

BIOLOGY, EXPLOITATION AND MANAGEMENT OF GROUPERS (SERRANIDAE, EPINEPHELINAE, EPINEPHELINI) AND SNAPPERS (LUTJANIDAE, LUTJANINAE, *Lutjanus*) IN THE GULF OF MEXICO

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INTRODUCTION

Groupers and snappers are reef fish of great commercial and recreational importance along the southeast coast of the U.S.A., Mexico, Bermuda, and in the Gulf of Mexico and the Caribbean Sea (Sadovy 1994). The Serranidae family includes 449 species in 62 genera and three sub-families (Serraninae, Anthiinae and Epinephelinae) (Nelson 1994). There are five tribes in the sub-family Epinephelinae, of which the Epinephelini tribe includes all the species known under the general term “groupers.” This tribe is comprised of 164 species that are classified into 14 genera (Nelson 1994). In the western Atlantic, along the American coast, there are 25 species of groupers belonging to the following seven genera: *Alphesthes*, *Cephalopholis*, *Dermatolepis*, *Epinephelus*, *Gonioplectrus*, *Mycteroperca* and *Paranthias* (Heemstra and Randall 1993). The Lutjanidae family, commonly known as snappers, consists of four sub-families (Lutjaninae, Paradicichthynae, Etelinae and Apsilinae), which include 17 genera and 103 species (Allen 1985). The American Atlantic coast is the second most important habitat in the world in terms of abundance of Lutjanidae genera (7) and species (19) (Druzhini 1970).

The Gulf of Mexico is one of the world’s 49 Large Marine Ecosystems (LME). These LME correspond to areas which are prone to growing tensions due to increased exploitation of renewable natural resources, damage to coastal zones, loss of habitat, and contamination (Sherman 1994). The Gulf of Mexico is characterized by its wide continental shelf, which represents 30% of the total area of the region and reaches 220 km width opposite the Louisiana coast, and 290 km opposite the southwestern coast of Florida and the north of the Yucatán Peninsula (Rabalais *et al.* 1999). These big extensions of continental shelf located both in the north and south of the Gulf represent the main commercial exploitation zones for groupers and snappers (Stevenson 1981).

Groupers and snappers share some biological characteristics that make them particularly vulnerable to human exploitation (Manooch 1987; Ralston 1987). The significant lack of biological knowledge about these species, the characteristics of the exploited stocks and the levels of exploitation, prevent the selection of the best management strategy for these resources (Sadovy 1994). The goal of this study is to synthesize the available information about the biology of the species of groupers and snappers in the Gulf of Mexico, as well as to analyze the most relevant aspects of their exploitation and management in this region.

THE SPECIES

In the Gulf of Mexico there are 23 species of groupers that belong to the seven genera of Tribe Epinephelini observed in the western Atlantic (Smith 1961, 1971, 1997; Bullock and Smith 1991; Heemstra and Randall 1993; Hoese and Moore 1998). The most important genus in terms of number of species present is *Epinephelus* (10), followed by the genera *Mycteroperca* (7), *Cephalopholis* (2), and *Alphesthes*, *Dermatolepis*, *Gonioplectrus* and *Paranthias* (with one species each) (Table 8.1).

Table 8.1. Groupers and snappers of the Gulf of Mexico: Species distribution and habitat. Sources: Smith 1961, 1971, 1997; Druzhini 1970; Fischer 1978; Allen 1985, 1987; Bannerot et al. 1987; Bullock and Smith 1991; Heemstra and Randall 1993; Colás-Marrufo et al. 1998; Hoese and Moore 1998; IUCN 2002; Musick et al. 2000.

Species <sup>1</sup>	Author	Common Names <sup>2</sup>		Distribution		Habitat <sup>5</sup>
		English	Spanish	Geographic <sup>3</sup>	Bathymetric (m)	
Serranidae (N=23)						
<i>Alphestes afer</i>	Bloch 1793	Mutton hamlet	Guaseta	E (SF)	—	CR;SG
<i>Cephalopholis cruentata</i> <sup>ES</sup>	Lacepede 1802	Graysby	Cherna enjambe	WG	< 170	CR;SG
<i>C. fulva</i> <sup>ES</sup>	Linnaeus 1758	Coney	Cherna cabrilla	WG	< 150	CR;CS
<i>Dermatolepis inermis</i> <sup>TS</sup>	Valenciennes	Marbled grouper	Mero marmol	WG	21–213	—
<i>Epinephelus adscensionis</i> <sup>ES</sup>	Osbeck 1765	Rock hind	Mero cabrilla	WG	< 100	CR; RR
<i>E. drummondhayi</i> <sup>ES, TS</sup>	Goode & Bean	Speckled hind	Mero pintaroja	N, E and S	25-183	RB
<i>E. flavolimbatus</i> <sup>ES, TS</sup>	Poey 1865	Yellowedge	Mero aleta amarilla	WG	64-275	RB; SB; MB
<i>E. guttatus</i> <sup>ES</sup>	Linnaeus 1758	Red hind	Mero colorado	WG	< 100	CR; RB
<i>E. itajara</i> <sup>ES, TS</sup>	Lichtenstein 1822	Jewfish	Mero guasa	WG	< 50	CR; M and E (j)
<i>E. morio</i> <sup>ES</sup>	Valenciennes	Red grouper	Mero americano	WG	< 150	RR; HB; SB; MB;
<i>E. mystacinus</i> <sup>ES</sup>	Poey 1852	Misty grouper	Mero listado	WG	100-400	
<i>E. nigritus</i> <sup>ES, TS</sup>	Holbrook 1855	Warsaw grouper	Mero negro	N, E and S	55-525	HB; SB
<i>E. niveatus</i> <sup>ES, TS</sup>	Valenciennes	Snowy grouper	Cherna pintada	WG	30-525	RB
<i>E. striatus</i> <sup>ES, TS</sup>	Bloch 1792	Nassau grouper	Cherna criolla	E (F) and S	< 90	RB
<i>Gonioplectrus hispanus</i>	Cuvier 1828	Spanish flag	Bandera espanol	WG	60-365	CR; HB; SG (j)
<i>Mycteroperca acutirostris</i>	Valenciennes	Comb grouper	Cuna negra	N and W	—	RB
<i>M. bonaci</i> <sup>ES, TS</sup>	Poey 1860	Black grouper	Cuna bonaci	N, E and S	10-30	RB; SG, M and
<i>M. interstitialis</i> <sup>ES, TS</sup>	Poey 1860	Yellow mouth	Cuna amarilla	E, W and S	20-150	CR; RB
<i>M. microlepis</i> <sup>ES, TS</sup>	Goode & Bean	Gag	Cuna aguají	WG	40-100	RB; SG and E (j)
<i>M. phenax</i> <sup>ES, TS</sup>	Jordan & Swain	Scamp	Cuna garopa	WG	70-100	RB; CR
<i>M. tigris</i> <sup>ES</sup>	Valenciennes	Tiger grouper	Cuna gata	E (SF), W and	10-40	CR; RB
<i>M. venenosa</i> <sup>ES</sup>	Linnaeus 1758	Yellowfin	Cuna de piedra	E (SF) and S	2-137	CR; RR; MB ; SG
<i>Paranthias furcifer</i>	Valenciennes	Creole-fish	Cuna lucero	WG	6-64	CR ; HB

Table 8.1. Continued

Lutjanidae (N=11)						
<i>Lutjanus ambiguus</i>	Poey 1860	Ambiguous	Pargo ambiguo	E (SF)	---	DR
<i>L. analis</i> <sup>ES, TS</sup>	Cuvier 1828	Mutton snapper	Pargo criollo	N, E and S	---	SG; M; E; CR
<i>L. apodus</i> <sup>ES</sup>	Walbaum 1792	Schoolmaster	Pargo amarillo	N, E and S	SW <sup>4</sup>	CR; SG; M
<i>L. buccanella</i> <sup>ES</sup>	Cuvier 1828	Blackfin snapper	Pargo sesí	WG	80-150	SB; RB
<i>L. campechanus</i> <sup>ES</sup>	Poey 1860	Red snapper	Pargo del Golfo	WG	10-190	RB; SB and MB y
<i>L. cyanopterus</i> <sup>ES, TS</sup>	Cuvier 1828	Cubera snapper	Pargo cubera	WG	< 40	CR; RB; M (j)
<i>L. griseus</i> <sup>ES</sup>	Linnaeus 1758	Grey snapper	Pargo prieto	WG	< 180	CR; RB; E; M
<i>L. jocu</i> <sup>ES</sup>	Bloch &	Dog snapper	Pargo jocú	N, E and S	---	CR; E (j)
<i>L. mahogoni</i>	Cuvier 1868	Mahogany	Pargo ojón	WG	SW <sup>4</sup>	RB; CR; SG
<i>L. synagris</i> <sup>ES</sup>	Linnaeus 1758	Lane snapper	Pargo biajaiba	WG	<400	CR; SG
<i>L. vivanus</i> <sup>ES</sup>	Cuvier 1828	Silk snapper	Pargo de lo alto	WG	90-200	SSc,i

<sup>1</sup>ES - commercially exploited species through fisheries. TS = threatened species

<sup>2</sup>According to FAO

<sup>3</sup>E -eastern Gulf, F - Florida, N - northern Gulf, W - western Gulf, YP - Yucatan Peninsula, S - southern Gulf, SF - southern Florida, WG - whole Gulf

<sup>4</sup>SW - shallow waters

<sup>5</sup>CR - coral reef, DR - deep reef, RR - rocky reef, CS - coastal shelf, E - estuary, SB - sandy bottom, HB - hard bottom, MB - muddy bottom, RB - rocky bottom, j - juvenile, M - mangrove, SG - seagrass, SSc,i - Continental and island shelf slope

Eleven snapper species of the genus *Lutjanus*, including the sub family Lutjaninae, occur in the Gulf of Mexico (Druzhini 1970; Allen 1985, 1987; Smith 1997; Hoese and Moore 1998) (Table 8.1).

## DISTRIBUTION AND HABITAT

With a few exceptions groupers and snappers are marine fish restricted to the tropical and subtropical zones of the oceans (Allen 1985; Heemstra and Randall 1993). Their worldwide geographic distribution generally coincides with that of coral reefs (Smith 1961; Druzhini 1970). The northern and southern distribution limits for groupers and snappers registered in the Gulf of Mexico are the coasts of Massachusetts, North Carolina and southern Florida in the USA, and the coasts of Venezuela and Brazil, respectively (Smith 1961, 1971, 1997; Fischer 1978; Allen 1985; Bullock and Smith 1991; Heemstra and Randall 1993; Hoese and Moore 1998). Only four grouper species of the Gulf occur outside the western Atlantic. *Epinephelus adscensionis* has also been reported in the eastern Atlantic (Ascension and St. Helen Island); *E. itajara* in the eastern Atlantic (Senegal, Congo and the Canary Islands) and eastern Pacific (from the Gulf of California to the coast of Peru); *E. mystacinus* in the eastern Pacific (Galapagos Islands), and *Paranthias furcifer* in the eastern Atlantic (Ascension Island and Gulf of Guinea) (Heemstra and Randall 1993).

With the exception of *Alphestes afer* and *Lutjanus ambiguus* which are observed only in the southern tip of Florida, and of *Mycteroperca acutirostris*, present exclusively in the northwestern Gulf, all other identified species (21 groupers and 10 snappers) are distributed along the whole coast of the Gulf of Mexico, from the Florida Keys in the USA to Cabo Catoche in the easternmost part of the Yucatán Peninsula in Mexico (Table 8.1).

Groupers and snappers are demersal fish generally associated with coral or rocky hard bottoms (Table 8.1). However, some groupers, such as *Epinephelus flavolimbatus* can also be found on sandy or muddy bottoms (Jones *et al.* 1989), and some snappers, such as *Lutjanus analis*, *L. apodus*, *L. cyanopterus* and *L. griseus* can live in coastal mangroves (Druzhini 1970). The majority of the species live in depths of less than 100 m, whereas some are found at up to 200 m or 400-500 m (*E. nigritus*, *E. niveatus* and *L. synagris*). The juveniles of many species of groupers are distributed in shallow coastal waters (Rivas 1979; Thompson and Munro 1978, 1983). The juveniles of *E. morio*, *Mycteroperca bonaci* and *M. microlepis* have been observed on rocky bottoms and in seagrass beds (Longley and Hildebrand 1941; Moe 1969; Smith 1971; Renan *et al.* 2003), and *E. itajara* has been observed in mangroves (Bullock and Smith 1991; Bullock *et al.* 1992). In the northern Gulf of Mexico the juveniles of *M. microlepis* are distributed in estuaries, on seagrass beds of *Zostera marina* or *Halodule wrightii*, and even on oyster reefs (Schirripa and Goodyear 1994). Frequently the young snapper are also found in shallow coastal waters, on sandy or muddy floors (*L. campechanus*), in mangroves (*L. cyanopterus*) and in estuaries, including downriver areas of some streams (*L. jocu* and *L. griseus*).

## BIOLOGY

### REPRODUCTION

To this date there is no information on the reproductive biology of all species of groupers and snappers. In the case of the Gulf of Mexico no information is available on the reproductive biology of *A. afer*, *Dermatolepis inermis*, *Cephalopholis fulva*, *Epinephelus mystacinus*, *E. nigrilus*, *E. striatus*, *Gonioplectrus hispanus*, *Mycteroperca acutirostris* and *M. tigris* (39% of the groupers in the Gulf), as well as *L. ambiguus*, *L. analis*, *L. apodus*, *L. buccanella*, *L. cyanopterus*, *L. jocu*, *L. mahogoni*, *L. synagris* and *L. vivanus* (82% the snappers in the Gulf) (Table 8.2).

### SEX

Several species of groupers are protogynous hermaphrodites whilst gonochorism is the most common sexual pattern in all snapper species (Grimes 1987; Shapiro 1987; Sadovy 1996). Considering the criteria defined by Sadovy and Shapiro (1987) to characterize hermaphroditism in fish, 11 species of groupers in the Gulf of Mexico clearly exhibit protogynous hermaphroditism and one (*E. striatus*) is considered gonochoristic with the potential to develop protogynous hermaphroditism (Sadovy and Colin 1995). The available data snappers sexual patterns is even scarcer. Based on histological studies of their gonads, *L. campechanus*, *L. griseus* and *L. synagris* were confirmed as gonochoristic species (Table 8.2).

### SEXUAL DIMORPHISM

In general the species of families Serranidae and Lutjanidae do not exhibit notable external sexual dimorphism. In the case of the western Atlantic snappers, no morphologic characteristic or color pattern related with sex can be observed (Thresher 1984; Grimes 1987). However, pigmentation differences have been reported in the body (*M. microlepis*) or on the fins (*M. bonaci*) of some species of groupers, according to the sex of the individuals (Gilmore and Jones 1992; Collins *et al.* 1997; Crabtree and Bullock 1998; Brule *et al.* 2003). Different coloration patterns have also been observed for males and females of *Epinephelus guttatus*, *E. striatus* and *M. tigris* during the reproductive period, in particular during the courting and spawning phases (Colin *et al.* 1987; Bullock and Smith 1991; Colin 1992; Shapiro *et al.* 1993a, b; Sadovy *et al.* 1994).

### SIZE AT FIRST SEXUAL MATURITY

Similar to many other reef fish, groupers and snappers exhibit late sexual maturity (Coleman *et al.* 2000). Generally, species reach their first sexual maturity when their size is between 33 and 74% (groupers) and between 23 and 84% (snappers) of the maximum reported length for each species (Grimes 1987; Sadovy 1996).

The populations of groupers and snappers in the Gulf of Mexico reach their first sexual maturity at sizes that vary between 33-80% and 23-85%, respectively, of the maximum reported lengths for each of the species under study (Table 8.2). In the case of protogynous hermaphrodite fish, this minimum size at the first sexual maturity only occurs in the females. Thus, the female

Table 8.2. Sex (S), first sexual maturity, reproduction period, absolute fecundity and spawning aggregations of groupers and snappers from the Gulf of Mexico. Where information is not available for the Gulf, some results are given for the northern Atlantic or the Caribbean.

