

“Greater” versus “Lesser” Strategies?

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ABSTRACT

There are 54 species of sciaenids in the Gulf of Mexico and Caribbean Sea. Here we review the life histories of the more common sciaenids with an emphasis on reproductive biology. Although all sciaenids have an extended reproductive season and are multiple spawners, analysis using principle component ordination and clustering on eight life history traits resulted in separation of three general groups. Whitemouth croaker (*Micropogonias furnieri*), black drum (*Pogonias cromis*), and red drum (*Sciaenops ocellatus*) are species of high commercial and recreational value, and can be termed “greater sciaenids.” These species have a longer life span, larger maximum size, larger size- and age-at-maturity, lower spawning frequency, and lower relative fecundity compared to other sciaenids. In contrast, silver perch (*Bairdiella chrysoura*), cubbyu (*Pareques umbrosus*), and star drum (*Stellifer lanceolatus*) are small sciaenids that are usually caught as trawl bycatch and used as bait or in the aquarium trade, and can be considered “lesser sciaenids.” These species have a short life span, small maximum size, small size- and age-at-maturity, short spawning season, high spawning frequency and high relative fecundity. Sharing traits of both groups is an intermediate group typified by moderate size, age and other life history traits.

This group includes ground croaker (*B. ronchus*), sand seatrout (*Cynoscion arenarius*), spotted seatrout (*C. nebulosus*), silver seatrout (*C. nothus*), banded drum (*Larimus fasciatus*), spot (*Leiostomus xanthurus*), southern kingfish (*Menticirrhus americanus*), gulf kingfish (*M. littoralis*), northern kingfish (*M. saxatilis*), and Atlantic croaker (*Micropogonias undulatus*). There are commercial fisheries for these species, but most are not typically as economically important as the larger sciaenids. Spotted seatrout and Atlantic croaker have several traits more similar to “greater sciaenids”, and historical data suggests overexploitation may have resulted in these species changing groups. Continued exploitation of sciaenids may result in changes to life history shifting traits and thus reclassification into different strategies.

KEY WORDS: Life history, reproduction, Sciaenidae

Evaluación de la Historia Reproductiva de la Vida del Sciaenidae en el Golfo de México y del Mar del Caribe: ¿ Estrategias de "Mayor" contra "Pocos"?

Hay 54 especies de sciaenidos en el Golfo de México y del Mar del Caribe. Aquí repasamos de las historias de la vida de los sciaenidos más comunes con un énfasis en la biología reproductiva. Mientras que todos los sciaenidos tienen una estación reproductiva extendida y desovian múltiples veces cada año, un análisis usando ordenación del componente principal y arracimando en ocho rasgos de la historia de la vida resultó en la separación en tres grupos generales. El ronco blanco (*Micropogonias furnieri*), el tambor negro (*Pogonias cromis*), y la corvineta ocelada (*Sciaenops ocellatus*) son especies del valor arriba comercial y recreacional, y se pueden llamar "sciaenidos mayores". Estas especies tienen una vida más larga, un tamaño máximo más grande, un tamaño y una edad-en-madurez más grande, frecuencias de desove más bajas, y fecundidades relativos más bajos comparados a otros sciaenidos. En contraste, el ronco amarillo (*Bairdiella chrysoura*), el payasito prieto (*Pareques umbrosus*), y la corvinilla lanza (*Stellifer lanceolatus*) son los sciaenidos pequeños que se cogen como especies accesorias de la red barredera y se utilizan generalmente como cebo o en el comercio del acuario, y pueden ser considerados "sciaenidos pocos". Estas especies tienen una vida corta, un tamaño máximo pequeño, un tamaño y una edad-en-madurez pequeña, frecuencias de desove altas y fecundidades relativos altos. Compartir características de ambos grupos es un grupo intermedio caracterizado por tamaño, edad y otros aspectos de la historia de la vida moderados. Este grupo incluye el ronco rayado (*B. ronchus*), la corvina pinta (*Cynoscion nebulosus*), la corvina arenera (*C. arenarius*), la corvina plateada (*C. nothus*), el croca (*Leiostomus xanthurus*), el berrugato zorro (*Menticirrhus americanus*), el berrugato del Golfo (*M. littoralis*), y la gurrubata (*Micropogonias undulatus*). Hay industrias pesqueras comerciales para estas especies, pero no son tan importante como los sciaenidos más grandes. *Cynoscion nebulosus* y *M. undulatus* tenga rasgos varios más similares de los "sciaenidos mayores", y los datos históricos sugieren que la explotación demasiado pudo haber dado lugar a estos grupos que cambian de la especie. La explotación continuada de sciaenids puede dar lugar a cambios a los rasgos que cambian de puesto de la historia de la vida y así a la reclasificación en diversas estrategias.

