

MORPHOLOGY AND EARLY LIFE HISTORY PATTERN OF SOME *LUTJANUS* SPECIES: A REVIEW

*Zubia Masood and Rehana Yasmeen Farooq

Department of Zoology, University of Karachi, Karachi-75270, Pakistan.

*email: masoodzubia@gmail.com

ABSTRACT

The present study was based on the literature review of the fishes belonging to the snapper family Lutjanidae. Data parameters about the morphology and early life history pattern not measured during the survey were taken from the FishBase data base (see www.fishbase.org and Froese *et al.*, 2000). These data parameters included, **L_{max}** (maximum length), **L_{inf}** (length infinity); **K** (growth rate); **M** (natural mortality); **LS** (life span); **L_m** (length at maturity); **t_m** (age at first maturity); **t₀** (age at zero length); **t_{max}** (longevity) and also the morphological data. Morphological and life history data were taken only for five species of fishes belongs to genus *Lutjanus* i.e., *L.johnii*, *L.malabaricus*, *L.lutjanus*, *L.fulvus*, *L.russellii*. The main objective of this study was to review some aspects of distribution, morphology and feeding habits, spawning and also acquired and analyze information on selected life history variables to described patterns of variation among different species of snappers.

Keywords: Lutjanidae, morphology, life history.

INTRODUCTION

This family is commonly known as “Snappers” are perch-like fishes, moderately elongated, fairly compressed (Allen and Talbot, 1985). Small to large fishes, ranging from 15cm-120cm or 1m in length and 40 kg in weight. Mouth is terminal, jaw bear large canine teeth (no canines in Apherius); Preopercle usually serrate. Dorsal fin continuous or slightly notched with 10-12 spines and 10-17 soft rays; anal fin with 3 spines and 7-11 soft rays; pelvic fins originating just behind pectoral base. Pelvic fins with 1 spine and 5 soft rays. Body is covered with moderate to small ctenoid scales. Anterior part of head (snout and preopercle area) is without scales; some rows of scales are found on cheek and gill cover (Allen, 1985; Nelson, 1994). Snappers are often long-lived (< 11 years), slow growing fishes with low rates of natural mortality (Ralston, 1987).

METHODOLOGY

Seventy samples of the five species of genus *Lutjanus* were collected from the landing specimens on Karachi fish harbor during the period January 2007-December 2008. All specimens were preserved in 10% formalin solution for later examination. Information about morphology and life history were collected from literature.

RESULT AND DISCUSSION

1.1: Taxonomy and Description of fishes of family Lutjanidae:

This family is composed of 17 genera and 103 species of mostly reef associated marine fishes, several deep-water (>100m) species and three freshwater species.

The family Lutjanidae is divided in four subfamilies.

Sub family Lutjaninae is the largest subfamily with six genera included (*Hoplopagrus*, *Ocyurus*, and *Rhomboplites*) are monotypic genera, genera *Macolor* and *Pinjalo* with two species each, and the genus *Lutjanus* with 66 species (Nelson, 1994).

Sub family Paradicichthyinae with two monotypic genera *Symphorus* and *Symphorichthys*;

Sub family Etelinae with five genera (*Aphareus*, *Aprion*, *Etelis*, *Pristipoides* and *Rhandallichthys*) with 18 species.

Sub family Apsilinae with four genera (*Apsilus*, *Lipocheilus*, *Paracesio* and *Parapristipoides*) and 10 Species (Allen, 1985; Nelson, 1994).

Froese and Pauly (2000) reported 32 species of family *Lutjanidae* from Pakistan coast. Out of which, 19 species were only belongs to genus *Lutjanus*; which include: *Etelis carbunculus*, *E.coruscans*, *Liphochilus carnolabrum*, *Lutjanus argentimaculatus*, *L.bengalensis*, *L.bohar*, *L.ehrenbergii*, *L.erythropterus*, *L.fulviflamma*, *L.fulvus*, *L.gibbus*, *L.johnii*, *L.kashmira*, *L.lemniscatus*, *L.lutjanus*, *L.malabaricus*, *L.quinquelineatus*, *L.rivulatus*, *L.russellii*,

L.sanguineus, *L.sebae*, *Macolar niger*, *Paracaesio xanthura*, *Pinjalo pinjalo*, *Pristipomoides filamentosus*, *P.multidens*, *P.sieboldii*, *P.zonatus*, *Aphareus furcatus*, *A.rutilans*, *A.virescens*.

