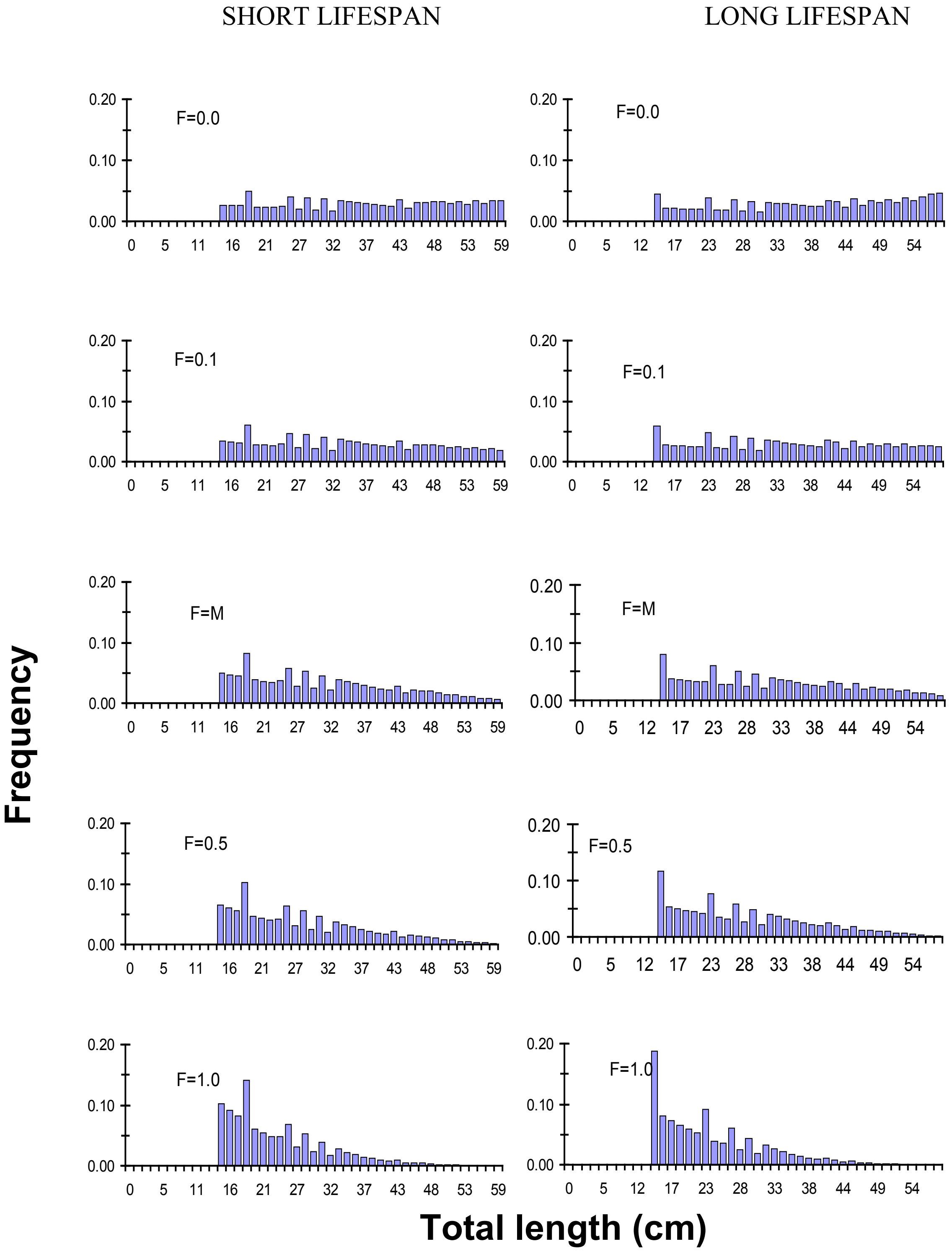


Figure 4.4 continued

(d) *Sp. chrysopterum.* Left panel t_λ=5, M=0.60. Right panel t_λ=8, M=0.37. Only size intervals equal or greater than size at first capture (L_c = 15 cm TL) are displayed.

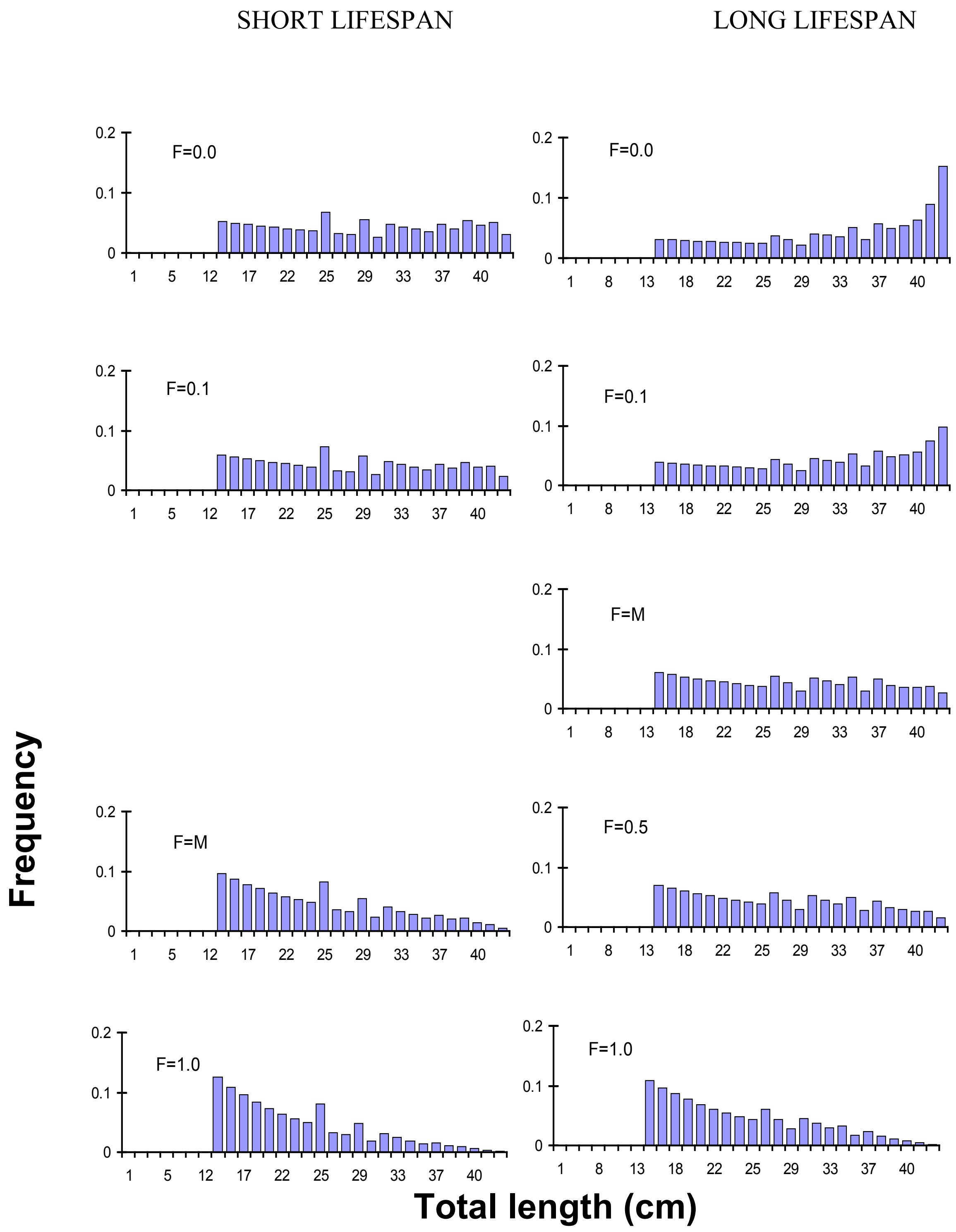
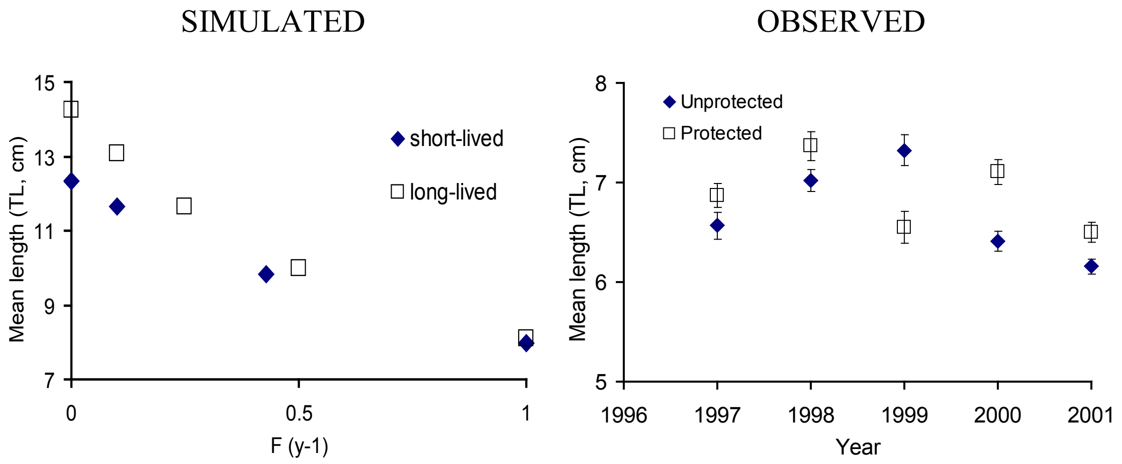


Figure 4.4 continued

(a) *Sc. iseri*



(b) *Sp. aurofrenatum*

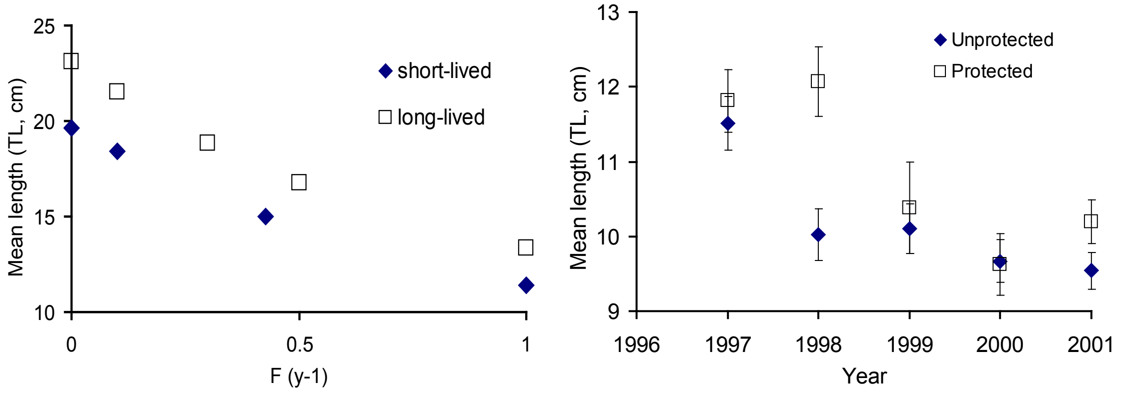
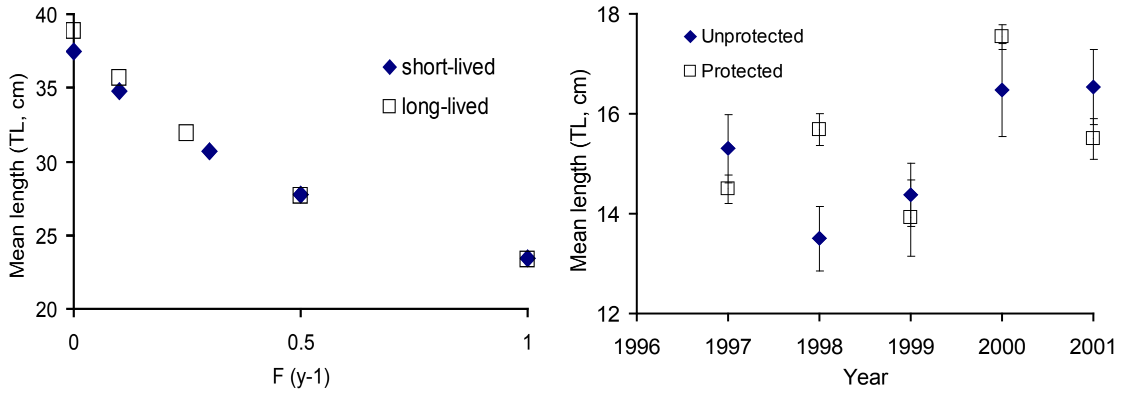


Figure 4.5: Simulated (left panel) mean body length at hypothetical levels of fishing mortality, and observed mean length (right panel) of parrotfish populations of the Florida Keys. Mean length is defined as the average length of potentially exploited phases (i.e., $t_c \geq 4$ cm TL in *Sc. iseri* and *Sp. aurofrenatum*, and $t_c \geq 15$ cm TL in *Sp. viride* and *Sp. chrysopterum*). Note length scales differ between simulated and observed data, and among species.