PALABRAS CLAVES : Sciaenidae, historia reproductiva, Golfo de México, Mar del Caribe

INTRODUCTION

Variation in life history traits of fishes is one approach that has been found useful to the development of a better understanding of how species respond evolutionarily to environmental conditions and potentially perturbations. In particular, examination of the reproductive life history of fishes has resulted in

the characterization of a series of reproductive guilds that are based on adaptations (i.e., ecological, physiological, etc.) to natural environmental conditions (Balon 1975). This concept of reproductive guilds was further enhanced by Winemiller and Rose (1992) who coupled demographic characters with life history traits. They proposed three primary life history strategies that result from tradeoffs among survivorship, fecundity, and size/age at maturation. The results of these analyses showed convergent evolution in that phylogenetically distinct species with similar reproductive life history traits were grouped together in the same guild or strategy. However, Winemiller and Rose (1992) noted that several of the larger freshwater and marine orders (Clupeiformes, Gadiformes, Perciformes, etc.) showed divergence in placement in any of the three primary life history strategies. For example, there were 71 species of Perciformes examined in their analysis and many life history traits varied widely (standard deviations exceeded the mean values), likely due to family differences within the order. This suggests that a highly specious family may also exhibit variation in reproductive life history traits, even though variation among genera within a family may be less than variation across families within an order.

There are 54 species of sciaenids in the Gulf of Mexico (GOM) and Caribbean Sea (Carpenter 2002). Many of these are prime targets for commercial as well as recreational fisheries (Carpenter 2002). However, little is known of the life history traits, especially reproductive biology, for many tropical sciaenids, even though they are also under fishing pressure. Aspects of the reproductive biology of a species can be used in countless ways to preserve or manage that species more effectively. For example, spawning season, spawning area, age-at-maturity, fecundity, and spawning frequency are important factors employed by fisheries managers to establish catch and size limits as well as the catch season (Everhart et al. 1975, Jennings et al. 2001).

We hypothesize that the Sciaenidae can be separated into different groups based on reproductive life history traits. Therefore, our objectives were to compile the available reproductive life history data on Sciaenidae in the GOM and Caribbean Sea and to analyze these data within a life history framework to identify suites of species exhibiting different reproductive life history strategies. Finally, the results of the analyses are interpreted in light of the impacts of the historic and current fishery practices.

MATERIALS AND METHODS

Literature for this review was searched in a hierarchical manner. First, various ecological and taxonomic guides were examined to determine which species of Sciaenidae inhabit the GOM and Caribbean Sea (Randall 1983, Humann 1989, Böhlke and Chaplin 1993, Hoese and Moore 1998, Smith-Vaniz et al. 1999, Carpenter 2002). Next, we searched Fish Base (<http://www.fishbase.org/>) for any additional GOM and Caribbean Sea species. Databases using selected keywords (Table 1) were searched in addition to the personal literature of the authors. After all relevant literature was collected, the literature cited section of each reference was checked for additional citations not identified in the procedures mentioned above. These included technical

reports, theses and dissertations, older references not incorporated in online databases, grey literature, etc. Finally, general searches were performed in Google (<http://www.google.com/>) using the keywords in Table 1.

Table 1. List of databases examined during literature search.

Database	Sources	Years	Keywords
Cambridge Scientific Abstracts Database Service	ASFA 1: Biological and Living Resources	1960 - current	genus and common name of each species; Sciaenidae; sciaenid; fish reproduction; gonadosomatic index; drum(s) AND any combination of these words
	Ecology Abstracts	1960 - current	
	Oceanic Abstracts	1960 - current	
	ERIC	1960 - current	
EBSCO Host Research Databases	Biological Abstracts (BIOSIS)	1969- current	
JSTOR	Ecology Section	1913 - 2000	
ISI Web of Knowledge: Web of Science	Science Citation Index Expanded	1994 - 2004	
INGENTA	INGENTA	1900 - current	

From this literature, we documented and tabulated nine traits related to reproduction. Only reproductive information specific for the GOM and Caribbean Sea were included. These nine traits were maximum size (mm total length (TL)), maximum age (yrs), age-at-maturity (yrs), size-at-maturity (mm TL or standard length (SL)), duration of peak spawning (mo), mean peak female gonadosomatic index (GSI, %), spawning frequency (days), relative fecundity (ova/g body weight (BW)), and batch fecundity (ova). Species were included only if some type of female reproductive trait was reported, and were not included if only general biological and non-reproductive information was available. This information was then used in subsequent analyses.

Statistical Analysis

Principle component analysis (PCA) in a two step procedure (Peterson and VanderKooy 1997) was used to compare the reproductive traits between the different sciaenid species. We ordinated species (11 species, 7 genera) based on eight life history traits using PCA of the correlation matrix, with varimax rotation to maximally resolve loadings. A scree test was used to determine the number of meaningful components. Any trait that loaded on a component at an absolute value of ≥ 0.50 was considered to contribute significantly to interpreting that component. Cluster analysis based on the unweighted pair group method with arithmetic mean (UPGMA) procedure was used on fourth-root transformed data to compare reproductive traits among the sciaenid species

with the Bray-Curtis similarity coefficient to examine species linkage using PRIMER (PRIMER-E Ltd, Plymouth, UK). The Bray-Curtis similarity coefficient values range from 0 % (no similarity) to 100 % (identical; Clark and Warwick, 2001). For both the PCA and cluster analysis, only species with data in all reproductive trait fields except spawning frequency were included.

