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Latitudinal Exploration of the Temporalities of Spawning for Some Tropical Fish Species (Epinephelidae: *Plectropomus* spp., *Mycteroperca* spp. and *Epinephelus* spp.)

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ABSTRACT

This study contributes to the existing knowledge of temporal reproduction patterns in tropical fish species which is potentially relevant to regional fisheries management. The latitudinal variation in Spawning Season Length (SSL) and its relationship with spawning season temperature (SPST) was explored, as well as the latitudinal variation in Spawning Aggregation Duration (SAD), through Spearman's rank coefficient. Additionally, the lunar synchrony of spawning and the time of day at which spawning occurs were described. We found variable trends for SSL with respect to latitude in the tropics; most patterns did not satisfactorily explain the variation in SSL. The minimum SPST consistently tended to be lower for longer spawning seasons, both within each species and for the entire dataset. We observed SSLs of one to six months across the entire range of latitudes (-30° to 35°) but most spawning seasons longer than six months were observed at latitudes lower than -4° or higher than 10°, where lower water temperatures can be found. The latitudinal tendencies of SAD were variable and poorly supported, but the data on *Epinephelus striatus* hinted that SSL may vary spatially. Furthermore, the studied species most likely follow lunar and semilunar spawning cycles which are likely to be related to specific daily spawning patterns.

Key words: Serranids, latitudinal pattern, spawning season length, spawning season temperature, spawning aggregation duration

INTRODUCTION

Reproduction of fish is a relevant issue regarding fish management and conservation and its knowledge is of importance for sustainable exploitation and conservation. Studies has been focused on different ways, general aspect on reproductive biology (Ramadan and El-Halfawy, 2007; Sivashanthini *et al.*, 2008; Chelemaal *et al.*, 2009; Kerdgari *et al.*, 2009; Sadeghi *et al.*, 2009), metabolism (Bouriga *et al.*, 2011; Sutharshiny and Sivashanthini, 2011) and physiology related to gonadal maturation (Khalil *et al.*, 2007), or reproductive behaviour (Hosseini *et al.*, 2009; Salcedo-Bojorquez and Arreguin-Sanchez, 2011), among others. However, of particular interest are the spawning aggregations where fishes are more vulnerable to fishing.

The spawning patterns of tropical fishes can occur on daily, lunar and seasonal time scales (Colin, 2012) and their interspecific and intraspecific geographic variations can be complex (Robertson, 1991). There are many tropical marine environments where fish breeding occurs and the temporality of breeding may be associated with environmental factors, the quality and availability of food, water chemistry and day length, among other variables. However, the processes that influence optimal breeding conditions are still poorly understood for most tropical fishes (Johannes, 1978; Lowe-McConnell, 1987; Wootton, 1998). Thus, the geographical variability of reproduction timing is a complex issue. Some tropical fishes exhibit longer spawning seasons nearer to the equator (Johannes, 1978; Craig, 1998) but such behaviour has not been explored for many species (Craig, 1998). Some questions that concern managers remain unanswered; e.g., what is the effect of fishing on those fish resources that form spawning aggregations and sustain brief spawning seasons at low latitudes? The timing of the spawning season for some epinephelid groupers is related to temperature and tends to occur during the summer in cooler latitudes and when temperatures are below the annual maximum in warmer, lower latitudes (Thresher, 1984; Samoilys, 1997). For example, there is evidence that the latitudinal shifts of *Epinephelus striatus*, whose spawning is restricted to a narrow range of temperatures, may be related to water temperatures (Colin, 1992) but other species may not respond in this way (Colin, 2012). The interest in this type of knowledge relates to the usage of spawning aggregations by fishermen and the need to regulate such exploitation to sustain fisheries. In this contribution, we explored the latitudinal variation of spawning season length and spawning aggregation duration and their relationships with water temperatures for fish species that form spawning aggregations in the Atlantic and Indo-Pacific Oceans. This study integrates information to find patterns that are useful for understanding the temporality of reproduction in tropical areas for regional fisheries management.

MATERIALS AND METHODS

Information on the temporality of grouper (Epinephelidae) reproduction, along with the geographical locations of temporal data, was collected from published scientific documents and FishBase (Froese and Pauly, 2009; www.fishbase.org). Google Earth version 5 was used for georeferencing locations whose geographical coordinates were not specified in the literature. The biological variables considered were spawning season length (SSL, in months), spawning aggregation duration (SAD, in days), the lunar phase during spawning, the time of day at which spawning occurred and the water temperature during the spawning season (minimum, maximum and average). The monthly temperatures during the spawning season were obtained from the POET database (<http://poet.jpl.nasa.gov/>) generated by the AVHRR Pathfinder algorithm version 5 using measurements with a resolution of 4 km of made by the AVHRR (Advanced Very-High-Resolution Radiometer) NOAA sensor.

The statistical relationships of SSL and SAD with latitude and the relationship of temperature with SSL were explored using Spearman's rank correlation coefficient (Spearman R) by species and hemisphere (northern and southern). The aim of the analyses was to determine the latitudinal pattern in the available information on reproductive temporality. The Spearman R was used because the data in each analysis set was scarce and non-normal (Zar, 2010). The coefficient ranges from 1 for a perfect positive correlation to -1 for a perfect inverse correlation, with 0 indicating complete independence (Spearman, 1904). The Spearman R was evaluated using Student's t test with n (number of data) and n-2 degrees of freedom with a significance threshold

of $p < 0.05$. Statistica 8.0 software (StatSoft Inc., USA) was used for statistical procedures. Finally, spawning temporality, the lunar synchrony of spawning events and the time of day of spawning were described.

RESULTS

Spawning season length: The Spawning Season Length (SSL) was correlated with latitude and spawning season temperature (SPST) for two *Plectropomus* spp., four *Mycteroperca* spp. and eight *Epinephelus* spp. (Table 1, Fig. 1) from areas of the southeast United States, the Gulf of Mexico, the Mexican Caribbean, the Bahamas, Cuba, the Cayman Islands, the Virgin Islands, Puerto Rico, Jamaica, Belize, the Netherlands Antilles, Colombia, Ascension Island and Brazil in the Atlantic Ocean and also Japan, the Marshall Islands, the Gulf of Mannar, the Federated States of Micronesia, Malaysia, Indonesia, Kenya, Seychelles, the Solomon Islands, the Torres Strait Islands, the Great Barrier Reef, Australia, Fiji, French Polynesia, New Caledonia and the Cook Islands in the Indo-Pacific Ocean.