Species	S <sup>1</sup>	Sexual Maturity <sup>(2)</sup>			Reproductive period		Fecundity <sup>(5)</sup>		Spawning Aggregation		Reference
		L <sub>min</sub> (mm)	L <sub>max</sub> (mm)	$\frac{L_{min}}{L_{max}}$ (%)	Month <sup>3</sup>	Region <sup>4</sup>	# oocytes (millions)	Region <sup>4</sup>	Type <sup>6</sup>	Region <sup>4</sup>	
<b>Serranidae</b>											
<i>Alphestes afer</i>	---	---	---	---	Dec	J	0.158-0.224	J	---	---	54
<i>Cephalopholis cruentata</i>	PH	165	305 SL	54	Jul-Aug	EG	0.263	J	---	---	9, 40, 44, 51
<i>C. fulva</i>	PH	145	275 FL	53	[Dec-Feb]	PR	0.067-0.282	J	---	---	44, 51, 54
<i>Epinephelus adscensionis</i>	---	275	375 SL	73	Jan-Jun	EG	0.761	EG	T, FM	---	9, 22, 31
<i>E. drummondhayi</i>	PH	560	770 TL	73	[Apr]	SG	---	---	---	PR	4
<i>E. flavolimbatus</i>	PH	(569)	1065 TL	---	Jan-Oct [May-Sep]	EG	---	---	---	---	11
<i>E. guttatus</i>	PH	305	381 SL	80	Apr, Jun-Aug	EG	0.097-0.526	J	T, FM, PS	---	22, 31, 48, 49, 51, 54
<i>E. itajara</i>	PH?	1250	2065 TL	61	Jun-Oct [Jul-Sep]	EG	38.9-56.6 <sup>(BF)</sup>	EG	T, FM	CS	9, 10, 22
<i>E. morio</i>	PH	260	790 SL	33	Dec-Jun [Apr-May]	EG	0.448-5.736	EG	---	EG	3, 20, 37, 55
		389	854 FL	46	Sep-Apr [Jan-Mar]	SG	0.024-2.322 <sup>(BF)</sup>	EG	---	---	
		381	980 TL	39	Feb-Jun [Mar-May]	EG					3, 20, 37, 55
<i>E. mystacinus</i>	---	---	---	---	Nov, Aug	J	---	---	---	---	54

Table 8.2. Continued

<i>E. niveatus</i>	PH?	379	1000 TL	38	Apr-Jul	EG	---	---	---	---	9, 31, 38
<i>E. striatus</i>	G/PH	425	730 SL	58	Dec-Feb	B	0.350-6.500	B	T, FM, GS	---	1, 14, 22, 45, 47
<i>M. bonaci</i>	PH	508	1310 TL	39	Jan-Dec [Dec-Mar]	EG	0.504	?	T?, FM?	CS EG	5, 21, 22, 24, 25, 51, 52
		580	1235 FL	47	Jan-Dec [Jan-Feb]	SG					
<i>M. interstitialis</i>	PH	420	747 TL	56	Jan-Dec [Apr-May]	EG	0.351-2.459 <sup>(BF)</sup>	EG	---	---	8, 9
<i>M. microlepis</i>	PH	450	1128 TL	40	Nov, Jan-Jul [Mar]	EG	0.656-1.46	EG	T, PS?	EG	6, 18, 22, 32, 33, 36
		490	1100 TL	45	Feb-Apr [Mar]	EG	0.011-0.865 <sup>(BF)</sup>	NEG			
		400	1150 SL	35	Feb-Apr [Mar]	EG					
		705	1100 FL	64	Oct-Apr [Jan-Mar]	SG					
<i>M. phenax</i>	PH	350	--- SL	---	Mar-May	EG	0.250-3.2 <sup>(BF)</sup>	NA	T	EG	9, 22, 30
		313	875 TL	36	Feb-Jul [Mar-May]	NA					
<i>M. tigris</i>	PH?	320	480 TL	67	Jan-Apr	PR	---	---	T, FM, PS		12, 22, 26, 46, 51
<i>M. venenosa</i>	PH	---	---	---	Mar, May- Aug	EG	1.995-2.875 <sup>(BF)</sup>	EG	T, FM	H, PR CS	9, 22, 25
		582	850 TL	69	Jan-Jun	C					
<i>Paranthias furcifer</i>	PH?	---	---	---	May-Sep	EG	0.177-0.640 <sup>(BF)</sup>	EG	---	---	9

Table 8.2. Continued

Lutjanidae											
<i>Lutjanus analis</i>	---	402	690 FL	58	Mar-Sep [Jun]	C	0.7-4.0	C	T, FM, GS?	EG	16, 22
<i>L. apodus</i>	---	♂250	570 FL	44	Feb-Jun, Aug-Nov	J	---	---	?	EG	29, 34, 39
		♀250	570 FL	44							
<i>L. buccanella</i>	---	♂260	490 FL	53	Feb-Nov [Apr, Sep]	J	0.67	C	---	---	29, 39, 42
		♀240	490 FL	49							
<i>L. campechanus</i>	G	334	941 FL	36	May-Nov [Aug-Sep]	EG	0.000013-3.4 <sup>(BF)</sup>	NEG	?	NEG, GE	2, 7, 17, 19, 28, 34, 56
		♂185	800 FL	23	Jan-Dec [Apr-Sep]	SG			?		
		♀189	818 FL	23							
		♂238	859 TL	28	Jan-Dec [May, Aug- Sep]	SG					
		♀245	833 TL	29							
<i>L. cyanopterus</i>	---	---	---	---	Jun-Aug	C	---	---	T?, FM	EG	22, 41
<i>L. griseus</i>	G	♂185	489 SL	38	Jun-Sep	EG	0.5	EG	T?, NM, GS?	EG	22, 23, 53
		♀195	489 SL	40							
		♂182	--- SL	---	[Jul-Aug]	EG					
		♀198	--- SL	---							
<i>L. jocu</i>	---	323	720 FL	45	Mar, Nov	J	1.28-8.46	C	?	EG, B	13, 22, 26, 29, 34, 39
									T, FM, GS?		



Table 8.2. Continued

<i>L. mahogoni</i>	---	---	---	---	May-Jul	C	---	---	---	---	41
<i>L. synagris</i>	G	♂85	275 FL	31	Mar-Sep [May]	C	0.099-1.1	C	?	EG, C	15, 22, 34, 35, 43
		♀85	310 FL	27					GS		
<i>L. vivanus</i>	---	♂525	720 FL	73	Jan-Dec (Mar)	T, J	0.009-0.299	VI	---		27, 50
					Mar-Nov [Mar, Sep]						
		♀575	680 FL	85							

<sup>1</sup> PH-protogynous hermaphroditism; G-gonochorism.

<sup>2</sup>  $L_{min}$  - minimum length at first sexual maturity,  $L_{max}$  - maximum length reached by the organisms, SL - standard length, FL - furcal length, TL -total length.

<sup>3</sup> Months during which females exhibit vitellogenic oocytes in their ovaries; [ ]-months during which higher frequency of females with vitellogenic or hyaline oocytes or and/or postovulatory follicles in their ovaries (spawning peak) were observed.

<sup>4</sup> NA - North Atlantic, B - Belize, C - Cuba, CS - Caribbean Sea, EG - Eastern Gulf, NEG - Northeastern Gulf, SG-Southern Gulf, J-Jamaica, PR-Puerto Rico.

<sup>5</sup> BF – batch fecundity.

<sup>6</sup> GS - group spawning, PS - spawning in pairs, FM - full moon, T - transitory.

References:

1-Aguilar-Perrera and Aguilar-Dávila (1996); 2-Bradley and Brian (1975); 3-Brulé *et al.* (1999); 4-Brulé *et al.* (2000); 5-Brulé *et al.* (2003b); 6-Brulé *et al.* (2003a); 7-Brulé *et al.* (2004); 8-Bullock and Murphy (1994); 9-Bullock and Smith (1991); 10-Bullock *et al.* (1992); 11-Bullock *et al.* (1996); 12- Byron *et al.* (2002); 13-Carter and Perrine (1994); 14-Carter *et al.* (1994); 15-Claro (1982); 16-Claro in García-Cagide *et al.* (2001); 17-Collins *et al.* (1996); 18-Collins *et al.* (1997); 19-Collins *et al.* (2001); 20-Collins *et al.* (2002); 21-Crabtree and Bullock (1998); 22-Domeier and Colin (1997); 23-Domeier *et al.* (1996); 24-Eklund *et al.* (2000); 25- García-Cagide and García (1996); 26-García-Cagide *et al.* (2001); 27-Gómez *et al.* (1996); 28-González y de la Rosa and Ré-Regis (2001); 29-Grimes (1987); 30-Harris *et al.* (2002); 31-Heemstra and Randall (1993); 32-Hood and Schlieder (1992); 33-Koenig *et al.* (1996); 34-Linderman *et al.* (2000); 35-Manickchand-Dass (1987); 36-McErlean and Smith (1964); 37-Moe (1969); 38-Moore and Labisky (1984); 39-Munro *et al.* (1973); 40-Nagelkerke in Heemstra and Randall (1993); 41-Naranjo in García-Cagide *et al.* (2001); 42-Pozo *et al.* in García-Cagide *et al.* (2001); 43-Rodríguez-Pino in García-Cagide *et al.* (2001); 44-Sadovy (1996); 45-Sadovy and Colin (1995); 46-Sadovy and Domeier (1994); 47 Sadovy and Eklund (1999); 48-Sadovy *et al.* (1992); 49-Shapiro *et al.* (1993a, b); 50- Silvestre *et al.* in Grimes (1987); 51-Smith (1959); 52-Smith (1961); 53-Starck and Schroeder (1970); 54-Thompson and Munro (1978); 55- Valdés and Padrón (1980); 56-Woods *et al.* (2003).

populations of *E. morio*, *M. bonaci* and *M. microlepis* of the Campeche Bank reach sexual maturity when their length is 46%, 47% and 64%, of their respective maximum sizes (Brule *et al.* 1999, 2003a, b). Males reach sexual maturity at the size that follows the process of sex reversion in the females. Shapiro (1987) observed that sex reversal in groups usually occurs in individuals that have between 33 and 100% of the maximum size exhibited by each species. For example, the sex reversal of populations of *E. morio*, *M. bonaci* and *M. Microlepis* of the Bank of Campeche can occur in organisms whose size oscillates, respectively, between 52%, 29% and 14% of the maximum reported size for each species. According to Shapiro (1987) the analysis of this data suggests that size (or age) of groupers is not a determining factor for the sex change of the organisms, which is more likely controlled by social factors that are intrinsic to the populations.

## REPRODUCTIVE PERIOD

According to Sadovy (1996) the reproduction period of groupers is restricted, whilst snappers are characterized by longer spawning periods.

The majority of groupers under study in the Gulf of Mexico exhibit reproduction periods that do not last more than 8 months of the year, except in the case of populations of *E. flavolimbatus*, *M. bonaci* and *M. interstitialis*, for which sexually active females (with vitellogenic oocytes present in the ovaries) are observed for 10 or 12 months of the year (Table 8.2). However, the spawning peaks for all the studied species in this region (months when the highest frequencies of vitellogenic or hyaline oocytes or and/or postovulatory follicles were observed in the ovaries) do not go beyond five months per year. For *L. campechanus* and *L. griseus*, the only species of snapper studied in the Gulf, active females were observed during 4 to 12 months of the year, and spawning peaks occurred for two to six months of the year (Table 8.2).

In the Gulf groupers reproduce in the winter and the start of the spring (*E. adscensionis*, *E. morio*, *M. bonaci* and *M. microlepis*), during the spring and the start of the summer (*E. drummondhayi*, *E. flavolimbatus*, *E. guttatus*, *E. niveatus*, *M. interstitialis*, *M. phenax*, *M. venenosa* and *P. furcifer*); or during the summer (*Cephalopholis cruentata* and *E. itajara*). In the case of the snappers in the Gulf, *L. griseus* reproduce during the spring and summer, and *L. campechanus*, during the spring and autumn (Table 8.2). Populations of a same species can present temporally out of phase reproduction periods according to their spatial distribution in the Gulf. *Epinephelus morio* and *M. microlepis* reproduce earlier in the year (January-March) in the southern region of the Gulf relative to the eastern region (March-May) (Moe 1969; Hood and Schlieder 1992; Koenig *et al.* 1996; Collins *et al.* 1997, 2002; Brule *et al.* 1999, 2004). The snapper *L. campechanus*, on the other hand, has two spawning peaks in the southern Gulf (one in spring and the other in summer-beginning of autumn) and only one spawning peak in the eastern Gulf (summer-beginning of autumn) (Futch and Bruger 1976; Brule *et al.* 2004).

## FECUNDITY

Fecundity is an essential parameter for estimating the reproductive potential of a species and for the evaluation of exploited stocks. Groupers and snappers are characterized by their capacity of producing a large number of oocytes, up to several million per female per year (Grimes 1987; Shapiro 1987; Sadovy 1996).

Fecundity values obtained for the species of the Gulf are very variable. They fluctuate between 11,000 (*M. microlepis*; 740 mm total length) and  $65.6 \times 10^6$  (*E. itajara*; 1,397 mm standard length) oocytes for groupers, and between 13 (*L. campechanus*; 417 mm total length) and  $8.5 \times 10^6$  (*L. jocu*) oocytes for snappers (Bullock and Smith 1991; Collins *et al.* 1997, 2001; Garcia-Cagide *et al.* 2001) (Table 8.2). These fluctuations can be caused by natural fecundity variations generally observed in fish at both inter- and intra-specific levels (fluctuations related to the size of the organisms and/or the year of the survey). The lack of a standardized method to estimate this parameter makes it difficult to perform a comparative study between surveys. However, based on an estimation of the fecundity by group and using the method hyaline oocytes and postovulatory follicles counts, some authors calculated the average spawning frequency of females of *E. morio* (26 per year), *M. microlepis* (8-27 per year), *M. phenax* (42 per year) and *L. campechanus* (21-35 per year), and thus estimated the potential annual fecundity of each of these species: between 613,000 and  $17 \times 10^6$  for *E. morio*; between 65,000 and  $61.4 \times 10^6$  for *M. microlepis* (700-1,065 mm total length); between  $1.3 \times 10^6$  and  $10.5 \times 10^6$  for *M. phenax* (445-712 mm total length); and, between 12,000 and  $59.7 \times 10^6$  for *L. campechanus* (349-820 mm total length) (Collins *et al.* 1996, 1997, 2002; Harris *et al.* 2002).

## SPAWNING AGGREGATIONS

During the reproductive period groupers and snappers release their gametes at the location the adults inhabit or in specific spawning areas after a migration. Generally, the larger species are the ones that migrate further for reproductive purposes, form spawning aggregations sometimes comprised of up to hundreds or thousands of individuals, during several days, in well defined geographic areas and periods of the year (Sadovy 1996).

Of the 14 species of groupers studied to date, nine form spawning aggregations in the western Atlantic (Table 8.2). Some aggregation sites in the Gulf of Mexico are located in its eastern part for four species: *E. itajara* in the southeast coast of Florida; *M. bonaci* in the Florida Keys (Florida Keys National Marine Sanctuary); *M. microlepis* and *M. phenax* in the northwestern coast of Florida (Florida Middle Ground). These aggregations are transient; they can occur during full moon (*E. itajara*; *M. bonaci*); they can form during winter for *M. Bonaci*, winter and spring for *M. microlepis* and *M. phenax*, or summer for *E. itajara*, and can lead to the formation of couples at the moment of spawning (*M. microlepis*) (Colin 1994; Coleman *et al.* 1996; Domeier and Colin, 1997; Eklund *et al.* 2000). For the southern part of the Gulf, Colas-Marrufo *et al.* (2002) and Tuz-Sulub *et al.* (2003) presented the first indications of the formation of probable spawning aggregations of *E. guttatus*, *M. bonaci*, *M. tigris* and *M. venenosa* in two areas of the Campeche Bank. Of the 11 studied snapper species, seven form spawning aggregations in the Gulf of Mexico (Table 8.2). Aggregation sites have been observed in the Florida Keys (Dry Tortugas and/or Key West) for *L. analis*, *L. apodus*, *L. cyanopterus*, *L. griseus*, *L. jocu* and *L. synagris*, and in northern Florida for *L. campechanus*. These aggregations are transient (*L. analis*, *L. cyanopterus* and *L. griseus*); they can occur during full moon (*L. analis* and *L. cyanopterus*) or new moon (*L. griseus*); they can form during spring and summer (*L. analis*, *L. apodus*, *L. cyanopterus* and *L. synagris*), or during summer (*L. griseus* and *L. jocu*), and can lead to the formation of spawning groups (*L. analis* and *L. griseus*) (Domeier *et al.* 1996; Domeier and Colin 1997; Lindeman *et al.* 2000).

## EMBRYOLOGICAL AND LARVAL DEVELOPMENT

The available taxonomic studies on eggs and larvae of groupers and snappers are still scarce and generally incomplete for the majority of the analyzed species. The embryological and larval development of *E. adscensionis*, *E. drummondhayi*, *E. flavolimbatus*, *M. acutirostris*, *M. interstitialis*, *M. tigris* and *M. venenosa* (30% of the groupers present in the Gulf) have still not been studied, neither have studies been carried out on *L. ambiguus*, *L. apodus*, *L. buccanella*, *L. cyanopterus*, *L. jocu*, *L. mahogoni* and *L. vivanus* (64% of the snappers present in the Gulf). In many cases, particularly for snappers, data on this subject was obtained through experimental laboratory cultures (Table 8.3).