(c) *Sp. viride*

SIMULATED OBSERVED



(d) *Sp. chrysopterum*

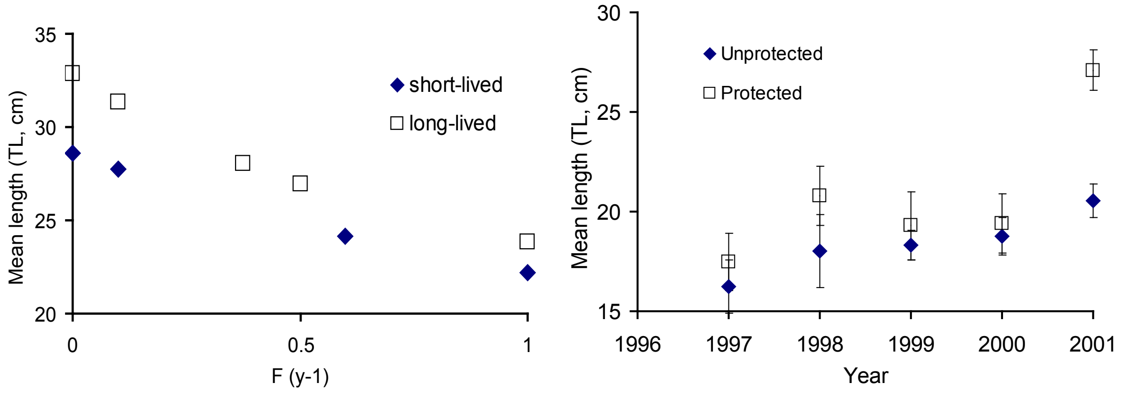
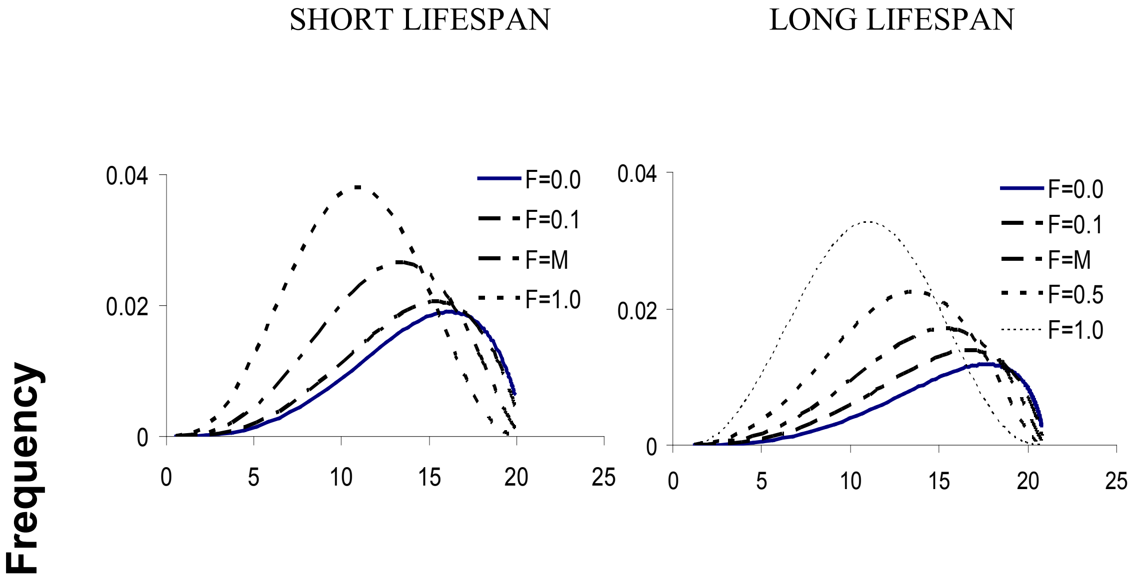


Figure 4.5 continued

(a) *Sc. iseri*



(b) *Sp. aurofrenatum*

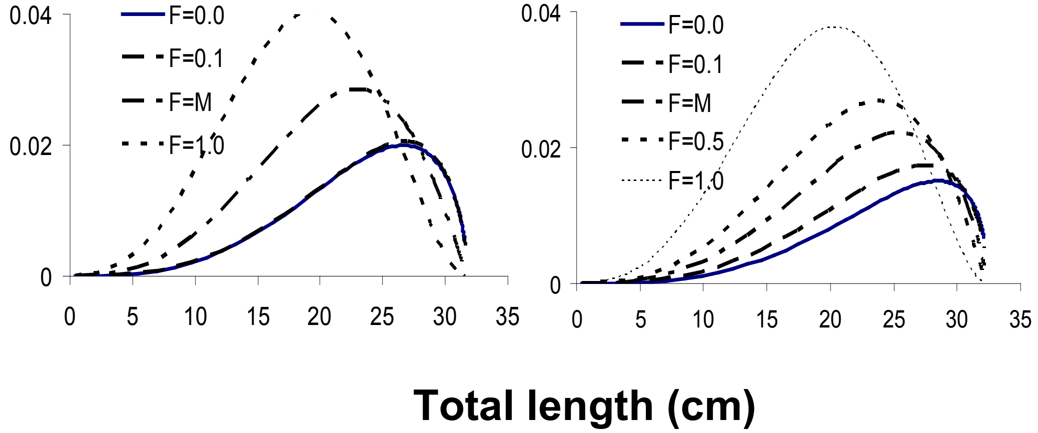
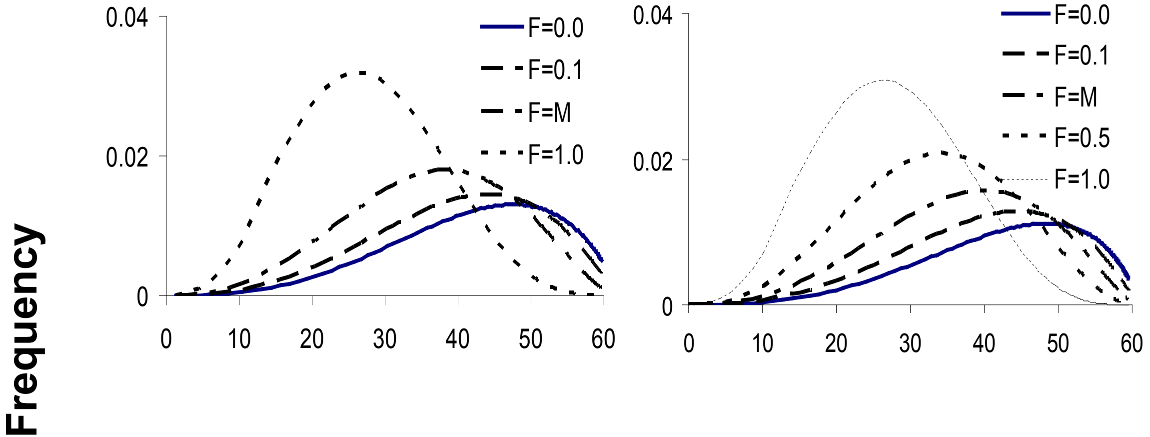


Figure 4.6: Predicted length distribution shapes at hypothetical levels of fishing mortality (F) of Florida Keys parrotfishes. Left panels: simulations assuming short longevity. Right panels: assuming long lifespan.

(c) *Sp. viride*

SHORT LIFESPAN LONG LIFESPAN



(d) *Sp. chrysopterum*

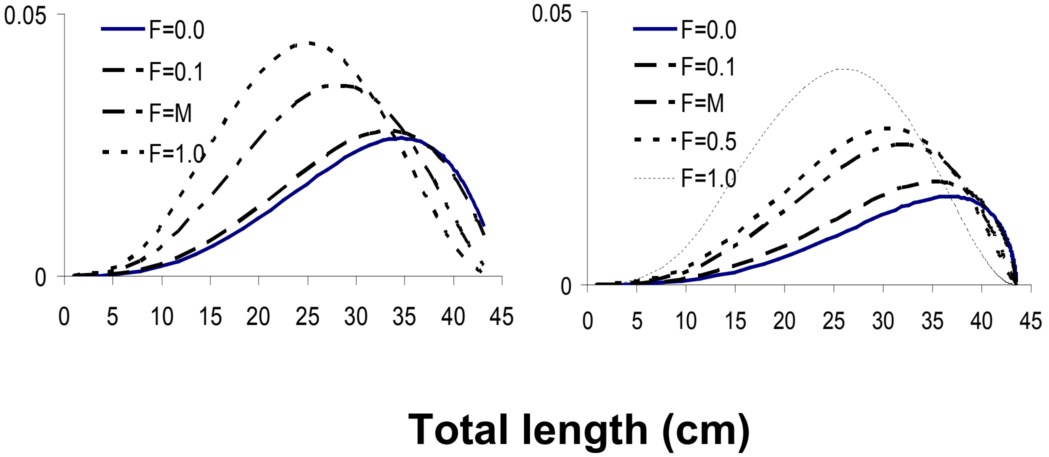


Figure 4.6 continued

Chapter 5: Fisheries ecology and management recommendations

5.1 Background

Sustainability of tropical reef fisheries is a complex goal that requires an integral combination of scientific protocols, participative processes, frameworks, governance, and implementation measures, in order to achieve selected objectives. The underlying principle is the aim to ensure ecosystem functionality, by protecting the processes that maintain the resources. This is achieved through management of species, communities, selected abiotic factors, and stakeholders, based on an understanding of the relationships among all components (Ault 1998, Jennings et al. 1998, Rosenberg et al. 2000, Ault et al. 2001, 2002, Garcia et al. 2003, Ault et al. 2006, Mumby 2006, Mumby et al. 2006, Ault et al. 2008). Concepts such as *Ecosystem-based Fisheries Management* (EBFM), *Ecosystem Approach to Fisheries* (EAF), *Environmental Management* (EM), *Biodiversity Management* (BM), *Systems Science Approach* (SSA), or *Ecosystem Approach* (EA) have been applied to describe this paradigm in fisheries management (Ault et al. 2001, Garcia et al. 2003).

Under this approach, several issues regarding parrotfish arise. Firstly, the status of South Florida scarid populations is of great importance. Due to their trophodynamic role, biomass, and abundance, parrotfishes have become major key grazers controlling the algal component in coral reef ecosystems (Bellwood and Choat 1990), moreover after the 1983 decline of the long-spined sea urchin, *Diadema antillarum* (Paddack et al. 2006), in the Great Caribbean Basin. Secondly, it has been suggested that Marine Protected Areas (MPAs) may have long-term negative impacts on parrotfishes, by protecting their predators (Mumby et al. 2006). Empirical data and simulation modeling that were used in this study may provide state-of-the-art tools to address this kind of issues.

Further efforts in ecosystem-based research include, but are not limited to, sampling design and gear performance improvements, modeling applications to understand and predict complex processes and dynamics, large-scale (both spatial and temporal) monitoring programs with fisheries-independent data, trophodynamics studies, essential fish habitat management, as well as marine protected area design and implementation.

5.1.1 Methodological issues

The comprehensive information gap analysis performed in this study combined with empirical data (e.g., Figure I.1 and Table 2.21) detected two major methodological issues for South Florida parrotfishes. Firstly, the absence of an optimal sampling design developed for scarid ecological studies. Secondly, a lack of species-specific, otolith-derived growth curves that accounted for the maximum size in the four most abundant parrotfishes observed in the Florida Keys.

Parrotfish from Biscayne Bay were collected following a simple Stratified Random Sampling scheme (StRS) primarily designed to collect pink shrimp (cf. sections 2.2.2 and 2.2.4). Under this design, sample size per stratum was proportional to habitat area, and within-stratum stations (sampling units) were randomly allocated. Because the parrotfish database was built from the sampling bycatch, optimizing the StRS to sample fish with scarid-like distributions for future surveys became an objective. Post-stratification theory provides a background to increase estimate precision, i.e., reduce variance. The practical advantage of this exercise is the minimization of sample size under a target level of uncertainty (measured as coefficient of variation). This is achieved by allocating the samples under stratification schemes newly defined according to actual variance data (Smith 1990, 1991, Ault et al. 1999a). That is, habitat use results can be applied to improve sampling design and estimate precision.

On the other hand, growth parameters accounting for the local characteristics of Florida Keys parrotfish populations were not found in the literature. Ageing studies were conducted in other Caribbean localities where maximum sizes were consistently smaller (Choat and Robertson 2002, Choat et al. 2003), thus alternative approaches had to be applied. In order to obtain curves that could explain demographic attributes observed in the Florida Keys populations, simulations based on observed data and on theoretical assumptions had to be performed.

Application of life invariant approaches, use of fisheries simulation programs (e.g., LBAR, REEFS), and simulation of growth curves based on available literature, may provide proxy population parameters, when local information gaps prevail for the biology of certain species.

5.1.2 Management aspects

Understanding, monitoring, and predicting vulnerability to exploitation and effects of management actions on fish species not targeted by fisheries is necessary under the precautionary principle. Approaches ranging from phylogenetics to modeling different scenarios have been applied (Jensen 1991, Chen et al. 1998, Jennings et al. 1998, Sponaugle et al. 2002), in an attempt to fill data gaps that prevent fisheries managers and scientists from having a complete picture of the stock status and ecosystem resilience.

Direct measurements and observed data on fisheries, stock status, and population dynamics are lacking for most of the Caribbean parrotfishes due to several factors, such as their low market value, identification issues, and complex social behavior. Because of the serial fishing already taking place in many areas of the Western Central Atlantic (Pauly et al. 1998), scarids might soon become an important substitute for top commercial fish Caribbean-wide and eventually get overexploited. In fact, this has already happened in a few localities, like Jamaica (Klomp et al. 2003).

Thus, to improve the understanding of the scarid population dynamics with relatively little empirical data available, this work applied a combination of published information, locally observed ontogenetic patterns of habitat use, size structure, and simulations of growth patterns and hypothetical fishing intensity levels.

Therefore, the objective of this chapter is to explore and further some of this study's contributions to fisheries ecology approaches and methodologies, management issues, and state of knowledge of habitat use and demographic aspects of the South Florida parrotfishes. Pertinent management recommendations are provided based on the understanding acquired with the analyses.

5.2 Materials and methods

5.2.1 Post-stratification analyses

Post-stratification theory (see equations on Table 5.1) was applied with two goals. Firstly, to select the best-performing sampling design applied to collect the samples, for habitat use analyses. Secondly, to propose a new parrotfish-customized stratification design, for future surveys in Biscayne Bay.

In order to find the optimal stratified sampling design that may provide the highest precision for density estimates, parrotfish distributions in Biscayne Bay were compared under different habitat classifications with post-stratification analyses (Smith 1990, 1991, Ault et al. 1999a). Analyses of density and variance of *N. usta*, *Sp. chrysopterum*, and *Sp. radians* were conducted for designs consisting on 9, 5, and 3 strata (described in Table 2.2), and Simple Random Sampling (SRS, no stratification assumed). Stratum specific estimates of density (D) and variance (S^2) were obtained by cruise as described in materials and methods of Chapter 2, and then overall values were computed by incorporating the weighting factor when applicable (see equations on Tables 2.5 and Table 5.1). Weighting factors were adjusted to each stratification design, accordingly.

With the goal of ensuring a desired precision level while minimizing the required sample size in future surveys, three new stratified sampling designs were developed based on observed abundances and distributions of each parrotfish (cf. Chapter 2). Each design was tested by season (spring, summer, fall) at target levels of adapted coefficient of variation of the mean ($CV\left[\overline{D}_k\right]$=CV) of 5, 10, 15, and 20% of the mean. The three new schemes with 4 to 6 strata are shown in Table 5.2. The three new schemes recognized two to three substrate types, namely seagrass, hardbottom and barebottom. Seagrass strata were divided into north and south components, but retaining cross-shelf / depth attributes. The north-south limit corresponded to the Featherbed Banks (25° 31.2' lat N), which appeared to act as a natural barrier for the parrotfishes. The largest stratum was seagrass deep north (SDN, 33.9% of total bay area), followed by seagrass deep south

(SDS, 15.8%). When pooled, seagrass shallow (SS_h, <2 m depth) represented 27.6%, while hardbottom and barebottom combined accounted for less than 25% of the surface area. For the assessment of proposed sampling scheme performances, cruises were pooled by season (spring, summer, and fall).