RESULTS AND DISCUSSION

Of the greater than 100 literature sources examined, 60 contained compiled or unique data used in this review. Sixteen sciaenid species distributed among 10 genera were found to have relevant information pertaining to this review (Table 2). An additional 38 species occur in the study area, but no specific reproductive data were found. Of the 16 species, only 11 were included in the PCA and cluster analysis because of missing reproductive traits. The PCA of the eight traits produced two components which explained 86.08% of the variance (Figure 1). Component 1 (PC I) comprises batch fecundity, relative fecundity, age-at-maturation, size-at-maturation, maximum length, and maximum age which we interpret as aspects of fish size that influence reproduction. Component 2 (PC II) includes duration of spawning season and mean peak GSI, and represents spawning season dynamics. Figure 1 suggests sciaenids have three different reproductive life history strategies. The first consist of whitemouth croaker (*Micropogonias furnieri*), black drum (*Pogonias cromis*), and red drum (*Sciaenops ocellatus*). The next group included ground croaker (*Bairdiella ronchus*), sand seatrout (*Cynoscion arenarius*), spotted seatrout (*Cynoscion nebulosus*), silver seatrout (*Cynoscion nebulosus*), banded drum (*Larimus fasciatus*), spot (*Leiostomus xanthurus*), and Atlantic croaker (*Micropogonias undulatus*). The last group was comprised of only one species, silver perch (*Bairdiella chrysoura*). The UPGMA cluster analysis (Figure 2) also identified three groups. Red drum, black drum and white mouth croaker (Group 1) clustered together with 95.82 % similarity. A second group, consisting of ground croaker, sand seatrout, spotted seatrout, silver seatrout, banded drum, spot, and Atlantic croaker (Group 2), were clustered with 90.96 % similarity. Finally, silver perch did not cluster with any other species and only had 82.46% similarity to Group 2. These two analyses support our hypothesis that sciaenids can be divided into different strategies based on reproductive life history traits. We termed these groups “greater”, “intermediate”, and “lesser” based on a socio-economic-ecological gradient.

Table 2. Life history traits of all sciaenid species included in this review.

Species	Max Age (yrs)	Max Length (mm TL)	Peak Spawning (mo)	Mean Peak GSI (%)	Spawning Frequency (days)	Relative Fecundity (ovary)	Batch Fecundity (ova)	Age-at-Maturity (yrs)	Size-at-Maturity (mm)	References
<i>Bairdiella chrysoura</i>	4-5	250	3	12	1.3-1.6	151-1387	2497-50,565	YOY	110-120 TL	7, 8, 35
<i>Bairdiella ronchus</i>	2	350	8	2.97-5.09		2212	188,964	YOY	158 TL	7, 21, 34
<i>Cynoscion arenarius</i>	3	590	6	4.5-5.5	2.8	176-1452	25,874-432,000	YOY	140-180 TL	13, 14, 15, 30, 31, 33, 36
<i>Cynoscion nebulosus</i>	9	700	6.5	~8	4-5	250-650	12,000-797,000	1+	272 TL	5, 6, 7, 24
<i>Cynoscion nothus</i>	2	400	6	3.5		419-1336	16,800-389,500	YOY	170-206 TL	7, 12, 30
<i>Larimus fasciatus</i>	2-3	220	4	5.5		1569	12,750-320,819	YOY	80-150 TL	7, 29, 32
<i>Leiostomus xanthurus</i>	2-3, 5	360	5	~4.5		267-2948	20,900-514,400	1+	127 TL	7, 11, 19, 28, 30,
<i>Menticirrhus americanus</i>	2-3	450-500	4					1	150-220 TL	1, 7, 17, 18
<i>Menticirrhus littoralis</i>	2	450-500	4						210 TL	1
<i>Menticirrhus saxatilis</i>	3	450-500	Spring and summer					1		1
<i>Micropogonias furnieri</i>	7	900	7	8.0	3-4	52-449	17,000-3,700,000	2	320 TL	7, 9, 22, 23,

Table 2. Continued.

Species	Max Age (yrs)	Max Length (mm TL)	Peak Spawning (mo)	Mean Peak GSI (%)	Spawning Frequency (days)	Relative Fecundity (ova/g)	Batch Fecundity (ova)	Age-at-Maturity (yrs)	Size-at-Maturity (mm)	References
<i>Microponias undulatus</i>	1-2, 8	357, 688	7	4.5		519 - 1581	27,300 - 1,075,600	YOY	140 - 170 TL	2, 20, 28, 30, 38
<i>Pareques umbrosus</i>		200	3		1.4 - 2.3		2000 eggs / spawn	Over 1 yr-captivity	150 mm SL in captivity	4, 7, 19
<i>Pogonias cromis</i>	43	1500	4	9 - 14	3 - 4	67 - 793	510,000 - 3,800,000	5	600 - 649 FL	3, 7, 16, 26, 27
<i>Sciaenops ocellatus</i>	35	1600	4	4 - 8	2 - 4	42 - 447	160,000 - 3,270,000	3 - 6	550 - 899 FL	7, 10, 25, 26, 39
<i>Stellifer anceolatus</i>	2.5 (A)	200	3					YOY (A)	80 - 100 TL (A)	7, 17, 37

