Variability in Life-History Traits of Groupers: Significance for Fisheries Management Plans

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ABSTRACT
Groupers (Subfamily: *Epinephelinae*) are important components of commercial fisheries in tropical and subtropical reef environments. More so than with typical temperate species, the unusual and complex biology and ecology of groupers mandates that their life-history characteristics be explicitly incorporated into any management strategy. Previous assumptions used in managing groupers are reevaluated in light of a comprehensive review and new findings on grouper life histories. Past overviews tend to generalize that groupers are protogynous hermaphrodites (changing sex from adult female to male), long lived, slow growing , sexually dimorphic in length and have female biased-sex ratios. Other general patterns have been related with size (e.g. smaller groupers do not aggregate and tend to spawn over extended periods). However, recent observations indicate that some species show different life-history characteristics, such as a predominantly gonochroristic sexual pattern, relatively short lifespan, wide size range overlap between sexes and a sex ratio close to unity. Also, small species appear to spawn in aggregations during a restricted period of time.

Key words: Plasticity, Life-History, Groupers, Fisheries, Management.

RESUMEN
Los meros (Subfamilia: *Epinephelinae*) constituyen un componente importante de las pesquerías arrecifales tropicales y subtropicales. Contrario a las especies en aguas templadas, la particular y compleja bio-ecología de los meros obliga a que las características de cada población se incorporen de manera individual dentro de las estrategias de manejo. Suposiciones utilizadas previamente en el diseño de planes de manejo para estas especies, son reevaluadas a la luz de nuevos descubrimientos en sus historias de vida. Evaluaciones previas tienden a generalizar que los meros son hermafroditas protogínicos (cambian de sexo de hembras adultas a machos), son longevos, crecen lentamente, sus sexos difieren en talla y las poblaciones se caracterizan por una mayor abundancia de hembras. Otros rasgos han sido relacionados con la talla (*e.j.* meros pequeños no forman agregaciones y tienden a desovar en períodos prolongados). Sin embargo, observaciones recientes indican que algunas especies muestran características diferentes, tales como un patrón sexual predominantemente gonocoristico (sexos separados), un período de vida relativamente corto, un solapamiento en la talla entre los sexos y una proporción de sexos cercana a la unidad. Las especies pequeñas, al igual que las de mayor talla, parece que forman agregaciones y desovan en períodos breves.

INTRODUCTION

Life-history studies have been oriented primarily to address the way in which a species lives. This is achieved through measuring age-specific, growth and mortality, as well as several aspects of reproductive biology for a particular population. This information can be used to further the theory of life-history strategies or used toward a practical consideration for stock assessment and fishery advice.

Much of what is known about commercially important species is based on studies at one or few locations. Small fisheries agencies with limited resources for collecting data tend to rely, at least partly, on population parameters established elsewhere (Sadovy 1994); quite often, information is extrapolated to higher taxonomic levels. Some trends are fairly consistent and allow this kind of generalization, others are so variable that generalizations do not hold, even within species.

The groupers (*Pisces, Serranidae*), defined as large members of the subfamily *Epinephelinae*, consist of the following 3 genera in American waters, *Paranthias*, *Epinephelus* and *Mycteroperca*. Worldwide studies tend to generalize that groupers are monandric protogynous hermaphrodites (where all males come from adult sex-reversed females) (Lavenda 1949, C. L. Smith 1959, 1965, Moe 1969, Bruslé and Bruslé 1975, Bouain and Siau 1983, Shapiro 1987), long lived and slow growing (Manooch 1987), sexually dimorphic in length (Thresher 1984), and female-biased (Shapiro 1987). Other traits, such as mating system and length of spawning season have been related to size (*e.g.* small groupers do not aggregate to spawn, they spawn over extended periods, and their males have small testes, while the opposite is expected for the large groupers; Sadovy et al. 1994, Sadovy, in press).