In Pakistan, common name of these fishes are “*Hira*” along the Sindh Coast and “*Kanulcha*” and “*Kunla*” along Makran Coast. Trawlers, gill-netters, Mechanized-cum-Sail Driven boats were used to caught these fishes. Currently, *Lutjanus argentimaculatus*, *L. johnii*, *L. russelli*, and *L. sebae* are successfully farmed in floating net cages in Pakistan, China, Singapore, Malaysia, Thailand, and the Philippines (Doi *et al.*, 1994; Emata, *et al.*, 1999, Hussain and Khaton, 2000).

1.2: Morphology:

1.2a: Colour is highly variable mainly from yellow through red to blue, often with blotches, lines or other patterns.

1.2b: Habitat and Distribution:

They are found in marine water, rarely found in estuaries. Many species are found in coral reef areas. A few species may even enter in rivers waters for feeding, especially in juvenile phase; others on soft bottom, in mangroves areas or in hyper saline lagoons. Snappers are occur in Arabian Sea, Chiku river, Coral sea, Great barrier reef, Gulf of Aden, Persian Gulf, Red Sea, South China Sea, Bay of Bengal, Tanshui River, Tsengwen River (Allen and Talbot, 1985).

1.2c: Depth:

These fishes are found at the depth ranging from 6m-450m depth (Blaber, 2000).

1.2d: Diet:

Most Snappers are large predators that occur in benthic habits and are usually active at night, feeding mainly on demersal organisms, including crustaceans and fishes, sometimes also cuttle fish and worms. Several are planktivores (e.g *Etelis* sp.). Most do well in aquaria, but grow too fast. Valued as food fish but sometimes a cause of ciguatera (Parrish, 1987).

The following species were collected from Karachi fish harbor, during survey (2007-2008). The diagnostic characters of each species are described below:

1.2e: *Lutjanus johnii*:

Allen (1985) reported it as “John's snapper”. Max. size is 97.0 cm TL. Dorsal spines (total): 10; Dorsal soft rays (total): 13 - 14; Anal spines: 3; Anal soft rays: 8. Dorsal profile of head steeply sloped. Preopercular notch and knob poorly developed. Scale rows on back parallel to lateral line. Center of each scale often with a reddish-brown spot, giving an overall appearance of series of horizontal lines on side of body. Generally yellow with a bronze to silvery sheen, shading to silvery white on belly and underside of the head. A large black blotch mainly above the lateral line below the anterior dorsal-fin rays. Adults probably frequent coral reef areas and shallow coastal water, oceanodromous; found at depth range? -80 m. Juveniles found in mangrove estuaries. Feeds on fishes and benthic invertebrates.

1.2f: *Lutjanus lutjanus*:

Allen (1985) reported it as “Big eye snapper”. Max. Size is 35.0 cm TL. Dorsal spines (total): 10 - 12; Dorsal soft rays (total): 12; Anal spines: 3; Anal soft rays: 8. Dorsal profile of head gently sloped. Preopercular notch and knob poorly developed. Scale rows on back rising obliquely above lateral line. Generally silvery white, with a broad yellow stripe running along the side from the eye to the caudal fin base. A series of faint narrow yellow horizontal lines is on the lower half of the body. The fins are pale yellow to whitish. Male is very much alike female. Inhabits offshore coral reefs and trawling grounds, found at depth range from 0 - 96 m. Feeds on bottom living fishes and crustaceans.

1.2g: *Lutjanus malabaricus*:

Allen (1985) reported it as “Malabar blood snapper”. Max. size is 100.0 cm TL. Dorsal spines (total): 11; Dorsal soft rays (total): 12 - 14; Anal spines: 3; Anal soft rays: 8 - 9. Dorsal profile of head steeply sloped. Preopercular notch and knob poorly developed. Scale rows on back rising obliquely above lateral line. Young with horizontal lines on sides. Inhabit both coastal and offshore reefs, found mostly at depth range 12 - 100 m. They tend to be associated with sponge and gorgonian-dominated habitats on the North West Shelf, and hard mud areas of the

Arafura Sea. Feed mainly on fishes, with small amounts of benthic crustaceans, cephalopods and other benthic invertebrates.