References: 1 = Armstrong and Muller (1996); 2 = Barger (1985); 3 = Beckman et al. (1990); 4 = Böhlke and Chaplin (1993); 5 = Brown-Peterson (2003); 6 = Brown-Peterson et al. (2002); 7 = Carpenter (2002); 8 = Chavance et al. (1984); 9 = Garcia-Cagide et al. (2001); 10 = Comyns et al. (1991); 11 = Cowan and Shaw (1988); 12 = DeVries and Chittenden (1982); 13 = Ditty (1986); 14 = Ditty et al. (1988); 15 = Ditty et al. (1991); 16 = Fitzhugh et al. (1993); 17 = Gunter (1938); 18 = Harding and Chittenden (1987); 19 = Holt and Riley (1999); 20 = Kobylinski and Sheridan (1979); 21 = Louis (1985); 22 = Macchi et al. (2003); 23 = Manickchand-Heileman and Kenny (1990); 24 = Murphy and Taylor (1994); 25 = Murphy and Taylor (1990); 26 = Dave L. Nieland (A) = Data for Atlantic Ocean

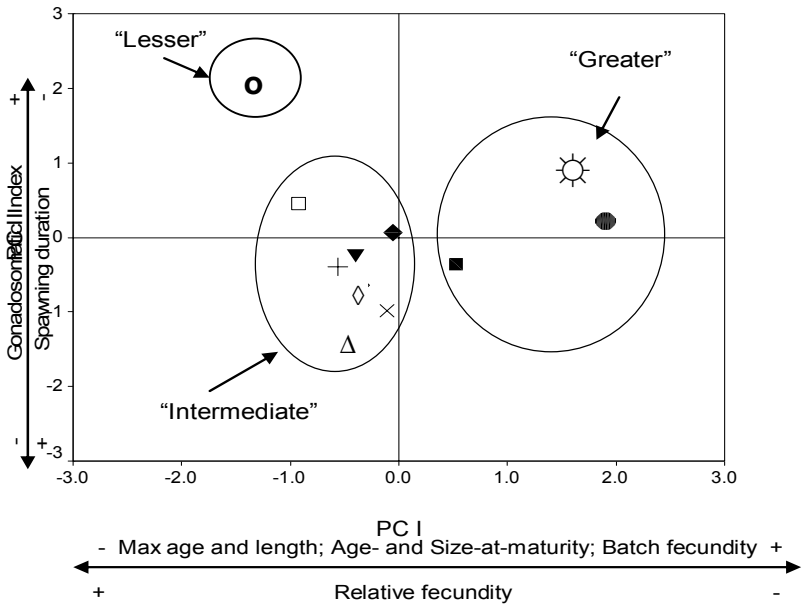


Figure 1. Plot of principle components I and II illustrating the distribution of sciaenid species relative to life history traits. “Greater”: ■ = *Micropogonias furnieri*; ☀ = *Pogonias cromis*; ● = *Sciaenops ocellatus*; “Intermediate”: Δ = *Bairdiella ronchus*; ▼ = *Cynoscion arenarius*; ◆ = *C. nebulosus*; ◇ = *C. nothus*; □ = *Larimus fasciatus*; + = *Leiostomus xanthurus*; X = *M. undulatus*; “Lesser”: ○ = *B. chrysoura*

“Greater Sciaenids”

The three species included as “greater sciaenids” were whitemouth croaker, red drum, and black drum. This group has a longer life span, larger maximum size, larger size- and age-at-maturity, lower spawning frequency, and lower relative fecundity compared to other sciaenids (Table 3). These species are of high commercial and recreational value. All three species spawn offshore but are estuarine dependent and use estuaries as nursery habitat (Patillo et al. 1997). Whitemouth croaker ranges from the Caribbean Sea into the southern Atlantic along the coast of South America (Carpenter 2002) and are one of the most economically important demersal fish in Trinidad (Manickchand-Heileman and Kenny 1990), Guianas and possibly Cuba (Carpenter 2002). Juveniles compose a significant portion of bycatch from shrimp trawlers (Manickchand-Heileman and Kenny 1990). Red drum and black drum are commercially and recreationally exploited. Red drum are found only in the GOM and along the Atlantic coast of the United States (U.S.). Black drum range from the Atlantic coast of the U.S. to the northern and western coasts of the GOM, throughout the Caribbean to the Atlantic coast of South America (Hoese and Moore 1998, Carpenter 2002). While all of the greater sciaenids have longer life spans and larger maximum sizes than the

other sciaenids, whitemouth croaker are much smaller and have a shorter life span than red drum and black drum, although whitemouth croaker may reach seven years of age (Manickchand-Heileman and Kenny 1990) and 900 mm TL (Carpenter 2002). Red drum have been reported to reach a maximum age of 35 yrs (Murphy and Taylor 1990) and maximum size of 1600 mm TL (Carpenter 2002), while black drum attain 1500 mm TL (Carpenter 2002) and 43 yrs of age (Beckman et al. 1990).