Bannerot (1984) pointed out the need to develop stock assessment models that account for the peculiarities of life history, and in general, groupers have been managed according to the above patterns as if they were universal. However, previous generalities may be misleading. Detailed studies exist for less than 20% of the 159 described species of groupers worldwide (Heemstra and Randall 1993), and most of these are for large groupers. Furthermore, few studies have accounted for environmental variability that may affect final phenotypic expressions.

The objectives of the present paper are (1) to determine the existence or not of common life-history patterns within the groupers and their correlating parameters (*e.g.* size, social organization), and (2) to compare life-history parameters in populations located along a latitudinal gradient in the western Atlantic. Results are interpreted in light of management considerations.

LIFE-HISTORY PATTERNS OF GROUPERS

Sexual pattern

As recent as 1987, no grouper had been discovered to be gonochoristic. However, Shapiro (1987) suspected that the existence of several protogynous groupers was not sufficient to conclude that all groupers were protogynous. Colin (1992) and Bullock *et al.* (1992) suspected gonochorism in two of the largest groupers, the Nassau grouper *Epinephelus striatus* (Bloch) and jewfish, *Epinephelus itajara* (Lichtenstein), respectively, while the sexual pattern of one of the smallest groupers, the Creole fish, *Paranthias furcifer* (Valenciennes), has been controversial and poorly defined for years (C. L. Smith 1959, 1965, Thompson and Munro 1974, 1978, Nelson *et al.* 1986, Bullock and G. B. Smith 1991).

A predominantly gonochoristic sexual pattern has been confirmed for both the Nassau grouper (Sadovy and Colin 1995) and the Creole fish (Posada 1996), while for jewfish further study is required. Moreover, the existence of two pathways of male developmental in groupers has been indicated by Sadovy *et al.* (1994) for the red hind, *Epinephelus guttatus* (Linnaeus) and by Siau (1994) for the east Atlantic grouper, *Cephalopholis taeniops* (Valenciennes).

Population structure

Monandric protogynous groupers have bimodal sex-specific size-frequency distributions (modal size of females is less than modal size of males) and female-biased sex ratios (Shapiro 1987). Oppositely, unfished populations of the gonochoristic Nassau grouper and Creole fish show only a slight female bias populations and little size difference between the sexes (Sadovy and Colin 1995, Posada 1996).

Mating system

Spawning aggregations at traditional sites have been commonly reported for large commercial groupers (see Auil-Marshalleck 1993, Sadovy 1994). Intensive fishing of these aggregations is one of the primary causes for overexploitation and stock collapse.

Smaller groupers were assumed to be protogynous hermaphrodites, not to aggregate, and have small testes [*e.g.* the coney, *Epinephelus fulvus* (Linnaeus), the graysby, *E. cruentatus* (Lacepède); Sadovy *et al.* 1994]. However, small aggregations have been reported for *E. fulvus* (Burnett-Herkes 1975, Carter *et al.*, 1994) and suggested for the Creole fish by Burnett-Herkes (1975) and by Posada (1996) based on the presence of large testis (up to 15.7% of the body weight).

Length of the spawning

While there is considerable interspecific and intraspecific variability on the duration of the spawning season within 12 studied western Atlantic groupers, it appears that peak of spawning lasts 1-3 months for most species (Figure 1). Sadovy (In press) indicated that scoring the months with vitellogenic oocytes tends to overestimate length of the spawning season. Posada (1996) observed that while female gonads with yolked oocytes and males expelling sperm were found from September to February in Paranthias furcifer, actual spawning occurred over a two-month period (November and December).

Sadovy (In press) suggested that length of the spawning season was linked with body size, with smaller grouper species tending to spawn over extended periods, and larger species exhibiting shorter reproductive seasons. However, the patterns shown in Figure 1 run counter to this hypothesis.

### Frequency of spawning and fecundity

From the previous section, it is easy to see that some researchers consider that female groupers spawn only once annually, while others suggest multiple spawnings. The number of spawnings is a critical assumption underlying fecundity estimation, particularly, in those groupers with brief spawning periods. Models used to assess the status of fish stock, as Spawning-stock-biomass-per-recruit (Goodyear 1989), require an unbias estimation of weight-specific fecundity estimation.