### *Eggs*

Groupers and snappers produce pelagic eggs that measure between 0.6 and 1.0 mm in diameter and present only one drop of oil with a diameter between 0.12 and 0.26 mm. According to the species and incubation temperature (21-30°C), the embryological development period was longer for groupers (23 to 44.5 hours after fecundation) than snappers (17 to 27 hours after fecundation) (Table 8.3).

### *Larvae*

The larvae of groupers and snappers are distinguished from each other by several morphological characteristics such as the degree of development of the bones of the dorsal fin, the size and width of indentations and little bones on the dorsal fin bones, the shape of the bones on the head and even the pigmentation pattern. In each family, the identification of the larvae is relatively easy up to the sub-family level, but reaching the species level is more complicated (Leis 1987). However, several authors succeeded in identifying and distinguishing the larvae of 10 species of groupers (*A. afer*, *C. cruentata*, *C. fulva*, *D. inermis*, *E. itajara*, *E. mystacinus*, *E. nigritus*, *E. niveatus*, *G. hispanus* and *P. furcifer*) and one snapper (*L. campechanus*) from environmental samples (Presley 1970; Collins *et al.* 1979; Kendall and Fahay 1979; Kendall 1979, 1984; Johnson and Keener 1984). Other authors have been able to describe larval stages of *E. morio*, *E. striatus*, *M. microlepis*, *L. analis*, *L. campechanus*, *L. griseus* and *L. synagris*, obtained in laboratory through artificial propagation, incubation and experimental larval cultures (Guitart-Manday and Juarez-Fernandez 1966; Rabalais *et al.* 1980; Richards and Saksena 1980; Roberts and Schlieder 1983; Powell and Tucker 1992; Colin *et al.* 1996; Clarke *et al.* 1997). The metamorphosis or transformation of the larvae was obtained between 25 and 62 days after hatching (dah) for two species of groupers (*E. morio* and *E. striatus*) and between 16 and 38 dah for two species of snappers (*L. analis* and *L. synagris*) (Table 8.3).

It has been observed that groupers and snappers larvae are not abundant in plankton samples, but are distributed preferentially in continental shelf rather than oceanic zones (Leis 1987).

## AGE AND GROWTH

Groupers and snappers are long-lived fish with slow growth and low natural mortality rates. In general the maximum age of the species exceeds ten years and the observed growth coefficient (K) of their populations fluctuates between 0.10 and 0.25/year (Manooch 1987). No growth information is available for populations of *A. afer*, *C. cruentata*, *C. fulva*, *D. inermis*, *E.*

Table 8.3. Main characteristics of the eggs and larvae of groupers and snappers from the Gulf of Mexico.

Species	Type <sup>1</sup>	Diameter (mm) <sup>2</sup>	Egg Oil Drop		Incubation		Larvae	Metamorphosis		Ref. <sup>5</sup>
			No.	Diameter (mm)	Time <sup>3</sup> (haf)	Temp. (°C)	Length <sup>4</sup> (mm)	Time <sup>3</sup> (dah)	Length <sup>4</sup> (mm)	
Serranidae										
<i>Alphesthes afer</i>	—	—	—	—	—	—	10.5-19.5 SL (17)	—	27.0-62.0 SL (8)	11
<i>Cephalopholis cruentata</i>	—	—	—	—	—	—	5.2-20.5 SL (46)	—	—	11
<i>C. fulva</i>	—	—	—	—	—	—	5.5-25.2 SL (7)	—	—	11
<i>Dermatolepis inermis</i>	—	—	—	—	—	—	6.8-10.5 SL (5)	—	—	11
<i>Epinephelus guttatus</i>	—	0.94	—	—	—	—	—	—	—	24
	—	0.62 <sup>HO</sup>	1	0.13	—	—	—	—	—	9
<i>E. itajara</i>	—	—	—	—	—	—	6.2-17.4 SL (5)	—	—	11
<i>E. morio</i>	—	<1.0	1	—	—	—	—	—	20-25 SL	16
	P (32)	0.95	1	—	30	24	2.5-9.6 SL (25)	25-27	12.2-26.2 SL (4)	6 <sup>L</sup>
	—	0.9 <sup>HO</sup>	1	0.21	—	—	—	—	—	3
<i>E. mystacinus</i>	—	—	—	—	—	—	20 SL (19)	—	—	11
<i>E. nigritus</i>	—	—	—	—	—	—	9.1 SL (1)	—	—	11
<i>E. niveatus</i>	—	—	—	—	—	—	5.5-10.3 SL (16)	—	—	18
	—	—	—	—	—	—	—	—	23.5-31.3 SL (7)	11
	—	—	—	—	—	—	10.2 SL (1)	—	—	12

Table 8.3. Continued

<i>E. striatus</i>	P	1.02	1	0.22	40	25	2.0-2.8 TL	—	—	10 <sup>L</sup>
	P (32)	0.92-0.97	1	0.20-0.26	27-29	25	1.8-13.2 NL/S (33)	—	—	17 <sup>L</sup>
<i>Gonioplectrus hispanus</i>	—	—	—	—	—	—	3.6-29.8 NL	45-62	—	25 <sup>L</sup>
	—	—	—	—	—	—	13.4-14.0 SL (2)	—	—	11
	—	—	—	—	—	—	13.4 SL (1)	—	—	13
	—	—	—	—	—	—	—	—	—	—
<i>Mycteroperca bonaci</i>	—	0.8	—	—	—	—	—	—	—	27 <sup>L</sup>
	—	0.87 <sup>HO</sup>	1	0.23	—	—	—	—	—	20
<i>M. microlepis</i>	P	0.92	1	0.22	44.5	21	2.1 TL	—	—	22 <sup>L</sup>
	—	—	—	—	—	—	4.0-35.4 SL (28)	—	—	12
	—	0.90 <sup>HO</sup>	1	0.21	—	—	—	—	—	4
	—	—	—	—	—	—	—	—	—	14
<i>M. phenax</i>	—	0.95	—	—	—	—	7.6 SL (3)	—	—	11
<i>Paranthias furcifer</i>	—	—	—	—	—	—	8.6 SL (1)	—	—	12
	—	—	—	—	—	—	—	—	—	24 <sup>L</sup>
	—	0.95	—	—	—	—	—	—	—	—
Lutjanidae										
<i>Lutjanus analis</i>	—	—	—	—	—	—	2.2-9.8 SL (37)	16-28	10.2-14.6 SL (8)	5 <sup>L</sup>
	P	0.73-0.88	1	—	17	27.7	2.6-9.7 NL	30-38	16.2-22.2 SL	26 <sup>L</sup>
<i>L. campechanus</i>	—	0.8	—	—	—	—	—	—	—	1 <sup>L</sup>
	P	0.77-0.85	1	0.15-0.19	24-27	23-25	2.2-2.6 SL	—	—	19 <sup>L</sup>
	—	—	1	—	20	27	—	—	—	15 <sup>L</sup>

Table 8.3. Continued

<i>L. campechanus</i>	—	—	—	—	—	—	4-7.6 SL (18)	—	—	7
<i>L. griseus</i>	—	—	1	—	—	—	—	—	10 SL	23
	P	0.70-0.80	1	0.12-0.18	20	27	—	—	—	8 <sup>L</sup>
					18	28				
					17	30				
	—	—	—	—	—	—	2.7-9.6 NL/S (13)	—	—	21 <sup>L</sup>
<i>L. synagris</i>	P	0.65-0.80	1	0.13-0.20	23	26	1.9-2.6	—	—	2 <sup>L</sup>
	—	0.7-0.75	1	—	—	—	2.0-9.8 SL (41)	20-22	10.0-12.4 SL (3)	5 <sup>L</sup>

<sup>1</sup> P - pelagic; Salinity at which the eggs float in parenthesis

<sup>2</sup> HO - measurements done with unfertilized hyaline oocytes

<sup>3</sup> haf - hours after fecundation, dah - days after hatching

<sup>4</sup> SL - standard length, NL - notochordal length, NL/S - notochordal or standard length, TL - total length; number of analyzed larvae in parenthesis

<sup>5</sup> L - laboratory results.

References: 1-Arnold *et al.* (1978); 2-Borrero *et al.* in Leis (1987); 3-Brulé *et al.* (1999); 4-Brulé, unpublished data; 5-Clarke *et al.* (1997); 6-Colin *et al.* (1996); 7-Collins *et al.* (1908); 8-Damas *et al.* in Leis (1987); 9-Falfan-Vazquez (2003); 10-Guitart-Manday and Juarez-Fernandez (1966); 11-Johnson and Keener (1984); 12-Kendall (1979); 13-Kendall and Fahay (1979); 14-Koenig in Tucker (1998); 15-Minton *et al.* (1983); 16-Moe (1969); 17-Powell and Tucker (1992); 18-Presley (1970); 19-Rabalais *et al.* (1980); 20-Renan *et al.* (2001); 21-Richards and Saksena (1980); 22-Roberts and Schlieder (1983); 23-Starck (1971); 24-Tucker (1998); 25-Watanabe *et al.* (1996); 26-Watanabe *et al.* (1998); 27-White in Tucker (1998).

*drummondhayi*, *E. flavolimbatus*, *E. mystacinus*, *E. nigritus*, *E. striatus*, *G. hispanus*, *M. acutirostris*, *M. tigris* and *M. venenosa* (57% of the groupers), or *L. ambiguus*, *L. apodus*, *L. buccanella*, *L. cyanopterus*, *L. griseus*, *L. jocu*, *L. mahogoni* and *L. vivanus* (73% of the snappers) in the Gulf of Mexico (Table 8.4).

### Age

Age determination was carried out successfully for the majority of the species of the Gulf (18 groupers and 8 snappers), by identification of annual growth marks in the otolith (in 23 species), scales (3 species of snapper), urohyal (3 species) and mesopterygoid bones (1 species), or by modal progressions of length classes analysis (4 species) (Table 8.4).

The maximum observed ages for these fish were 41 years for the grouper *E. nigritus* (Manooch and Mason 1987) and 47 years for the snapper *L. campechanus* (Allman *et al.* 2002).

### Growth

The growth coefficient (K) for populations of the Gulf of Mexico fluctuated between 0.08 (*M. interstitialis*) and 0.20 (*E. guttatus*) in the case of groupers, and between 0.07 (*L. campechanus*) and 0.28 (*L. synagris*) for snappers (Table 8.4). According to Manooch (1987) these values indicate that species reach their maximum size slowly and the populations exhibit low rates of natural mortality. For several species the calculated asymptotic length values ( $L_{\infty}$ ) are above one meter: *E. itajara* with 2,006 mm total length (TL) (Bullock *et al.* 1992), *E. niveatus* with 1,320 mm TL (Moore and Labisky 1984), *M. bonaci* with 1,306 mm TL (Crabtree and Bullock 1998), *M. microlepis* with 1,180 mm TL (Hood and Schlieder 1992) and *L. campechanus* with 1,023 mm furcal length (Fischer 2002). The asymptotic weight values ( $P_{\infty}$ ), calculated through  $L_{\infty}$  values and the length-weight equations ( $W = aL^b$ ) of the species, reached maximum values of 166 kg total weight (TW) in the case of the grouper *E. itajara* (Bullock *et al.* 1992) and 12 kg tw in the case of the snapper *L. campechanus* (Fischer 2002).

### FEEDING

Groupers and snappers are opportunistic carnivores characterized by a diet comprised predominantly of fish and crustaceans. According to their depth distribution intervals these species can feed from zones of shallow water to depths of 400 to 500 m. (Randall 1967; Parrish 1987). Most species capture a large part of their prey on or near the substrate. Groupers are characterized for being more sedentary than snappers and for ambushing their prey (Parrish 1987). The feeding habits of some grouper and snapper populations in the Gulf are still unknown, including *A. afer*, *C. cruentata*, *C. fulva*, *D. inermis*, *E. striatus*, *G. hispanus*, *M. acutirostris*, *M. tigris* and *M. venenosa* (39% of the groupers present in the Gulf) and *L. ambiguus*, *L. buccanella* and *L. cyanopterus* (27% of the snappers present in the Gulf) (Table 8.5).



Table 8.4. Age and growth parameters, in length and weight, of groupers and snappers from the Gulf of Mexico. In cases where data for the Gulf was not available some results for the northern Atlantic or the Caribbean are given.

Species	R <sup>1</sup>	M <sup>2</sup>	Amax <sup>3</sup> (years)	Growth in Length <sup>4</sup>				Growth in Weight				Ref.
				L <sub>∞</sub> (mm)	K (per year)	t <sub>0</sub> (year)	Lmax (mm)	W = aL <sup>b</sup>		P <sub>∞</sub> (kg)	Wmax <sup>5</sup> (kg)	
								a	b			
Serranidae												
<i>Alphesthes afer</i>	J	—	—	—	—	—	260 TL	—	—	—	—	49
	—	—	—	—	—	—	330 TL	—	—	—	—	26
<i>Cephalopholis cruentata</i>	NA	O	13	451 TL	0.12	-1.24	405 TL	8.81 x 10 <sup>-6</sup>	3.12	1.7 TW	—	44
<i>C. fulva</i>	NA	O	11	372 TL	0.32	-0.20	397 TL	2.59x10 <sup>-5</sup>	2.94	0.9 TW	—	44
<i>Dermatolepis inermis</i>	J	—	—	—	—	—	690 TL	—	—	—	—	49
	—	—	—	—	—	—	900 TL	—	—	—	>10	26
<i>Epinephelus adscensionis</i>	NA/EG	O	12	499 TL	0.17	-2.50	—	6.00x10 <sup>-9</sup>	3.19	2.4 TW	—	43
	EG	—	—	—	—	—	375 SL	1.30x10 <sup>-8</sup>	3.04	—	—	12
	—	—	—	—	—	—	600 TL	—	—	—	—	26
<i>E. drummondhayi</i>	NA	O	25	967 TL	0.13	-1.01	1096 TL	1.10x10 <sup>-8</sup>	3.07	16.9	—	32
	EG	—	—	—	—	—	—	—	3.03	—	21.0 EW	12
	SG	—	—	—	—	—	960 TL	1.29x10 <sup>-8</sup>	—	—	17.3 TW	5
<i>E. flavolimbatus</i>	EG	O	27	800 SL	—	—	—	—	—	—	—	10
	EG	—	—	—	—	—	—	—	2.86	—	14.0	12
	—	—	—	—	—	—	1150 TL	2.94 x 10 <sup>-8</sup>	—	—	—	26
<i>E. guttatus</i>	NA/EG	O	11	471 TL	0.2	-2.40	491 TL	—	2.61	1.7 TW	—	43
	EG	—	—	—	—	—	396 SL	1.80x10 <sup>-7</sup>	—	—	1.8 TW	12

Table 8.4. Continued

<i>E. itajara</i>	EG	O	37	2006 TL	0.13	-0.49	2160 TL	—	3.06	165.6 TW	—	13
	EG	—	—	—	—	—	—	$1.31 \times 10^{-8}$	3.02	—	—	12
	—	—	—	—	—	—	2500 TL	$1.50 \times 10^{-8}$	—	—	320.0	26
<i>E. morio</i>	EG	O	25	672 SL	0.18	-0.45	772 SL	—	—	—	—	35
	EG	—	—	—	—	—	—	—	2.90	—	—	12
	SG	O	14	928 TL	0.11	-0.09	700 TL	$5.42 \times 10^{-8}$	2.59	7.1	—	38
	SG	U	21	860 FL	0.10	-1.50	—	$1.47 \times 10^{-4}$	3.00	10.3	—	51
	SG	O	20	802 TL	0.16	-1.21	—	$1.62 \times 10^{-5}$	3.00	7.1 TW	—	19
	SG	O	12	820 TL	0.19	-0.67	—	$1.38 \times 10^{-5}$	3.07	8.9 EW	—	47
		M	12	891 TL	0.12	0.56	—	$1.02 \times 10^{-5}$	—	11.5 EW	—	
	SG	LF	—	985	0.17	-0.27	—	—	—	—	14.4	3
	SG	—	—	—	—	—	880 FL	—	3.05	—	12 TW	4, 9
	—	—	—	—	—	—	900 TL	$1.24 \times 10^{-2}$	—	—	—	26
<i>E. mystacinus</i>	EG	—	—	—	—	—	1150 SL	—	—	—	49 EW	12
<i>E. nigritus</i>	NA	O	41	2394 TL	0.05	-3.62	2261 TL	—	2.98	246.6	190.0	29
								$2.10 \times 10^{-5}$	—	—	160.0	12
<i>E. niveatus</i>	EG	O	27	1320 TL	0.09	-1.01	1180 TL	—	2.93	34.8 TW	25.4 TW	36
	—	—	—	—	—	—	970 SL	$2.45 \times 10^{-8}$	—	—	24.0	12
<i>E. striatus</i>	C	O	—	760 TL	0.12	-1.11	—	—	2.98	7.9	—	15
	—	—	—	—	—	—	1000 TL	$1.98 \times 10^{-2}$	—	—	25.0	26
<i>Gonioplectrus hispanus</i>	—	—	—	—	—	—	230 SL	—	—	—	—	26
<i>Mycteroperca acutirostris</i>	—	—	—	—	—	—	800 TL	—	—	—	4.0	26