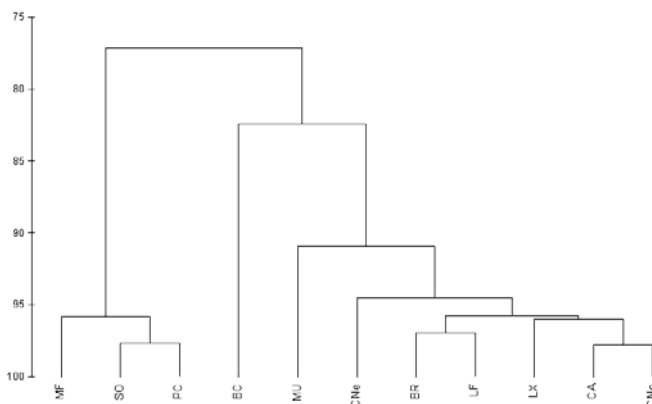


Figure 2. The UPGMA cluster analysis of sciaenid species based on Bray-Curtis similarity of eight reproductive traits. “Greater”: MF = *Micropogonias furnieri*; PC = *Pogonias cromis*; SO = *Sciaenops ocellatus*; “Intermediate”: BR = *Bairdiella ronchus*; CA = *Cynoscion arenarius*; CNe = *C. nebulosus*; CNo = *C. nothus*; LF = *Larimus fasciatus*; LX = *Leiostomus xanthurus*; MU = *M. undulatus*; “Lesser”: BC = *B. chrysoura*

In general, the “greater sciaenids” have a greater size- and age-at-maturity than the other groups. Red drum and black drum both mature at an older age and larger size than the aforementioned species. Red drum mature between three and six years of age and 550 – 899 mm fork length (FL) (Murphy and Taylor, 1990; Wilson and Nieland, 1994), and black drum mature at 640 – 649 mm FL and five years of age (Nieland and Wilson 1993). In contrast, whitemouth croaker females mature by age two at 320 mm TL (Manickchand-Heileman and Kenny 1990). Whitemouth croaker spawn most actively from February to August (seven months) in the Caribbean, with maximum mean female GSI values of 8 % and a spawning frequency of 3 – 4 d (Manickchand-Heileman and Kenny 1990, García-Cagide et al. 2001, Macchi et al. 2003). Red drum spawn from August to November (4 mo) with a GSI peak in September of 4 – 8 % and a spawning frequency of 2 – 4 d (Murphy and Taylor, 1990; Comyns et al. 1991, Wilson and Nieland 1994). Black drum spawn for four months in the northern GOM (January – April) with GSI peaks in February and March of 9 – 14 % and a spawning frequency of 3 – 4 d (Fitzhugh et al. 1993, Nieland and Wilson 1993).

Batch fecundity within the “greater sciaenids” is generally higher compared to other sciaenids while relative fecundity is lower (Table 3). Batch fecundity is positively related to fish size, but size explains no more than 44 % (Sheridan et al. 1984, Nieland and Wilson 1993, Brown-Peterson, 2003) of the variation in fecundity for any species. The ranges in batch fecundity for the “greater sciaenids” are listed in Table 2.

Table 3. Summary of mean values of life history traits in each group with the “intermediate” group calculated with and without Atlantic croaker and spotted seatrout. N = number of species; MA = maximum age; ML = maximum length; PS = peak spawning; SF = spawning frequency (number of species); BF = batch fecundity; RF = relative fecundity; AM = age-at-maturity; SM = size-at-maturity; MG = mean maximum GSI.

	N	MA	ML	PS	SF	BF	RF	AM	SA	MG
Greater	3	28	127 3	5	3 (3)	1,909,50 0	225	4	549	9
Intermediate	7	4	468	6	3.6 (2)	255,259	120 8	1	166	5
Lesser	1	5	250	4	1.6 (2)	20,181	769	1	115	12
Intermediate without CNe and MU	5	3	382	6	2.8 (1)	210,409	138 6	1	147	4.8
Atlantic Croaker (MU)	-	2	357	7	-	551450	105 0	1	155	4.5
Spotted seatrout (CNe)	-	9	700	7	4.5	183,316	474	2	272	8

“Lesser Sciaenids”

In contrast to the “greater sciaenids”, “lesser sciaenids” are small sciaenids that are usually caught as trawl bycatch, used as bait, or in the aquarium trade. Members of this group are species which inhabit estuaries and reefs. There is a limited amount of life history information available for “lesser sciaenids”, and the suite of reproductive life history traits used to define this group is based on a single species, silver perch. However, we were able to place the star drum (*Stellifer lanceolatus*) and cubbyu (*Pareques umbrosus*) in this group based on comparison of the limited information on their reproductive traits (Table 2) to those of the “lesser sciaenids” (Table 3). As a whole, these “lesser sciaenids” appear to have a short life span, smaller maximum size, small size- and age-at-maturity, shorter spawning season, high spawning frequency, and high relative fecundity.