Figure 1 (opposite). Interspecific and intraspecific variability on the duration of the spawning season within 12 western Atlantic grouper species, ranked by size categories (1=largest, 4=smallest). Black areas refers to specific description of the spawning period. Sources: 1=Bannerot (1984), 2=Bullock and G.B. Smith (1991), 3=Bullock and Murphy (1994), 4=Bullock et al.(1992), 5=Burnett-Herkes (1975), 6=Carter et al. (1994), 7=Colin (1994), 8=Colin et al. (1987), 9=Collins et al.(1987), 10=Erdman (1956), 11=Hood and Schlieder (1992), 12=Koenig et al.(In press), 13=Manooch and Haimovici (1978), 14=Matheson et al.(1986), 15=Moe (1969), 16=Moore and Labisky (1984), 17=McErlean (1963), 18=Munro et al.(1973), 19=Nagelkerken (1979), 20=Nelson et al. (1986), 21=Perez-Villarroel (1982), 22=Sadovy et al.(1994), 23=Schroeder (1924), 24=Shapiro et al. (1993), 25=C.L. Smith (1958), 26=C.L. Smith (1961), 27=C.L. Smith (1971), 28=C.L.Smith (1972), 29=G.B. Smith (1976), 30=Taylor and McMichael (1983), 31=Thompson and Munro (1974), 32=Thompson and Munro (1978), 33=Tucker et al. (1993), 34=Posada (1996), 35=pers. obs.
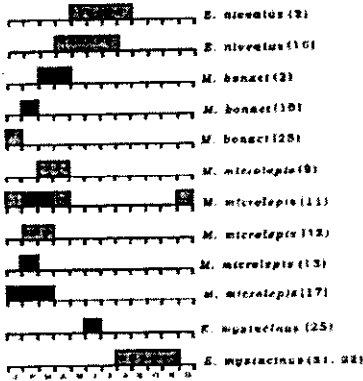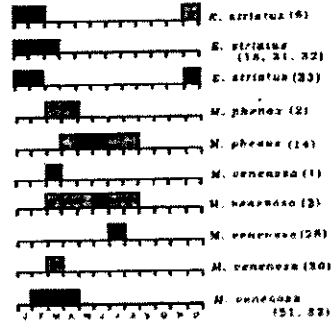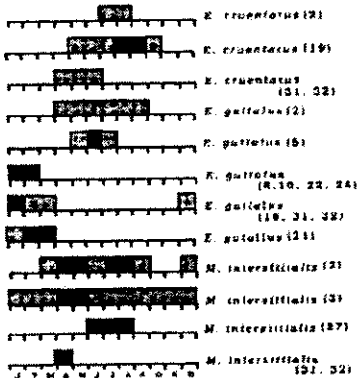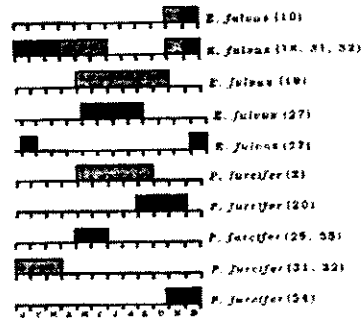
Determininate fecundity (*i.e.* potential annual fecundity becomes fixed prior to the onset of spawning) is most likely in those species, populations or individuals that spawn over restricted periods each year (Sadovy in press). This appears to be the case for the red hind. Sadovy *et al.* (1994) following the modal progression of oocytes diameters in this species; observed spawning occurred more than once during the course of the spawning season, but no evidence for recruitment of non-vitellogenic oocytes was found. However, Posada (1996) suggested that the Creole fish, from Puerto Rico, may be an indeterminate spawner and that brief spawning periods and determinate fecundity do not correlate. Estimation of total fecundity is meaningless if, during the spawning season, oocytes are added to the stock of advanced oocytes (Hunter *et al.* 1992)

Time of the spawning
Several studies have correlated spawning seasonality to simple environmental variables, *e.g.* day length, water temperature (Moe 1969, Burnett-Herkes 1975, Nagelkerken 1979, Pérez-Villarroel 1982, Tucker *et al.* 1993, Sadovy and Colin 1995). Although it is beyond the scope of the present analyses to explore in detail the validity or not of such correlations, its is important to notice the presence of some apparent trends along a latitudinal gradient.