Table 8.4. Continued

<i>M. bonaci</i>	EG	O	33	1306 TL	0.17	-0.77	1518 TL	—	3.22	37.7 TW	—	18
	EG	—	—	—	—	—	1260 SL	$3.49 \times 10^{-6}$	3.21	—	50.9	12
	SG	—	—	—	—	7.50	1320 FL	$3.42 \times 10^{-9}$	3.17	—	35.2 TW	6, 9
<i>M. interstitialis</i>	EG	O	28	828 TL	0.08	—	—	$6.40 \times 10^{-3}$	2.89	7.0	—	11
	EG	—	—	—	—	—	646 SL	$2.59 \times 10^{-5}$	2.97	—	6.0	12
<i>M. microlepis</i>	EG	O	13	—	—	-0.74	—	$1.56 \times 10^{-8}$	—	—	—	33
	EG	O	21	1180 TL	0.17	—	1222 TL	—	3.06	20.4 TW	—	27
	EG	—	—	—	—	—	1050 SL	$8.13 \times 10^{-6}$	—	—	24.5	12
	SG	—	—	—	—	-1.49	1160 FL	—	3.19	—	20.5 TW	7, 9
<i>M. phenax</i>	EG	O	17	720 TL	0.17	—	—	$5.30 \times 10^{-3}$	—	—	—	24
	—	—	—	—	—	—	—	—	3.07	—	—	12
	—	—	—	—	—	-1.88	900 TL	$8.99 \times 10^{-9}$	—	—	14.0	26
<i>M. tigris</i>	C	O	18	740 TL	0.11	—	755 TL	—	3.12	6.4	—	23
	—	—	—	—	—	—	1000 TL	$9.40 \times 10^{-3}$	—	—	10.0	26
<i>M. venenosa</i>	J	O	15	860 TL	0.10	—	860 TL	—	—	—	—	49
	EG	—	—	—	—	—	810 FL	—	—	—	—	12
	—	—	—	—	—	-0.25	900 TL	—	—	—	15.0	26
<i>Paranthias furcifer</i>	G	O	—	372 FL	0.22	—	—	—	—	—	—	40
	—	—	—	—	—	—	304 SL	—	—	—	—	12
Lutjanidae												
<i>Lutjanus ambiguus</i>	—	—	—	—	—	—	< 400 TL	—	—	—	—	1
<i>L. analis</i>	NA/EG	O	14	862 TL	0.15	-0.58	860 TL	—	3.05	9	—	31
	—	—	—	—	—	—	800 TL	$1.00 \times 10^{-8}$	—	—	—	1

Table 8.4. Continued

<i>L. apodus</i>	J	LF	—	570 FL	0.18	—	—	—	—	3.8	—	39
	—	—	—	—	—	—	620 TL	—	—	—	—	1
<i>L. buccanella</i>	NA	U	—	602 FL	0.10	-3.16	—	—	—	4.3	—	20
<i>L. campechanus</i>	—	—	—	—	—	—	620 TL	—	—	—	—	1
	EG	O	5	—	—	—	678 FL	—	—	—	—	22
	NG	S/O	13	941 TL	0.17	-0.10	—	—	—	—	—	42
	NG	O	10	925 TL	0.14	-0.10	—	—	—	—	—	41
	NG	O	47	—	—	—	—	—	—	—	—	2
	NWG	S	4	—	—	—	—	—	—	—	—	37
	NWG A	O	34	884 FL	0.21	-0.63	916 FL	—	2.94	11.9 TW	—	21
	L	O	37	873 FL	0.24	-0.73	913 FL	$2.57 \times 10^{-8}$	3.03	12.2 TW	—	
	T	O	45	1023 FL	0.07	-2.92	844 FL	$1.54 \times 10^{-8}$	—	—	—	
	SG	S	9	908 FL	0.14	-0.76	—	—	2.83	11.1EW	—	25
	LF	—	860 TL	0.13	-0.36	—	$4.71 \times 10^{-5}$	—	—	—		
SG?	—	—	—	—	—	833 TL	—	2.91	—	8.4 EW	8, 9	
?	—	—	—	—	—	859 TL	$1.8 \times 10^{-2}$	2.94	—	8.0 EW		
<i>L. cyanopterus</i>	—	—	—	—	—	—	1600 TL	$1.6 \times 10^{-2}$	—	—	—	1
	C	—	—	—	—	—	—	—	3.12	—	—	16
<i>L. griseus</i>	NA	O	21	890 TL	0.10	-0.32	—	$0.98 \times 10^{-2}$	—	—	—	30
	C	O	9	548 FL	0.23	-1.07	520 FL	—	2.92	2.5 TW	2.0 TW	14
	EG	S	9	—	—	—	—	$2.07 \times 10^{-2}$	—	—	3.6	48

Table 8.4. Continued

<i>L. jocu</i>	NA	O	—	854 FL	0.10	-2.00	—	—	—	—	—	17
	?	O	—	964 FL	0.08	-2.14	—	—	—	—	—	
<i>L. mahogoni</i>	—	—	—	—	—	—	480 TL	—	—	—	—	1
<i>L. synagris</i>	NG	O	—	454 FL	0.13	-4.26	—	—	—	—	—	28
	SG	S	6	428 FL	0.10	-6.44	—	—	2.65	1.1 TW	—	50
		LF	—	410 FL	0.25	-1.82	—	1.25 x 10 <sup>-4</sup>	—	—	—	
	SG	LF	—	428 FL	0.28	-0.07	—	—	—	1.2	—	34
	SG	LF	—	352 FL	0.26	—	—	—	—	—	—	46
	C	U	—	729 FL	0.09	-2.64	—	—	—	—	—	45
<i>L. vivanus</i>	—	—	—	—	—	—	800 TL	—	—	—	—	1

<sup>1</sup> Region: NA - North Atlantic, C - Cuba, G - Gulf of Mexico, EG - Eastern Gulf, NG - Northern Gulf, NWG - Northwestern Gulf (A - Alabama, L - Louisiana, T - Texas), SG - Southern Gulf, J-Jamaica

<sup>2</sup> Study method: S - Scales, LF - length frequency, M - mesopterygoid, O- otolith, U - urohyal

<sup>3</sup> A<sub>max</sub> - maximum observed age

<sup>4</sup> L<sub>max</sub> - maximum observed length; SL - standard length, FL - furcal length, LT - total length

<sup>5</sup> W<sub>max</sub> maximum observed weight, EW - eviscerated weight of fish, TW - total weight (whole fish).

References:

1-Allen (1985); 2-Allman *et al.* (2002); 3-Arreguin-Sanchez *et al.* (1987); 4-Brule *et al.* (1999); 5-Brule *et al.* (2000); 6-Brule *et al.* (2003b); 7-Brule *et al.* (2003a); 8- Brule *et al.*(2004); 9-Brule, unpublished data; 10-Bullock and Godcharles in Manooch (1987); 11-Bullock and Murphy (1994); 12Bullock and Smith (1991); 13-Bullock *et al.* (1992); 14-Claro (1983); 15-Claro in Claro and Garcia-Arteaga (2001); 16-Claro and Garcia-Arteaga (2001); 17-Claro *et al.* in Claro and Garcia-Arteaga (2001); 18-Crabtree and Bullock (1998); 19-Doi *et al.* (1981); 20-Espinoza *et al.* in Claro and Garcia-Arteaga (2001); 21-Fischer (2002); 22-Futch and Bruger (1976); 23-Garcia-Arteaga *et al.* in Claro and Garcia-Arteaga (2001); 24-Godcharles and Bullock in Manooch (1987); 25-Gonzalez and de la Rosa (1988); 26-Heemstra and Randall (1993); 27-Hood and Schlieder (1992); 28-Johnson *et al.* in Claro and Garcia-Arteaga (2001); 29 - Manooch and Mason (1987); 30-Manooch and Matheson in Manooch (1987); 31-Mason and Manooch (1985); 32-Matheson and Huntsman (1984); 33-McErlean (1963); 34-Mexicano and Arreguin-Sanchez in Claro and Garcia-Arteaga (2001); 35-Moe (1969); 36-Moore and Labisky (1984); 37-Moseley (1966); 38-Muhlia-Melo (1976); 39-Munro in Claro and Garcia-Arteaga (2001); 40-Nelson *et al.* in Claro and Garcia-Arteaga (2001); 41-Nelson *et al.* in Manooch (1987); 42-Nelson and Manooch in Manooch (1987); 43-Potts and Manooch (1995); 44-Potts and Manooch (1999); 45-Pozo *et al.* in Claro and Garcia-Arteaga (2001); 46-Rivera-Arriaga *et al.* in Claro and Garcia-Arteaga (2001); 47-Rodriguez-Sanchez (1986); 48-Starck (1971); 49-Thompson and Munro (1978); 50-Torres and Chavez (1987); 51-Valdes and Padron (1980).

Table 8.5. Diet composition of groupers and snappers from the Gulf of Mexico. Where information is not available for the Gulf, some results are given for the northern Atlantic or the Caribbean.

Species	n <sup>1</sup>	Main Categories of Prey Identified in the Diet <sup>2</sup>							R <sup>3</sup>	Ref.
		Fish	Shrimp	Crabs	Other Crustaceans	Other Benthic Invertebrates	Cephalopods	Plankton		
<i>Alphesthes afer</i>	30	V7	V7	V77	V7	—	V3	—	VI/PR	24
<i>Cephalopholis cruentata</i>	— A	+ Pom	—	—	—	—	—	—	Cu	18
	— J	x	+	—	—	—	—	—	—	—
	26	V66	V17	V4	V9 Sto	V4 Gas	—	—	VI	24
<i>C. fulva</i>	29	V46 Pom	V21	V17	V16 Sto	—	—	—	VI/PR	24
<i>Epinephelus adscensionis</i>	—	17%(3)	67%(3)	—	—	—	—	—	WG	21
	—	—	x	x	—	—	—	—	EG	8
<i>E. drummondhayi</i>	31 A r	x	x	x	x Lob	x Asc	x Oct Sq	—	EG	8
<i>E. flavolimbatus</i>	—	—	—	—	—	x Biv	—	—	WG	21
	— r	x	—	x	x	x Ech Asc	x	—	EG	8
<i>E. guttatus</i>	—	V21	V10	V40	V>7	V>2	V7 Oct	—	G	22
<i>E. itajara</i>	2 J	x	x	—	—	—	—	—	EG	8
	32	x	—	x	x Lob	x Gas	—	—	—	—
	—	x	—	x	+ Lob	—	—	—	G	22
	2	—	—	+	—	—	—	—	SG	25
<i>E. morio</i>	—	+	+	+	+	—	x	—	G	22
	—	x	x	—	x Lob Sto	—	X Oct	—	EG	14
	—	x	x	x	x Lob	—	x Oct Sq	—	EG	16
	— J	—	x	—	x Amp	—	—	—	EG	8
	23 J/A r	x	x	x	—	x Gas	X Oct	—	—	—
	—	x	+	+	+ Sto	x Mol	—	—	SG	27
163 J	F>4	F<3	F>30	F<4 Sto	F<3 Gas	F<3 Oct	—	SG	5	

Table 8.5. Continued

<i>E. morio</i>	37 A	x	x	x	x Sto	x Biv	X Oct	—	SG	6
	855									
	J/A	F28	F18	F48	x Lob Sto	x Ech	x Oct Sq	—	SG	12
<i>E. mystacinus</i>	—	x	—	—	—	—	X Sq	—	G	22
	1	—	—	x	—	—	—	—	EG	8
<i>E. nigritus</i>	—	x	x	x	x Lob	—	—	—	—	13
	1	—	—	—	x Lob	—	—	—	EG	8
<i>E. niveatus</i>	32 ci	F72	F13	F16	x Sto	F3 Gas F9 Pol	F28	—	EG	2
<i>E. striatus</i>	—	F45-66	F3-14	F30-62	x Sto	—	x Oct Sq	—	NE/WG	10
<i>Mycteroperca bonaci</i>	2	—	x	—	x Amp	—	—	—	EG	23
<i>M. interstitialis</i>	—	x	—	—	—	—	—	—	EG	8
	25	x Pom	—	—	—	—	—	—	EG	7
<i>M. microlepis</i>	134	N26	N72	—	N3 Amp	—	—	—	EG	23
	53	x	x	—	—	—	—	—	EG	8
	—	V95-100	—	V0-3	—	—	—	—	EG	19
<i>M. phenax</i>	91	+	x	x	—	—	X Oct	—	NA	15
	2	x	—	—	—	—	—	—	EG	8
<i>M. tigris</i>	34	V100	—	—	—	—	—	—	VI/PR	24
<i>M. venenosa</i>	51	V95	V1	—	—	—	V4 Sq	—	VI/PR	24
<i>Paranthias furcifer</i>	252	—	—	—	—	—	—	+ Cop	WG	24
Lutjanidae										
<i>Lutjanus analis</i>	—	+	—	—	+	x Gas	—	—	G	22
<i>L. apodus</i>	—	x	x	x	—	x Wor	—	—	G	22
<i>L. buccanella</i>	24	F33	F8	F4	F46 Iso	—	F8	—	VI	4
<i>L. campechanus</i>	2431	F66	F9	F20	F36 Sto	x Asc	F16 Sq	x	NA/G	20
	1	x	—	—	—	—	—	—	G	1
	56	N46	N4	N13	N30	N4	—	—	EG	11

Table 8.5. Continued

<i>L. campechanus</i>	258 J	F20	F46	F14	F>13	—	—	—	NWG	3
	190 A	F52	F15	F10	F8	x Uro	—	—		
	73 J	V14	V26	V3	V32 Sto	—	x	+	NWG	17
	114 A	V55	V14	V3	x	x Uro Mol Pol	x	Urop		
	14 J	—	F93	—	—	—	—	Urop	SG	9
	24 A	F42	F33	F12	—	F4 Gas	F4 Oct	—		
<i>L. cyanopterus</i>	11	V100	—	—	—	—	—	—	VI/PR	24
<i>L. griseus</i>	—	+	+	+	x	—	—	—	G	22
<i>L. griseus</i>	636	F35	F27	F25	F22	x	F0.8	x	EG	26
<i>L. jocu</i>	—	61%(3)	—	—	—	x	—	—	G	22
	34	+	x	+	+ Lob	x Mol	x Oct	—	—	26
<i>L. mahogoni</i>	32	+	x	x	—	—	x Oct	—	G	22
<i>L. synagris</i>	—	+	x	—	+	x Ane Mol	—	x	G	22
<i>L. vivanus</i>	—	+	x	x	x	x Uro	x	—	G	22

<sup>1</sup> n - number of full stomachs analyzed: A - adults, ci - intestinal content, J - juveniles, r - regurgitated contents

<sup>2</sup> Symbols: F - frequency of a category of prey (%), N - percentage category of prey in number of individuals, V - percentage of a category of prey in volume, + - abundant, x - present; Percentage of stomachs analyzed. Particular prey: Amp - Amphipods, Ane - annelids, Asc - ascidians, Biv - bivalves, Sq - squid, Cop - copepods, Ech - Echinoderms, Sto - stomatopods, Gas - gastropods, Wor - worms, Iso - isopods, Lob - lobsters, Mol - molluscs, Pol - polychaeta, Pom - Pomacentridae Fish, Oct - octopus, Uro - urochordates, Urop - pelagic urochordates

<sup>3</sup> Region: NA - northern Atlantic, C - Cuba; Cu - Curaçao, G - Gulf of Mexico, EG - Eastern Gulf, NEG - Northeastern Gulf, NWG - Northwestern Gulf, WG - Western Gulf, SG - Southern Gulf, VI - Virgin Islands, PR - Puerto Rico.