5.2.2 Status and management of South Florida parrotfish populations

Long-term series of mean length estimates for the major four species of parrotfishes were obtained from the same Reef Fish Visual Census (RVC) database used in Chapter 2 (see sections 2.2.3 and 2.2.4 for a detailed description), and additional survey sampling efforts from 1979 to 1996. This addition to the database was generously provided by Jerald Ault of the Rosenstiel School of Marine and Atmospheric Sciences (RSMAS) Miami, and James Bohnsack of the National Marine Fisheries Service (NMFS, NOAA), Miami (Ault et al. 1998).

Mean length estimates were computed with all individuals ≥ 4 cm TL that were recorded in the visual censuses (i.e., juveniles were excluded), to avoid misidentifications or under-counts. Based on the Stratified Random Sampling (StRS) design for the Florida Keys domain (cf. section 2.2.4), parrotfish abundance and mean size were compared between protected and unprotected sites (cf. Table 2.4).

Management fishing benchmarks were calculated with the REEFS algorithm from empirical and simulated data obtained in Chapters 3 and 4 (see sections 3.2 and 4.2 for details), following equations shown in Table 4.2. Additionally, the Spawning Potential Ratio (SPR) was estimated as the fraction of the exploited stock biomass ($SSB_{exploited}$) with respect to the equilibrium unexploited SSB (i.e., at F = 0), such that SPR = $SSB_{exploited}$/ $SSB_{unexploited}$), but expressed as a percentage (Ault et al. 1998, 2008).

5.3 Results and discussion

5.3.1 Contributions in fishery ecology methods

An ecosystem-based approach integrating ontogenetic habitat uses and population dynamics was developed to assess population risks from exploitation and environmental changes on non-target reef fishes. The goal was to provide valuable tools for the sustainable use of coastal marine resources in the Caribbean nations, by developing statistically robust approaches while optimizing data acquisition that could be applicable to tropical habitats and species. The method employed a combination of fisheries and ecological theory, and a suite of simulation techniques to study South Florida parrotfishes. Recommended steps in this systems approach, whose flowchart is shown in Figure I.1, are: (I) analysis of information gaps for the stocks, guild or taxon under consideration, including systematics, biogeography, population dynamics, reproductive ecology, trophodynamics, habitat use, and fisheries catch and fleet dynamics (Chapter 1); (II) determination of primary objectives from prioritization of information gap analyses of Step I; (III) determination of essential fish habitats from integration of stratified sampling design (Cochran 1977, Smith 1990) for fisheries-independent surveys and habitat selection theory-based analyses (Manly et al. 1993). Conducted in two domains, Biscayne Bay and Florida Keys, these length-based analyses included ontogenetic shifts, migrations, and connections between reefs and adjacent habitats subject to fisheries (Chapter 2); (IV) refined estimation of population dynamics and fisheries-specific parameters encompassing life history demographics from empirical data or comparisons to theoretical expectations adapted to local conditions (Chapter 3); and (V) simulation modeling of a realistic range of fishing scenarios and demographic characteristics using

REEFS (Reef Ecosystem Exploited Fisheries Simulator) and size-based mortality estimation (LBAR) to evaluate the efficacy of potential traditional fisheries and spatial management strategies (Chapter 4).

This work studied lightly exploited stocks, which is a rare opportunity anywhere in the Caribbean basin. The information found was scattered, and in many topics it was not explored beyond certain specific objectives, as it commonly happens with non-target species. The gap analysis provided a baseline for prioritization of objectives to address. For example, because use of habitats has been considered a driving force in the evolution and biological success of scarids (Streelman et al. 2002), its study became a priority of this research.

Lack of fisheries data from other heavily exploited locations prevented understanding effects of fishing and protection on this family. Simulations were performed to study several scenarios and contrast expected outputs against observed data.

5.3.1.1 Estimation precision and sampling optimization: post-stratification analyses

The Biscayne Bay sampling designs applied in this study targeted the pink shrimp population, for which high precision was successfully achieved (CV ~6-14%) (Ault et al. 1999a). The post-stratification analyses concluded less precise estimates (CV≥14%) for parrotfishes (Table 5.3). CV values ranged from 14-25 (*Sp. chrysopterum*) to 22-100% (*Sp. radians*), although this outcome did not preclude sensible conclusions regarding habitat shifts. For uncommon species with CV≥50%, such as *Sp. radians*, the uncertainty is undeniable high; nevertheless, the low standard errors allowed detection of abundance differences within the range of twofold differences in density (i.e., 100% increase).

There was similar precision among all designs tested, and no unique design performed optimally for all species in all cruises.

When applying the same principles to optimize sample allocation for future parrotfish surveys, the potential performance of proposed 4, 5 and 6 stratum designs ranged 15 to 26% for *N. usta*, 15 to 22% for *Sp. chrysopterum*, and 25 to 100% for *Sp. radians* (Table 5.4). Resulting seasonal calculations of sample size required to achieve a target precision level, n*, indicated that *N. usta* and *Sp. chrysopterum* would require the least amount of samples in spring surveys, and *Sp. radians* in summer, regardless of the design (not shown). Conversely, the largest n* values were in fall, summer, and spring surveys for *N. usta*, *Sp. chrysopterum*, and *Sp. radians*, respectively.

A global n* was computed to compare required sample size among proposed designs. All the proposed stratified classifications required fewer samples than a simple random design at any target level of precision (Figure 5.1), and the 6-stratum design provided the smallest n* values at all target levels. The proposed 6 habitat types (Table 5.2) retain the main characteristics of the 9-stratum scheme, by recognizing 4 types of seagrass habitats, defined by (a) depth (deep vs. shallow), (b) north and south components (deep seagrass only), and (c) cross-shelf (basin axis, and mainland and leeward sides of shallow seagrass). The remaining two strata simplified hardbottom and barebottom habitats by pooling their corresponding cross-shelf categories.

The shapes of the curves in Figure 5.1 suggested that an ideal target of 10% CV would require an average of ~250-290 samples for *N. usta* and *Sp. chrysopterum*, but 480 for *Sp. radians*. Reducing desired precision to 15% CV decreases n* to nearly half, closer to the actual sample sizes of this study.

Once the 6-stratum design and a target 10% CV were chosen, the optimal or Neyman's sample allocation among strata were computed (Cochran 1977). Total sample size varied with season (Table 5.5), ranging 224-350 (*N. usta*), 209-320 (*Sp. chrysopterum*), and 381-1184 (*Sp. radians*), but always allocated the largest amount of samples in the seagrass deep north habitat. *Sp. chrysopterum* benefited most from this optimized allocation. This parrotfish was slightly more abundant than *N. usta* in this work, but ranked much lower in Campos (1985)'s study (cf. Table 2.6). The resulting Neyman's sampling allocation was comparable to that proposed for pink shrimp in Biscayne Bay ($n^* = 158\text{-}333$) (Ault et al. 1999a). However, given that densities of pink shrimp were about 3 orders of magnitude higher than those of parrotfishes, its target CV could be as low as 5% without requiring larger sample sizes.

In summary, to obtain a target 10% uncertainty in mean density estimates of parrotfishes, the best sampling scheme is the 6-stratum design, which is considered efficient (Cochran 1977, Ault et al. 1999a). It required nearly 250 to 300 samples, ~60% allocated in the north deep seagrass stratum for *N. usta*, but only 40-50% for *Sp. chrysopterum*. Targeting *Sp. radians* for monitoring studies would require sample sizes ≥ 400 units. This design could be applied to study other fishes with distributions similar to that of parrotfishes, with smaller sample sizes if they were more abundant.

5.3.1.2 Estimation precision: visual censuses in the Florida Keys.

Figure 5.2 shows a long-term series of mean length estimates for the four major parrotfish species in the Florida Keys. Two major conclusions can be drawn from these results. Firstly, precision mean estimates improved after 1997 due to a combination of factors, such as the increase of sampling effort, the application of stratified sampling designs, and the improved identification skills of the divers. Secondly, mean length of scarids showed no major effect from implementation of marine protected areas, including the Florida Keys Marine Sanctuary (1990) and the network of no-take protected zones (1997) (Waddell 2005). While minor differences among protected and unprotected areas can now be detected more readily (Figure 5.2), no trends were observed in modes of size frequency distribution, minimum and maximum lengths (cf. Table 2.21), habitat selection (cf. Table 2.22), density (cf. Figure 2.16), and frequency distribution (cf. section 4.3) except for *Sp. chrysopterum* (cf. Figure 4.3d). These results suggested that the long-term negative effects of MPAs on parrotfishes predicted by (Mumby et al. 2006) were not detected in the Florida Keys during and prior to the study period. Thus, MPA implementation represents no danger to parrotfish populations in this domain.

As a limitation of the visual census, a natural tendency to round off observed lengths towards multiples of 5 (e.g., 30, 35, 40 cm) for larger species could be detected in the modes of length distributions shown in Figure 4.2 (Chapter 4). This rounding usually occurs within ± 1.5 cm of error (H. Molina-Ureña, pers. obs.) and in larger specimens is not a major issue. However, this artifact can be readily corrected as the divers get more trained and experienced.

Misidentification issues must be addressed constantly, especially in a phenotypically complex guild, such as the scarids. Small-size specimens require more attention, due to their camouflaged coloration and interspecific schooling behavior (H. Molina-Ureña, pers. obs.). Separating juvenile, initial and terminal phases in the census may help hone in identification skills, and provide more precise data on the relationship between life stage and habitat use.

5.3.1.3 Growth simulations and life stage designations

Published otolith growth models were adapted by following a numerical technique previously used to model the Chesapeake Bay oyster growth pattern (Rothschild et al. 1994). Equations, assumptions, and other considerations were described in Chapter 3. The availability of otolith studies of parrotfishes from other Caribbean areas (Choat and Robertson 2002, Choat et al. 2003), and local data (Paddack 2005) was an advantage that the mollusk study did not have. On the other hand, scarids have shown great demographic flexibility (Gust et al. 2002), distinctive sex-specific growth profiles (Munday et al. 2004), large plasticity of initial growth rates (J.H. Choat, 2004, pers. comm.), and variable longevity (Paddack 2005), let alone the expected changes in size composition due to exploitation (Ault et al. 1998). All evidence has suggested that the observed demographic variability is not exclusively due to a sampling artifact or fishing effects, but rather is a result of adaptability to localized conditions related to habitat characteristics (van Rooij et al. 1996a), as well as social organization (J.H. Choat, 2004, pers. comm.).

Because genetic studies have demonstrated scarids have relatively open populations and high level of migration (Geertjes et al. 2004), this plasticity is phenotypical in nature and implies the need of an increased effort in sampling wider ranges of habitats at any particular domain. Obtaining direct age data for each condition may be desirable, but unfeasible. Because lack of growth parameters is always a major limitation when assessing stock status, simulation techniques integrated to the knowledge of habitat-dependent distributions are valuable managing tools.

The constraints applied to growth simulations (Chapter 3) ensured parameter estimates biologically tenable. Firstly, fitting the von Bertalanffy model unconstrained could lead to overestimated t_o and L_∞ values that may give erroneous K estimates (Choat and Robertson 2002, Grandcourt 2002). Secondly, by using observed maximum sizes as constraint, the growth curves simulated hereby not only considered local demographic attributes, but also corrected for the possibility of juvenescence effect of fishing that may have affected the empirical data elsewhere in the Caribbean.

The extensive length overlaps between color phases in different species were corroborated in this study, but both combined with length and habitat distribution may help explain ontogenetic patterns. It is suggested that future surveys include the phase color besides a length or weight measure.

The family Acanthuridae (surgeonfishes) is another reef fish taxon that shows great demographic adaptability (Gust et al. 2002). Thus, simulation techniques could be applied to different taxa until direct otolith data can be obtained.

Applying multivariate techniques to designate life stages is a complementary approach for ontogenetic studies. The use of Principal Components Analysis helped grouping size intervals with respect to fish density at each stratum. If the primary objective is to detect developmental changes, this technique is useful whether the source of variation is due to actual ontogenetic habitat shifts or to size-related catchability changes.

5.3.2 Habitat use by South Florida parrotfishes

In Chapter 2, it was concluded that Biscayne Bay parrotfishes used deeper seagrass substrates during younger stages, expanding seaward as they grow, but remaining concentrated in the northern half of the bay near Safety Valve, the wide opening that connects the bay to offshore waters. *Nicholsina usta* apparently restricts its life cycle to seagrass substrates in semi-closed waters (e.g., Biscayne Bay) and probably open waters, skipping reef habitats. However, the fate of the largest individuals was unknown because of gear selectivity and catchability issues. Thus, in order to clarify whether the bay acts as nursery grounds only, or as full cycle habitat for *N. usta*, it is recommended to obtain trawl samples from ocean waters 20-100 m depth off the South Florida coast, focusing on habitats similar to those of the Eastern Atlantic population (Randall 1983, Gushchin and Girardin 2000). Mark and recapture techniques can also be useful for this purpose.

On the contrary, while scarce in Biscayne Bay, *Sc. iseri* and *Sp. aurofrenatum* were ubiquitous in the Florida Keys. The former showed cross-shelf ontogenetic shifts from inshore to offshore reefs, with generalized habitat requirements. The latter displayed a similar type of cross-shelf ontogenetic shift, but avoiding inshore areas, and concentrating in the mid-shelf reefs.

Sparisoma viride was rare in bay waters, but appeared more frequently in the upper Keys than the middle and lower Keys regions. Although the inshore-to-offshore pattern of habitat use was obscured by interannual abundance variations and the strong influence of local conditions on its demography, this parrotfish had more affinity for midchannel and shallow forereefs. It also appeared to prefer unprotected reefs and was found in protected areas. Finally, *Sp. chrysopterum* was the only parrotfish occurring significantly in both domains. Biscayne Bay might be an important recruitment ground, where part of the population may remain; another proportion migrates through Safety

Valve onto the adjacent reef environment, soon after the tail morphology changes from truncated to concave at six months of age. Its ontogenetic pattern is partially reversed (offshore to inshore), with Terminal Phase fish still showing more affinity for offshore reefs.

Given the striking within-population differences in habitat use, it is recommended that all available seagrass, mangrove, onshore and offshore reefs be surveyed when addressing South Florida scarids. Seagrass substrate is abundant in Biscayne Bay and Florida Bay, as well as the inshore areas of the Florida Keys. Gulf coast of Florida should also be explored, especially in lobster trap areas.

5.3.3 Fisheries simulations

A review on the assumptions underlying the algorithms of the Reef Ecosystem Exploited Fisheries Simulator (REEFS) and the $\overline{L}$ -based mortality estimator (LBAR) used in Chapter 4 (cf. Table 4.2) was performed. One of the major assumptions of REEFS and LBAR algorithms is constant recruitment (cf. section 4.4.3). As shown by App. Figure A.2, this assumption held for the three most abundant parrotfishes during the study period.