1.2h: *Lutjanus russellii*:

Allen (1985) reported it as "Russell's snapper". Max. size is 50.0 cm TL. Mostly they are reef-associated; brackish; marine; Dorsal spines (total): 10; Dorsal soft rays (total): 14; Anal spines: 3; Anal soft rays: 8. Dorsal profile of head steeply to moderately sloped. Preopercular notch and knob poorly developed. Scale rows on back rising obliquely above lateral line. Generally whitish or pink with silvery sheen, frequently brownish on the upper part of the head and back. A black spot which is sometimes faint is on the lateral line below the anterior portions of the soft dorsal fin. Juveniles from the western Pacific whitish with four black stripes on sides and with a round black spot on upper back. Male is very much alike female. Inhabit offshore coral reefs and also inshore rocky and coral reefs, found at depth range from 10 - 80 m, usually 20 - 50 m. Juveniles frequent mangrove estuaries and lower reaches of freshwater streams. Feed on benthic invertebrates and fishes.

Table 1. Summary of morphological characteristics of five snappers (Allen and Talbot, 1985).

Species Name	Body Shape		Dorsal head profile	Position of Mouth	No. of Lateral lines	No. of Scales on Lateral line
	Lateral	Cross section				
<i>Lutjanus malabaricus</i>	fusiform	Oval	clearly Concave	Terminal	1	47-50
<i>Lutjanus russellii</i>	fusiform	Oval	Straight	Terminal	1	47-50
<i>Lutjanus fulvus</i>	fusiform	Oval	Straight	Terminal	1	47-50
<i>Lutjanus johnii</i>	fusiform	Oval	steeply sloped	Terminal	1	47-50
<i>Lutjanus lutjanus</i>	fusiform	Oval	Convex	Terminal	1	48-50

Scales rows above the Lateral line	Gill Rakers		Dorsal fin spines		Anal fin spines		Pectoral fin		Pelvic fin	
	on lower limb	on upper limb	Spines	Soft rays.	Spines	Soft rays	Spines	Soft rays.	Spines	soft rays.
6-7 rows	12- 14	4-7	XI	12	III	9	0	16-17	I	5
6-7 rows	7-11	6-7	X	14	III	8	0	16-17	I	5
6-7 rows	10-13	6-7	X	13-14	III	8	0	16-17	I	5
6-7 rows	10-12	6-8	X	13-14	III	8	0	16-17	I	5
4-5 rows	17-19	6-8	X-XII	12	III	8	0	16-17	I	5

1.2 i: *Lutjanus fulvus*:

Allen (1985) reported it as "Blacktail snapper". Max. Size is 40.0 cm TL. Dorsal profile of head steeply sloped. Preopercular notch and knob well developed. Scale rows on back rising obliquely above lateral line. Generally tinged are Brownish to pale yellow-white. Scales with brownish to yellow margins. The caudal and dorsal fins are blackish with narrow white margins; the anal pectoral and pelvic fins are yellow. Striped when young. Both sexes are same. Inhabit lagoon and semi-protected seaward reefs. Benthopelagic. Juveniles sometimes found in shallow mangrove swamps and the lower parts of freshwater streams. Feed at night on fishes, shrimps, crabs, holothurians and cephalopods. Mostly they are found in reef-associated; freshwater; brackish; marine water; at depth range from 1 - 75 m.

The five *Lutjanus* species individual descriptions are followed by a summary of their morphological characters (Table 1) which should enable identification of most species found on Karachi Coast.

1.3: Life history:

1.3a: Spawning:

Spawning occurs at night near open water and its time is coinciding with spring tides at new and full moons. Lutjanids are higher fecund, with large females producing 5-7x1,000,000 ova (Grimes, 1987). Lutjanids are batch spawners with individual females generally spawning several times during the year. Batch and annual fecundities are highly variable with female size (Grimes, 1987; Parrish, 1987). During spawning season the same medium and larger species form large aggregations and migrate towards off- shore areas where they spawn near the surface.