References: 1-Baughman in Parrish (1987); 2-Bielsa and Labisky (1987); 3-Bradley and Bryan (1975); 4-Brownell and Rainer in Parrish (1987); 5-Brulé and Rodriguez-Canche (1993); 6-Brulé and Deniel (1996); 7-Bullock and Murphy (1994); 8-Bullock and Smith (1991); 9-Camber (1955); 10-Claro et al. (1990); 11-Futch and Bruger (1976); 12-Gimenez *et al.* (2001); 13-Heemstra and Randall (1993); 14-Longley and Hildebrand (1941); 15-Matheson *et al.* (1986); 16-Moe (1969); 17-Moseley (1966); 18-Nagelkerken in Bullock and Smith (1991); 19-Naughton and Saloman in Dodrill et al. (1993); 20-Naughton and Saloman in Parrish (1987); 21-Nelson in Bullock and Smith (1991); 22-Parrish (1987); 23-Peters in Bullock and Smith (1991); 24-Randall (1967); 25-Smith (1967); 26-Starck (1971); 27-Valdez and Padron (1980).



### *Diet Composition*

The analysis of the stomach or gut contents as well as regurgitation residues indicated that both groupers and snappers feed on a wide variety of prey, among which fish, crustaceans (crabs, shrimp, stomatopods and lobsters) and cephalopods stand out (Table 8.5). In global terms, however, snappers exhibit a more varied diet composition than groupers. Snappers tend to consume more planktonic organisms (pelagic urochordates) and benthic invertebrates other than crustaceans (ascideans, urochordates, polychaetes, molluscs) than groupers. Some species such as *A. afer*, *E. adscensionis*, *E. guttatus* and *E. morio* consume more crustaceans (Randall 1967; Parrish 1987; Nelson, in Bullock and Smith 1991; Gimenez *et al.* 2001), whereas others such as *M. tigris*, *M. venenosa*, *L. cyanopterus* and *L. jocu* feed more on fish (Randall 1967; Parrish 1987). Among the groupers of the Gulf, *P. furcifer* differs from the other species as it is the only serranid that feeds of planktonic organisms, particularly copepods (Nelson, in Bullock and Smith 1991).

### *Variations in Diet*

A variation in the composition of the diet was observed for some species depending on the ontogenetic development of the organisms. Juveniles of *C. cruentata*, *E. morio*, *E. striatus* and *L. campechanus* consume more crustaceans, whereas the adults eat more fish (Camber 1955; Moseley 1966; Bradley and Bryan 1975; Claro *et al.* 1990; Nagelkerken, in Bullock and Smith 1991; Brule and Rodriguez-Canche 1993; Gimenez *et al.* 2001). In terms of the nycthemeral rhythm of feeding activity, some species seek food both at day and night time (*E. morio*, *E. striatus*, *L. analis*, *L. apodus* and *L. synagris*), whereas others are more active at night (*L. griseus*, *L. mahogoni* and *L. vivanus*) (Longley and Hildebrand 1941; Randall 1967; Starck 1971; Parrish 1987; Brule *et al.* 1994).

## EXPLOITATION

In the western Atlantic, groupers and snappers are commercially exploited by industrial, artisanal and recreational fisheries throughout the southeastern coast of the U.S.A., Bermuda, the Caribbean Sea and the whole Gulf of Mexico (Sadovy 1994). Of the total of the species considered in the present study, 18 groupers and 9 snappers are commonly exploited in the Gulf of Mexico (Table 8.1) (Bannerot *et al.* 1987). The most abundant species in commercial catches in this region are: *E. morio*, *M. microlepis*, *M. phenax* and *M. bonaci* for groupers and *L. campechanus* for snappers. Other groupers such as *E. nigritus*, *E. flavolimbatus*, *E. niveatus* and *E. drummondhayi* come from deep water fisheries (70-300 m) (Bannerot *et al.* 1987; Bullock and Smith 1991; Colas-Marrufo *et al.* 1998; D.O.F. 2000).

Groupers and snappers can be particularly sensitive to the impact of fishing activities (Coleman *et al.* 2000). They exhibit slow growth and late sexual maturity, high longevity, low rates of natural mortality and reach high asymptotic sizes. According to the theory of demographic strategies of marine fish, these characteristics indicate that groupers and snappers are species close to those of the K-type. Simulation studies and recently acquired experience in fisheries analyses indicate that species with a K-type strategy achieve maximum yield per recruit when there is a low fishing mortality level and high recruitment age. In addition, the low natural mortality rates observed for these species indicate that grouper and snapper populations have low

rates of renovation and productive capacity. Because of these biological characteristics the grouper-snapper complex constitutes a resource with a high potential risk of reaching the over-exploitation level (Ralston 1987).

Very frequently, the fisheries effort exerted over a given stock is selectively directed towards larger individuals in terms of size and age, which are generally adult reproductive organisms. In the long run this can cause a change in the size and age demographic structure of the stock for both hermaphrodite and gonochoristic species, and lead to a progressive elimination of the largest, and consequently most prolific females (Coleman *et al.* 2000). In the case of protogynous hermaphrodite groupers, the selective capture of the largest individuals can also lead to a gradual decrease in the number of males in the exploited stock and, in extreme cases, to a deficit in the amount of male gametes necessary for the fertilization of the oocytes produced by the females during the reproductive period of the species (Bannerot *et al.* 1987). In the case of the stock of *M. microlepis* in the northeastern Gulf of Mexico, Koenig *et al.* (1996) observed a reduction in the average size of females and males, as well as in the proportion of males (from 17% to 2%) between 1980 and 1991-93. In the eastern Gulf, Coleman *et al.* (1996) observed that females of this species reached their first sexual maturity and started the process of sex reversion at a smaller size between 1991 and 1993, than had been observed by Hood and Schlieder (1992) between 1977 and 1980 in the same region. According to McGovern *et al.* (1998) these changes in demographic and biological characteristics of *M. microlepis* would be the consequence of the considerable increase in fisheries pressure on the stock of this species. Similar observations were made for the *M. phenax* stock in the Gulf, which exhibited a decrease in the percentage of males from 36% at the end of the 1970s to 18% at the beginning of the 1990s (Coleman *et al.* 1996). According to Coleman *et al.* (1996) this loss of males can have serious consequences on the reproductive behavior of mature females, such as non-participation in the formation of aggregations, and/or inhibition of ovulation and oviposition followed by re-absorption of the vitellogenic oocytes by the ovaries (atresias).

The observed changes in the average size of the organisms and proportion of each sex may also be a consequence of the fisheries pressure exerted specifically on spawning aggregations (Koenig *et al.* 1996). *M. microlepis* and *M. phenax* are species that migrate to specific spawning places where they form small aggregations of dozens to hundreds of individuals dispersed over an extensive geographic area. Gilmore and Jones (1992) observed that the fisheries effort was more intense during the season of these aggregations formation. Koenig *et al.* (1996) suggested that the selective fisheries of *M. microlepis* males in these aggregations were, to a great extent, responsible for the decrease in their numbers in the stocks of the Gulf of Mexico. The opposite occurred in the case of *E. morio*, also an intensively exploited species, but which does not form spawning aggregations. No change was observed in the proportion of sexes in stocks of this species in the eastern Gulf during 25 to 30 years (Coleman *et al.* 1996). Due to the yearly formation of spawning aggregations in the same geographical sites and periods of the year, they can be very vulnerable to irresponsible fisheries efforts (Sadovy 1997). The capture of a large number of organisms during several years in a row can lead to the definitive disappearance of aggregations, as was the case of several spawning aggregations of *E. striatus* that used to occur in specific places of the Caribbean (Sadovy 1994; Sadovy and Eklund 1999).

The species that are presently considered overexploited or at risk of overexploitation in the southeastern United States are *E. morio*, *E. drummondhayi*, *E. itajara*, *E. nigritus*, *E. niveatus*, *E. striatus*, *M. microlepis*, *M. phenax* and *L. campechanus* (Shipp 1999; Coleman *et al.* 2000). In the southern Gulf, the stocks of *E. morio* and *L. campechanus* in Campeche Bank are

considered overexploited and exploited to maximum sustainable level, respectively (Burgos and Defeo 2000; D.O.F. 2000). In the case of *L. campechanus*, the juveniles of the age classes 0 and 1 exhibit a high mortality rate because they are a part of the bycatch of shrimp trawlers. These juveniles occur with shrimp on soft bottoms until reaching a size between 150 a 200 mm, at which length they migrate to reef areas where they are less vulnerable to trawl nets (Shipp 1999).

As a consequence of fisheries exploitation and the degradation of critical or essential habitats, as occurred with the spawning aggregation zones of *M. microlepis* and *M. Phenax* along the east coast of Florida (Koenig *et al.* 2000), 11 species of groupers and two of snappers of the Gulf were included in the list of threatened species by the International Union for Conservation of Nature and Natural Resources (IUCN 2007) and/or by the American Fisheries Society (Musick *et al.* 2000) (Table 8.1). This high number of grouper and snapper species requiring protection is not surprising. In fact, among the most important commercial species, those at greatest risk of becoming endangered or extinct are iteroparous, which grow to substantial size, exhibit late sexual maturity and have sporadic recruitment (Sadovy 2001). These characteristics are generally observed in both groupers and snappers. In addition, according to Sadovy (2001), there are few empirical and theoretical bases that substantiate the classical hypothesis that the species that have high fecundity, such as groupers and snappers, are at lower risk of becoming threatened than species with low fecundity.

## MANAGEMENT

The rational management of a renewable natural resource can be achieved by the application of conventional measures (fisheries management) or non-conventional methods (conservation management). These two types of management have applications both in the maintenance and rehabilitation of the optimum productivity level of a fisheries resource (Bohnsack 1996). The objective of fisheries management is the preservation of the economic value of the fishery. This implies in the implementation of a series of regulations that lead to an economic benefit through the sustainable exploitation of the fisheries target species. Conservation management seeks to regulate human activities in order to minimize the direct and indirect negative impacts on valuable sites and/or species, with the objective of preserving certain species or biodiversity in general (Sale 2002).

### CONVENTIONAL MANAGEMENT

Fisheries management seeks to ensure that a sufficient number of fish are not captured, attempting to reduce or restrain the effective fisheries effort (input control), or restricting the total capture to predetermined limits (output control). Current conventional methods include: minimum capture length, catch limits, restrictions on fishing gear, closure periods and areas, and control of access to fishing zones (King 1995; Bohnsack 1996).

In response to multiple threats to grouper and snapper stocks in the Gulf of Mexico, the governments of the U.S.A. and Mexico have implemented policies to regulate their exploitation. However, relative to current federal fisheries control measures in the U.S.A., the Mexican regulation for these same fisheries seems less restrictive (Table 8.6). The official regulatory measures regarding commercial fisheries of groupers and snappers in Mexican waters (D.O.F. 2000, 2003; SEMARNAP 2000) consist of the following:

Table 8.6. Current conventional regulations for grouper and snapper fisheries in federal waters of the U.S. Gulf of Mexico.

Species	Commercial Fisheries			Sports Fisheries			
	Minimum capture size <sup>1</sup>	Quota per trip (Tons) <sup>1</sup>	Total quota (Tons) <sup>1</sup>	Closure <sup>1</sup>	Minimum capture size <sup>1</sup>	Daily catch <sup>7</sup>	Closure <sup>1</sup>
Serranidae							
Deep water groupers			726 <sup>3</sup>				
<i>Epinephelus mystacinus</i>	n	n	—	n	n	5/p	n
<i>E. niveatus</i>	n	n	—	n	n	5/p	n
<i>E. flavolimbatus</i>	n	n	—	n	n	5/p	n
<i>E. nigritus</i>	n	n	—	n	n	1/b	n
<i>E. drummondhayi</i>	n	n	—	n	n	1/b	n
Shallow water groupers			4.446 <sup>4</sup>				n
<i>Mycteroperca bonaci</i>	610 mm TL	n	—	15/02-15/03 <sup>6</sup>	559 mm TL	5/p	n
<i>M. microlepis</i>	610 mm TL	n	—	15/02-15/03 <sup>6</sup>	559 mm TL	5/p	n
<i>E. morio</i>	508 mm TL	n	—	15/02-15/03 <sup>6</sup>	508 mm TL	5/p	n
<i>M. venenosa</i>	508 mm TL	n	—	n	508 mm TL	5/p	n
<i>M. phenax</i>	406 mm TL	n	—	n	406 mm TL	5/p	n
<i>M. interstitialis</i>	n	n	—	n	n	5/p	n
<i>E. adscencionis</i>	n	n	—	n	n	5/p	n
<i>E. guttatus</i>	n	n	—	n	n	5/p	n
Protected Groupers							
<i>E. itajara</i>	—	—	—	Permanent	—	—	Permanent
<i>E. striatus</i>	—	—	—	Permanent	—	—	Permanent

Table 8.6. Continued

Lutjanidae							
<i>Lutjanus campechanus</i>	381 mm TL	0.907 & 0.091 <sup>2</sup>	2.109 & 1.388 <sup>5</sup>	See footnote <sup>5</sup>	406 mm TL	4/p	n
<i>L. synagris</i>	203 mm TL	n	n	n	203 mm TL	20 rf	n
<i>L. griseus</i>	305 mm TL	n	n	n	305 mm TL	10/p	n
<i>L. analis</i>	406 mm TL	n	n	n	406 mm TL	10/p	n
<i>L. mahogoni</i>	305 mm TL	n	n	n	305 mm TL	10/p	n
<i>L. apodus</i>	305 mm TL	n	n	n	305 mm TL	10/p	n
<i>L. jocu</i>	305 mm TL	n	n	n	305 mm TL	10/p	n
<i>L. cyanopterus</i>	305 mm TL	n	n	n	305 mm TL	10/p	n
<i>L. buccanella</i>	n	n	n	n	n	10/p	n
<i>L. vivanus</i>	n	n	n	n	n	10/p	n

<sup>1</sup> n = no restrictions (Gulf of Mexico Fishery Management Council, 2003a, b). TL = total length

<sup>2</sup> Depending on type of fishing license (class 1 or class 2).

<sup>3</sup> Includes *M. phenax* when the quota for shallow water groupers is reached.

<sup>4</sup> Includes all groupers that are not included in the deep-water classification.

<sup>5</sup> Authorized fishing during the first 10 days of each month from February 1st until the first quota is reached and from October 1st until the second quota is reached.

<sup>6</sup> Includes the ban on commercialization of *M. bonaci*, *M. microlepis* and *E. morio* during this period.

<sup>7</sup> b - per boat, p - per person (all species together, with the exception of *E. itajara* and *E. striatus* for groupers, and *L. campechanus* and *L. synagris* for snappers), rf - reef fish (all species together)

- Limited license emission for the commercial exploitation of finfish (including groupers and snappers)
- Temporary closure seasons of one month for groupers (all species) from February 15 to March 15 (established in 2003).
- A capture quota of 3,900 tons of groupers and snappers for the Cuban fisheries fleet
- Use of the “huachinanguero” hook No. 7 or 8 for the capture of groupers (to ensure that 50% of the captured organisms are >370 mm TL).

A minimum length of 300 mm TL is recommended for the first catch of all species of groupers. However, this length was determined based exclusively on commercial criteria (minimum catch size) without taking into account the biology of the species (size at first sexual maturity). To date, this measure is not included in the Normas Oficiales Mexicanas (NOM; Official Mexican Standards) for the protection of fisheries. There is no specific regulation for sports fisheries of groupers and snappers in Mexico.

One of the most problematic conventional methods, regarding its application for the control of grouper and snapper fisheries, is the requirement of a minimum catch length. Its use is facilitated and it reaches maximum efficiency with highly selective fishing methods that prevent the capture of fish below the legal length. When non-selective fishing techniques are used, on the other hand, this measure requires the return of fish below the minimum size (bycatch) to the sea. In these cases the fishing method should not harm the captured fish and the probability of survival of the returned fish should be very high, so that this measure does not become counter-productive. Many groupers and snappers captured in deep waters reach the surface with dilated or burst swim bladders and their internal organs compressed or expelled through their mouth or anus, thus promoting their short-term death. According to Wilson and Burns (1996) the survival rates of *E. morio* and *M. phenax* returned to the sea were between 86% and 100% for organisms captured at a 44 m depth, and of 0% and 50-25% for those captured between 54 and 75 m. The survival rate of *M. microlepis* captured between 54 and 75 m depth was 0%. Patterson *et al.* (2002) observed that the survival rate for *L. campechanus* returned to the sea was statistically significantly lower when captured at 32 m (87%) than at 21 m (91%) depth. In the northwestern Gulf the amount of captured *E. morio* and *M. microlepis* below the minimum catch length (<508 mm tl) fluctuates between 36 and 62% of the total commercial catch (Johnson *et al.*, Panama City Laboratory, NMFS, NOAA, unpublished data). In the U.S.A. the Florida Sea Grant College Program is seeking to increase survival rates by recommending that fishermen to use special syringes to remove the excess of gases in the visceral cavity before returning the fish to the sea.