Algorithms of REEFS and LBAR are based on the von Bertalanffy body growth model (VB) (cf. section 4.2 and Table 4.2). The VB model (cf. Eq. 3.2) is widely applied to fishes and other aquatic animals because of its empirical description of growth patterns for most species (Quinn and Deriso 1999). This model relies on the principle that the body growth rate slows down as the individual gets older until reaching an asymptotic size, and somatic growth occurs throughout most of their size range (Choat and Robertson 2002).

However, unlike other taxa, the maximum size is reached early in the scarid life cycle and stays constant through most of their adult life (cf. Figure 3.2 and section 3.4.2), and their sexual maturity is achieved at a relatively early age, but close to their maximum size (Choat and Robertson 2002). These adaptations may reduce predation and improve their reproductive success in ecologically complex environments. Furthermore, growth patterns of western Atlantic parrotfishes suggest a life strategy different from other scarids, characterized by higher early growth rates and natural mortality in combination with a shorter lifespan and ontogenetic shifts of habitat. Competition and predation, as well as social behavior, might have been strong selective forces in Caribbean reefs. The down side is that this strategy might not be optimally explained by the VB model.

Another limitation is that the high natural mortality rates derived from longevity may underestimate actual M levels (cf. section 4.4.3). The alternative Beverton-&-Holt-derived M estimates (right panels in App. Figure A.1), nearly twice as high (cf. App. Table A.1), could be an upper limit to the actual M values. However, the B&H estimates did not improve the fit between simulated and observed length frequency distributions.

Therefore, it is suggested that the growth (size at age) curves of scarids should be revised for alternative equations that may better apply to the patterns observed. Otolith sampling of the largest specimens should also be conducted, and collecting sites should consider that terminal phase parrotfishes prefer deeper reefs (>18 m).

5.3.4 Management issues and recommendations

Despite empirically recording low fishing mortality for the Florida Keys major scarid species, fisheries simulation outputs rather matched a scenario characterized by high natural mortality (M), a short lifespan (t_λ) and fishing mortality rates (F) close to natural mortality (F = M) (cf. section 4.4).

Table 5.6 synthesizes results obtained from Chapters 2, 3, and 4. Assuming that the four most abundant parrotfish species of the Florida Keys domain were exploited at a fishing rate for maximum sustainable yield, i.e., the upper bound of allowed fishing mortality $F_{MSY} = M$ (Williams and Shertzer 2003), their spawning potential ratio (SPR) are currently below the 30% overfishing threshold established by the U.S. Federal standards. It is hereby proposed the selected length at first capture (L_c) as the size corresponding to the estimated age at first sexual maturity (Table 5.6), even maintaining the current F levels. This alone would increase the SPR up to at least ~45% in all cases, well above the U.S. Federal standards, and render larger mean lengths (Table 5.6).

Most stock assessment methods rely on landings and catch information, thus the management actions usually are remedial rather than preventive. In the context of the precautionary principle and ecosystem-based management, it is necessary to identify those species vulnerable to exploitation before their populations start showing effects of overfishing. Monitoring seagrass and reef fishes in coastal areas subjected to intense urban development and anthropogenic activities is strongly advised. The major current sources of fishing mortality of South Florida parrotfishes, i.e., targeted ornamental trade and incidental captures in shrimp and lobster fisheries bycatch, represented an annual removal of < 0.2% of the mean population size only (cf. section 4.4.2). However, it is advisable to keep those species monitored by seasonal beam roller surveys in Biscayne Bay, annual visual censuses in the Florida Keys, and permanent trip ticket surveys of ornamental trade.

Local trends due to complex dynamics and demographic plasticity obscure overall patterns. Thus, understanding habitat use, stratum distribution, and potential locality-specific fishing mortality of these populations becomes fundamental. Because of the reported capacity for high gene flow in members of this family (Geertjes et al. 2004), it is desirable to determine what proportion of the populations is found in each stratum, and make pertinent adjustments by estimating weighed overall parameters, if necessary.

Sampling optimization techniques are useful for researchers and budget administrators, who will have the ultimate decision about the trade-offs between sampling costs and precision levels. Time required to process the samples is an important factor to take into account because sampling costs include not only the actual collecting and measuring of the specimens, but also the sorting of the samples and identification of all species and lifestages of interest. Color phase should be used as a second criterion to express the lifestage when assessing members of the families Scaridae and Labridae in Biscayne Bay and the Florida Keys. The marginal cost of recording this information is minimal compared to the wide possibilities it opens.

Corrections by selectivity and catchability factors are important considerations for population size composition analyses. However, uncorrected databases from Biscayne Bay are still useful tools because they give species composition, size structure, and abundance of the shrimp fishery bycatch. Incidental fishing mortality is another aspect that should be part of an integral approach to fish management, including species that could be more impacted by the roller beam trawls. For example, pinfish (*Lagodon rhomboides*), gulf toadfish (*Opsanus beta*), grunts (*Haemulon plumieri*, *H. sciurus*), silver jenny (*Eucinostomus gula*), filefishes (*Monacanthus ciliaris*, *M. hispidus*), bronze cardinalfish (*Astrapogon alutus*), and scrawled cowfish (*Lactophrys quadricornis*) ranked among the top 10 species in the Biscayne Bay collection (J. Ault, J. and H. Molina-Ureña, 2006. unpubl. data).

Both anthropogenic and natural disturbances have been suggested to have direct effect on scarids and their role in the reef ecosystem. Firstly, the new field studying endocrine disrupting chemicals (EDCs) has brought water pollution issues under a paradigm different from ecotoxicology (Crews et al. 2000). This component has to be assimilated into ecosystem-based management. For many decades, Biscayne Bay and the Florida Keys have been exposed to both natural and anthropogenic materials from local activities and far removed sources (Rumbold and Snedaker 1999, Grabe and Barron 2004, Poor et al. 2004, Wurl and Obbard 2004). Many of these pollutants may be ECDs whose impact on local parrotfish populations is yet to be studied. Secondly, efficacy of parrotfish grazing is sensitive to hurricane frequency (Mumby 2006). Mumby's (2006) models predicted that in areas where severe hurricanes occur on a decadal basis or less (e.g., Florida), parrotfish grazing will not be enough to allow the corals recover from the damage, unless a major grazer like *Diadema antillarum* was present in significant numbers. In areas where these disturbances occurred every $\geq$ 20 years (e.g., Central America), parrotfishes would have enough time to crop algal growth, and coral would be able to recover, as long as the scarids were not depleted by overfishing. Understanding these aspects should soon become a priority as part of an ecosystem-based approach.

Parrotfish current bycatch levels in South Florida could be considered negligible to light, as long as no significant changes in the shrimp and lobster trap fisheries take place. Nevertheless, it is advisable to have bycatch studies, such as that of Matthews and

Donahue (1997) every 5 years. As for the ornamental trade, the following steps are recommended:

(1) To maintain the regulation as "restricted species" for Florida scarids, granted in the Marine Life Rule 68B-42 (Fish and Wildlife Conservation Commission), stating that they should be landed alive only.

(2) To advertise the notion that parrotfishes are considered high maintenance or difficult care level species among aquarium hobbyists, so by keeping the demand in check, low levels of exploitation can be maintained. Several sellers, aquarists, and scientists (Fenner 1998; F.M. Greco, private aquarist, 2001, pers. comm.; H. Molina-Ureña, pers.obs.) concur with these observations. Simultaneously, the listings of marine fish unsuitable for captivity prepared by Frank Greco, Reefs UK[22], should be constantly reviewed and updated, with collaborations from aquarium experts, hobbyists, and reef fish scientists worldwide.

(3) The State of Florida's management authorities could have a more proactive role in recording ornamental trade activities, and reporting landings to the Global Marine Aquarium Database, in order to achieve accurate accounts of exploitation, survival in captivity, and export.

Uninterrupted annual reef fish visual surveys have taken place in the Florida Keys since 1979. This combined effort by the National Marine Fisheries Service of the National Oceanographic and Atmospheric Administration (NMFS, NOAA), the Rosenstiel School of Marine and Atmospheric Science of the University of Miami (RSMAS, UM), and National Underwater Research Center (NURC) has provided a

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[22] Reefs UK http://www.reefsuk.org, link to **Captive Breeding** articles, link to **Unsuitable Marine Fish For Captivity**

sound database, and must be continued. Recent improvements included the continuous sampling optimization targeting selected fish species, the coordination of coral and fish surveys, the recording of standardized habitat features that may help find habitat predictors of abundances of distributions of fish, systematization of geographic coordinates for digital mapping, and the recording of protection categories that will help monitor the impact of marine protected area networks on fish species at different trophic levels.

Table 5.1: Post-stratification and optimal sample size equations.

VARIABLE	EQUATION	NOTATION	NOTES
Mean density per stratum	$\overline{D}_h = \frac{1}{\mathrm{n_h}} \sum_h D_j$	D_j= density per sampling unit, e.g., fish m^{-2} n_h= number of samples taken within stratum h	
Number of total possible samples within a stratum	$N_h = \frac{A_h}{\overline{U}_h}$	A_h=total area of stratum h U_h=sample unit area	$\overline{U}_h$~600 m^2 for shrimp trawls
Desired variance	$V = (CV[\overline{D}_k] * \overline{D}_h)^2$	$CV[\overline{D}_k]$= Target "coefficient of variation" of the mean density	Target CVs: 5, 10, 15, 20%
Required sample size to achieve target CV	$n^* = \frac{\left(\sum_h w_h s_h\right)^2}{V + \frac{1}{N}\sum_h w_h s_h^2}$	w_h= Weighting factor for stratum h $s^2{}_h$=sample variance of density in stratum h s_h= $s_h = \sqrt{s_h^2}$	
Optimal ("Neyman") sample allocation	$n_h = n \frac{w_h s_h}{\sum_h w_h s_h}$		Assuming equal sampling costs among strata

Table 5.2: Alternative sampling designs proposed in this work for future parrotfish surveys in Biscayne Bay.

Code name	Stratum name	Depth (m)	Equivalency to other designs	General location	Total area (Km^2)
6-stratum design					
SDN	Seagrass deep north	>2	SBA, North	Midbasin North of 25.52 lat N	130.8
SDS	Seagrass deep south	>2	SBA, South	Midbasin South of 25.52 lat N	61.2
SSM	Seagrass shallow mainland	1-2	SMS	East shore, north and south of bay	81.2
SSL	Seagrass shallow leeward	1-2	SLS	West shore, north and south of bay	25.3
HBt	Hardbottom	>1	HMS, HBA, HLS	South half of bay	61.6
BBt	Barebottom	>1	BMS, BBA, BLS	North half of bay	26.2
5-stratum design					
SDN	Seagrass deep north	>2	SBA, North	Midbasin North of 25.52 lat N	130.8
SDS	Seagrass deep south	>2	SBA, South	Midbasin South of 25.52 lat N	61.2
SSh	Seagrass shallow	1-2	SMS, SLS	East and West shores, north and south of bay	106.5
HBt	Hardbottom	>1	HMS, HBA, HLS	South half of bay	61.6
BBt	Barebottom	>1	BMS, BBA, BLS	North half of bay	26.2
4-stratum design					
SDN	Seagrass deep north	>2	SBA, North	Midbasin North of 25.52 lat N	130.8
SDS	Seagrass deep south	>2	SBA, South	Midbasin South of 25.52 lat N	61.2
SSh	Seagrass shallow	1-2	SMS, SLS	East and West shores, north and south of bay	106.5
HBB	Hard / bare bottom	>1	HMS, HBA, HLS BMS, BBA, BLS	North and south of bay	87.7

Table 5.3: Estimate precision obtained for *N. usta*, *Sp. chrysopterum*, and *Sp. radians* under 3 actual stratified sampling designs (3, 5, and 9 strata), and a simple random sampling (SRS) design, Biscayne Bay. Stratum descriptions from Table 2.1.

		3-stratum			5-stratum			9-stratum			Random design		
Cruise	n	Mean density	SE (D)	CV	Mean density	SE (D)	CV	Mean density	SE (D)	CV	Mean density	SE (D)	CV
N. usta													
April 1996	118	0.124	0.032	25.81	0.131	0.033	25.24	0.113	0.029	25.44	0.145	0.031	21.71
March 1997	122	0.226	0.056	24.91	0.279	0.069	24.86	0.272	0.066	24.42	0.232	0.063	27.14
March 2000	110	0.683	0.112	16.40	0.949	0.253	26.60	0.704	0.113	16.05	0.614	0.112	18.23
August 1996	93	0.391	0.098	24.99	0.389	0.110	28.33	0.411	0.129	31.36	0.386	0.102	26.37
September 1997	151	0.469	0.084	17.86	0.582	0.092	15.85	0.583	0.104	17.90	0.501	0.098	19.67
November 1996	150	0.742	0.177	23.85	0.755	0.163	21.54	0.781	0.183	23.45	0.755	0.185	24.51
November 1997	120	0.698	0.171	24.55	1.008	0.248	24.64	0.705	0.172	24.42	0.745	0.180	24.20
November 1999	119	0.875	0.183	20.97	1.101	0.203	18.42	0.929	0.191	20.51	0.893	0.195	21.88
Sp. chrysopterum													
April 1996	118	0.482	0.076	15.85	0.514	0.080	15.57	0.498	0.074	14.93	0.475	0.073	15.41
March 1997	122	0.281	0.050	17.74	0.331	0.057	17.29	0.326	0.055	16.96	0.291	0.054	18.50
March 2000	110	0.440	0.080	18.29	0.594	0.096	16.18	0.499	0.082	16.48	0.499	0.082	16.48
August 1996	93	0.573	0.128	22.24	0.554	0.132	23.90	0.546	0.135	24.67	0.597	0.122	20.44
September 1997	151	0.344	0.061	17.65	0.432	0.073	16.96	0.421	0.071	16.91	0.369	0.071	19.28
November 1996	150	0.591	0.084	14.21	0.609	0.086	14.05	0.597	0.082	13.71	0.597	0.087	14.53
November 1997	120	0.856	0.163	19.03	1.206	0.208	17.25	0.845	0.140	16.63	0.913	0.164	17.99
November 1999	119	0.373	0.077	20.78	0.413	0.079	19.18	0.396	0.077	19.56	0.396	0.077	19.56