The relationship between SSL data and latitude showed a patchy distribution between 10° Lat and 35° Lat for the species from the Atlantic Ocean (*M. phenax*, *M. bonaci*, *M. venenosa*, *M. tigris*, *E. itajara*, *E. guttatus*, *E. striatus* and *E. adscensionis*) and for one of the species from the Indo-Pacific Ocean (*E. merra*). These SSLs ranged from one to twelve months. The latitude-SSL correlations in the above-mentioned latitudes were negative in two cases and positive in seven cases, but none were statistically different from zero (Fig. 1). The minimum SPST-SSL correlations were negative for all mentioned species and were statistically significant for *E. itajara* (Spearman R = -0.71) and *E. guttatus* (-0.41), indicating that low values of SSL corresponded to high values of minimum SPST (Table 1). Some maximum SPST-SSL and average SPST-SSL correlations were negative whereas, others were positive and the maximum SPST-SSL correlations were only statistically significant for *M. bonaci* (Spearman R = 0.75), *E. guttatus* (Spearman R = 0.41) and *E. striatus* (Spearman R = 0.35), indicating that longer SSL values corresponded with higher maximum SPSTs (Table 1).

Table 1: Spearman rank correlation of the minimum, maximum and average temperature during spawning season respect to spawning season length of some tropical groupers

Species	N	Minimum SPST - SSL			Maximum SPST - SSL			Average SPST - SSL		
		R	t _{N,2}	p	R	t _{N,2}	p	R	t _{N,2}	p
<i>Plectropomus leopardus</i>	23	-0.05	-0.22	0.83	0.14	0.63	0.53	0.03	0.14	0.89
<i>Plectropomus areolatus</i>	44	-0.51	-3.86	<0.01*	-0.02	-0.14	0.89	-0.32	-2.20	0.03*
<i>Mycteroperca phenax</i>	7	-0.36	-0.86	0.43	-0.41	-1.01	0.36	-0.21	-0.48	0.65
<i>Mycteroperca bonaci</i>	18	-0.28	-1.17	0.26	0.75	4.55	<0.01*	-0.13	-0.52	0.61
<i>Mycteroperca venenosa</i>	19	-0.23	-0.99	0.34	0.38	1.67	0.11	0.10	0.43	0.68
<i>Mycteroperca tigris</i>	5	-0.54	-1.12	0.34	0.35	0.65	0.56	0.00	0.00	1.00
<i>Epinephelus ongus</i>	4	-0.95	-4.24	0.05	-0.32	-0.47	0.68	-0.95	-4.24	0.05
<i>Epinephelus polyphkadion</i>	32	-0.80	-7.42	<0.01*	-0.33	-1.88	0.07	-0.69	-5.26	<0.01*
<i>Epinephelus fuscoguttatus</i>	31	-0.42	-2.47	0.02*	-0.02	-0.13	0.90	-0.27	-1.53	0.14
<i>Epinephelus itajara</i>	11	-0.71	-3.05	0.01*	-0.35	-1.14	0.28	-0.58	-2.11	0.06
<i>Epinephelus guttatus</i>	24	-0.41	-2.12	0.04*	0.41	2.09	0.04*	-0.21	-1.01	0.32
<i>Epinephelus striatus</i>	57	-0.01	-0.05	0.96	0.35	2.81	0.01*	0.16	1.20	0.24
<i>Epinephelus adscensionis</i>	5	-0.56	-1.18	0.32	0.29	0.52	0.64	-0.56	-1.18	0.32
<i>Epinephelus merra</i>	6	-0.06	-0.13	0.91	-0.11	-0.22	0.83	-0.19	-0.38	0.72

SSL: Spawning season length, SPST: Spawning season temperature, N: No. of data, R: Spearman rank correlation coefficient, t_{N,2}: Student's t-test with N (number of data) less two degrees of freedom, p: probability of significance, *Significant correlation