1.3b: Eggs & Larvae:

Lutjanid eggs are pelagic, spherical in shape, with a diameter ranging from 0.65 to 1.02 mm, and usually contain a single oil droplet 0.12 – 0.20 mm in diameter (except in *L. erythropterus*, where no oil droplet is present) which provides buoyancy. Eggs are similar to most pelagic eggs, which makes them difficult to identify from plankton samples. Eggs hatch after 17 to 36 hours, depending on the species and incubation temperature, and the just- hatched larvae are also similar to the vast majority of larvae coming from pelagic eggs. Snapper eggs and/or newly hatched larvae are transported by surface currents to in-shore waters while they remain as part of the zooplankton. After larvae arrive in coastal waters, there is a marked difference in the habitat selected depending on the species. The juveniles of some species of the genus *Lutjanus* are found in estuaries while juveniles of other species, including also the genus *Lutjanus*, are found in coastal waters at depths ranging generally from 20 – 40 meters. Lu Suifen, (1981) gave the identification and description about the eggs of *L.lutjanus*. Lutjanids larvae are capture with the help of neuston type nets.

Lutjanids larvae were relatively easy to identify by using the characteristics in a given Table 2. Larvae of sub family Lutjaninae were identifying by using the following characters (Lies and Rennis, 1983):-

Table 2. Larval characteristics of sub family Lutjaninae.

Characters	Sub family Lutjaninae
Fin spines.	Smooth to coarsely serrate.
Length of second dorsal spine.	Moderately to very long.
Body shapes.	Moderately to very deep and strongly compressed.
Dorsal fins.	X-XII, 11-17 soft rays.
Anal fins.	III, 8-9 soft rays.
Tail pigment in preflexion larvae.	Ventral series of many melanophores.
Pigment present on the membrane of dorsal fin in preflexion larvae.	Yes or no
Supra ocular ridge serrate.	Yes
Formation of third anal spine.	Late.

Newly hatched lutjanids larvae measure less than 2 mm TL, have a large yolk sac, unpigmented eyes, no mouth and limited swimming abilities. The yolk sac reserves last for 3 – 4 days and by this time the eyes are pigmented and the mouth becomes functional. After a few more days, snapper larvae develop spines on the head and some have particularly long dorsal and pelvic fins what make them relatively easy to identify at this point. These spines reach a maximum length when larvae are about 7 – 8 mm SL and then decrease in relative size and remain only slightly elongated at settlement. Lutjanids larvae have 24 myomeres. Larvae of the subfamilies Lutjaninae and

Paradicichthyinae are most common in coastal waters while Apsilinae and Etelinae larvae are more common in offshore areas. The larval pelagic stage last for 25 – 47 days, when larvae are between 12 and 20 mm TL (Allen, 1985; Leis, 1987; Lindeman, *et al.*, 2001).

After settlement juveniles remain on nursery grounds usually for a period of 2 to 4 years, until they reach maturity, and then move to other areas joining the adult population. On average, lutjanids reach their maturity at about 43 to 51 % of the maximum total length, with males maturing at a slightly smaller size than females (Allen, 1985; Everson, *et al.*, 1989).

1.4: Sexual dimorphism:

Snappers are dioecious and gonochoristic organisms; this means that they have separate sexes and that the sexual differentiation remains constant throughout their life span. Sexual dimorphism in structure or color pattern is rare and only reported in two species (genus *Pristipomoides*) from the Indo-west Pacific Ocean. The ventral lobe of the caudal fin of female *Pristipomoides auricilla* from the Guam contains slight yellow traces. Large males with 270mm FL usually have a distinct yellow blotch on the ventral lobe of the caudal fin (Grimes, 1987). In family Lutjanidae, sexes remain fixed throughout life.

1.5: Life history data:

The present study analyzed through several methods the sources of life history variation among different species of snappers. Life history variables selected for study were given in table 3:

Table 3. Life history data for fishes of Family Lutjanidae (Froese *et al.*, 2000).

No. of obs.	Species names.	Lmax	Linf	K	M
1.	<i>L.malabaricus</i>	100 cm TL	96.9 cm TL	0.15/year	0.21-0.49/year
2.	<i>L.russellii</i>	50.0 cm TL	52.0 cm TL	0.31/year	0.4-0.92/year
3.	<i>L.fulvus</i>	40 cm TL	41.7 cm TL	0.38/year	0.48-1.1/year
4.	<i>L.johnii</i>	97 cm TL	72.4 cm TL	0.37/year	0.45-1.04/year
5.	<i>L.lutjanus</i>	35.0 cm TL	27.6 cm TL	0.53/year	0.76-1.75

Table Continued.....