Table 5.3 continued

		3-stratum			5-stratum			9-stratum			Random design		
Cruise	n	Mean density	SE (D)	CV	Mean density	SE (D)	CV	Mean density	SE (D)	CV	Mean density	SE (D)	CV
Sp. radians													
April 1996	118	0.031	0.014	44.27	0.033	0.014	43.33	0.031	0.014	45.50	0.042	0.015	34.49
March 1997	122	0.057	0.020	34.50	0.068	0.023	33.15	0.063	0.022	34.46	0.062	0.021	34.36
March 2000	110	0.009	0.009	99.99	0.009	0.009	99.99	0.011	0.011	99.99	0.010	0.010	104.6
August 1996	93	0.108	0.037	34.24	0.122	0.050	41.37	0.138	0.049	35.52	0.116	0.040	34.29
September 1997	151	0.202	0.058	28.66	0.274	0.073	26.70	0.261	0.066	25.07	0.220	0.070	31.81
November 1996	150	0.116	0.033	28.28	0.117	0.031	26.29	0.124	0.034	27.70	0.117	0.034	29.48
November 1997	120	0.257	0.065	25.32	0.351	0.077	22.07	0.245	0.060	24.52	0.271	0.066	24.47
November 1999	119	0.034	0.016	45.99	0.043	0.022	49.89	0.044	0.018	41.05	0.037	0.019	50.17

Table 5.4: Estimate precision obtained for *N. usta*, *Sp. chrysopterum*, and *Sp. radians* under 3 proposed stratified sampling designs (4, 5, and 6 strata), and a simple random sampling (SRS) desig. Stratum descriptions from Table 5.2

		4-stratum			5-stratum			6-stratum			Random design		
Cruise	n	Mean density	SE (D)	CV	Mean density	SE (D)	CV	Mean density	SE (D)	CV	Mean density	SE (D)	CV
N. usta													
April 1996	118	0.126	0.030	23.53	0.125	0.032	25.87	0.122	0.032	25.85	0.145	0.031	21.71
March 1997	122	0.227	0.054	23.65	0.230	0.054	23.70	0.232	0.055	23.57	0.232	0.063	27.14
March 2000	110	0.656	0.110	16.72	0.724	0.116	16.03	0.754	0.193	15.33	0.614	0.112	18.23
August 1996	93	0.497	0.139	27.87	0.473	0.137	28.90	0.442	0.135	30.51	0.386	0.102	26.37
September 1997	151	0.508	0.088	17.21	0.488	0.080	16.35	0.552	0.092	16.73	0.501	0.098	19.67
November 1996	150	0.702	0.170	24.17	0.697	0.168	24.13	0.719	0.169	23.50	0.755	0.185	24.51
November 1997	120	0.739	0.175	23.72	0.690	0.164	23.72	0.686	0.159	23.21	0.745	0.180	24.20
November 1999	119	0.813	0.177	21.82	0.849	0.183	21.60	0.914	0.193	21.14	0.893	0.195	21.88
Sp. chrysopterum													
April 1996	118	0.508	0.076	15.00	0.515	0.080	15.57	0.513	0.080	15.59	0.475	0.073	15.41
March 1997	122	0.303	0.605	20.00	0.301	0.061	20.15	0.302	0.061	20.14	0.291	0.054	18.50
March 2000	110	0.493	0.081	16.35	0.492	0.081	16.40	0.493	0.081	16.40	0.499	0.082	16.48
August 1996	93	0.613	0.142	23.20	0.574	0.014	23.61	0.525	0.130	24.79	0.597	0.122	20.44
September 1997	151	0.382	0.064	16.76	0.377	0.064	16.85	0.424	0.070	16.48	0.369	0.071	19.28
November 1996	150	0.553	0.715	12.92	0.552	0.071	21.92	0.554	0.072	12.91	0.597	0.087	14.53
November 1997	120	0.847	0.149	17.61	0.816	0.144	17.68	0.809	0.129	15.91	0.913	0.164	17.99
November 1999	119	0.351	0.072	20.37	0.361	0.074	20.55	0.382	0.076	19.82	0.396	0.077	19.56

Table 5.4 continued

Cruise	n	Mean density	SE (D)	CV	Mean density	SE (D)	CV	Mean density	SE (D)	CV	Mean density	SE (D)	CV
Sp. radians													
April 1996	118	0.372	0.015	40.50	0.033	0.014	43.93	0.328	0.014	43.93	0.042	0.015	34.49
March 1997	122	0.562	0.020	35.72	0.053	0.018	34.79	0.590	0.020	34.05	0.062	0.021	34.36
March 2000	110	0.011	0.011	99.99	0.011	0.011	99.99	0.105	0.011	99.99	0.010	0.010	104.6
August 1996	93	0.147	0.054	36.45	0.137	0.052	37.53	0.143	0.052	36.59	0.116	0.040	34.29
September 1997	151	0.197	0.049	24.95	0.193	0.049	25.13	0.259	0.065	24.95	0.220	0.070	31.81
November 1996	150	0.117	0.034	28.79	0.117	0.034	28.79	0.122	0.034	27.59	0.117	0.034	29.48
November 1997	120	0.276	0.074	26.95	0.252	0.064	25.38	0.250	0.062	24.66	0.271	0.066	24.47
November 1999	119	0.033	0.015	46.22	0.043	0.022	49.89	0.417	0.017	41.31	0.037	0.019	50.17

Table 5.5: Sample allocation for a 6-stratum sampling design for *N. usta*, *Sp. chrysopterum*, and *Sp. radians* under the 6-stratum sampling design during different seasons. Symbology: n*=sample size required for a 10% CV target precision. Stratum codes are given in Table 5.2.

Season	SPRING	SUMMER	FALL
N. usta			
n*	224	248	350
SDN	134	141	200
SDS	10	19	36
SSM	17	26	11
SSL	10	34	71
HBt	34	0	0
BBt	19	28	32
Sp. chrysopterum			
n*	230	320	209
SDN	112	130	123
SDS	42	62	20
SSM	17	41	17
SSL	10	40	32
HBt	37	16	4
BBt	12	31	13
Sp. radians			
n*	1184	381	496
SDN	516	177	224
SDS	146	51	61
SSM	114	40	0
SSL	147	77	105
HBt	108	1	35
BBt	153	35	71

Table 5.6: Current and proposed estimates of exploitation benchmarks for South Florida populations of parrotfishes. F = Fishing mortality, F_{msy} = Fishing mortality for maximum sustainable yield, t_m = mean age at first sexual maturity (months of age), t_c = mean age at first capture (months of age), L_c = mean length at first capture (cm Total Length), $\overline{L}$ = mean length in exploitable phase (cm Total Length) observed in protected (Prot) and unprotected (Unprot) sites, SPR = Spawning Potential Ratio.

	CURRENT							PROPOSED			
Species	F/F_{msy}	t_m	t_c	L_c	$\overline{L}$ Prot	$\overline{L}$ Unprot	SPR	t_c	L_c	$\overline{L}$	SPR
Sc. iseri	1.0	24.4	4.9	4	6.50	6.38	23.7	24.4	13.1	9.7	46.7
Sp. aurofrenatum	1.0	18.4	2.4	4	9.92	9.48	25.3	18.4	16.3	16.7	44.8
Sp. viride	1.0	40	11	15	15.3	13.2	23.5	40	39.1	26.5	48.4
Sp. chrysopterum	1.0	19	7.1	15	19.7	17.1	26.1	19	23.2	20.6	47.5

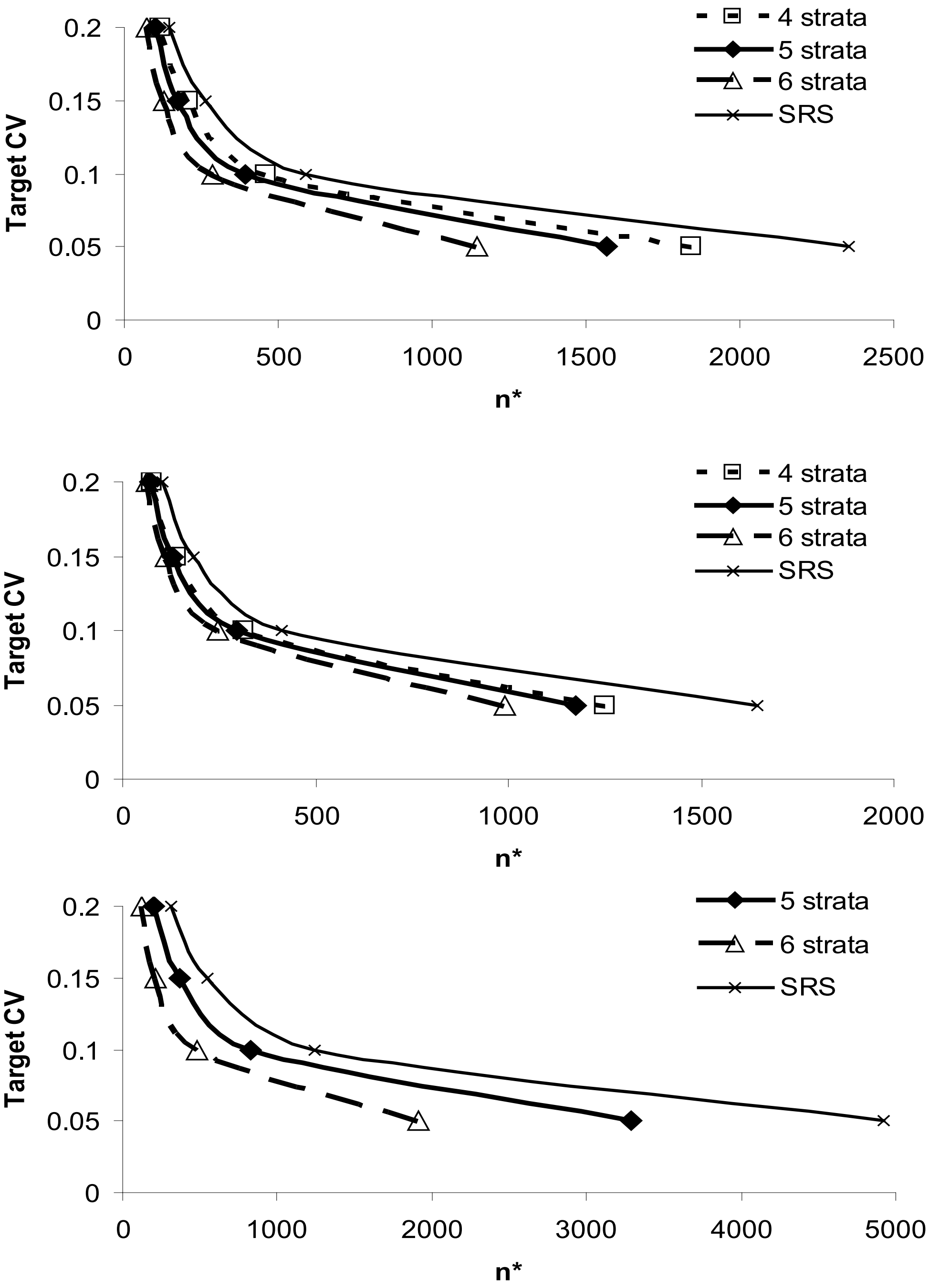

Figure 5.1: Number of samples required to achieve a target coefficient of variation (CV) of density estimates under 4 different sampling designs: 4, 5, and 6 strata, and simple random sampling (SRS). Top panel: *N. usta*. Medium panel: *Sparisoma chrysopterum*. Bottom panel: *Sp. radians*. Note different scales on the X axis in each graph.

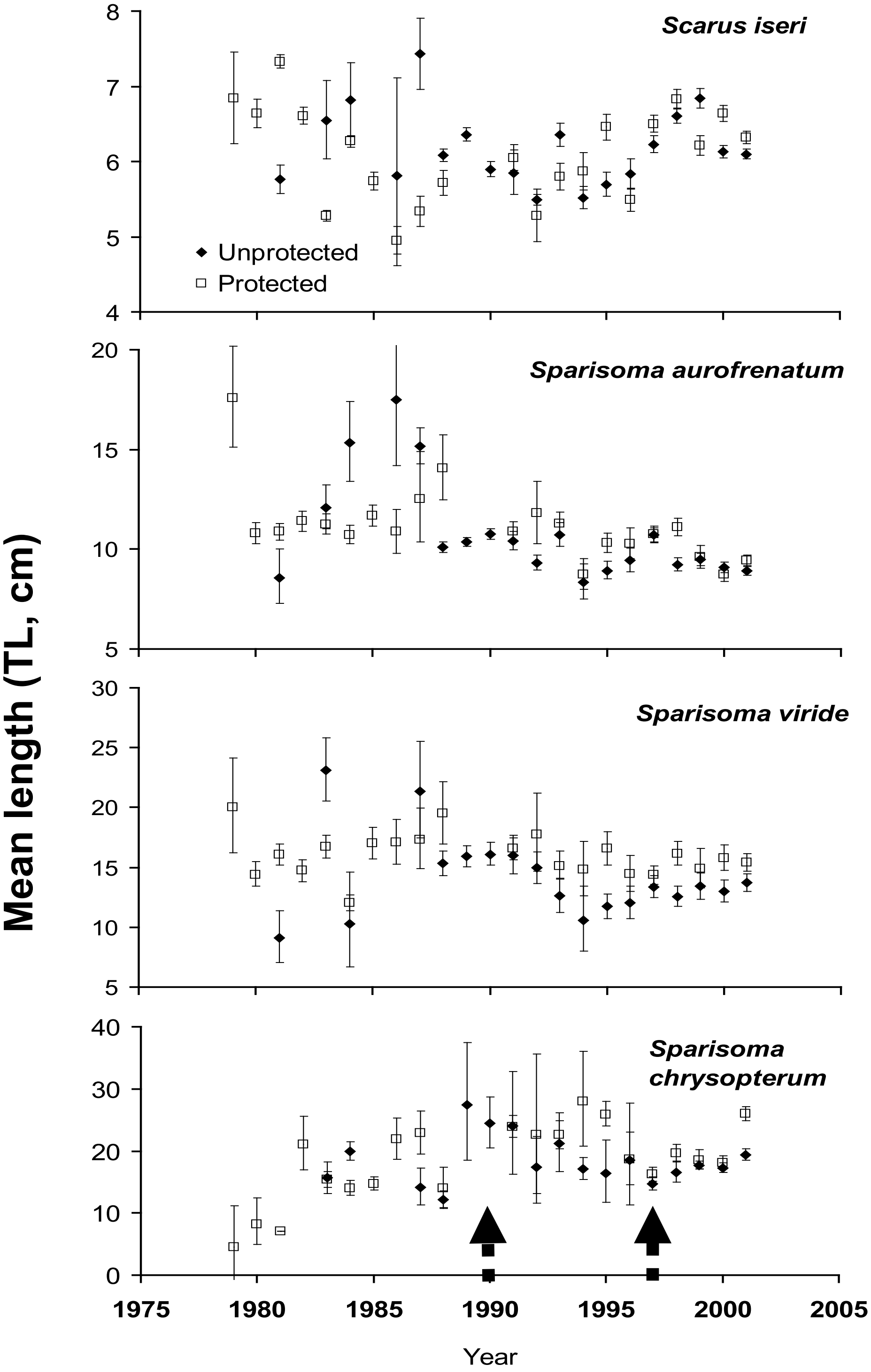

Figure 5.2: Mean lengths of Florida Keys populations of parrotfishes, 1979-2001. Hatched vertical arrows mark the implementation of the Florida Keys National Marine Sanctuary Law (1990) and the network of no-take protected zones (1997), which coincided with the massive 1997-1998 coral bleaching event (Turgeon et al. 2002). Note the Y axis have different scales, according to the species characteristics.