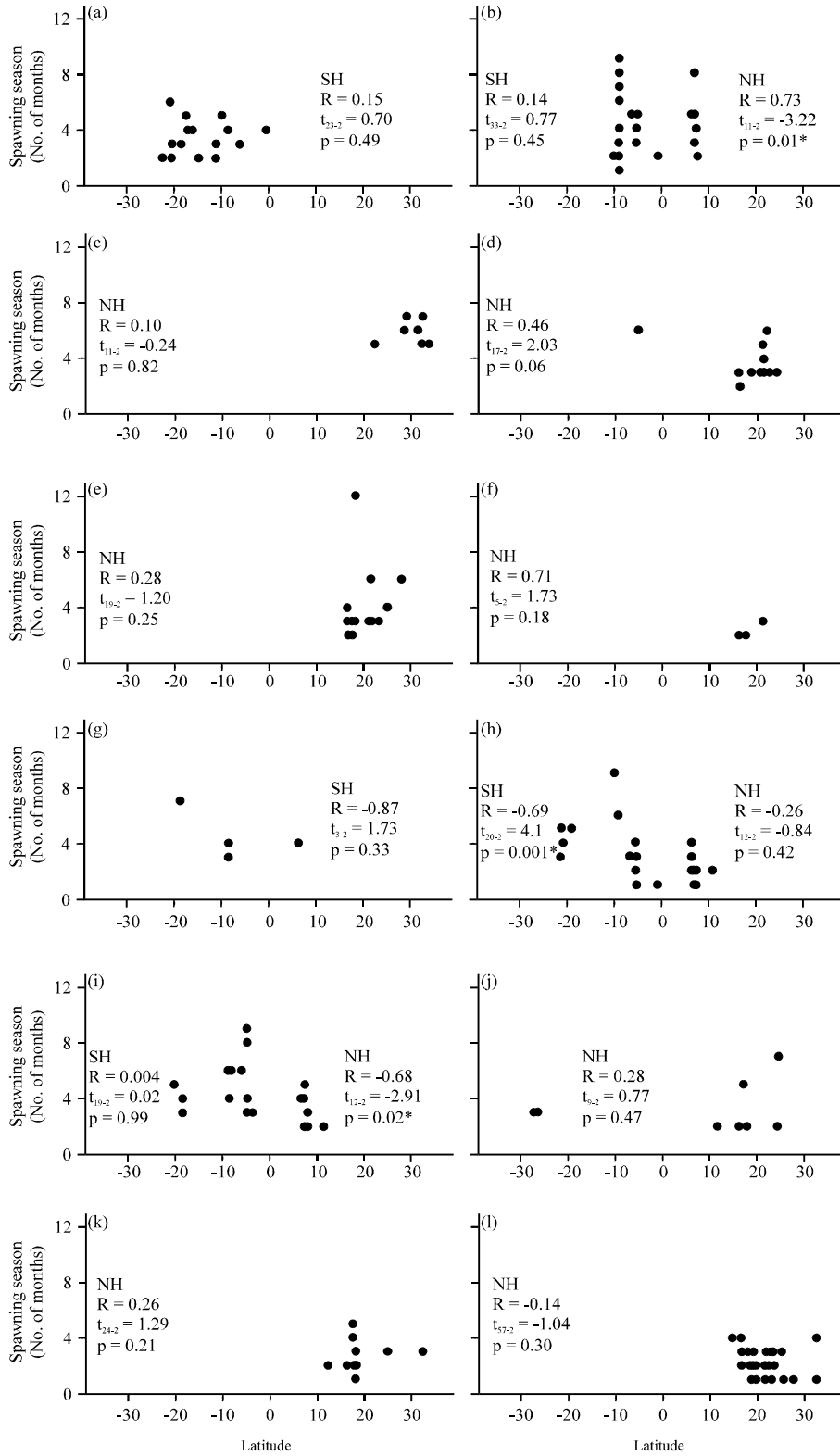


Fig. 1(a-n): Continue

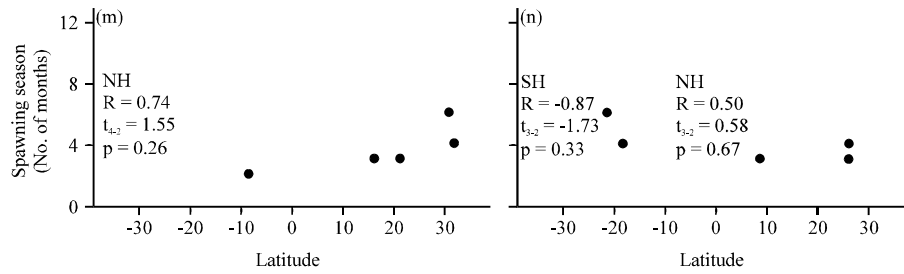


Fig. 1(a-n): Relationships of spawning season lengths, showing distribution with respect to latitude. SH, southern, NH, northern, R, the Spearman rank correlation, t, the t-test and p, probability level where, *indicates a statistically significant relationship, (a) *Plectropomus leopardus*, (b) *Plectropomus areolatus*, (c) *Mycteroperca phenax*, (d) *Mycteroperca bonaci*, (e) *Mycteroperca venenosa*, (f) *Mycteroperca tigris*, (g) *Epinephelus ongus*, (h) *Epinephelus polyphekadion*, (i) *Epinephelus fuscoguttatus*, (j) *Epinephelus itajara*, (k) *Epinephelus guttatus*, (l) *Epinephelus striatus*, (m) *Epinephelus adscensionis* and (n) *Epinephelus merra*

SSL data for other species from the Indo-Pacific Ocean (*P. leopardus*, *P. areolatus*, *E. ongus*, *E. polyphekadion* and *E. fuscoguttatus*) showed a patchy distribution mostly below 10° Lat, where SSL ranges from one to nine months. The latitude-SSL correlations were negative in the northern hemisphere between 0° Lat and 10° Lat and were statistically significant for *P. areolatus* (Spearman R = -0.73) and *P. fuscoguttatus* (Spearman R = -0.68), indicating that the shorter SSLs occurred at higher latitudes. However, the latitude-SSL correlations between 0° Lat and -25° Lat in the southern hemisphere were both negative and positive and were statistically significant for *E. polyphekadion* (Spearman R = -0.69), indicating that SSLs were longer at more southerly latitudes (Fig. 1). The minimum SPST-SSL correlations were negative for all species from the Indo-Pacific Ocean and were statistically different from zero for *P. areolatus* (Spearman R = -0.51), *E. polyphekadion* (Spearman R = -0.80) and *E. fuscoguttatus* (Spearman R = -0.42), indicating that low values of SSL corresponded to high values of minimum SPST (Table 1). The maximum SPST-SSL and average SPST-SSL correlations were negative in most cases except for *P. leopardus*. The average SPST-SSL correlations were only significant for *P. areolatus* (Spearman R = -0.32) and *E. polyphekadion* (Spearman R = -0.69), indicating that lower SSL values corresponded to higher average SPSTs (Table 1).

The latitude-SSL correlations were statistically insignificant for all species in both the northern (Spearman R = 0.11, $t_{179} = 1.54$, $p = 0.13$) and the southern (Spearman R = -0.11, $t_{103} = -1.1$, $p = 0.28$) hemispheres. However, the minimum SPST had a negative and significant correlation with SSL in both hemispheres (northern: Spearman R = -0.23, $t_{179} = -3.10$, $p = 0.002$; southern: Spearman R = -0.22, $t_{103} = -2.30$, $p = 0.02$). The maximum SPST-SSL correlation was significant in the northern hemisphere (Spearman R = 0.35, $t_{179} = 5$, $p < 0.001$), although the average SPST-SSL correlation was not (Spearman R = -0.06, $t_{179} = -0.74$, $p = 0.46$). The correlations of maximum SPST-SSL (Spearman R = 0.05, $t_{103} = 0.54$, $p = 0.59$) and average SPST-SSL (Spearman R = -0.11, t_{103} , $p = 0.27$) were not statistically significant in the southern hemisphere. Figure 2 shows the distribution of all SSL and temperature data with respect to latitude, where SSLs from one to six months occurred across the entire range of latitudes (-30° to 35°), but most spawning seasons that were longer than six months were observed at latitudes lower than -4° or higher than 10°.