LS (years)	Lm	tm (years)	to (year)	tmax
19.2	37.9-68.0 cm TL	4.1	0.82	19
9.2	21.7-38.9 cm TL	2.2	0.46	17
7.5	17.8-31.9 cm TL	1.8	0.4	4
7.8	29.2-52.4 cm TL	1.7	0.35	14
5.4	12.3-22.0 cm TL	1.4	0.31	4

To compare variations in life history data among the different species of snappers, it is observed that the smallest species (*L.lutjanus*) had 27.6 cm TL asymptotic length; medium species (*L.russellii*); large species (*L.malabaricus*) had 96.9 cm TL asymptotic length. Further comparison of these species indicated that larger species had low growth rate (0.15/year in *L.malabaricus*) than small species (0.53/year in *L.lutjanus*) and low mortality rate (0.21-0.49/year of *L.malabaricus* and 0.76-1.75/year of *L.lutjanus*). Large species matured later and at larger sizes (*L.malabaricus* had “tm” value 4.1 years and “Lm” value was 37.9-68.0 cm in TL) than the medium and small species (*L.lutjanus* had “tm” value 1.4 years and “Lm” value was 12.3-22.0 cm in TL); and had longer life spans (19.2 years in *L.malabaricus*) than small species (5.4 years in *L.lutjanus*).

Result of analysis of life history variables for the species of snappers in table 3 and comparison of correlations (r) between different life history variables indicating that size at which species mature (Lm) was depend upon maximum size (Lmax); moderate correlations occurred between mortality (M) and growth rates (K); age at maturity (tm) did not depend on Lm and Lmax or Life span (LS); the high correlations were also occurred between Lm (maturity length), Lmax (max. length) and Linf (Infinite length). Low correlations occurred between tmax (longevity) and tm (age at maturity) indicating that species of snappers mature at relatively constant age, regardless of the number of years they live or maximum size they reach. High correlation occurred between tmax (longevity) and life spans. Low correlations occurred between size variables (Linf, Lm, Lmax) and longevity (tmax) indicated that size is not depend upon life span, so small species could reach at long life spans.

1.6: Seasonality:

Based on larval abundance, two types of seasonal reproductive patterns are common to the family Lutjanidae; continental populations and species have restricted summer spawning season, whereas insular or year around populations and species associated with oceanic islands reproduce year around in a more or less continuous pattern with peak activity in the spring and fall (Allen, 1985; Grimes, 1987).

1.7: Economic importance and commercial landing:

They are of high commercial value. Their flesh is of delicate taste. Marketed mostly fresh, also dried salted. Some species have occasionally been reported to cause poisoning (ciguatera). Atlantic dog snapper contain toxin. They are caught mainly with bottom trawls, hand lines and traps (Allen and Talbot, 1985). *L. argentimaculatus*, *L. bohar*, *L. fulviflamma*, *L. sebae*, *L. fulvus*, *L. rivulatus*, are included in the list of dangerous fishes of Pakistan which cause ciguatera poisoning. *L. argentimaculatus*, *L. erythropterus*, *L. johnii*, *L. rivulatus*, *L. russellii*, *L. sebae*, included in the list of aquaculture species of Pakistan. *L. argentimaculatus*, *L. fulviflamma*, *L. erythropterus*, *L. johnii*, *L. erythropterus*, *L. lunulatus*, *L. lutjanus*, *L. malabaricus*, *L. sebae* are included in the list of commercially important marine fishes of Pakistan (Froese and Pauly, 2000). The catch of snappers recorded from Sindh coast, were about [In 1995: 3,123 metric tons, in 1996: 1,989 metric tons, in 1997: 2,342 metric tons, in 1998: 3,176 metric tons, in 1999: 3,112 metric tons, in 2000: 2,976 metric tons, in 2001: 2,709 metric tons, in 2002: 2,670 metric tons, in 2003: 2,190 metric tons]. The catch of Red snappers recorded from Sindh coast, were about [In 2004: 2260 metric tons, in 2005: 2169 metric tons, in 2006: 2009 metric tons, in 2007: 1890 metric tons, in 2008: 2111 metric tons], respectively. Total catch of species of family Lutjanidae are decreasing since 1999 to 2003.

The present paper can provide the useful information about the morphology and life history pattern of lutjanid fishes that could be helpful to the researchers in taxonomy and management of these fishes in the future.