## NON-CONVENTIONAL MANAGEMENT

Conservation management includes methods such as less harmful and destructive fishing practices, repopulation operations using aquaculture breeding methods, restoration or modification of habitat (implantation of artificial reefs) and the establishment of marine protected areas (MPA) (Bohnsack 1996).

Marine protected areas are currently considered as one of the most attractive and promising non-conventional fisheries management methods. Among the types of MPA available, the marine fisheries reserves or no-take marine reserves are well-delimited geographic areas, in which restrictions on the use of natural resources are imposed, or which constitute permanently closed areas for all consumption purposes (Chiappone *et al.* 2000). These reserves can contribute to: the protection of critical habitats necessary for the development of fisheries resources that

have been exhausted by over fishing or by the destruction of their natural habitat; the conservation of the marine biodiversity; and, in some circumstances, the increase of the productivity of stocks in adjacent areas (Conover *et al.* 2000). Although the efficiency of the creation of these reserves on fisheries productivity has not been completely proven, several authors, such as Bohnsack (1996) and Russ (2002), estimate that the implementation of this type of management measure must be promoted. These reserves represent the most viable option for fisheries management in developing countries. Contrary to what generally occurs with the requirement of controls over the catch and/or fisheries effort, MPAs can have better acceptance by the human societies that undertake artisanal or subsistence fisheries. In fact, MPAs frequently offer a range of associated benefits, such as income generated by tourism (Russ 2002).

MPAs appear to be an efficient tool for the protection of groupers. Results obtained to date indicate that they have a positive effect on this resource, such as: increased densities, biomass, average size and species abundance. These benefits have been observed for species considered small (*C. cruentatus* and *C. fulvus*), medium sized (*E. adscencionis* and *E. guttatus*) or large (*E. striatus*, *M. bonaci*, *M. tigris* and *M. venenosa*) (Sluka *et al.* 1997; Sadovy 1999; Chiappone *et al.* 2000; Koenig *et al.* 2000). However, MPAs could have a very limited interest in the case of more mobile species or those that exhibit reproductive migrations and whose movement would take them outside protected areas (Sadovy 1999; Bohnsack 2000; Tupper 2002).

Aquaculture of these species could represent a good complementary option for the management of natural resources. This could have the objective of growing organisms to commercial sizes or producing juveniles for the repopulation of wild stocks. The development of aquaculture of groupers and snappers of the western Atlantic has not yet gone beyond experimental levels. Induced reproduction, embryo and larvae development in the laboratory have been successfully carried out for several species of groupers and snappers from the Gulf such as *E. morio* (Colin *et al.* 1996), *E. striatus* (Guitart and Juarez 1966; Tucker 1991, 1998; Watanabe *et al.* 1996), *M. microlepis* (Roberts and Schlieder 1983), *L. analis* (Watanabe *et al.* 1998), *L. campechanus* (Arnold *et al.* 1978; Rabalais *et al.* 1980; Minton *et al.* 1983), *L. griseus* (Gonzalez *et al.* 1979) and *L. synagris* (Millares *et al.* 1979). However, low larval survival rates are presently the main problem limiting the development of this activity (Tucker 1998; Chigbu *et al.* 2002). Some repopulation experiments were carried out with *E. morio* (Colin *et al.* 1996) and *E. striatus* (Roberts *et al.* 1995).

## CONCLUSIONS

Groupers and snappers are important components of the reef fish communities of the Gulf of Mexico both at the ecological and economic level (Bannerot *et al.* 1987). According to Sadovy (1994) assessments of the populations of groupers in the central-western Atlantic reveal the symptoms of overexploitation for the majority of the studied species (abrupt reduction in average size and weight of the catch; decrease in the catch and landings by effort unit; alarming reduction or disappearance of reproductive aggregations). As a consequence, much of the grouper stocks, which are exploited both in continental and island zones, are at the point of or have already reached the stage of growth and/or recruitment overexploitation.

The protection of grouper stocks is generally inadequate or non-existent, and due to the high commercial value of the species that comprise them, it is common to quickly reach fisheries overexploitation levels (Levin and Grimes 2002). Few of the existing regulations for fisheries

management of reef fish are based on a quantitative evaluation of stocks, and none have explicitly considered the effect of inter-specific relationships or of reproductive strategies of the species (such as the protogynous hermaphroditic characteristics of several groupers) (Bannerot *et al.* 1987).

Since the sustainable management of resources is based on the evaluation of stocks and an understanding of the biology of the exploited species (Sadovy 1997), more information on these aspects is necessary for the implementation and improvement of management strategies of groupers and snappers in the Gulf. The reproductive biology, in particular, of several species of groupers and snappers of this region has not yet been studied. Many of these species, such as *E. mystacinus*, *E. nigrilus*, *E. striatus*, *M. tigris*, *L. analis*, *L. buccanella*, *L. jocu* and *L. Synagris*, have commercial importance and/or are threatened. Sexual patterns of all the species in the Gulf have not yet been characterized. Fecundity data is scarce and often imprecise. Reproduction, spawning aggregation and nursing areas in several regions of the Gulf are still unidentified. The main stages of the embryological and larval development of the majority of groupers and snappers have not been studied. The lack of biological information is particularly problematic for the management of stocks in the southern Gulf. The grouper-snapper complex of the continental shelf of the Yucatán Peninsula (Campeche Bank) is exploited in sequential manner by large and small Mexican fleets, and represents a resource that is shared with Cuba. It is a multi-specific resource that includes 18 species of grouper of the genera *Cephalopholis*, *Epinephelus* and *Mycteroperca*, and 10 species of snapper of the genus *Lutjanus* (Colas-Marrufo *et al.* 1998; Tuz-Sulub 1999; D.O.F. 2000). All these species are of commercial interest and 12 are considered threatened. Despite the commercial and ecological importance of these resources for the region, their reproduction has only been studied for *E. morio*, *M. bonaci*, *M. microlepis* and *L. campechanus*. Studies on growth have only been carried out for *E. morio*, *L. campechanus* and *L. synagris*, and on feeding habits, for *E. morio* and *L. campechanus*.

It is probable that the implementation of several administrative measures for fisheries management will be necessary in order that carry out the rational management of grouper and snapper resources, for the maintenance of sustainable production. Conventional management methods should not be rejected, even though their application has not prevented the deterioration of fisheries (deficiencies in the control of fisheries effort and in the prevention of the overexploitation of recruits) (Russ 2002). Although the efficiency of marine reserves as a non-conventional management method has not been proven to this date, they still represent one of the most viable options for resource management (Russ 2002). The creation of these reserves requires acquiring better understanding of the location and extension of the adult spawning areas, parental reproductive behavior (formation or not of spawning aggregations, type and timing of pairing), location of nursing areas as well as settlement processes, and biology of juveniles in such areas. The protection of the species from the negative effects of fisheries exploitation requires that future marine reserves include critical habitats where one of the crucial stages of the life cycle of target species takes place (Sadovy 1999). However, it does not seem appropriate to consider marine reserves as a possible replacement for all other fisheries management measures (Sadovy 1999; Trexler and Travis 2000; Russ 2002). Marine reserves must be considered as a potential support tool for preventive management measures (Russ 2002). When these reserves are used as complementary measures to conventional fisheries management regulations, they offer greater flexibility for the management of fisheries and the protection of marine resources (Bohnsack 2000).



## LITERATURE CITED

- Aguilar-Perera, A. and W. Aguilar-Dávila. 1996. A spawning aggregation of Nassau grouper *Epinephelus striatus* (Pisces: Serranidae) in the Mexican Caribbean. *Environmental Biology of Fishes* 45:351-361.
- Allen, R. G. 1985. *FAO Species Catalogue. Vol. 6. Snappers of the World: An Annotated and Illustrated Catalogue of Lutjanid Species Known to Date*. FAO Fisheries Synopsis No. 125. Rome: Food and Agriculture Organization of the United Nations. 208 pp.
- \_\_\_\_\_. 1987. Synopsis of the circumtropical fish genus *Lutjanus* (Lutjanidae). Pp. 33-88 in J.J. Polovina, J. L. and S. Ralston (eds.), *Tropical Snappers and Groupers: Biology and Fisheries Management*. Boulder, Colorado: Westview Press.
- Allman, R. J., L. A. Lombardi-Carlson, G. R. Fitzhugh, and W. A. Fable. 2002. Age structure of red snapper (*Lutjanus campechanus*) in the Gulf of Mexico by fishing mode and region. *Proceedings of the Gulf and Caribbean Fisheries Institute* 53:482-495.
- Arnold, C. R., J. M. Wakeman, T. D. Williams, and G. D. Treece. 1978. Spawning of red snapper (*Lutjanus campechanus*) in captivity. *Aquaculture* 15:301-302.
- Arreguin-Sánchez F., M. A. Cabrera, and G. Mexicano. 1987. Dinámica de la población de *Epinephelus morio* del Banco de Campeche, México. Pp. 81-88 in: M. Ramírez-Rodríguez (ed.), *Memorias del Simposium sobre Investigación en Biología y Oceanografía Pesquera en México*. La Paz, Baja California Sur, México.
- Bannerot, S., W. W. Fox Jr., and J. E. Powers. 1987. Reproductive strategies and the management of snappers and groupers in the Gulf of Mexico and Caribbean. Pp. 561-603 in J. J. Polovina and S. Ralston (eds.), *Tropical Snappers and Groupers: Biology and Fisheries Management*. Boulder, Colorado: Westview Press.
- Bielsa, L. M. and R. F. Labisky. 1987. Food habits of blueline tile fish, *Caulolatilus microps*, and snowy grouper, *Epinephelus niveatus*, from the lower Florida Keys. *Northeast Gulf Science* 9:77-87.
- Bohnsack, J. A. 1996. Maintenance and recovery of reef fishery productivity. Pp. 283-314 in: N. V. C. Polunin and C. M. Roberts (eds.), *Reef Fisheries*. London: Chapman & Hall.
- \_\_\_\_\_. 2000. A comparison of the short-term impacts of no-take marine reserves and minimum size limits. *Bulletin of Marine Science* 66:635-650.
- Bradley, E. and C. E. Bryan. 1975. Life history and fishery of the red snapper (*Lutjanus campechanus*) in the northwestern Gulf of México: 1970-1974. *Proceedings of the Gulf and Caribbean Fisheries Institute* 27:77-106.
- Brulé, T. and C. Denié. 1996. Biological research on the red grouper (*Epinephelus morio*) from the southern Gulf of Mexico. Pp. 28-42 in: F. Arreguin-Sánchez, J. L. Munro, M.C. Balgos, and D. Pauly (eds.), *Biology, Fisheries and Culture of Tropical Groupers and Snappers. Conference proceedings 48*. Manila, Philippines: ICLARM (International Center for Living Aquatic Resources Management).
- \_\_\_\_\_. and L. G. Rodríguez-Canché. 1993. Food habits of juvenile red groupers, *Epinephelus morio* (Valenciennes, 1828) from Campeche Bank, Yucatán, México. *Bulletin of Marine Science* 52:772-779.
- \_\_\_\_\_, T. Colás-Marruf, A. Tuz-Sulub, and C. Denié. 2000. Evidence for protogynous hermaphroditism in the serranid fish *Epinephelus drummondhayi* (Perciformes: Serranidae) from the Campeche Bank in the southern Gulf of Mexico. *Bulletin of Marine Science* 66:513-521.

- \_\_\_\_\_, C. Déniel, T. Colás-Marrufo, and X. Renán. 2003a. Reproductive biology of gag in the southern Gulf of Mexico. *Journal of Fish Biology* 63:1501-1520.
- \_\_\_\_\_, \_\_\_\_\_, \_\_\_\_\_, and M. Sánchez-Crespo. 1999. Red grouper reproduction in the southern Gulf of Mexico. *Transactions of the American Fisheries Society* 128:385-402.
- \_\_\_\_\_, D. Ordaz-Avila, M. Sánchez-Crespo, and C. Déniel. 1994. Seasonal and diel changes in diet composition of juvenile red grouper (*Epinephelus morio*) from Campeche Bank. *Bulletin of Marine Science* 55:255-262.
- \_\_\_\_\_, J. C. Sámano-Zapata, T. Colás-Marrufo, E. Pérez-Díaz, and C. Déniel. 2004. Primeros resultados sobre la reproducción del pargo del Golfo *Lutjanus campechanus*, de la plataforma continental de la Península de Yucatán, México. *Proceedings of the Gulf and Caribbean Fisheries Institute* 55:797.
- \_\_\_\_\_, X. Renán, T. Colás-Marrufo, Y. Hauyon, A. Tuz-Sulub, and C. Déniel. 2003b. Reproduction in the protogynous black grouper (*Mycteroperca bonaci* Poey) from the southern Gulf of Mexico. *Fishery Bulletin* 101:463-475.
- Bullock, L. H. and M. D. Murphy. 1994. Aspects of the life history of the yellowmouth grouper, *Mycteroperca interstitialis*, in the eastern Gulf of Mexico. *Bulletin of Marine Science* 55:30-45.
- \_\_\_\_\_ and G. B. Smith. 1991. Seabasses (Pisces: Serranidae). *Memoirs of the Hourglass Cruises* 8(2): 1-243.
- \_\_\_\_\_, M. F. Godcharles, and R. E. Crabtree. 1996. Reproduction of yellowedge grouper, *Epinephelus flavolimbatus*, from the eastern Gulf of Mexico. *Bulletin of Marine Science* 59:216-224.
- \_\_\_\_\_, M. D. Murphy, M. F. Godcharles, and M. E. Mitchell. 1992. Age, growth, and reproduction of jewfish *Epinephelus itajara* in the eastern Gulf of Mexico. *Fishery Bulletin* 90:243-249.
- Burgos, R. and O. Defeo. 2000. Un marco de manejo precautorio para la pesquería de mero (*Epinephelus morio*) del Banco de Campeche, México. *Oceánides* 15:129-140.
- Byron, D., D. M. Wyanski, B. M. Eleby, and C. G. Lilyestrom. 2002. Tiger grouper (*Mycteroperca tigris*): Profile of a spawning aggregation. *Bulletin of Marine Science* 70:233-240.
- Carter, J. and D. Perrine. 1994. A spawning aggregation of dog snapper, *Lutjanus jocu* (Pisces: Lutjanidae) in Belize, Central America. *Bulletin of Marine Science* 55:228-234.
- Carter, J., G. J. Marrow, and V. Pryor. 1994. Aspects of the ecology and reproduction of Nassau grouper, *Epinephelus striatus*, off the coast of Belize, Central America. *Proceedings of the Gulf and Caribbean Fisheries Institute* 43:65-111.
- Camber, I. C. 1955. A survey of the red snapper fishery of the Gulf of Mexico, with special reference to the Campeche Banks. *Florida State Board of Conservation Technical Series* 12:1-64.
- Chiappone, M., R. Sluka, and K. S. Sealey. 2000. Groupers (Pisces: Serranidae) in fished and protected areas of the Florida Keys, Bahamas and northern Caribbean. *Marine Ecology Progress Series* 98:261-272.
- Chigbu, P., T. Ogle, J. T. Jeffreu, M. M. Lotz, and E. L. Coleman. 2002. Some aspects of the culture of red snapper. *Proceedings of the Gulf and Caribbean Fisheries Institute* 53:228-233.