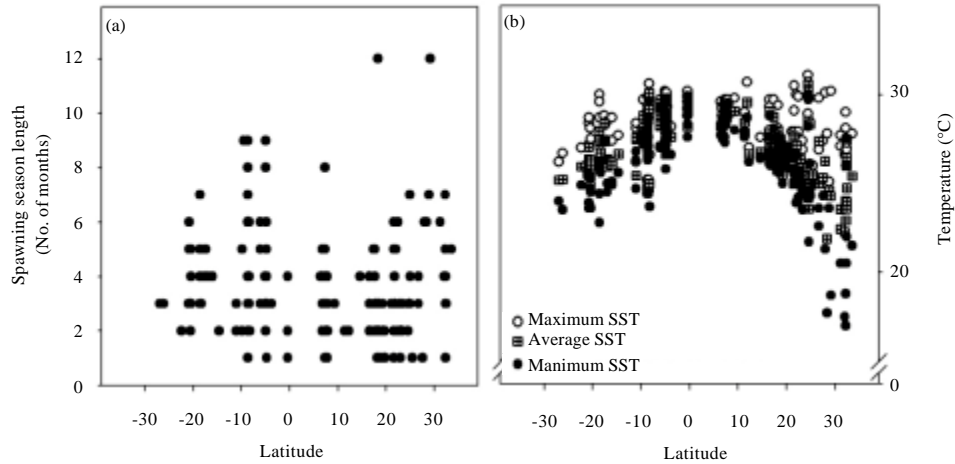


Fig. 2(a-b): Distribution showing global trends for (a) Spawning season length and (b) Spawning season temperatures with respect to latitude

Spawning aggregation duration: The Spawning Aggregation Duration (SAD) was correlated with latitude for two *Plectropomus* spp., two *Mycteroperca* spp. and four *Epinephelus* spp., (Fig. 3) from areas southeast of the Mexican Caribbean Sea and from the Bahamas, the Cayman Islands, the Virgin Islands, Puerto Rico and Belize in the Atlantic Ocean and from the Federated States of Micronesia, the Maldives Islands, Papua New Guinea and the Great Barrier Reef in the Indo-Pacific Ocean.

Most of the latitude-SAD correlations were negative except for *P. areolatus*, *M. tigris* and *E. fuscoguttatus* in the northern hemisphere. Only the correlation of SAD-latitude for *E. striatus* (Spearman $R = -0.36$) was statistically different from zero, indicating that lower values of SAD corresponded to higher latitudes (Fig. 3).

The latitude-SAD correlation was statistically insignificant for all species in both the northern (Spearman $R = -0.03$, $t_{72} = 1.54$, $p = -0.28$) and southern hemispheres (Spearman $R = 0.25$, $t_{44} = 0.25$, $p = 0.09$).

Lunar day of spawning: Few spawning events have been observed for the *Plectropomus* spp., *Mycteroperca* spp. and *Epinephelus* spp., included in this study. Spawnings have been observed near or within the full and third-quarter phases of the moon in species from the Atlantic Ocean and an occur from two days before the full moon to the third quarter in *E. striatus*. In the Indo-Pacific Ocean, spawnings for *P. areolatus*, *E. polyphekadion* and *E. fuscoguttatus* have been observed near or within the full and new phases of the moon, whereas spawning has been observed during the new moon for *P. leopardus* and around the full moon for *E. merra* (Table 2).

Time of day of spawning: Spawning activity has been recorded between afternoon and midnight in species from the Atlantic Ocean. In the Indo-Pacific Ocean, spawnings for *P. areolatus*, *E. polyphekadion* and *E. fuscoguttatus* can occur in the early morning to morning and from dusk to midnight. *P. leopardus* can spawn at dusk and *E. merra* can spawn during the night (Table 2).

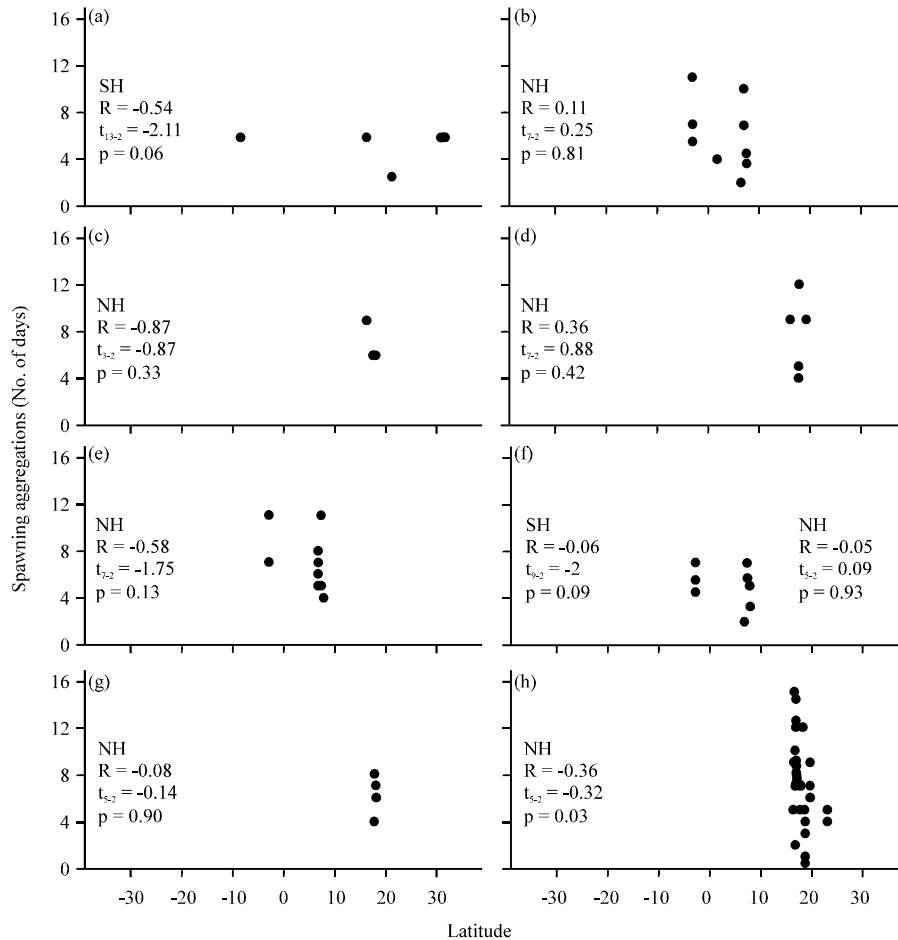


Fig. 3(a-h): Relationships between spawning aggregation duration and latitude. SH, southern, NH, northern, R, the Spearman rank correlation, t: the t-test and p, probability level, (a) *Plectropomus leopardus*, (b) *Plectropomus areolatus*, (c) *Mycteroperca venenosa*, (d) *Mycteroperca tigris*, (e) *Epinephelus polyphekadion*, (f) *Epinephelus fuscoguttatus*, (g) *Epinephelus guttatus* and (h) *Epinephelus striatus*

DISCUSSION

The spawning seasons of marine fishes are characteristically longer at latitudes nearer the equator (Johannes, 1978). Our analysis showed variable trends for SSL with respect to latitude in the tropics but only three cases were statistically significant, showing longer spawning periods nearer to the equator for *P. areolatus* and *E. fuscoguttatus* in the northern hemisphere and shorter spawning periods for *E. polyphekadion* in southern hemisphere. For most species, latitude was not a significant source of variation in SSL. This could be due to weak correlations, few records, or intraspecific inconsistencies, for example, *E. polyphekadion*, whose SSL increases closer to the equator in the northern hemisphere and decreases closer to the equator in the southern hemisphere.