Sadovy (In press) suggested that in the Caribbean region, groupers tend to spawn from December to March, while in more northerly areas such as Florida and Bermuda, the same species tend to spawn between April and August. An extended latitudinal comparison between 18 of the western Atlactic groupers, shown in Figure 2, appears to confirm such pattern (Figure 2). Robertson (1991) was skeptical to accept a pattern of geographical variation in spawning cycle for tropical western Atlantic snappers and groupers because the existence of some exceptions, but those exceptions noted by Robertson (1991) appear to be more related to Lutjanids.

Age-(size-) at-first maturation
Maximum life span in groupers does not appear to predict age-at-first maturation. Table 1 shows a great variability in age-at-first maturation for some of the large long-lived groupers, while most of smaller species tend to mature when 2 years old. Size is a better predictor than age. For 20 populations of groupers, Sadovy (In press) calculated the following regression between length-at-maturity (L_m) and asymptotic size ($L\infty$)(TL, for females): $L_m = 0.5165 \cdot L\infty - 16.46$ (N = 20, $r^2 = 0.87$).

In protogynous species, the size (age) of sexual transition represents that of male maturation (Sadovy, In press). Conversely, the similarity of female and male maturation size (age) in the Nassau grouper and the Creole fish reflect their predominantly gonochoristic sexual pattern (Sadovy and Colin 1995, Posada 1996).
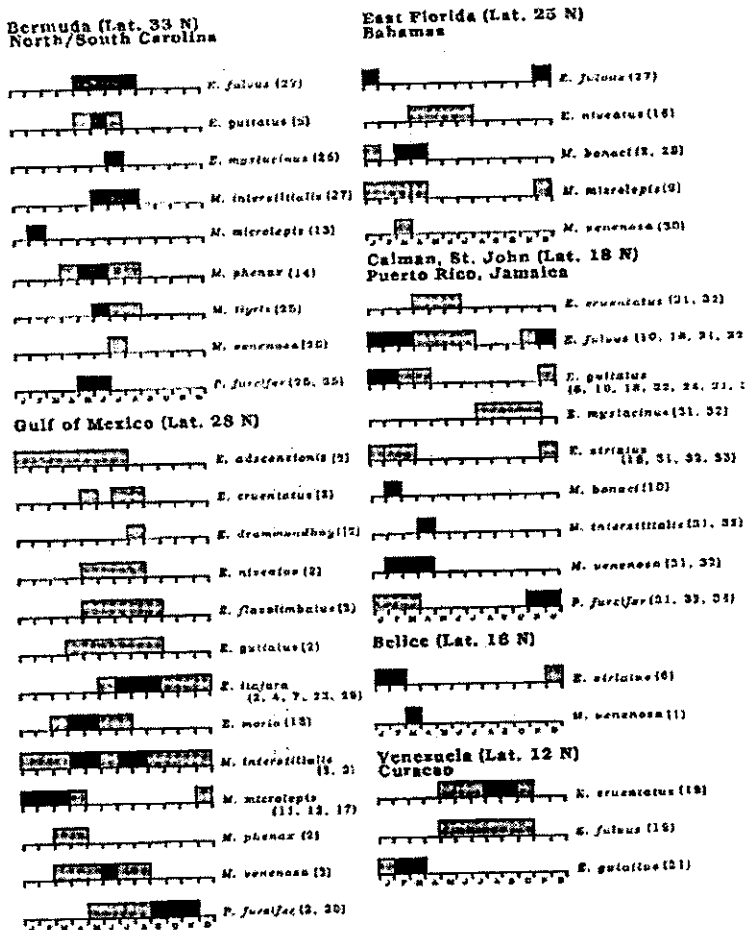
Figure 2. Comparison in the time of spawning along a latitudinal gradient within 18 western Atlantic grouper species. Shadow areas refers to presence of ripe specimens in the population. Black areas refers to specific description of the spawning period. Sources: as in Figure 1.