- Clarke, M. E., M. L. Domeier, and W. A. Laroche. 1997. Development of larvae and juveniles of the mutton snapper (*Lutjanus analis*), lane snapper (*L. synagris*) and yellowtail snapper (*L. chrysurus*). *Bulletin of Marine Science* 66:721-728.
- Claro, R. 1982. *Ecología y Ciclo de Vida de la Biajaiba, Lutjanus synagris (Linnaeus), en la Plataforma Cubana. IV: Reproducción*. Reporte de Investigación del Instituto de Oceanología, No. 5. Havana, Cuba: Academia de Ciencias de Cuba.
- \_\_\_\_\_, and J. P. García-Arteaga. 2001. Growth patterns of fishes of the Cuban shelf. Pp. 149-178 in R. Claro, K. C. Lindeman, and L. R. Parenti (eds.), *Ecology of the Marine Fishes of Cuba*. Washington, D.C.: Smithsonian Institution Press.
- Claro, R. J. 1983. *Ecología y Ciclo de Vida del Caballerote, Lutjanus griseus (Linnaeus), en la Plataforma Cubana. II: Edad y Crecimiento, Estructura de las Poblaciones y Pesquerías*. Reporte de Investigación del Instituto de Oceanología No. 8. Havana, Cuba: Academia de Ciencias de Cuba 26 pp.
- \_\_\_\_\_, A. García-Cagide, L. M. Sierra, and J. P. García-Arteaga. 1990. Características biológico-pesqueras de la cherna criolla, *Epinephelus striatus* (Bloch) (Pisces: Serranidae) en la plataforma cubana. *Ciencias Biológicas* 23:23-43.
- Colás-Marrufo, T. C., T. Brulé, and C. Deniél. 1998. Análisis preliminar de las capturas de meros realizadas a través de unidades de la flota mayor en el sureste del Golfo de México. *Proceedings of the Caribbean Fisheries Institute* 50:780-803.
- Colás-Marrufo, T. C., A. Tuz-Sulub, and T. Brulé. 2002. Observaciones preliminares sobre la pesquería de meros (Serranidae: Epinephelinae) en el parque marino Nacional "Arrecife Alacranes", Yucatán, México. *Proceedings of the Gulf and Caribbean Fisheries Institute* 53:431-445.
- Coleman, F. C., C. C. Koenig, and L. A. Collins. 1996. Reproductive styles of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. *Environmental Biology of Fishes* 47:129-141.
- \_\_\_\_\_, \_\_\_\_\_, G. R. Huntsman, J. A. Musick, A. M. Eklund, J. C. McGovern, R. W. Chapman, G. R. Sedberry, and C. B. Grimes. 2000. Long-lived reef fishes: The grouper-snapper complex. *Fisheries* 25:14-21.
- Colin, P. L. 1992. Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) and its relationship to environmental conditions. *Environmental Biology of Fishes* 34:357-377.
- \_\_\_\_\_. 1994. Preliminary investigations of reproductive activity of the jewfish, *Epinephelus itajara* (Pisces: Serranidae). *Proceedings of the Gulf and Caribbean Fisheries Institute* 43:138-147.
- \_\_\_\_\_, Koenig C. C., and W. A. Laroche. 1996. Development from egg to juvenile of the red grouper (*Epinephelus morio*) (Pisces: Serranidae) in the laboratory. Pp. 399-414 in F. Arreguín-Sánchez, J. L. Munro, M. C. Balgos and D. Pauly (eds.), *Biology, Fisheries and Culture of Tropical Groupers and Snappers: Conference Proceedings 48*. Manila, Philippines: ICLARM (International Center for Living Aquatic Resources Management).
- \_\_\_\_\_, D. Y. Douglas, Y. Shapiro, and D. Weiler. 1987. Aspects of the reproduction of two groupers, *Epinephelus guttatus* and *E. striatus* in the Western Indies. *Bulletin of Marine Science* 40:220-230.
- Collins, L. A., J. H. Finucane, and L. E. Barger. 1979. Description of larval and juvenile red snapper, *Lutjanus campechanus*. *Fishery Bulletin* 77:965-974.

- \_\_\_\_\_, A. G. Johnson, and C. P. Keim. 1996. Spawning and annual fecundity of the red snapper (*Lutjanus campechanus*) from the northeastern Gulf of Mexico. Pp. 174-188 in F. Arreguín-Sánchez, J. L. Munro, M. C. Balgos and D. Pauly (eds.), *Biology, Fisheries and Culture of Tropical Groupers and Snappers: Conference Proceedings 48*. Manila, Philippines: ICLARM (International Center for Living Aquatic Resources Management).
- \_\_\_\_\_, C. C. Koenig, and M. S. Baker, Jr. 1997. Reproductive patterns, sex ratio, and fecundity in gag, *Mycteroperca microlepis* (Serranidae), a protogynous grouper from the northeastern Gulf of Mexico. *Fishery Bulletin* 96:415-427.
- \_\_\_\_\_, G. R. Fitzhugh, L. A. Lombardi, H. M. Lyon, W. T. Walling, and D. V. Oliver. 2002. *Characterizations of Red Grouper (Serranidae: Epinephelus morio) Reproduction from the eastern Gulf of Mexico*. Panama City Laboratory Contribution Series 2002-07. Panama City, Florida: National Marine Fisheries Service. 21 pp.
- \_\_\_\_\_, L. Mour, L. A. Lombardi-Carlson, W. T. Walling, Jr., W. A. Fable Jr., M. R. Burnett, and R. J. Allman. 2001. Preliminary results from a continuing study of spawning and fecundity in the red snapper (Lutjanidae: *Lutjanus campechanus*) from the Gulf of Mexico, 1988-1999. *Proceedings of the Gulf and Caribbean Fisheries Institute* 52:34-47.
- Conover, D. O., J. Travis, and F. Coleman. 2000. Essential fish habitat and marine reserves: an introduction to the Second Mote Symposium on Fisheries Ecology. *Bulletin of Marine Science* 66:527-534.
- Crabtree, R. E. and L. H. Bullock. 1998. Age, growth, and reproduction of black grouper, *Mycteroperca bonaci*, in Florida waters. *Fishery Bulletin* 96:735-753.
- Diario Oficial de la Federación (D.O.F.). 2000. Tomo CLXIII, 28 de agosto:63-67.
- Diario Oficial de la Federación (D.O.F.). 2003. Tomo DXCIII, 13 de febrero:48-49
- Dodrill, J., C. S. Manooch III, and A. B. Manooch. 1993. Food and feeding behavior of adult snowy grouper *Epinephelus niveatus* (Valenciennes) (Pisces: Serranidae), collected off the Central North Carolina coast with ecological notes on major food groups. *Brimleyana* 19:101-135.
- Doi, T., D. Mendizábal, and M. Contreras. 1981. Análisis preliminar de la población de mero, *Epinephelus morio* (Valenciennes) en el Banco de Campeche. *Ciencia Pesquera* 1:1-15.
- Domeier, M. L. and P. L. Colin. 1997. Tropical reef fish spawning aggregations: defined and reviewed. *Bulletin of Marine Science* 60:698-726.
- \_\_\_\_\_, C. Koenig, and F. Coleman. 1996. Reproductive biology of the gray snapper (*Lutjanus griseus*), with notes on spawning for other western Atlantic snapper (Lutjanidae). Pp. 189-201 in F. Arreguín-Sánchez, J. L. Munro, M. C. Balgos and D. Pauly (eds.), *Biology, Fisheries and Culture of Tropical Groupers and Snappers: Conference Proceedings 48*. Manila, Philippines: ICLARM (International Center for Living Aquatic Resources Management).
- Druzhini, A. D. 1970. The range and biology of snappers (Fam. Lutjanidae). *Journal of Ichthyology* 10:717-736.
- Eklund, A. M., D. B. McClellan, and D. E. Harper. 2000. Black grouper aggregation in relation to protected areas within the Florida Keys National Marine Sanctuary. *Bulletin of Marine Science* 66:721-728.
- Falfán-Vázquez, E. 2003. Estudio sobre la fecundidad del mero colorado *Epinephelus guttatus* (Linnaeus, 1758) del Banco de Campeche. Tesis de maestría. CINVESTAV-Unidad Mérida, Mérida, Yucatán, México. 83 pp.

- Fischer, W. 1978. *FAO Species Identification Sheets for Fisheries Purposes, Western Central Atlantic (Fishing Area 31)*, Vols. 1-7, Rome: Food and Agriculture Organization of the United Nations.
- \_\_\_\_\_. 2002. Age growth of red snapper *Lutjanus campechanus*, in the northwestern Gulf of Mexico implications to the unit stock hypothesis. *Proceedings of the Gulf and Caribbean Fisheries Institute* 53:497-505.
- Futch, R. B. and G. E. Bruger. 1976. Age, growth, and reproduction of red snapper in Florida waters. *Proceedings of the Colloquium of Snapper-grouper Fishery Resources of the Western Atlantic Ocean* 17:165-184.
- García-Cagide, A. and T. García. 1996. Reproducción de *Mycteroperca bonaci* y *Mycteroperca venenosa* (Pisces: Serranidae) en la plataforma cubana. *Revista de Biología Tropical* 44:771-780.
- \_\_\_\_\_, R. Claro, and B. V. Koshelev. 2001. Reproductive patterns of fishes of the Cuban shelf. Pp. 73-114 in R. Claro, K. C. Lindeman, and L. R. Parenti (eds.), *Ecology of the Marine Fishes of Cuba*. Washington, D.C.: Smithsonian Institution Press.
- Gilmore, R. G. and R. S. Jones. 1992. Color variation and associated behavior in the Epinepheline groupers, *Mycteroperca microlepis* (Goode and Bean) and *M. phenax* Jordan and Swain. *Bulletin of Marine Science* 51:83-103.
- Giménez, E., B. Anderes, V. Moreno, and R. Burgos. 2001. Aspectos de la conducta alimentaria del mero (*Epinephelus morio*) del Banco de Campeche. *Ciencia Pesquera* 15:165-170.
- Gómez, C. J., R. A. Guzmán, and L. A. Marcano. 1996. Biological aspects of the yellow eye snapper (*Lutjanus vivanus*) (Pisces: Lutjanidae) from the Los Hermanos Islands, Eastern Venezuela. Pp/ 48 in F. Arreguín-Sánchez, J. L. Munro, M. C. Balgos and D. Pauly (eds.), *Biology, Fisheries and Culture of Tropical Groupers and Snappers: Conference Proceedings* 48. Manila, Philippines: ICLARM (International Center for Living Aquatic Resources Management).
- González, E., T. Damas, N. Millares, and M. Borrego. 1979. Desove inducido en el caballero (*Lutjanus griseus* Linné 1758) en condiciones de laboratorio. *Revista Cubana de Investigación Pesquera* 4:43-63.
- González y de la Rosa, M. E. 1988. Estudio de la pesquería del huachinango (*Lutjanus campechanus* Poey) del Banco de Campeche. Tesis de maestría, CINVESTAV-Unidad Mérida, Mérida, Yucatán, México.: 46 pp.
- González y de la Rosa, M. E. and C. Regis. 2001. Aspectos de la reproducción de *Lutjanus campechanus* en Campeche, México. *Ciencia Pesquera* 15:141-146.
- Grimes, C. B. 1987. Reproductive biology of the Lutjanidae: a review. Pp. 239-294 in J. J. Polovina and S. Ralston (eds.), *Tropical Snappers and Groupers: Biology and Fisheries Management*. Boulder, Colorado: Westview Press.
- Guitart, D. and M. Juárez. 1966. Desarrollo embrionario y primeros estadios larvales de la cherna criolla, *Epinephelus striatus* (Bloch) (Perciformes: serranidae). *Estudios del Instituto de Oceanografía de la Habana* 1:35-45.
- Harris, P. J., D. M. Wyanski, D. B. White, and J. L. Moore. 2002. Age, growth, and reproduction of scamp, *Mycteroperca phenax*, in the southwestern North Atlantic, 1979-1997. *Bulletin of Marine Science* 70:113-132.
- Heemstra, P. C. and J. E. Randall. 1993. *FAO species catalogue. Vol. 16. Groupers of the World (Family Serranidae, Subfamily Epinephelinae). An annotated and illustrated Catalogue of the Grouper, Rock Cod, Hind, Coral Grouper and Lyretail Species Known to Date.*

- FAO Fisheries Synopsis No. 125. Rome: Food and Agriculture Organization of the United Nations. 382 pp.
- Hoese, H. D. and R. H. Moore. 1998. *Fishes of the Gulf of Mexico: Texas, Louisiana, and adjacent waters*. College Station, Texas: Texas A&M University Press. 327 pp.
- Hood P. B. and R. A. Schlieder. 1992. Age, growth, and reproduction of gag, *Mycteroperca microlepis* (Pisces: Serranidae) in the eastern Gulf of Mexico. *Bulletin of Marine Science* 5:337-352.
- International Union for Conservation of Nature and Natural Resources (IUCN). 2007. Available at: [mwww.redlist.org](http://mwww.redlist.org). Accessed on June 27, 2007.
- Johnson, G. D. and P. Keener. 1984. Aid to identification of American grouper larvae. *Bulletin of Marine Science* 34:106-134.
- Jones, R. S., E. J. Gutherz, W. R. Nelson, and C. Matlock. 1989. Burrow utilization by yellowedge grouper, *Epinephelus flavolimbatus*, in the northwestern Gulf of Mexico. *Environmental Biology of Fishes* 26:277-284.
- Kendall, A. W. 1979. *Morphological comparisons of North American Sea Bass Larvae (Pisces: Serranidae)*. NOAA Technical Report, NMFS Circular 428. Washington, D.C.: U.S. Department of Commerce, National Oceanic and Atmospheric Administration. 50 pp.
- \_\_\_\_\_. 1984. Serranidae: Development and relationships. Pp. 499-510 in H. D. Moser, M. Richards, A. Fahay, and S. Richardson (eds.), *Ontogeny and Systematics of Fishes*. Lawrence, Kansas: American Society of Ichthyologists and Herpetologists.
- Kendall, A. W., Jr. and M. P. Fahay. 1979. Larva of the Serranid fish *Gonioplectrus hispanus* with comments on its relationships. *Bulletin of Marine Science* 29:117-121.
- King, M. 1995. *Fisheries biology. Assessment and Management*. Oxford: Fishing News Books. 352 pp.
- Koenig, C. C., F. C. Coleman, L. A. Collins, Y. Sadovy, and P. L. Colin. 1996. Reproduction in gag (*Mycteroperca microlepis*) (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregation. Pp. 307-323 in F. Arreguín-Sánchez, J. L. Munro, M. C. Balgos and D. Pauly (eds.), *Biology, Fisheries and Culture of Tropical Groupers and Snappers: Conference Proceedings 48*. Manila, Philippines: ICLARM (International Center for Living Aquatic Resources Management).
- \_\_\_\_\_, \_\_\_\_\_, C. B. Grimes, G. R. Fitzhugh, K. M. Scanlon, C. T. Gledhill, and M. Grace. 2000. Protection of fish spawning habitat for the conservation of warm-temperate reef-fish fisheries of shelf-edge reefs of Florida. *Bulletin of Marine Science* 66:593-616.
- Leis, J. M. 1987. Review of the early life history of tropical groupers (Serranidae) and snappers (Lutjanidae). Pp. 189-237 in J. J. Polovina and S. Ralston (eds.), *Tropical Snappers and Groupers: Biology and Fisheries Management*. Boulder, Colorado: Westview Press.
- Levin, P. S. and C. B. Grimes. 2002. Reef fish ecology and grouper conservation and management. Pp. 377-389 in P. Sale (ed.), *Coral Reef Fishes*. San Diego, California: Elsevier Science.
- Lindeman, K. C., R. Pugliese, G. T. Waugh, and J. S. Ault. 2000. Developmental patterns within a multispecies reef fishery: management applications for essential fish habitats and protected areas. *Bulletin of Marine Science* 66:929-956.
- Longley, W. and S. F. Hildebrand. 1941. *Systematic Catalogue of the Fishes of Tortugas Florida*. Papers from Tortugas Laboratory 34:1-331, Carnegie Institute of Washington Publication No. 535. Washington, D.C.: Carnegie Institute. 331 pp.

- Manickchand-Dass, S. C. 1987. Reproduction, age and growth of the lane snapper, *Lutjanus sinagrays* (Linnaeus) in Trinidad, West Indies. *Bulletin of Marine Science* 40:22-28.
- Manooch, C. S., III. 1987. Age and growth of snappers and groupers. Pp. 329-373 in J. J. Polovina and S. Ralston (eds.), *Tropical Snappers and Groupers: Biology and Fisheries Management*. Boulder, Colorado: Westview Press.
- \_\_\_\_\_ and D. L. Mason. 1987. Age and growth of the Warsaw grouper and black grouper from the southeast region of the United States. *Northeast Gulf Science* 9:65-75.
- Mason, D. L. and C. S. Manooch, III. 1985. Age and growth of mutton snapper along the East coast of Florida. *Fisheries Research* 3:93-104.
- Matheson, R. H., III and G. R. Huntsman. 1984. Growth, mortality, and yield-per recruit models for speckled hind and snowy grouper from the United States South Atlantic Bight. *Transactions of the American Fisheries Society* 113:607-616.
- \_\_\_\_\_, \_\_\_\_\_ and C. S. Manooch, III. 1986. Age, growth, mortality, food and reproduction of the scamp, *Mycteroperca phenax* collected off North Carolina and South Carolina. *Bulletin of Marine Science* 38:300-312.
- McErlean, A. J. 1963. A study of the age and growth of the gag, *Mycteroperca microlepis* Goode and Bean (Pisces Serranidae) on the west coast of Florida. *Florida State Board of Conservation Marine Laboratory* 41:1-29.
- \_\_\_\_\_ and C. L. Smith. 1964. The age of sexual succession in the protogynous hermaphrodite *Mycteroperca microlepis*. *Transactions of the American Fisheries Society* 93:301-302.
- McGovern, J. C., D. M. Wyanski, O. Pashuk, C. S. Manooch II, and G. S. Sedberry. 1998. Changes in the sex ratio and size at maturity of gag, *Mycteroperca microlepis*, from the Atlantic coast of the southeastern United States during 1976-1995. *Fishery Bulletin* 96:797-807.
- Millares, N., M. Borrego, T. Damas, and E. González. 1979. Desove inducido de la biajaiba. *Revista Cubana de Investigación Pesquera* 41:1-20.
- Minton, R. V., J. P. Hawke, and W. M. Tatum. 1983. Hormone induced spawning of red snapper, *Lutjanus campchanus*. *Aquaculture* 30:363-368.
- Moe, M. A. 1969. *Biology of the Red Grouper Epinephelus morio (Valenciennes) from the Eastern Gulf of Mexico*. Florida Department of Natural Resources, Marine Research Laboratory, Professional Papers Series No. 10. St. Petersburg, Florida: Florida Department of Natural Resources. 95 pp.
- Moore, C. M. and R. F. Labisky. 1984. Population parameters of relatively unexploited stock of snowy grouper in the Lower Florida Keys. *Transactions of the American Fisheries Society* 113:322-329.
- Moseley, F. N. 1966. Biology of the red snapper, *Lutjanus aya* Bloch, of the Northwestern Gulf of Mexico. *Publications of the Institute of Marine Science, University of Texas* 11:90-101.
- Muhlia-Melo, A. F. 1976. Aspectos biológico-pesqueros de *Epinephelus morio* (Val.) "mero". Pp. 223-265 in *Simposium Nacional sobre Recursos Pesqueros Masivos de México*. México, D.F.: Instituto Nacional de la Pesca.
- Munro, J. L., V. C. Gaut, R. Thompson, and P. H. Reeson. 1973. The spawning seasons of Caribbean reef fishes. *Journal of Fish Biology* 5:69-84.