Silver perch are one of the top five most abundant species of sciaenids in estuaries along the GOM and the Atlantic coast of the U.S. (Chao and Musick 1977, Rooker et al. 1998, Gelwick et al. 2001), and support a small commercial fishery in the southern GOM (Ocaña-Luna and Sánchez-Ramírez 1998). Star drum is very similar in appearance to silver perch, but is not as abundant in estuaries. It is also caught as bycatch in bottom trawls and is found in the

GOM and along the Atlantic coast of the U.S. (Hoese and Moore 1998, Carpenter 2002). There is limited information on star drum in the GOM.

The cubbyu is another small sciaenid with little information available about its life history. This fish is found from Chesapeake Bay into the GOM and along the Atlantic coast of South America (Randall 1983, Böhlke and Chaplin 1993, Carpenter 2002) and is taken as bycatch in trawl fisheries (Carpenter 2002). In addition to the cubbyu, other small reef sciaenids such as the highhat (*Pareques acuminatus*), jack-knife fish (*Equetus lanceolatus*) and spotted drum (*Equetus punctatus*) are sought after in the aquarium trade (Smith-Vaniz et al. 1999, Carpenter, 2002). However, there is no reproductive biology information available regarding these and other small sciaenid species. It is unknown if they can be classified as “lesser sciaenids”.

Silver perch reach a maximum size of 250 mm TL (Carpenter 2002) and in the GOM, a maximum age of four to five years (Waggy 2004). Star drum are similar and may attain 200 mm TL (Carpenter, 2002) and 2.5 years of age on the Atlantic coast (Welsh and Breder 1923). Cubbyu, smallest of the three, may reach 200 mm TL (Böhlke and Chaplin 1993, Carpenter 2002), but maximum age is unknown.

“Lesser sciaenids” mature at a young age and small size (Tables 2 and 3). Silver perch mature just before their first birthday between 91 and 95 mm SL (Waggy 2004), and star drum at one year of age and 80 mm – 100 mm TL (Welsh and Breder 1923, Hildebrand and Cable 1934). Holt and Riley (1999) observed cubbyu in captivity to spawn when they were 150 mm SL and over one year old.

Silver perch and star drum are spring – summer spawners. Silver perch spawning from March – May with mean peak GSI values of 12 % in April (Waggy 2004). Spawning occurs in star drum from April – June (Gunter 1938). The spawning season for cubbyu is unknown, however Holt and Riley (1999) observed captive cubbyu to have a spawning frequency of 1.4 – 2.3 d (three to five times a week). In comparison, silver perch spawn almost daily (Waggy 2004). The spawning frequency for star drum is unknown.

The “lesser sciaenids” have the lowest batch fecundity of the groups, but mean relative fecundity is higher than that of the greater sciaenids (Table 3). Relative fecundity of silver perch was estimated from data presented by Chavance et al. (1984), and was found to be between 151 and 1387 ova / g BW, and batch fecundity was estimated to be between 2497 – 50,565 ova. Cubbyu spawning in captivity released a mean of 2000 eggs per spawning event (Holt and Riley 1999). Information for star drum is unavailable.

“Intermediates”

Sharing traits of both the “greater” and “lesser” sciaenids is an intermediate group which is typified by moderate size, age, and other life history traits. Some members of this group support commercial fisheries, and although they are generally not as important as the larger sciaenids, they are more economically valuable than the “lesser sciaenids.” Many of these species are caught as bycatch, and most are sought by recreational fishermen.

The species in this group cover a wide range in the western Atlantic, GOM and Caribbean. Atlantic croaker occur from the Gulf of Maine to southern

Florida, in the GOM, and down to Argentina. Spot, banded drum, silver seatrout and spotted seatrout are found along the coast of the western Atlantic and in the GOM (DeVries and Chittenden 1982, Sheridan et al. 1984, Pattillo et al. 1997, Hoese and Moore 1998, Carpenter 2002). Sand seatrout are similar in appearance and life history to silver seatrout; however, they live only in the GOM (Hoese and Moore 1998, Carpenter 2002). Ground croaker inhabit the Caribbean Sea and southward along the coast of South America (Carpenter 2002). In addition to these seven intermediate species with well documented reproductive life history traits, three species of *Menticirrhus* can be added to this group based on available information (Table 2). The northern kingfish (*M. saxatilis*), southern kingfish (*M. americanus*) and Gulf kingfish (*M. littoralis*) are all found along the coast of the western Atlantic and GOM, with the southern and Gulf kingfish extending along the coast of South America (Hoese and Moore 1998, Carpenter, 2002).