Temperature is a common variable influencing the time at which fishes spawn in tropical areas (Colin, 2012; Craig, 1998; Pankhurst and Porter, 2003). Consistently, the results showed that the

Table 2: Lunar day of spawning and spawning period of day of some tropical groupers

Species	Lunar day of spawning	Period of day of spawning	References
<i>Plectropomus leopardus</i>	29	Dusk	h, r, z, hh, jj, qq
<i>Plectropomus areolatus</i>	15, 29	Dawn, morning, dusk and night	j, n, o, p, q, z, aa
<i>Mycteroperca phenax</i>		Dusk and night	k, w, ff
<i>Mycteroperca bonaci</i>		Dusk and night	c, l, ii
<i>Mycteroperca venenosa</i>	15, 26	Dusk and night	c, ll
<i>Mycteroperca tigris</i>	15, 20		e, nn
<i>Epinephelus polyphkadion</i>	13, 15, 28, 29	Early morning, morning and night	g, j, o, z, cc, ee
<i>Epinephelus fuscoguttatus</i>	15, 29	Morning, night and midnight	a, j, o, p, u, z, aa, ee
<i>Epinephelus itajara</i>		Dusk, night and midnight	f, s, v
<i>Epinephelus guttatus</i>	12, 22	Dusk	d, gg, pp
<i>Epinephelus striatus</i>	13 to 20, 22	Afternoon, dusk and night	b, c, e, i, y, ii, mm, nn, oo
<i>Epinephelus merra</i>	15, 18	Night	m, p, t, bb, kk

Lunar day of spawning: the 1st day representing the day after the new moon or the beginning of the cycle, the 8th day representing the first quarter phase, the 15th day representing the full moon phase, the 22nd day representing the last quarter phase and the 29th day representing the new moon phase. References: a: Avala *et al.* (1996), b: Carter *et al.* (1994), c: Claro and Lindeman (2003), d: Colin *et al.* (1987), e: Colin (1992), f: Colin (1994), g: Colin (2010), h: Doherty *et al.* (1994), i: Guitart and Juarez (1966), Aguilar-Perera (1994), j: Hamilton *et al.* (2004), k: Harris *et al.* (2002), l: Heyman and Kjerfve (2008), m: Jagadis *et al.* (2007), n: Johannes (1989), Johannes *et al.* (1999), o: Johannes *et al.* (1994), p: Johannes (1981) Russell (2001), q: Johannes and Squire (1988), Russell (2001), r: Juncker and Granger (2007), s: Koenig and Coleman (2009), t: Lee *et al.* (2002), u: Lim *et al.* (1990), Johannes *et al.* (1994), v: Mann *et al.* (2009) w: MARMAP by Sedberry *et al.* (2004), y: Paz and Grimshaw (2001), z: Pet and Muljadi (2001), aa: Pet *et al.* (2005), bb: Randall and Brock (1960), Lee *et al.* (2002), cc: Rhodes and Sadovy (2002), ee: Robinson *et al.* (2008), ff: Rocha *et al.* (2008), gg: Sadovy *et al.* (1994), hh: Samoilys and Squire (1994), ii: Sala *et al.* (2001), jj: Samoilys (1997), kk: Soyano *et al.* (2003), ll: Starr *et al.* (2007), mm: Tucker *et al.* (1993), nn: Whaylen *et al.* (2004), oo: Whaylen *et al.* (2006), pp: Whiteman *et al.* (2005), qq: Zeller (1998)

minimum SPST tended to be lower for longer spawning seasons, in individual species as well as for the whole dataset. In fact, we observed SSLs from one to six months across the entire range of latitude (-30° to 35°), but most spawning seasons longer than six months were observed at latitudes lower than 4°S or higher than 10°N, where lower water temperatures can be found (Lowe-McConnell, 1987; Colin, 2012). Additionally, this suggests that the high intraspecific variability of SSLs in similar ranges of latitude could be associated with the presence of different temperature regimes (variation in temperature between locations) at similar latitudes due to differences in habitats, such as those cases where neritic waters are more dynamic with greater variation in temperatures than deeper waters (Lowe-McConnell, 1987).

The variability in SSL suggests that there is a need to scrutinise the reproductive ecology of fishes and compare different tropical habitats for a better understanding of the variability in reproductive tactics. In addition, the minimum SPST could be investigated as an indicator of SSL for fish resources. Hypothetically, we could predict that if the minimum SPST were to rise in an anomalously warm year with respect to a normal year, a certain reduction in SSL could be expected. This could be useful for decision making processes in fisheries.

We are not aware of any studies that relate latitude to SAD; we found variable tendencies between species, but only one such relationship was statistically significant. We found that SAD is lower at higher latitudes for *E. striatus* across a short latitude interval (15° to 25° Lat). For *E. striatus*, the relationship of SSL with latitude was not significant but was clearly negative, suggesting that a shorter SSL occurs at higher latitudes. Statistically, the error level could be high

in the observation data and, consequently, in the distributions of the data, as field observations of this type are difficult; however, if the above tendency is assumed to be realistic, a shorter SAD could correspond to shorter SSLs in some areas between 10° and 30° Lat. This result suggests that reproductive output could be lower at higher latitudes in *E. striatus* and also that, hypothetically, some environmental conditions could be determining the SAD (Robertson, 1991). It is known that some spawning aggregations have disappeared in some areas of Mexico, the Bahamas, Belize, Puerto Rico, Bermuda and the Cayman Islands which is usually explained by over-fishing (Aguilar-Perera, 2006; Colin, 1992; Johannes *et al.*, 1999; Sadovy and Eklund, 1999; Sala *et al.*, 2001; Whaylen *et al.*, 2004). If environmental conditions cause a low SSL in some areas, those spawning sites could be more vulnerable to fishing activities than other areas; although our results indicate that this could be possible, more research is needed.