Summary and conclusions

This study aimed at designing a pathway towards ecosystem-based approaches for fisheries management, by developing methods to fill important gaps of information pertaining non-target, herbivorous fish in a coral reef ecosystem and adjacent habitats. While developed with South Florida populations, this approach is intended to be useful in different locations around the Wide Caribbean Basin. Ecosystem-based management refers to a form of fisheries governance based on the understanding of ecological, socio-economic and biophysical components, including the resilience of such complex systems (Bellwood et al. 2004). However, this concept is constantly evolving, due in part to the difficulty of turning these principles into operational objectives.

Few studies have addressed population dynamics, trophodynamics, and habitat use of non-target populations because those species have often been neglected in traditional fisheries management plans. Besides, unless there are records of incidental captures, reliable catch data is usually unavailable for analyses of their fisheries dynamics. Taxonomy, ecology, reproductive biology, and local abundances might be better known on some non-target fish stocks, but this information is seldom integrated to relate life history patterns to observed population structure and dynamics. Thus, lack of integrated information is pervasive and deters further analyses of the status of this type of populations. The pathway hereby proposed intends to use all available information with the aim of improving the knowledge of different aspects of the life history of species that could be (a) vulnerable to exploitation, (b) important prey items for target fishes, and (c) key species in coral reef ecosystems of the world.

With respect to the South Florida populations of parrotfishes, four questions were examined: How do these species use habitats in Biscayne Bay and Florida Keys? What is the current status of the parrotfish populations? What are the effects of marine protected areas? What could be the effects of the trend of fishing down from high quality carnivores to less valuable herbivores or planktivores, known as serial fishing?

A three-step approach was proposed as a viable, integrating alternative designed to detect and prioritize major biological information voids, and to attempt to fill those gaps (cf. Figure I.1). Step I was an analysis of information gaps. Step II prioritized the information within a framework including ecosystem relationships and data gathering opportunities, in order to determine the amount and scope of the studies that can be carried out. Step III consisted of the techniques, approaches, and analyses that were applied to answer the top priorities.

Step I. A thorough literature search aimed at obtaining all background necessary for an *a priori* picture about the role of the stock or taxon within the ecosystem, and the population dynamics of this component. The search included population dynamics, behavior and reproductive strategies, trophodynamics and other ecological relationships (e.g., symbiosis, competition), habitat, biosystematics, taxonomy, biogeography, and evolution. In order to have a more complete picture, especially in the context of shifting baselines, this first step also reviewed information on human activities that may have effects on the studied species, focusing on fisheries dynamics across the geographic range of the Western Atlantic parrotfishes. For this study, the search was restricted to peer-reviewed journals, and government reports. The proposed approach should enhance the scope of the search and sharing of information by a network of government agencies, research institutions, non-governmental organizations (NGOs), and sources of gray literature (e.g., local agency reports, environmental impact studies, theses, etc.).

Step II. In order to prioritize the questions that needed answer, and the possibility of addressing them, several aspects were considered. The information available on the role of the stock, taxon, or guild in the ecosystem was analyzed within an integrative framework, considering three aspects: (a) the paradigm of shifting baselines, i.e., our baselines pertaining reef ecosystems are built on less than five decades of research, while the ecosystem has been evolving during much longer time scales. Thus, standards to assess changes should be based on palaeoecological, archaeological, and historical information besides recent empirical data; (b) how the local conditions of the study area related to the findings on each species obtained from different locations of its geographic range; and (c) what type of data was available, which had to be generated, and what were the possibilities of answering the questions with observed data.

The information gap analysis determined that habitat use and feeding modes were tightly related, and this relationship drove the evolution of the parrotfishes to a certain extent. This family is very abundant, frequent, and specious in most Caribbean reefs. Scarids play a major role as bioeroders and grazers, the latter likely being enhanced since the decline of the populations of the sea urchin, *Diadema antillarum*, in the last two decades. This taxon also acts as a trophic link to commercial species, such as groupers, snappers, jacks, and barracudas, as well as marine birds (e.g., cormorant). Small parrotfish species are under predation pressure during the whole life cycle, while the larger species might be most vulnerable at younger developmental stages. Vulnerability of the spawners and their products to predation is not well documented, but the coexistence of spawning aggregations, group spawning, and pair spawning strategies in the same species may indicate different selective pressures by locality.

The gap analysis also concluded that, besides a phenotypic plasticity of local demographic patterns of several Atlantic scarids, the published growth models of selected parrotfish species from elsewhere in the Caribbean did not account for the patterns observed in the Florida Keys. Regarding fishing dynamics, available data suggested very low fishing pressure from ornamental trade, and lobster fisheries bycatch. No data was found on the shrimp fishery in Biscayne Bay. Effects of implementation of marine protected areas in the Florida Keys had not been studied on a large scale, while studies from other localities were mostly based on simulations rather than empirical data. Finally, the possibility to participate in two major projects based on large scale fishery-independent surveys in South Florida provided an opportunity to examine adjacent domains. One study surveyed the seasonal abundances of pink shrimp, *Farfantepenaeus duorarum*, in Biscayne Bay (Diaz 2001), in which bycatch data from bottom trawls were used. The other project consisted of a long term, Keys-wide reef fish visual census by divers in the Florida reef tract.

Step III. Given the information gaps and the data gathering opportunities, four major objectives were selected as priorities:

1- To determine ontogenetic habitat uses by parrotfishes in Biscayne Bay and the Florida Keys.

2- To evaluate the effects of habitat protection in the Florida Keys on parrotfishes.

3- To determine the current status of parrotfish populations in the Florida Keys.

4- To forecast potential effects of targeted fishing on South Florida parrotfishes, given the current knowledge of their population dynamics.

Habitat use was studied in two domains, a coastal bay and a reef tract. Biscayne Bay was surveyed with nighttime bottom trawls with a sampling design following a simple stratified random scheme customized for pink shrimp, based on three attributes: substrate type, distance from shore, and depth. The Florida Keys reef fish visual censuses (RVC) were conducted during daylight on a 2-stage stratified random design, defined by distance from shore, depth, and protection level.

Three measures of habitat affinity were applied by domain, species, lifestage, cruise or year (Manly et al. 1993): *probability of use of a habitat unit in stratum h*, $p(\text{use})_h$, *per unit amount of use*, PUA, and *relative population amount of use*, p(P) vs. p(A). This ecological technique proved useful to improve the understanding of parrotfish distribution and habitat use, which in turn was a valuable input to improve the sampling design. In the Biscayne Bay trawls, the three most abundant scarids were *Sparisoma chrysopterum* (Redtail parrotfish), *Nicholsina usta* (Emerald parrotfish), and *Sp. radians* (Bucktooth parrotfish), ranking among the top 24 of a total of 177 species sampled. Little has changed in the relative abundance of those three species, even 20+ years after the fish trap ban, and despite the continuous removal as bycatch by the shrimp fisheries.

Three to four lifestages (juvenile phase, JP; subadult, SP; initial phase, IP; and terminal phase, TP) were determined. Within-bay habitat use by the three top parrotfishes showed similar patterns: an affinity for seagrass and use of barebottom substrates based on this habitat's area availability. The outcome of this study supported the dual use of seagrass habitats and ocean waters, rather than coral reefs or mangroves, by *N. usta*. This parrotfish has its own reproductive population in Biscayne Bay with little exchange with the Keys, but probably using offshore (18-50 m depth) waters as an adult habitat. This population remains in the bay mostly during the wet, warm months (summer, fall), and a considerable portion of the population leaves this domain in winter and spring. A prolonged influx of new recruits into the bay likely reflected a protracted spawning activity, although the actual spawning grounds of *N. usta* have not been determined. A progressive expansion onto nearby substrates associated with growth was observed, but no sharp ontogenetic within-bay habitat shifts were detected. Because gears used in most studies were size-selective towards smaller fish, the fate of the older individuals >20 cm TL is unknown. In order to clarify whether the bay acts as nursery grounds for open water populations of *N. usta*, or constitutes a lifelong habitat, it is recommended to obtain trawl samples from ocean waters 20-100 m depth off the South Florida coast. The results also suggested little exchange with the Florida Keys for bay populations of *Sp. radians*. However, given its preference for seagrass, mangrove and sandy substrates, its avoidance of high rugosity reefs, and its permanent territorialism reported in the literature, it is likely that the whole life cycle of this parrotfish may take place within the bay and inshore seagrass habitats.

In the Florida Keys, the four parrotfishes most abundantly recorded in the RVC were *Scarus iseri* (Striped parrotfish)*, Sparisoma aurofrenatum* (Redband parrotfish), *Sp. viride* (Stoplight parrotfish), and *Sp. chrysopterum*. These populations showed an onshore-to-offshore ontogenetic pattern, in which the smaller individuals occupied the near shore reefs, progressively expanding to midshelf, offshore and forereefs as the fish grew, driven by substrate availability. TPs concentrated in fore reefs $\geq$ 6 m deep.

Indirect evidence suggested a seagrass-reef connection for *Sp. chrysopterum*, in which an influx of young IPs (TL $\geq$ 12 cm), leaving the bay via Safety Valve, may enter the Florida reefs along midshelf strata. Results suggested settlement grounds other than reefs. The onset of a change in tail shape from truncated to concave in *Sp. chrysopterum* (at ~9-11 cm TL) may indicate an ecomorphological adaptation for longer sustained swimming ability. The timing of this event would coincide with the hypothesized ontogenetic emigration from the bay waters onto the reef habitats. Finally, an apparent reversal of the ontogenetic pattern was observed towards the middle of the shelf.

The study of life history parameters concluded that *Sc. iseri* and *Sp. chrysopterum* have isometric growth (b=3), no differences in their weight-length relationship among color phases, and an extensive size overlap between IP and TP. *Nicholsina usta* and *Sp. radians* showed a small positive allometry, with 95% confidence limits $3.1 \leq b \leq 3.4$.

In order to develop growth curves adjusted to the demographic characteristics observed in the Florida Keys parrotfishes, growth parameter estimates of South Florida populations of *Sc. iseri*, *Sp. aurofrenatum*, *Sp. chrysopterum*, and *Sp. viride* were adapted from otolith-based von Bertalanffy Growth Functions (VBGF) (Choat and Robertson 2002, Choat et al. 2003, Paddack 2005). The procedure consisted in an iterative numerical recombination of reported parameter estimates under a set of constraints, using observed data from the Reef fish Visual Censuses (RVC) as initial inputs. Two candidate growth models were selected for each species, denoted as "short" (low maximum life time, t_{λ}) and "long" (high t_{λ}) lifespan. Longevity estimations ranged from 5 to 12 years, shorter than those for Indo-Pacific scarids. Brody growth parameter, $\hat{K}$, values differed little between the short-lived ($\hat{K}$ range = 0.32, 0.70) and long-lived ($\hat{K}$ range = 0.34, 0.62) assumptions. Estimates were comparable to empirical data from Caribbean and Pacific species (Choat and Robertson 2002), but lower than those from Paddack (2005). Steepness of growth curves decreased in the following order: *Sp. aurofrenatum*, *Sp. chrysopterum*, *Sc. iseri*, and *Sp. viride*. Nonetheless, simulation outcomes retained the tendency found in Indo-Pacific and Atlantic scarids to a determinant growth in which the fish reach the maximum size early in their life, and stay at that size for the rest of their lifespan (Choat and Robertson 2002).

The discrepancy in the maximum length reported for each parrotfish species between otolith studies and this dissertation, can be explained by the considerably larger sampling effort of this study, in terms of amount of sampling units, total area surveyed, habitat types visited, and absolute numbers of fish observed. This allowed recording between 1,600 and >19,000 individuals of the four most abundant scarids in the Florida Keys domain, which in turn increased the probability of detecting larger, less common specimens in those populations.

Based on empirical proportion for unsexed data (Froese and Binohlan 2000) applied to the short lifespan model, age at first maturity ranged from ~1.5 year old (*Sp. aurofrenatum* and *Sp. chrysopterum*), to ~2 and >2.5 y.o. (*Sc. iseri* and *Sp. viride*, respectively), at lengths comparable to observed maturity schedules of Caribbean parrotfish populations. Estimations of size and age at sex change based on empirical species-specific length proportions from Panama, ranging 0.56-0.81 of maximum length (Robertson and Warner 1978), were adapted to the larger maximum sizes found in the Florida Keys parrotfish populations. These estimates suggested that sex change occurs within 4 months before (*Sc. iseri*) or 3-10 months after (*Sparisoma* spp.) the time of first maturity. The invariant theory (Allsop and West 2003b) holds better for species in which all individuals undergo transformation. Diandry, and other cases in which not all individuals change sex, may not follow the predicted proportions.

Empirical data from this study also concluded that habitat protection, by means of marine protected areas, showed no negative effects on parrotfishes, as predicted by Mumby (2006). The species considered here showed no trends on habitat preference between protected and unprotected sites.

To address potential effects of increased fishing pressure, outputs of two models, Reef Ecosystem Exploited Fisheries Simulator (REEFS)[24] and a length-based mortality estimating algorithm (LBAR) (Ault et al. 1996), were used to simulate different levels of fishing mortality, based on the life history parameters as adapted to South Florida parrotfishes. The endpoints of the simulations were: average length of exploited population ($\overline{L}$), instantaneous rate of total mortality (Z), and size frequency distribution. Outputs of the simulations suggested that the high Z values yielded Spawning Potential Ratios slightly below the U.S. Federal standard (i.e., SPR<30%). Should the need to commercially exploit South Florida parrotfishes arise, this study recommends a combination of fishing mortality at maximum sustainable yield ($F_{MSY} = M$) with a minimum size at first capture equal to the size at first maturity ($t_c = t_m$), such that SPR stays at a minimum of 45%.

REEFS and LBAR simulation outputs validations against empirical data concluded that, based on the von Bertalanffy model, scarids displayed high total mortalities (Z), suggesting either high natural mortality rates, or unreported exploitation

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[24] Ault, J.S. 1998. Tropical coral reef fishery resource decision dynamics. Unpubl. manuscript.

levels. An alternative explanation is that this model does not fit the determinant growth shown by the Atlantic parrotfishes. Therefore, a different growth function should be developed for species belonging to this family.

Information voids on scarids that still should be addressed include, but are not limited to: physiology and ethology of sex change and territorial behavior, effects of endocrine disruption processes in sequential hermaphrodites, otolith-based growth curves with larger specimens of each species, body growth models for determinant growth, fisheries data from other Western Atlantic localities, and actual feeding habits of each species at different stages of their life cycle.