- Musick, J. A., M. M. Harbin, S. A. Berkeley, G. H. Burgess, A. M. Eklund, L. Findley, R. G. Gilmore, J. T. Golden, D. S. Ha, G. R. Huntsman, J. C. McGovern, S. J. Parker, S. G. Poss, E. Sala, T. W. Schmidt, G. R. Sedberry, H. Weeks, and S. G. Wright. 2000. Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). *Fisheries* 25:6-30
- Nelson, J. S. 1994. *Fishes of the World, 3<sup>rd</sup> Edition*. New York: John and Wiley and Sons, Inc. 599 pp.
- Parrish, J. D. 1987. The trophic biology of snappers and groupers. Pp. 405-439 in: J. J. Polovina and S. Ralston (eds.), *Tropical Snappers and Groupers: Biology and Fisheries Management*. Boulder, Colorado: Westview Press.
- Patterson, W. F., III, G. W. Walter-Ingram Jr., R. L. Shipp, and J. H. Cowan Jr. 2002. Indirect estimation of red snapper (*Lutjanus campechanus*) and gray triggerfish (*Balistes capriscus*) release mortality. *Proceedings of the Gulf and Caribbean Fisheries Institute* 53:526-535.
- Potts, J. C. and C. S. Manooch, III. 1995. Age and growth of red hind and rock hind collected from North Carolina through the Dry Tortugas, Florida. *Bulletin of Marine Science* 56:784-794.
- \_\_\_\_\_ and \_\_\_\_\_. 1999. Observations on the age and growth of graysby and coney from the Southeastern United States. *Transactions of the American Fisheries Society* 128:751--757.
- Powell, A. B. and J. W. Tucker Jr. 1992. Egg and larval development of laboratory-reared Nassau grouper *Epinephelus striatus* (Pisces, Serranidae). *Bulletin of Marine Science* 50:171-185.
- Presley, R. F. 1970. *Larval Snowy Grouper Epinephelus niveatus (Valenciennes, 1828) from the Florida Straits*. Florida Department of Natural Resources Marine Research Laboratory, Leaflet Series IV, Part 1 (Pisces), No. 18. St. Petersburg, Florida: Florida Department of Natural Resources. 6 pp.
- Rabalais, N. N., R. S. Carney, and E. G. Escobar-Briones. 1999. Overview of continental shelf benthic communities of the Gulf of Mexico. Pp. 171-195 in H. Kumpf, K. Steidinger, and K. Sherman (eds.), *The Gulf of Mexico Large Marine Ecosystem: Assessments, Sustainability and Management*. Malden, Massachusetts: Blackwell Science.
- Rabalais, N. N., S. C. Rabalais, and C. R. Arnold. 1980. Description of eggs and larvae of laboratory reared red snapper (*Lutjanus campechanus*). *Copeia* 4:704-708.
- Ralston, S. 1987. Mortality rates of snappers and groupers. Pp. 375-404 in J. J. Polovina and S. Ralston (eds.), *Tropical Snappers and Groupers: Biology and Fisheries Management*. Boulder, Colorado: Westview Press.
- Randall, J. E. 1967. Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography* 5:665-847.
- Renán, X., T. Brulé, T. Colás-Marrufo, Y. Hauyon, and C. Déniel. 2001. Preliminary results of the reproductive cycle of the black grouper, *Mycteroperca bonaci* from the southern Gulf of Mexico. *Proceedings of the Gulf and Caribbean Fisheries Institute* 52:1-14.
- \_\_\_\_\_, K. Cervera-Cervera, and T. Brulé. 2003. Probable nursery areas for juvenile groupers along the northern coast of the Yucatan Peninsula, Mexico. *Proceedings of the Gulf and Caribbean Fisheries Institute* 54:1496-1505.



- Richards, W. J. and V. P. Saksena. 1980. Description of larvae and early juveniles of laboratory-reared gray snapper, *Lutjanus griseus* (Linnaeus) (Pisces, Lutjanidae). *Bulletin of Marine Science* 30:515-522.
- Rivas, L. R. 1979. Review of the *Lutjanus campechanus* complex of red snappers. *Quarterly Journal of the Florida Academy of Sciences* 15:117-135.
- Roberts, D. E. Jr. and R. A. Schlieder. 1983. Induced sex inversion, maturation, spawning and embryogeny of the protogynous grouper, *Mycteroperca microlepis*. *Journal of World Mariculture Society* 14:639-649.
- Roberts, M. R., N. Quinn, J. W. Tucker Jr., and P. N. Woodward. 1995. Introduction of hatchery-reared Nassau grouper to a coral reef environment. *North American Journal of Fisheries Management* 15:159-164.
- Rodríguez-Sánchez, H. 1986. Determinación de la edad y crecimiento del mero (*Epinephelus morio* Valenciennes) del Banco de Campeche utilizando dos estructuras óseas diferentes (otolito y hueso mesopterigoides). Tesis profesional, Universidad Autónoma de Nuevo León, San Nicolás de los Garza, Nuevo León, México. 22 pp.
- Russ, G. R. 2002. Yet another review of marine reserves as reef fishery management tools. Pp. 421-443 in P. Sale (ed.), *Coral Reef Fishes*. San Diego, California: Elsevier Science.
- Sadovy, Y. 1994. Grouper stocks of the western central Atlantic: the need for management and management needs. *Proceedings of the Gulf and Caribbean Fisheries Institute* 43:43-64.
- \_\_\_\_\_. 1996. Reproduction of reef fishery species. Pp. 15-59 in N.V.C. Polunin and C. M. Roberts (eds.), *Reef Fisheries*. London: Chapman and Hall.
- \_\_\_\_\_. 1997. Problems of sustainability in grouper fisheries. Pp. 321-324 in *Proceedings of the Fourth Asian Fisheries Forum*. Beijing, China: China Ocean Press.
- \_\_\_\_\_. 1999. MPAs as generic tool. With emphasis on protection of long-lived fishes, such as groupers. *Fisheries Research Report* 5:43-45.
- \_\_\_\_\_. 2001. The threat of fishing to highly fecund fishes. *Journal of Fish Biology* 59:90-108.
- \_\_\_\_\_ and P. L. Colin. 1995. Sexual development and sexuality in the Nassau grouper. *Journal of Fish Biology* 46:961-976.
- \_\_\_\_\_ and M. L. Domeier. 1994. Aggregation and spawning in the tiger grouper, *Mycteroperca tigris* (Pisces: Serranidae). *Copeia* 2:511-516.
- \_\_\_\_\_ and A. M. Eklund. 1999. Synopsis of biological data on the Nassau grouper, *Epinephelus striatus* (Bloch, 1792), and the jewfish, *E. itajara* (Lichtenstein, 1822) NOAA Technical Report NMFS 146, FAO Fisheries Synopsis No. 157. Seattle, Washington: U.S. Department of Commerce, National Oceanic and Atmospheric Administration. 65 pp.
- \_\_\_\_\_ and D.Y. Shapiro. 1987. Criteria for the diagnosis of hermaphroditism in fishes. *Copeia* 1:136-156.
- \_\_\_\_\_, M. Figuerola, and A. Román. 1992. Age, growth of *Epinephelus guttatus* in Puerto Rico and St. Thomas. *Fishery Bulletin* 90:516-528.
- \_\_\_\_\_, A. Rosario, and A. Román. 1994. Reproduction in an aggregating grouper, the red hind, *Epinephelus guttatus*. *Environmental Biology of Fishes* 41:269-286.
- Sale, P. F. 2002. The science we need to develop for more effective management. *Coral Reef Fishes*. Pp. 361-375 in P. Sale (ed.), *Coral Reef Fishes*. San Diego, California: Elsevier Science.

- Schirripa, M. J. and C. P. Goodyear. 1994. Status of the vermilion snapper (*Rhomboplites aurorubens*), red snapper (*Lutjanus campechanus*), and gag (*Mycteroperca microlepis*) in the U.S. Gulf of Mexico. *Proceedings of the Gulf and Caribbean Fisheries Institute* 51:139-151.
- SEMARNAP. 2000. *Sustentabilidad y Pesca Responsable en México: Evaluación y Manejo 1997-1998*. México, D.F.: Secretaría de Medio Ambiente, Recursos Naturales y Pesca-INP. 691pp.
- Shapiro, D.Y. 1987. Reproduction in groupers. Pp. 295-327 in J. J. Polovina and S. Ralston (eds.), *Tropical Snappers and Groupers: Biology and Fisheries Management*. Boulder, Colorado: Westview Press.
- \_\_\_\_\_, Y. Sadovy, and M. A. McGehee. 1993a. Periodicity of sex change and reproduction in the red hind, *Epinephelus guttatus*, a protogynous grouper. *Bulletin of Marine Science* 53:1151-1162.
- \_\_\_\_\_, \_\_\_\_\_ and \_\_\_\_\_. 1993b. Size, composition and spatial structure of the annual spawning aggregation of the red hind, *Epinephelus guttatus* (Pisces: Serranidae). *Copeia* 1993(2):399-406.
- Sherman, K. 1994. Sustainability, biomass yields, and health of coastal ecosystems: An ecology perspective. *Marine Ecology Progress Series* 112:277-301.
- Shipp, R. 1999. Status of exploited fish species in the Gulf of Mexico. Pp. 196-203 in H. Kumpf, K. Steidinger, and K. Shermam (eds.), *The Gulf of Mexico Large Marine Ecosystem: Assessments, Sustainability and Management*, Malden, Massachusetts: Blackwell Science.
- Sluka, R., M. Chiappone, K. M. Sullivan, and R. Wright. 1997. The benefits of marine fishery reserve for Nassau grouper *Epinephelus striatus* in the central Bahamas. *Proceedings of the 8<sup>th</sup> International Coral Reef Symposium* 2:1961-1964.
- Smith, C. L. 1959. Hermaphroditism in some serranid fishes from Bermuda. *Papers of the Michigan Academy of Science, Arts and Letters* 41:111-119.
- \_\_\_\_\_. 1961. *Synopsis of Biological Data on Groupers (Epinephelus and Allied Genera) of the Western North Atlantic*. FAO Fisheries Biology Synopsis No. 23. Rome: Food and Agriculture Organization of the United Nations. 67 pp.
- \_\_\_\_\_. 1967. Contribution to a theory of hermaphroditism. *Journal of Theoretical Biology* 17:76-90.
- \_\_\_\_\_. 1971. A revision of the American groupers: *Epinephelus* and allied genera. *Bulletin of the American Museum of Natural History* 146:67-242.
- \_\_\_\_\_. 1997. *National Audubon Society Field Guide to Tropical Marine Fishes of the Caribbean, the Gulf of Mexico, Florida, the Bahamas, and Bermuda*. New York: Alfred A. Knopf, Inc. 720 pp.
- Starck, W. A. 1971. Biology of the gray snapper, *Lutjanus griseus* (Linnaeus), in the Florida Keys. *Studies in Tropical Oceanography, University of Miami* 10:11-150.
- \_\_\_\_\_ and R. E. Schroeder. 1970. *Investigations on the Gray Snapper, Lutjanus griseus*. Studies in Tropical Oceanography No. 10. Miami, Florida: Rosenstiel School of Marine and Atmospheric Science. 224 pp.
- Stevenson, D. K. 1981. *A Review of the Marine Resources of the Western Central Atlantic Fisheries Commission (WECAFC) Region*. FAO Fisheries Technical Paper No. 211. Rome: Food and Agriculture Organization of the United Nations. 118 pp.

- \_\_\_\_\_. 1978. Aspects of the biology and ecology of Caribbean reef fishes: Serranidae (hinds and groupers). *Journal of Fish Biology* 12:115-146.
- Thompson, R. and J. L. Munro 1978. Aspects of the biology and ecology of Caribbean reef fishes: Serranidae (hinds and groupers). *Journal of Fish Biology* 12:115-146.
- \_\_\_\_\_ and \_\_\_\_\_. 1983. The biology, ecology and bionomics of the snappers, Lutjanidae. *ICLARM Technical Report* 7:94-109.
- Thresher, R. E. 1984. *Reproduction in Reef Fishes*. Neptune City, New Jersey: T. F. H. Publications. 399 pp.
- Torres, R. and E. Chávez. 1987. Evaluación y diagnóstico de la pesquería de rubia (*Lutjanus synagris*) en el estado de Yucatán. *Ciencias Marinas* 13:7-29.
- Trexler, J. C. and J. Travis. 2000. Can marine protected areas restore and conserve stock attributes of reef fishes? *Bulletin of Marine Science* 66:853-873.
- Tucker, J. W., Jr. 1991. Induced spawning of Nassau grouper *Epinephelus striatus*. *Journal of the World Aquaculture Society* 22:187-191.
- \_\_\_\_\_. 1998. *Marine Fish Culture*. Boston: Kluwer Academic Publishers. 760 pp.
- Tupper, M. 2002. Essential fish habitat and marine reserves for groupers in the Turks & Caicos Islands. *Proceedings of the Gulf and Caribbean Fisheries Institute* 53:606-622.
- Tuz-Sulub, A. N. 1999. Composición, distribución e importancia pesquera de los serránidos (Subfamilia Epinephelinae) en el Banco de Campeche, Yucatán, México. Tesis de maestría, CINVESTAV-Unidad Mérida, Mérida, Yucatán, México: 76 pp.
- \_\_\_\_\_. N., K. Cercera-Cervera, T. Colás-Marrufo, and T. Brulé. 2003. Primeros indicios sobre la formación de agregaciones de reproducción de meros (Epinephelinae: Epinephelini) en el Banco de Campeche. *Proceedings of the Gulf and Caribbean Fisheries Institute* 54:652-667.
- Valdés, E. and G. Padrón. 1980. Pesquerías de palangre. *Revista Cubana de Investigación Pesquera* 5:38-52.
- Watanabe, W. O., S. C. Ellis, E. P. Ellis, V. G. López, P. Bass, J. Ginoza, and A. Moriwake. 1996. Evaluation of first-feeding regimens for larval Nassau grouper *Epinephelus striatus* and preliminary, pilot-scale culture through metamorphosis. *Journal of the World Aquaculture Society* 27:323-331.
- \_\_\_\_\_, E. P. Ellis, S. C. Ellis, J. Chavez, C. Manfredi, R. W. Hagood, M. Sparsis, and S. Arneson. 1998. Artificial propagation of mutton snapper *Lutjanus analis*, a new candidate marine fish species for aquaculture *Journal of the World Aquaculture Society* 29:176-186.
- Wilson, R. W. Jr. and K. M. Burns. 1996. Potential survival of released groupers caught deeper than 40 m based on shipboard and in-situ observations, and tag-recapture data. *Bulletin of Marine Science* 58:234-24
- Woods, M. K., A. J. Fischer, J. H. Cowan Jr., and D. L. Nieland. 2003. Size and age at maturity of female red snapper *Lutjanus campechanus* in the northern Gulf of Mexico. *Proceedings of the Gulf and Caribbean Fisheries Institute* 54:527-537.