Lunar cues influence the behaviour and reproductive activities of various species of fish (Johannes, 1978; Taylor, 1984; Robertson *et al.*, 1990; Robertson, 1991), synchronising spawning activity at intervals of one month (lunar spawning cycle), two weeks (semi-lunar spawning cycle) or daily based on tidal changes (tidal spawning season) (Takemura *et al.*, 2010). Present results suggest that some grouper species probably follow a lunar spawning cycle which may have a relationship with the timing of spawning behaviour between afternoon and midnight. Others may exhibit semilunar spawning, which could be related to spawning between the early morning and morning and from dusk to midnight. These spawning periodicities are based on the lunar days on which spawning has been observed (Robertson *et al.*, 1990; Robertson, 1991; Takemura *et al.*, 2010). For some species and localities, spawning is highly predictable during the spawning season because of lunar periodicities, making species vulnerable to over-fishing (Claro and Lindeman, 2003; Claydon, 2005; Domeier and Colin, 1997; Johannes *et al.*, 1999).

CONCLUSION

The variability in SSL for tropical Epinephelidae fishes indicated that spawning seasons could be longer at cooler latitudes. Our analysis also suggests that the minimum SPST is probably a good indicator of SSL for several fish resources. We also found evidence that for *E. striatus*, SAD may vary with latitude with lower values towards higher latitudes. We propose two hypotheses: first, that a shorter SAD could correspond to a shorter SSL in *E. striatus* and second, that lunar and semilunar spawning behaviour could be associated with specific daily spawning patterns.

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REFERENCES

- Aguilar-Perera, A., 1994. Preliminary observations of the spawning aggregation of Nassau grouper *Epinephelus striatus*, at Mahahual, Quintana Roo, Mexico. Proc. Gulf Carib. Fish. Inst., 43: 112-122.
- Aguilar-Perera, A., 2006. Disappearance of a Nassau grouper spawning aggregation off the Southern Mexican Caribbean coast. Mar. Ecol. Prog. Ser., 327: 289-296.

- Avala, M.N.R., M.L.L. Dolar and J.A. Luchavez, 1996. Natural spawning of four *Epinephelus* species reared in the laboratory. Proceedings of the Seminar-Workshop on Breeding and Seed Production of Cultured Finfishes in the Philippines, May 4-5, 1993, Tigbauan, Iloilo, Philippines, pp: 65-77.
- Bouriga, N., M. Cherif, G. Hajjej, S. Selmi, J.P. Quignard, E. Faure and M. Trabelsi, 2011. Growth, reproduction and seasonal variation in the fatty acid composition of the sand smelt *Atherina* sp. from Kerkennah islands, Tunisia. *J. Fish. Aquat. Sci.*, 6: 322-333.
- 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. *Proc. Gulf Carib. Fish. Inst.*, 43: 65-111.
- Chelemal, M., S. Jamili and I. Sharifpour, 2009. Reproductive biology and histological studies in Abu Mullet, Liza abu in the water of the Khozestan Province. *J. Fish. Aquat. Sci.*, 4: 1-11.
- Claro, R. and K.C. Lindeman, 2003. Spawning aggregation sites of snapper and grouper species (*Lutjanidae* and *Serranidae*) on the insular shelf of Cuba. *Gulf Carib. Res.*, 14: 91-106.
- Claydon, J.A.B., 2005. The structure and dynamics of spawning aggregations of coral reef fish. Ph.D. Thesis, School of Marine Biology and Aquaculture, James Cook University, Australia.
- Colin, P.L., 1992. Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) and its relationship to environmental conditions. *Environ. Biol. Fish.*, 34: 357-377.
- Colin, P.L., 1994. Preliminary investigations of reproductive activity of the jewfish, *Epinephelus itajara* (Pisces: Serranidae). *Proc. Gulf Caribbean Fish. Inst.*, 43: 138-147.
- Colin, P.L., 2010. Aggregation and spawning of the humphead wrasse *Cheilinus undulatus* (Pisces: Labridae): General aspects of spawning behaviour. *J. Fish Biol.*, 76: 987-1007.
- Colin, P.L., 2012. Timing and Location of Aggregation and Spawning in Reef Fishes. In: Reef Fish Spawning Aggregations: Biology, Research and Management, De Mitcheson, Y.S. and P.L. Colin (Eds.). Springer, New York, USA., pp: 117-158.
- Colin, P.L., D.Y. Shapiro and D. Weiler, 1987. Aspects of the reproduction of two groupers, *Epinephelus guttatus* and *E. striatus* in the West Indies. *Bull. Mar. Sci.*, 40: 220-230.
- Craig, P.C., 1998. Temporal spawning patterns of several surgeonfishes and wrasses in American Samoa. *Pac. Sci.*, 1: 35-39.
- Doherty, P.J., A.J. Fowler, M.A. Samoily and D.A. Harris, 1994. Monitoring the replenishment of coral trout (Pisces: Serranidae) populations. *Bull. Mar. Sci.*, 54: 343-355.
- Domeier, M.L. and P.L. Colin, 1997. Tropical reef fish spawning aggregations: Defined and reviewed. *Bull. Mar. Sci.*, 60: 698-726.
- Froese, R. and D. Pauly, 2009. Fish Base. World Wide Web Electronic Publication, UK.
- Guitart, D. and M. Juarez, 1966. Embryonic and early larval stages of the Nassau grouper *Epinephelus striatus* (Bloch) (Perciformes: Serranidae). *Acad. Cienc. Cuba. Stud. Oceanol. Inst.*, 1: 32-45.
- Hamilton, R.J., M. Matawai and T. Potuku, 2004. Spawning aggregations of coral reef fish in New Ireland and Manus provinces, Papua New Guinea: Local knowledge field survey report. TNC Pacific Island Countries Report No. 4/04, The Nature Conservancy, Papua Nueva Guinea. http://pdf.usaid.gov/pdf_docs/PNADI905.pdf
- Harris, P.J., D.M. Wyanski, D. Byron White and J.L. Moore, 2002. Age, growth and reproduction of scamp, *Mycteroperca phenax*, in the Southwestern North Atlantic, 1979-1997. *Bull. Mar. Sci.*, 70: 113-132.
- Heyman W.D. and B. Kjerfve, 2008. Characterization of transient multi-species reef fish spawning aggregations at Gladden Spit, Belize. *Bull. Mar. Sci.*, 83: 531-551.