This study is unique because South Florida parrotfish populations presented an extraordinary opportunity for the holistic approach on fisheries management, as well as for comparing simulated to observed data as a tool to assess the current status and predict potential effects of fishing and management actions on non-target stocks. This research has provided medium and large scale analyses of temporal and spatial patterns of habitat use within and among an adjacent seagrass embayment and a coral reef by South Florida scarids. In Biscayne Bay, the results demonstrated the importance of seagrass beds as settlement, recruitment, and nursery areas for parrotfish, with seasonal patterns. In the Florida Keys, there was evidence of ontogenetic shifts from inshore to offshore habitats, and annual variability of abundance and distribution of fish. By following the only species with significant presence in both sampling domains, the results suggested a role of Biscayne Bay as source of juveniles and subadults of *Sp. chrysopterum* to the Florida reef tract.

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Appendix A: REEFS and LBAR simulation inputs, outputs and empirical data supporting recruitment assumption.

Table A.1: Input values of life history parameter estimates as predicted by simulations and invariant theory under two levels of natural mortality (high and medium). Longevity (t_λ), weight-length parameters (α, β), ultimate length and weight (L_∞, W_∞), Von Bertalanffy curvature coefficient (K), maximum observed length and weight (L_λ, W_λ), size and age at recruitment (L_r, t_r) size and age at first maturity (L_m, t_m), size and age at first capture (L_c, t_c), natural mortality estimates from 5% survivorship ($M_{(5\%)}$) and Beverton & Holt invariant M=1.5*K ($M_{(B\&H)}$). Length: (mm) TL (SL). Weight: (g)

Parameter estimates	*Sc. iseri*	*Sp. aurofrenatum*	*Sp. viride*	*Sp. chrysopterum*
t_λ (y)	7	7	10	5
Weight – Length				
α	0.0126	0.0162	0.0226	0.0152
β	3.1426	3.2321	2.9298	3.0274
L_∞	205 (172)	277 (255)	62.5 (47.9)	455 (357)
W_∞	97	410	4076	1590
K	0.5203	0.7020	0.3242	0.6808
L_∞	205 (172)	277 (255)	62.5 (47.9)	455 (357)
W_∞	97	410	4076	1590
L_λ	200 (168)	275 (254)	60.0 (46.1)	440 (345)
W_λ	155	405	3662	1436
L_r	12.5 (10)	12.5 (10)	12.5 (10)	12.5 (10)
t_r (months)	1.4	0.7	0.8	0.5
L_m	135 (114)	184 (168)	406 (316)	294 (236)
W_m	45	102	1170	422
t_m (months)	24.4	18.4	40	19
L_c	40 (33)	40 (33)	150 (123)	150 (118)
W_c	1	0.6	63	55
t_c (months)	4.9	2.4	11	7.1
$M_{(5\%\ Surv)}$	0.4280	0. 4280	0. 2996	0. 5991
$M_{(B\&H)}$	0. 7955	1.0530	0. 4863	1.0212

Table A.2: Predicted parameter estimates by simulations with REEFS and LBAR algorithms (Ault et al. 1996, Ault 1998, Ault et al. 1998). Total instantaneous mortality is given as a rate and as percentage of the population, as calculated by Ricker (1975). Asterisks indicate the models that fitted better the observed size frequency distributions in each species.

Parameter estimate	*Sc. iseri*		*Sp. aurofrenatum*	
	M=0.43	M=0.80	M=0.43	M=1.05
Z (y^{-1}, % population)				
At F=0.0	0.45 (36)	0.84 (57)	0.48 (38)	1.23 (71)
At F=0.1	0.56 (43)	0.95 (61)*	0.59 (45)	1.35 (74)*
At F=0.5	-	1.40 (75)	-	1.89 (85)
At F=1.0	1.55 (79)	1.98 (86)	1.72 (82)	-
At F=1.5	-	-	-	3.43 (>95)
At F=M	0.91 (60)	1.74 (82)	0.98 (62)	2.71 (93)
Frequency of maximum length (%)				
At F=0.0	9.8	3.3	8.8	0.7
At F=0.1	7.4	2.3	6.0	0.4
At F=0.5	-	0.6	-	0.07
At F=1.0	0.4	0.1	0.1	-
At F=1.5	-	-	-	0.00
At F=M	2.7	0.2	0.2	0.00

	Sp. viride		*Sp. chrysopterum*	
	M=0.30	M=0.49	M=0.60	M=1.02
Z (y^{-1}, % population)				
At F=0.0	0.31 (27)	0.50 (39)	0.64 (47)	1.10 (67)
At F=0.1	0.41 (34)	0.61 (46)*	0.75 (53)	1.21 (70)*
At F=0.5	0.84 (57)	-	-	1.67 (81)
At F=1.0	1.39 (75)	1.60 (80)	1.76 (83)	-
At F=1.5	-	-	-	2.89 (94)
At F=M	0.62 (46)	1.03 (64)	1.30 (73)	2.29 (90)
Frequency of maximum length (%)				
At F=0.0	3.4	1.2	3.0	0.8
At F=0.1	1.9	0.6	2.3	0.6
At F=0.5	0.2	-	-	0.2
At F=1.0	0.00	0.00	0.1	-
At F=1.5	-	-	-	0.00
At F=M	0.6	0.05	0.5	0.02

(a) Sc. iseri. Left panel: M=0.43 Right panel: M=0.8

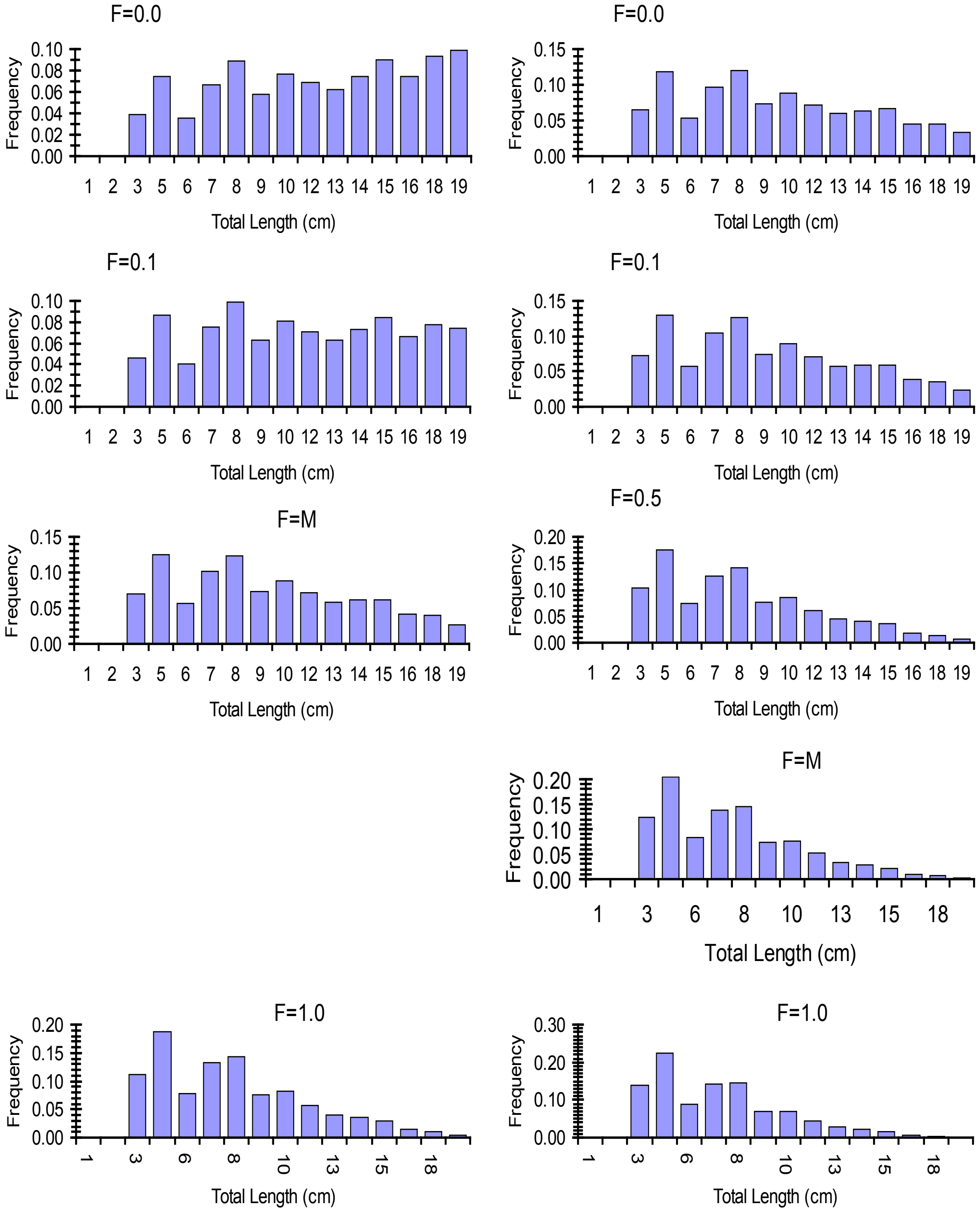

Figure A.1: Predicted length distribution histograms from REEFS and LBAR models for parrotfishes of the Florida Keys. Left panel represents simulations assuming low M. Right panel represents high M. Original standard length outputs are converted to TL units for comparison purposes.