Most sciaenids in the intermediate group reach a maximum size ≤ 500 mm TL and a maximum age of two to three years (Tables 2 and 3). Spot reach 360 mm TL in size (Carpenter, 2002) and have a life span up to five years (usually two to three years) (Pattillo et al. 1997). Banded drum achieve a maximum length of 220 mm TL (Carpenter, 2002) and have a life span of two to three years (Standard and Chittenden 1984). Sand seatrout attain a size of 590 mm TL (Trent and Pristas 1977) and a maximum age of three years (Shlossman and Chittenden 1981). Silver seatrout reach 400 mm TL (Carpenter, 2002) with an estimated maximum life span of two years (DeVries and Chittenden 1982). Ground croaker grow to a maximum size of 350 mm TL (Carpenter 2002) and have a life span of two years (Louis 1985). Southern kingfish, Gulf kingfish and northern kingfish all have a maximum size of 450 – 500 mm TL and may have a life span of three to four years (Harding and Chittenden 1987, Amstrong and Muller 1996). However, Atlantic croaker and spotted seatrout are larger and older than the other “intermediate” sciaenids.” Atlantic croaker may attain a size of 668 mm TL and maximum age of eight years in the GOM (Barger 1985, Pattillo et al. 1997). However, specimens from the north-western GOM (TX, LA) have been reported to have life spans of only one to two years and a maximum size of 357 mm TL (White and Chittenden 1977, Sheridan et al. 1984). In the GOM, spotted seatrout may attain an age of nine years (Murphy and Taylor 1994) and a size of 700 mm TL (Carpenter 2002).

All “intermediate sciaenids” reach sexual maturity in their first year of life at relatively small sizes (Table 2). In Atlantic croaker, maturation occurs near the end of their first year of life at 140 – 170 mm TL (White and Chittenden 1977, Sheridan et al. 1984). Spotted seatrout reach sexual maturity after their first birthday at around 250 mm SL (Brown-Peterson 2003). Female spot mature at 127 mm SL and age 1 in the GOM (Sheridan et al. 1984). Standard and Chittenden (1984) found banded drum to mature in their first year of life between 80 – 130 mm SL. Sand seatrout mature between 140 and 180 mm TL as young-of-the-year fish just before their first birthday (Shlossman and Chittenden 1981, Ditty et al. 1991, Brown-Peterson et al. In prep.) as do silver seatrout which mature at 140 – 170 mm SL (DeVries and Chittenden 1982, Sheridan et al. 1984). Ground croaker mature at about 158 mm TL (Torres-Castro et al. 1999); age at maturation is unavailable. Southern kingfish mature

at age 1 and between 150 – 220 mm TL (Harding and Chittenden 1987). Limited information is available for both the northern and Gulf kingfish; however, they appear to have a similar size- and age-at-maturation (Armstrong and Muller 1996).

While spawning season varies within the “intermediate sciaenids”, duration of spawning is similar. Atlantic croaker exhibit a protracted spawning season from September through March peaking in October with GSI values of 4.5 % (White and Chittenden 1977, Sheridan et al. 1984, Pattillo et al. 1997). Spot spawn from November through March in the northern GOM with maximum mean GSI values of 4.5 % (Sheridan et al. 1984, Cowan and Shaw 1988) with the season becoming more prolonged as latitude decreases (Pattillo et al. 1997). Spotted seatrout spawn from April to September in the GOM (Brown-Peterson 2003) with maximum GSI ranging from 5 – 14 % (Brown-Peterson et al. 2002). They spawn every four to five days (Brown-Peterson, 2003). Banded drum are generally fall spawners (September – November) with a minor spring period from April – June in the GOM with mean peak GSI values of 5.5 % (Ross 1984, Standard and Chittenden 1984). Sand seatrout display two distinct spawning peaks during a seven month reproductive period, a spring (March – May) peak and a late summer peak (August – September) with mean peak GSI values of 4.5 – 5.5 % (Shlossman and Chittenden 1981, Sheridan et al. 1984, Ditty 1986; Ditty et al. 1988, Brown-Peterson et al. In prep.). Sand seatrout display spawning frequencies of 2.8 d during peak spawning times (Brown-Peterson et al. In prep.). Silver seatrout spawn throughout the late spring and summer (March – October) with two distinct peaks in spawning and maximum mean GSI values of 3.5 % (DeVries and Chittenden 1982, Sheridan et al. 1984). Spawning of ground croaker occurs from March to October in the Caribbean with GSI values ranging between 3.0 – 5.1 % (Louis 1985, Torres-Castro et al. 1999). Southern kingfish spawn in two peaks from February – November (spring and late summer peak) (Gunter 1938, Harding and Chittenden 1987). Northern kingfish and Gulf kingfish are also reported to spawn in the spring and late summer (Armstrong and Muller 1996). The spawning frequency for Atlantic croaker, spot, banded drum, silver seatrout, northern kingfish, southern kingfish, Gulf kingfish, and ground croaker is unknown.

Batch and relative fecundity of the “intermediate sciaenids” were similar among all species (Table 2). The relative fecundity of Atlantic croaker, spot, sand seatrout, and silver seatrout was estimated from data presented by Sheridan et al. (1984), and banded drum relative fecundity was estimated from Standard and Chittenden (1984). Batch fecundity and relative fecundity for the three species of kingfish is unknown.