- Hosseini, S.A., S. Jamili, T. Valinassab, G. Vosoghi and S.M.R. Fatemi, 2009. Feeding and spawning of *Sphyaena jello* in the North-West of Persian Gulf. *J. Fish. Aquat. Sci.*, 4: 57-62.
- Jagadis, I., B. Ignatius, D. Kandasami and M.A. Khan, 2007. Natural spawning of honeycomb grouper *Epinephelus merra* Bloch under captive conditions. *J. Mar. Biol. Assoc. India*, 49: 65-69.
- Johannes, R.E. and L. Squire, 1988. Spawning aggregations of coral trout and maori wrasse on the Great Barrier Reef Marine Park. Report, CSIRO, Cairns, QDPI. Hobart, Australia.
- Johannes, R.E., 1978. Reproductive strategies of coastal marine fishes in the tropics. *Environ. Biol. Fish.*, 3: 65-84.
- Johannes, R.E., 1981. Words of the Lagoon: Fishing and Marine Lore in the Palau District of Micronesia. University of California Press, Berkeley, USA.
- Johannes, R.E., 1989. A spawning aggregation of the grouper, *Plectropomus areolatus* (Ruppel) in the Solomon Islands. Proceedings of the 6th International Coral Reef Symposium Executive Committee, August 8-12, 1988, Townsville, Australia, pp: 751-755.
- Johannes, R.E., L. Squire and T. Graham, 1994. Developing a protocol for monitoring spawning aggregations of palauan serranids to facilitate the formulation and evaluation of strategies for their management. Report No. 94/28, Forum Fisheries Agency, Solomon Islands. http://www.spc.int/digitalibrary/doc/fame/ffa/reports/ffa_1994_028.pdf
- Johannes, R.E., L. Squire, T. Graham, Y. Sadovy and H. Renguul, 1999. Spawning aggregations of groupers (*Serranidae*) in Palau. Marine Conservation Research Series Publication No. 1, The Nature Conservancy, pp: 144. <http://www.conservationgateway.org/file/spawning-aggregations-groupers-serranidae-palau>
- Juncker, M. and B. Granger, 2007. Main spawning areas of reef fishes in the Northern Province (New Caledonia). Phase 1: Survey of Ecological Knowledge, Report. Noumea: Program ZoNeCo (in French), http://www.reefbase.org/pacific/pub_A0000004667.aspx
- Kerdgari, M., T. Valinassab, S. Jamili, M.R. Fatemi and F. Kaymaram, 2009. Reproductive biology of the Japanese threadfin bream, *Nemipteru japonicus*, in the Northern of Persian Gulf. *J. Fish. Aquat. Sci.*, 4: 143-149.
- Khalil, N.A., A.E.H.E. El-Gamal, S.A. Gaber and M.A. Mousa, 2007. Immunohistochemical localization of gonadotropin-releasing hormone and somatolactin during sexual maturation and spawning of *Lates niloticus*. *J. Boil. Sci.*, 7: 1102-1111.
- Koenig, C.C. and F.C. Coleman, 2009. Population density, demographics and predation effects of adult goliath grouper. MARFIN Project Final Report No. NA05NMF4540045, National Oceanic and Atmospheric Administration (NOAA), Florida, USA. <http://teens4oceans.org/GGreport09.pdf>
- Lee, Y.D., S.H. Park, A. Takemura and K. Takano, 2002. Histological observations of seasonal reproductive and lunar-related spawning cycles in the female honeycomb grouper *Epinephelus merra* in Okinawan waters. *Fish. Sci.*, 68: 872-877.
- Lim, L.C., T.M. Chao and L.T. Khoo, 1990. Observations on the breeding of brown-marbled grouper, *Epinephelus fuscoguttatus* (Forsk.) in Singapore. *J. Primary Ind.*, 18: 66-84.
- Lowe-McConnell, R.H., 1987. Ecological Studies in Tropical Fish Communities. Cambridge University Press, London, pp: 73.
- Mann, D.A., J.V. Locascio, F.C. Coleman and C.C. Koenig, 2009. Goliath grouper *Epinephelus itajara* sound production and movement patterns on aggregation sites. *Endangered Species Res.*, 7: 229-236.
- Pankhurst, N.W. and M.J.R. Porter, 2003. Cold and dark or warm and light: Variations on the theme of environmental control of reproduction. *Fish Physiol. Biochem.*, 28: 385-389.