Table 1. Age and length (at maturation and maximum) reported for some of the western Atlantic female groupers.

Species	Age (years)		Length (mm,TL)		Source
	at maturation	maximum	at maturation	maximum	
s *Epinephelus cruentatus*	2	9	140	415	Nagelkerken (1979)
m *Epinephelus guttatus*	2	9	195	480	Sadovy et al. (1994)
a					Shapiro et al. (1993)
l *Mycteroperca interstitialis (Poey)*	2	16	420	750	Bullock and Murphy (1994)
l *Paranthias furcifer*	2	9	169	423	Nelson et al. (1986)
	2	8	174	267	Posada (1996)
l *Epinephelus itajara (Lichtenstein)*	6	37	1200	2006	Bullock et al. (1992)
a *Epinephelus morio (Valenciennes)*	4	24	441	792	Moe (1969)
r *Epinephelus niveatus (Valenciennes)*	4	15	450	1000	Moore and Labisky (1984)
g *Epinephelus striatus*	9	21	502	846	Sadovy and Colin (1995)
e *Mycteroperca microlepis (Goode and Bean)*	3	20.5	600	1100	Colins et al. (1987)
	2	16	450	1110	Hood and Schlieder (1992)
	5	10.5	≈610	≈1000	McErlean (1963)
					McErlean and Smith (1964)

Recruitment

Little is known about recruitment for the majority of grouper species, however, juvenile of several species of grouper depend on shallow, near shore habitats, prior to their migrating offshore (Keener *et al.* 1988, Sadovy 1994, Eggleston 1995). All of these are species that reside primarily over the shelf. Other species such as the Creole fish and the misty grouper, *Epinephelus mystacinus* (Poey) are primarily slope species (Thompson and Munro 1974, 1978, Posada, 1996) and their juveniles could be associated with a different environment. Small specimens of the Creole fish have been found in the stomachs of yellowfin and skipjack tunas (Dragovich 1970), and a juvenile misty grouper was observed around an abandoned fish trap in water 27 m deep (Sutherland *et al.* 1983). There could be differences on recruitment pattern and ontogenetic migration between primarily slope dwellers and relatively shallow water species. An understanding of the species-specific habitats for juvenile and adult stages need to be incorporated into management strategies.

Growth pattern and mortality

Small groupers are relatively short lived (mean = 7.6 years) and attain asymptotic length at a faster rate than larger, long lived groupers (see Manooch 1987). Appeldoorn (1992) recommended that growth parameters be plotted on a Log-Log scale to assess variability and look for trends. Figure 3 plots the von Bertalanffy parameters for groupers from Table 2. The plot shows that there is considerable variability both within and among species. However, these follow specific relationships. Intraspecific variations follow the ø' relationship of Pauly and Munro (1984), *i.e.* not significantly different from the theoretical ø'-value of slope -2 at 95% confidence limits. The average ø'-line is illustrated in the figure 3 for parameters of the red hind, for which multiple estimates are available. Interspecific variations follow the Φ' relationship of Appeldoorn (1992). A regression of all estimates yielded the following relationship: Log (k) = 1.167 - 0.696 Log (L∞), r^2 = 0.56. The slope of this relationship is not significantly different from the theoretical Φ'- value of 0.75. When comparative data are available, the combined use of ø' and Φ' can aid in the estimation or validation of growth parameters. By this method, the estimate of Munro and Thompson (1974, 1978) for *Epinephelus fulvus* appears to be an outlier.