Many reproductive life history traits of Atlantic croaker and spotted seatrout have a stronger affinity with the “greater sciaenid” group than the “intermediate” group (Table 3). Indeed, prior to analysis, we assumed spotted seatrout to be a “greater sciaenid” based on maximum age, spawning frequency, relative fecundity, and their commercial and recreational importance. The commercial fishery for spotted seatrout has been closed in some of the coastal states along the GOM in the U.S. due to decreased landings from overexploitation and habitat destruction (Pattillo et al. 1997). However,

spotted seatrout are still greatly sought after and heavily fished recreationally along the GOM (Pattillo et al. 1997), where they are one of the primary target species of anglers (VanderKoooy and Muller 2004). Analysis of otoliths from prehistoric populations of spotted seatrout in Texas (800 – 5,000 years ago) suggest there was a greater percentage of the oldest (age 9) spotted seatrout in prehistoric times and that contemporary populations grow faster than prehistoric populations (Colura and Vickers 1998). Colura and Vickers (1998) note that the percentage of older age fish (not only spotted seatrout, but also Atlantic croaker, red drum, and black drum) was greater in prehistoric times, demonstrating the impact modern fishing pressure has on the populations of these sciaenids. Thus, spotted seatrout may have been considered a “greater sciaenid” historically, but life history adaptations due to heavy fishing pressure (i.e., faster growth, smaller size/age at maturation, reduced batch fecundity) which may be related to decreases in population size (Brown-Peterson and Warren 2001), could explain the current inclusion of this species in the “intermediate sciaenid” category.

The historical change in life history traits of Atlantic croaker is even more striking than that for spotted seatrout. In prehistoric times, Atlantic croaker from St. Augustine, FL reached 15 years of age (Hales and Reitz 1992), and prehistoric Atlantic croaker populations in Texas were older than contemporary populations (Colura and Vickers 1998). Due to overfishing in some areas, Atlantic croaker has decreased in maximum size and age, age- and size-at-maturity (Diamond *et al.* 2000) and is considered overexploited in the GOM (Pattillo et al. 1997). While large (668 mm TL, Pattillo et al. 1997) and old (eight years, Barger 1985), Atlantic croaker have been reported from the GOM, current trends indicate ages 0 and 1 fish (<366 mm TL) are most commonly captured (White and Chittenden 1977, Colura and Vickers 1998). Thus, Atlantic croaker appear to be correctly classified as “intermediate sciaenids” based on current reproductive life history traits (Table 3). However, historically this species was older, larger, and supported an extensive commercial fishery in the GOM (Diamond et al. 1999), and could have been considered a “greater sciaenid” at that time.

CONCLUSIONS

We have found that the Sciaenidae indigenous to the GOM and Caribbean Sea can be divided into three reproductive life history strategies. “Greater sciaenids” have a long life span, larger maximum size, larger age- and size-at-maturity, lower spawning frequency, high batch fecundity, and low relative fecundity compared to the other sciaenids. The “lesser sciaenids” mature quickly with low batch fecundity, a shorter spawning season, high spawning frequency, and high relative fecundity. “Intermediate sciaenids” are between these groups with more moderate traits. The “greater” and “intermediate” sciaenids fall into the periodic strategy proposed by Winemiller and Rose (1992), whereas the traits of “lesser sciaenids” are more similar to the opportunistic strategists. Periodic strategists delay maturation to attain a sufficient size for large clutch (batch fecundity) production with synchronous spawning, and opportunistic strategists mature at small sizes and have small clutch sizes

but high relative reproductive effort (Winemiller and Rose 1992). Pianka (2000) also described reproductive strategies, but in terms of the $r - K$ selection continuum based on the maximal instantaneous rate of increase (r_{\max}), which takes into account the simultaneous processes of birth and death. Small organisms have higher r_{\max} values corresponding to shorter generation times and high reproductive effort (r strategists). Larger organisms tend to delay reproduction (i.e., greater size-at-maturity) which results in reduced r_{\max} values (K strategists) (Pianka 2000). Overall, the “greater sciaenids” appear to exhibit a k -selected life history, while the “lesser sciaenids” seem to be r -selected. These attributes may play a significant role in the sustainability of the species under various scenarios of overfishing in the GOM and Caribbean Sea.

Management of species groups is complex; even those classified together may have subtle differences within their reproductive life histories. Thus, a management strategy may work with one species, but negatively affect others in the same group (Winemiller and Rose 1992). Additionally, latitudinal differences within the same species cause deviations in life history traits (Snyder and Peterson 1999, Brown-Peterson et al. 2002), and management strategies should be adjusted accordingly. Overexploitation can change life history traits and demographics of a species, resulting in changes in ordination space and shifting the species along the gradient, resulting in possible classification into a different group. This appears to be the case with Atlantic croaker. Furthermore, our analysis, in conjunction with historical data and current fishery practices, suggest the shift of spotted seatrout from the “greater” to the “intermediate” group is a recent occurrence. Continued exploitation may result in other species shifting among reproductive life history strategies.

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