REFERENCES

- Allen, G.R. (1985). FAO species catalogue 6. Snappers of the world. Annotated and illustrated catalogue of lutjanid species known to date. FAO fish. Synop. 6 (125). 208p.
- Allen, G.R., and F.H. Talbot (1985). Review of the snappers of the genus *Lutjanus* (Pices: Lutjanidae) from the Indo-Pacific, with the description of a new species. *Indo Pac. Fish.* 11: 1-87 (Bernice P. Bishop Mus., Honolulu).
- Anderson, W.D., Jr. (1981). A new species of Indo-West Pacific *Etelis* (Pisces, Lutjanidae), with comments on other species of the genus. *Copeia*, (4): 820-825.
- Blaber, S. J. M. (2000). *Tropical estuarine fishes*. Ecology, Exploitation and conservation. Blackwell sciences, USA, 372pp.
- Doi, M., H. Kohno and T. Singhagraiwan (1994). Morphological development of eggs, larvae and juveniles of the red snapper, *Lutjanus argentimaculatus* (Pisces: Lutjanidae). *Journal of the Tokyo University of Fisheries*, 81(2):165.
- Emata, A.C., J.P. Damaso and B.E. Eullaran (1999). Growth, maturity and induced spawning of mangrove red snapper, *Lutjanus argentimaculatus*, broodstock reared in concrete tanks. *Israeli Journal of Aquaculture*, 51(2):58-64.
- Everson, A.R., H.A. Williams and B.M. Ito (1989). Maturation and reproduction in two Hawaiian eteline snappers, Uku, *Aprion virecens*, and Onaga, *Etelis coruscans*. *Fish. Bull.* 87: 877-888.
- Froese, R and D. Pauly. (2000). FishBase 2000: *Concepts design and data sources*. Los Baflos and Laguna, Manila, Philippines. ICLARM. 344pp.
- Froese, R., M.L.D. Palomares and D. Pauly (2000). Estimation of Life-History Key Facts. In: *FishBase 2000: concepts design and data sources* (R. Froese and D. Pauly eds.). Manila, Philippines, ICLARM, p. 167-175.
- Grimes, C. B. (1987). Reproductive Biology of Lutjanidae. 239-294pp. In: *Tropical snappers and groupers. Biology and Fisheries Management*. (J.J.Polovina and S. Ralston eds.). West view Press. Boulder and London.
- Hussain, S.M. and Z. Khatoon (2000). Preliminary Studies on Cage Culture of *Lutjanus johnii* (Snapper) and *Pomadysys kaakan* (Grunt) Marine Fishes. *Pakistan Journal of Zoology*, 32(1): 85-91.
- Lies, J.M., and D.S. Rennis (1983). The larvae of the Indo-Pacific coral reef fishes. New South Wales University Press, Sydney, and University of Hawaii Press, Honolulu, 269pp.
- Lies, J.M. (1987). Review of the early life history of tropical groupers (Serranidae) and snappers (Lutjanidae). 189-237pp. In: *Tropical snappers and groupers. Biology and Fisheries Management*. (J.J.Polovina and S. Ralston eds.). West view Press. Boulder and London.

- Lindeman, K.C., T.N.Lee, W.D.Wilson, R. Claro and J.S. Ault (2001). Transport of larvae originating in southwest Cuba and the Dry Tortugas: Evidence for partial retention in grunts and snappers. *Proceedings of the Gulf and Caribbean Fisheries Institute*, 52: 732-747.
- Lu Suifen (1981). Observations on the fish eggs and larvae on the black striped snapper. *Lutjanus vitta* (Quoy et Gaimard). [In Chin., Engl. Abstr.] *Trans. Chin. Ichthyol. Soc.* 1:49-56.
- Nelson, J. S. (1994). *Fishes of the world*. John Wiley and Sons, Inc. New York. 3rd edition. 600 pp.
- Parrish, J.D. (1987). The Tropic Biology of Snappers and Groupers. 405-464pp. In: *Tropical snappers and groupers. Biology and Fisheries Management*. (J.J.Polovina and S. Ralston eds.) . West view Press. Boulder and London.
- Ralston, S. (1987). Mortality rates of Snappers and Groupers. 375-404pp In: *Tropical snappers and groupers. Biology and Fisheries Management*. (J.J.Polovina and S. Ralston eds.). West view Press. Boulder and London.

(Accepted for publication November 2010)