Pauly (1981) for fishes in general, and Manooch (1987) for groupers argue that a given species will attain a larger asymptotic size and a lower growth coefficient in the cooler temperatures of higher latitudes. However, Manooch (1987) failed to demonstrate such a pattern. The expanded data shown in Figure 3 also fails to support this argument.

General remarks

Ideally management strategies should be established for each of the more important species in a fishery since the behavior of the resource depends on the

Table 2. Growth parameters (Asymptotic length, L and growth coefficient, k) reported for some of the western Atlantic groupers.

	Species	Area
1	*Epinephelus adscensionis* (Osbeck)	Southeastern U.S.
2	*Epinephelus cruentatus*	Curacao
s 3		Jamaica
4	*Epinephelus fulvus*	Jamaica
m 5		Virgin Is.
6	*Epinephelus guttatus*	Bermuda
a 7		Jamaica
8		Southeastern U.S.
l 9		Puerto Rico
10		Virgin Is.
l 11	*Paranthias furcifer*	Gulf of Mexico
12		Puerto Rico
13		Puerto Rico
14	*Epinephelus drummondhayi* Goode and Bean	Southeastern U.S.
15	*Epinephelus itajara* (Lichtenstein)	Gulf of Mexico
l 16	*Epinephelus morio*	Gulf of Mexico
17		Gulf of Mexico
a 18		Southeastern U.S.
19	*Epinephelus nigritus* (Holbrook)	Southeastern U.S.
r 20	*Epinephelus niveatus*	Southeastern U.S.
21		Florida Keys
g 22	*Epinephelus striatus*	Virgin Is.
23	*Mycteroperca bonaci* (Poey)	Southeastern U.S.
e 24	*Mycteroperca microlepis*	Southeastern U.S.
25		Gulf of Mexico
26	*Mycteroperca venenosa* (Linnaeus)	Jamaica

| L∞ (mm, TL)	k (year-1)	Source
499	0.167	Potts and Manooch (1995)
41	0.130	Nagelkerken (1979)
340	0.340	Thompson and Munro (1974,1978)
340	0.630	Thompson and Munro (1974, 1978)
340	0.300	Beets et al. (1990)
507	0.180	Burnett-Herkes(1975)
520	0.240	Thompson and Munro (1974, 1978)
471	0.200	Potts and Manooch (1995)
514	0.101	Sadovy et al. (1992)
601	0.075	Sadovy et al. (1992)
423	0.220	Nelson et al. (1986)
312	0.282	Posada and Appeldoorn (In press)
267	0.306	Posada (1996)
967	0.130	Matheson and Huntsman (1984)
2006	0.126	Bullock et al. (1992)
928	0.113	Melo (1975)
792	0.180	Moe (1969)
938	0.153	Stiles and Burton (1994)
2394	0.054	Manooch and Mason (1987)
1255	0.074	Matheson and Huntsman (1984)
1320	0.087	Moore and Labisky (1984)
900	0.090	Randall (1962, 1963)
1352	0.116	Manooch and Mason (1987)
1290	0.122	Manooch and Haimovici (1978)
1190	0.166	Hood and Schlieder (1992)
860	0.100	Thompson and Munro (1974, 1978)
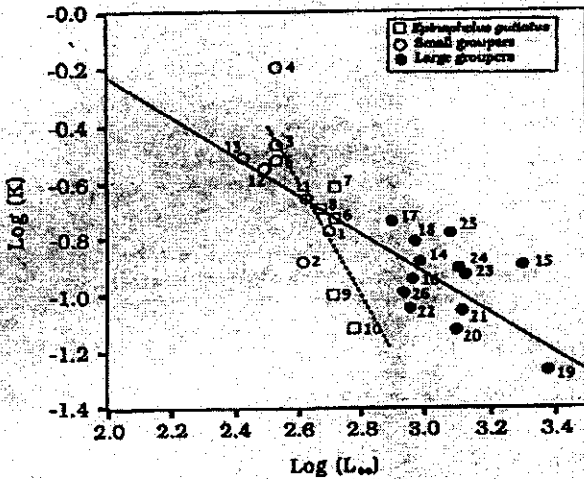
Figure 3. Log-log of von Bertalanffy growth parameters, L∞ and k, covering 14 western Atlantic grouper species given in Table 2. Solid line represent Φ'-value for interspecific comparisons. Dashed line represent the theoretical ø-value for intraspecific comparison, illustrated with the red hind.