- Paz, G.E. and T. Grimshaw, 2001. Status report on nassau grouper (*Epinephelus striatus*) aggregations in Belize, Central America. Technical Report, Green Reef Environmental Institute, Belize. <http://eprints.eriub.org/1182/>
- Pet, J.S. and A.H. Muljadi, 2001. Spawning and aggregations of groupers (Serranidae) and Napoleon wrasse (Labridae) in the Komodo National Park. Monitoring Report, The Nature Conservancy, Indonesia. <http://www.komodonationalpark.org/downloads/fish%20monitoring%2098-01.pdf>
- Pet, J.S., P.J. Mous, A.H. Muljadi, Y.J. Sadovy and L. Squire, 2005. Aggregations of *Plectropomus areolatus* and *Epinephelus fuscoguttatus* (groupers, Serranidae) in the Komodo National Park, Indonesia: Monitoring and implications for management. *Environ. Biol. Fish.*, 74: 209-218.
- Ramadan, A.M. and M.M. El-Halfawy, 2007. Common forms of Atresia in the ovary of some red sea fishes during reproductive cycle. *Pak. J. Biol. Sci.*, 10: 3120-3125.
- Randall, J.E. and V.E. Brock, 1960. Observations on the ecology of Epinepheline and Lutjanid fishes of the Society Islands, with emphasis on food habits. *Trans. Am. Fish. Soc.*, 89: 9-16.
- Rhodes, K.L. and Y. Sadovy, 2002. Temporal and spatial trends in spawning aggregations of camouflage grouper, *Epinephelus polyphekadion*, in Pohnpei, Micronesia. *Environ. Biol. Fish.*, 63: 27-39.
- Robertson D.R., C.W. Petersen and J.D. Brawn, 1990. Lunar reproductive cycles of benthic brooding reef fishes: Reflections of larval biology or adult biology? *Ecol. Monogr.*, 60: 311-329.
- Robertson, D.R., 1991. The Role of Adult Biology in the Timing of Spawning of Tropical Reef Fishes. In: *The Ecology of Fishes on Coral Reefs*, Sale, P.E. (Ed.). Academic Press, San Diego, USA., pp: 356-386.
- Robinson, J., M. Samoilys and P. Kimani, 2008. Reef Fish Spawning Aggregations in the Western Indian Ocean: Current Knowledge and Implications for Management. In: *Ten Years after Bleaching: Facing the Consequences of Climate Change in the Indian Ocean*, Obura, D.O., J. Tاملander and O. Linden (Eds.). CORDIO, Mombasa, Kenya, pp: 263-276.
- Rocha, L., J.C. McGovern, M.T. Craig, J.H. Choat, B. Ferreira, A.A. Bertoncini and M. Craig, 2008. *Mycteroperca phenax*. IUCN Red List of Threatened Species. <http://www.iucnredlist.org/apps/redlist/details/132729/0>
- Russell, M., 2001. Spawning Aggregations of Reef Fishes on the Great Barrier Reef: Implications for Management. Great Barrier Reef Marine Park Authority, Townsville, Australia, ISBN-13: 9781876945008, Pages: 37.
- Sadeghi, M.S., F. Kaymaram, S. Jamili, M.R. Fatemi and M.S. Mortazavi, 2009. Patterns of reproduction and spawning of the *Scomberomorus commerson* in the coastal waters of Iran. *J. Fish. Aquatic Sci.*, 4: 32-40.
- Sadovy, Y. and A.M. Eklund, 1999. Synopsis of biological data on the nassau grouper, *Epinephelus striatus* (Bloch, 1972) and the jewfish, *E. itajara* (Lichtenstein, 1822). NOAA Technical Report NMFS 146, <http://spo.nwr.noaa.gov/tr146.pdf>
- Sadovy, Y., A. Rosario and A. Roman, 1994. Reproduction in an aggregating grouper, the red hind, *Epinephelus guttatus*. *Environ. Biol. Fish.*, 41: 269-286.
- Sala, E., E. Ballesteros and R.M. Starr, 2001. Rapid decline of Nassau grouper spawning aggregations in Belize: Fishery management and conservation needs. *Fisheries*, 26: 23-30.
- Salcedo-Bojorquez, S. and F. Arreguin-Sanchez, 2011. An exploratory analysis to identify reproductive strategies of billfishes. *J. Fish. Aquat. Sci.*, 6: 578-591.
- Samoilys, M.A. and L.C. Squire, 1994. Preliminary observations on the spawning behavior of coral trout, *Plectropomus leopardus* (Pisces: Serranidae), on the Great Barrier Reef. *Bull. Mar. Sci.*, 54: 332-342.

- Samoilys, M.A., 1997. Periodicity of spawning aggregations of coral trout *Plectropomus leopardus* (Pisces: Serranidae) on the northern Great Barrier Reef. *Mar. Ecol. Prog. Ser.*, 160: 149-159.
- Sedberry, G.R., C.L. Cooksey, S.F. Crowe, J. Hyland, P.C. Jutte, C.M. Ralph and L.R. Sautter, 2004. Characterization of deep reef habitat off the southeastern U.S., with particular emphasis on discovery, exploration and description of reef fish spawning sites. Report, project NA16RP2697. South Carolina: USA, Marine Resources Research Institute.
- Sivashanthini, K., G.A. Charles and S. Shutharshan, 2008. Fecundity studies of *Gerres abbreviatus* (BLEEKER, 1850) from the Jaffna lagoon, Sri Lanka. *J. Fish. Aquatic Sci.*, 3: 320-327.
- Soyano, K., T. Masumoto, H. Tanaka, M. Takushima and M. Nakamura, 2003. Lunar related spawning in honeycomb grouper, *Epinephelus merra*. *Fish Physiol. Biochem.*, 28: 447-448.
- Spearman, C., 1904. The proof and measurement of association between two things. *Am. J. Psychol.*, 15: 72-101.
- Starr, R.M., E. Sala, E. Ballesteros and M. Zabala, 2007. Spatial dynamics of the nassau grouper (*Epinephelus striatus*) in a Caribbean atoll. *Mar. Ecol. Prog. Ser.*, 343: 239-249.
- Sutharshiny, S. and K. Sivashanthini, 2011. Lipid reserves of *Scomberoides Lysan* (Pisces: Carangidae) from the Sri Lankan waters. *Int. J. Biol. Chem.*, 5: 170-183.
- Takemura A., M.S. Rahman and Y.J. Park, 2010. External and internal controls of lunar related reproductive rhythms in fishes. *J. Fish Biol.*, 76: 7-26.
- Taylor, M.H., 1984. Lunar synchronization of fish reproduction. *Trans. Am. Fish. Soc.*, 113: 484-493.
- Thresher, R., 1984. *Reproduction in Reef Fishes*. T.F.H. Publications, New Jersey, ISBN: 0876668082..
- Tucker, J.W., P.G. Bush and S.T. Slaybaugh, 1993. Reproductive patterns of Cayman Islands nassau grouper (*Epinephelus striatus*) populations. *Bull. Mar. Sci.*, 52: 961-969.
- Whaylen, L., C.V. Pattengill-Semmens, B.X. Semmens, P.G. Bush and M.R. Boardman, 2004. Observations of a Nassau grouper, *Epinephelus striatus*, spawning aggregation site in Little Cayman, Cayman Islands, including multi-species spawning information. *Environ. Biol. Fish.*, 70: 305-313.
- Whaylen, L., P. Bush, B. Johnson, K.E. Luke and C. McCoy *et al.*, 2006. Aggregation dynamics and lessons learned from five years of monitoring at a Nassau grouper (*Epinephelus striatus*) spawning aggregation in Little Cayman, Cayman Islands, BWI. *Proceedings of the 59th Gulf and Caribbean Fisheries Institute*, November 9-11, 2006, Belize, pp: 413-421.
- Whiteman, E.A., C.A. Jennings and R.S. Nemeth, 2005. Sex structure and potential female fecundity in a *Epinephelus guttatus* spawning aggregation: applying ultrasonic imaging. *J. Fish Biol.*, 66: 983-995.
- Wootton, R.J., 1998. *Ecology of Teleost Fishes*. 2nd Edn., Kluwer Academic Publishers, Dordrecht, Netherlands, ISBN-13: 9780412642005, Pages: 386.
- Zar, J.H., 2010. *Biostatistical Analysis*. 5th Edn., Prentice-Hall, Upper Saddle River, New Jersey, Englewood, USA., Pages: 662.
- Zeller, D.C., 1998. Spawning aggregations: Patterns of movement of the coral trout *Plectropomus leopardus* (Serranidae) as determined by ultrasonic telemetry. *Mar. Ecol. Prog. Ser.*, 162: 253-263.