(b) *Sp. aurofrenatum.* Left panel: M=0.43 Right panel: M=1.05

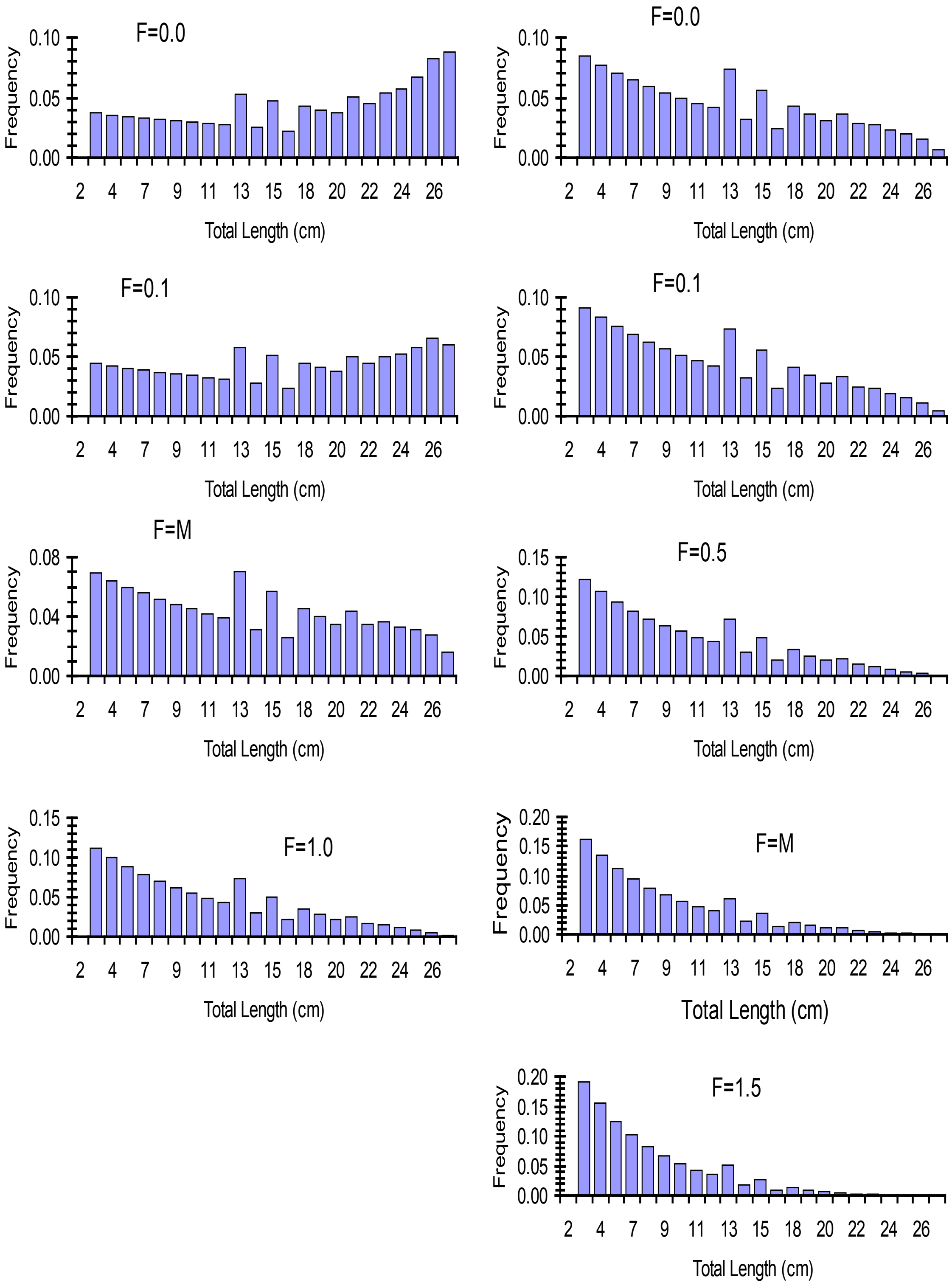

Figure A.1 continued

(c) *Sp. viride.* Left panel: M=0.30 Right panel: M=0.49

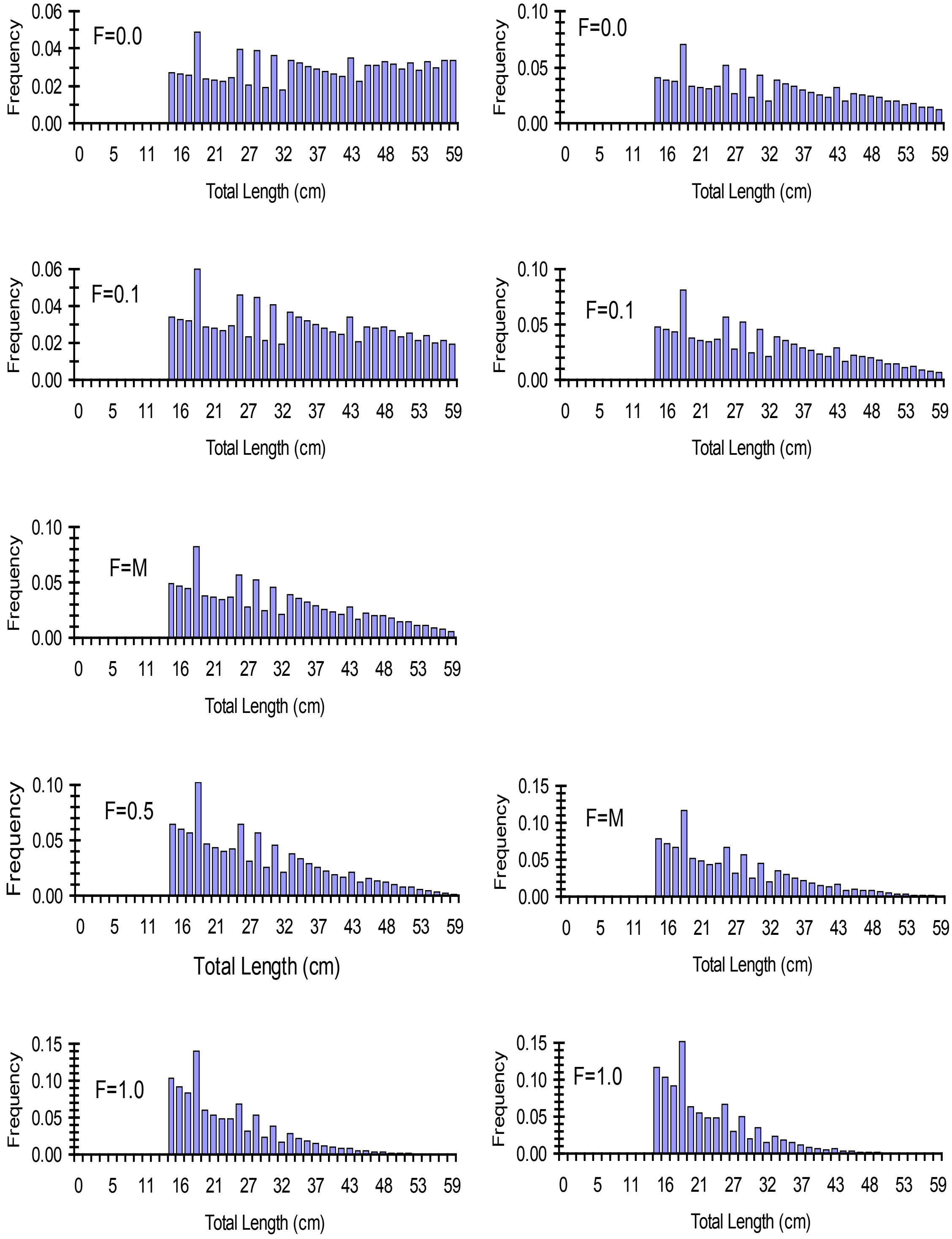

Figure A.1 continued

(d) *Sp. chrysopterum.* Left panel: M=0.60 Right panel: M=1.02

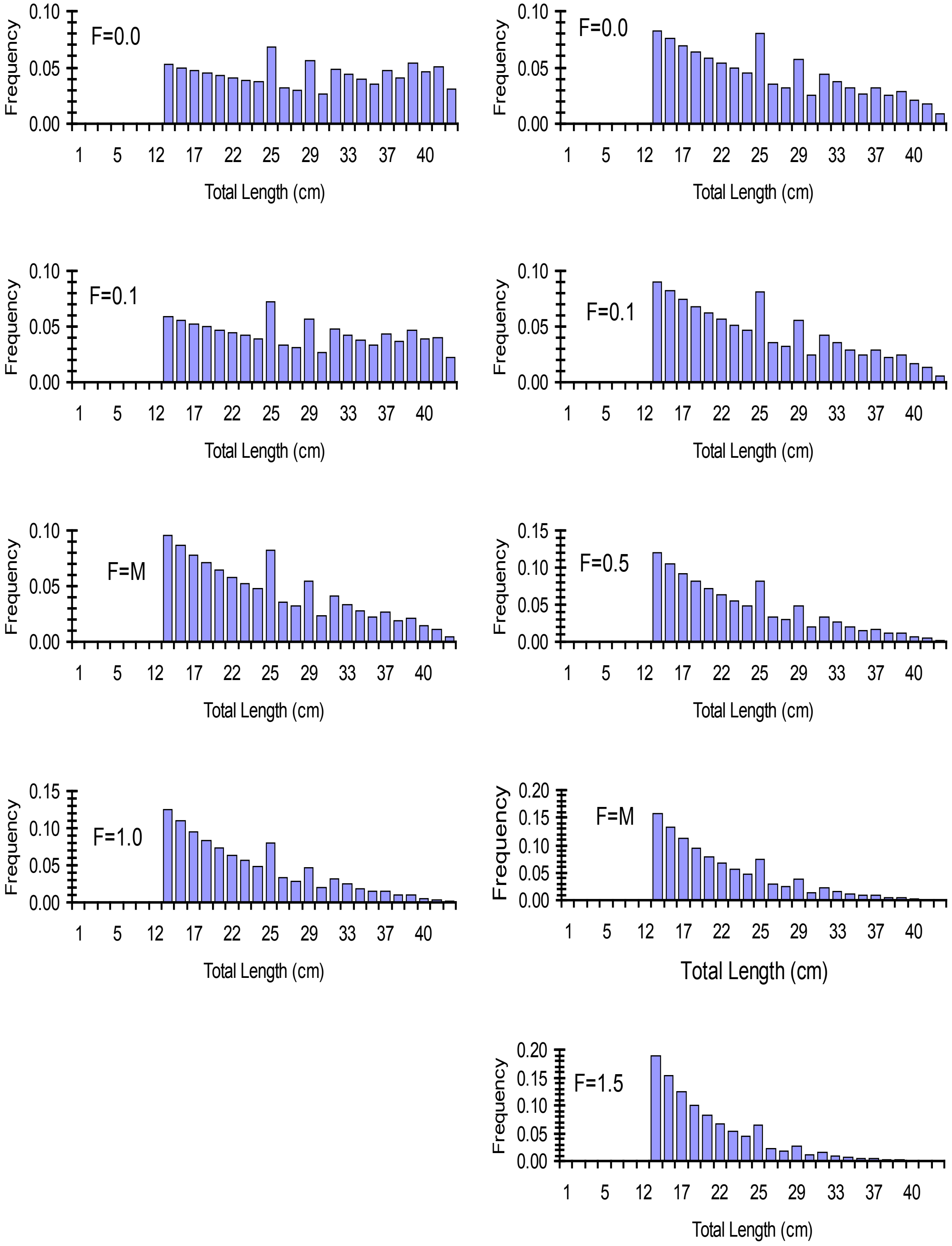

Figure A.1 continued

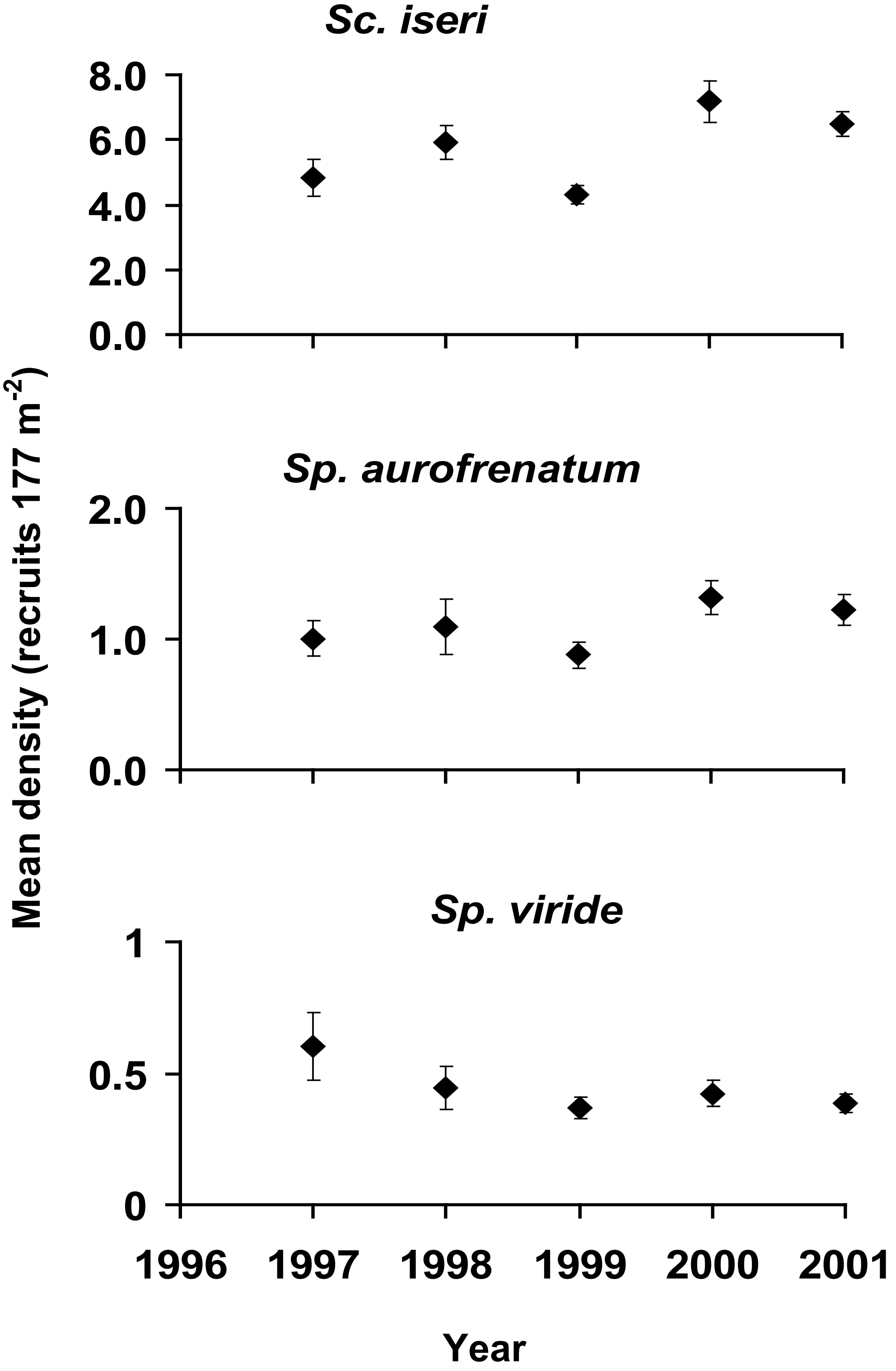

Figure A.2: Density of scarid recruits (< 6 cm TL) in the Florida Keys.

Appendix B: Glossary

Browser	feeding mode in which the fish removes pieces of epilithic algae, fragments of macroalgae and seagrasses with oral jaw teeth, without scraping or scarring the substrate
Ceratobranchial	longest bones or cartilages of the branchial arches, situated immediately below the angle of the arch, between the epibranchials and the hypobranchials.
Clade	a monophyletic group of organisms
Cladism	a branch of biology that determines the evolutionary relationships between organisms based on *derived* similarities
Denticle	a small outgrowth similar in structure to a tooth
Diandry	both primary and secondary males are present in the same population
EDC	Endocrine disrupting chemical, which can mimic estrogens (e.g., DDT, some PBCs), or antagonize their effects (e.g., PAHs)
Epibranchial	bone or cartilage forming the upper part of the gill arch, immediately above the angle of the arch.
Epilithic	growing on stone
Excavator	a fish that removes pieces of substrate during feeding, leaving distinct grazing scars
Gonadosomatic index	percentage of gonad weight relative to body weight
Gonochorist	individual that lack the genetic capacity to change sex
Harem	a group of females within a male territory, that mate nearly exclusively with that one male
Homonym	a word that has the same pronunciation and spelling as another word, but a different meaning
Homoplasy	similarity that may result from convergent or parallel evolution, change, or by chance alone, not due to common ancestry.
Initial phase	female or male characterized by a disruptive, dull coloration
Invertivore	fish that consumes mostly invertebrates
Molecular clock	a technique in genetics, which researchers use to date when two species diverged. It deduces elapsed time from the number of minor differences between their DNA sequences
Monandry	all males present in a population are transformed from females in a protogynous species
Monophyly	condition of a taxonomic group that consists of a common ancestor and all its descendants
MSY	Maximum sustainable yield, the largest long-term average yield/catch that can be taken from a species' stock without depressing the species ability to reproduce

Glossary (continued)

Ontogeny	describes the origin and the development of an organism from the fertilized egg to its mature form
PAHs	Polycyclic aromatic hydrocarbons, a group of over 100 different chemicals that are formed during the incomplete burning of coal, oil and gas, garbage, or other organic substances like tobacco or charbroiled meat.
Paraphyly	condition of a taxonomic group that contains some but not all descendants of the most recent common ancestor
PCBs	Polychlorinated biphenyls, mixtures of up to 209 individual chlorinated compounds (known as congeners). There are no known natural sources. PCBs have been used as coolants and lubricants in transformers, capacitors, and other electrical equipment because they don't burn easily and are good insulators. Also found in old (<1977) fluorescent lighting fixtures and electrical devices containing PCB capacitors, and old microscope and hydraulic oils.
Pharyngocleithral	muscualr process that establishes physical contact of the pharyngeal jaw with the cleithrum
Pharyngognathy	gill arch elements that have become secondarily modified into a feeding apparatus of versatile biting jaws
Polychromatic	a species having many different coloration forms among its individuals
Polyphyly	condition of a taxonomic group that contains organisms but not their common ancestor
Prematurational sex change	testes are derived from ovaries without ever being a functional female in a protogynous species
Primary male	individual that are not product of sexual transformation
Protogyny	sequential hermaphroditism in which the female sex occurs before the male sex
Scraper	feeding mode in which the fish removes material from the surface of the substrate with a non excavating bite that rarely scars the substrate
Secondary male	individual resulting from sex reversal in protogyneous species
Sphincter	a ring of muscle that contracts to close an opening
Terminal phase	a male that underwent color change to a bright coloration, predominantly green and blue with cephalic and opercular markings in red, orange or blue

Vita

Helena Molina-Ureña was born in San José, Costa Rica, first child to José Guillermo Molina and María Cecilia Ureña and sister to Silvia and Ronald. She received her elementary education at Escuela República del Perú and her secondary education at Colegio Superior de Señoritas. After she graduated *Suma Cum Laude* with a B.S. degree in Biology at Universidad de Costa Rica, she was awarded a Fulbright Graduate Program scholarship to pursue a Master's degree. Once she got her M.S. in Oceanography at Oregon State University, in Corvallis, she returned to Costa Rica to work at her home university at the Research Center for Marine Science and Limnology (CIMAR). In 1991, she became faculty at the School of Biology, Universidad de Costa Rica, where she has been Associate Professor since 1997. She became a member at large of the Phi Sigma Biological Sciences Honor Society, Chapter Omega Omega in 2002. A Fulbright-LASPAU scholarship allowed her to start her doctorate studies at the Rosenstiel School of Marine and Atmospheric Science, University of Miami, where she was granted a Ph.D. degree in Marine Biology and Fisheries in May 2009.

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