biological and exploitation characteristics of individual species. However, such an approach is difficult, particularly for multispecies tropical marine fisheries. Evaluation of variability in life-history parameters within a particular taxon may prove valuable in providing some needed estimates or simplifying assumptions.

Life-history parameters such as life span, asymptotic length or size (age)-at-first sexual maturation vary greatly within the grouper subfamily. Nevertheless, there exists among these parameters certain consistent correlated trade-offs, as previously indicated by Beverton and Holt (1959), Ni (1978), Pauly (1980) and Ralston (1987). These trade-offs have been expressed into mathematical functions such as Ralston's (1987) equation to predict natural mortality, Sadovy's (In press) equation to predict size-at-first maturation and Pauly and Munro's (1984) and Appeldoorn's (1992) equations for growth parameter estimation. In spite of relying only on a single parameter, these functions have proved very useful in the context of fishery science as estimation or verification tools.

Other parameters, in particular those relate with the reproductive biology of groupers, also show high variability. Some expected generalities were supported [e.g. Sadovy's (In press) suggestion of temperature dependent spawning in the northwestern Atlantic] while others did not hold. An examination of the available

data offers possible explanations and suggests new trends. For example, Sadovy *et al.* (1994) and Sadovy (In press) hypothesized that small groupers are protogynous, do not aggregate and spawn over extended periods. With the Creole fish being small but being predominately gonochoristic, spawning over a short period and possibly forming aggregations, this hypothesis is unsupported. As a substitute hypothesis, we offer an alternative classification for groupers based on sex ratio, sexual pattern and confirmed or suggested spawning pattern, following ideas presented by Charnov (1982) based on sex-ratio and by Sadovy and Colin (1995) and Sadovy (In press) based on the testis size for reef fishes in general. Predominantly gonochoristic species (*e.g.* the Nassau grouper and the Creole fish) have a near balanced sex-ratio and group-spawning. Sex-reversing groupers have a female-bias sex ratio and pair-spawning.

Most of the variability observed in length of spawning season could result from differences in methodology. Some reports refer only to the presence of ripe specimens, while others are more specific in describing the spawning period. Spawning frequency in groupers, as in most tropical fish species is poorly described and not well understood (Shapiro 1987, Sadovy, In press). All groupers may not be deterministic spawners. Some large species appear to have protracted spawning periods (*e.g.* the yellowmouth grouper, *Mycteroperca interstitialis* (Poey) (Bullock and Smith 1991, Bullock and Murphy 1994). Limitations on body cavity volume may induce indeterminate spawning in some of the small groupers.

Important aspects of the reproductive biology of fishes are, in many instances, socially mediated. Fishing activities may have a significant impact on the demographic population structure, with not well understood consequences. Current and future management strategies should consider that not all groupers share the same sexual patterns. The development and application of assessment models that expressly model sexual pattern (*e.g.* Bannerot 1984) for a particular grouper stock may not necessarily be generalized to all stocks, other species, or to species complexes.

Protection of spawning aggregations areas have been recommended as important management strategies for large groupers (see Bannerot *et al.* 1987, Auil-Marshalleck 1993, Sadovy 1994). A similar argument can be made for smaller species. Smaller groupers are gaining importance as the large ones are driven to commercial extinction (*e.g.* Bermuda; Butler *et al.* 1993). The reproductive strategies and the existence or not of spawning aggregations in such small species should be identified previous to any severe fishing exploitation.

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