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Reproductive Biology of the Lutjanidae: A Review

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ABSTRACT

Available information on the reproductive biology of over 40 species of the Lutjanidae found throughout the world's oceans is reviewed. The lutjanids are apparently gonochoristic, there being no histological evidence to the contrary. Population sex ratio as well as sex ratio at size is frequently skewed; however, evidence suggests this results from differential growth and mortality rates between the sexes.

Sexual maturity occurs at approximately 40-50% of maximum length. Analysis of covariance of length at maturity (with maximum length as a covariate) revealed that populations and species associated with islands mature at a significantly higher ($0.005>P>0.001$) proportion of maximum length (51%) than continental species and populations (43%). Deep (>91 m) dwelling species and populations mature at a significantly higher ($0.005>P>0.001$) proportion of maximum size (49%) than shallow (<91 m) species (43%).

Lutjanids are highly fecund, with large females producing 5-7 x 10^6 ova.

Two patterns of reproductive seasonality are apparent: Continental populations and species exhibit extended summer spawning, and insular populations and species reproduce year round with pulses in spring and fall.

Spawning appears to take place at night, sometimes timed to coincide with spring tides at new and full moons. Courtship behavior culminates in an upward spiral swim with gametes released at the apex.

Individual fish spawn more than once each reproductive season.

Many features of the reproductive biology of the lutjanids (e.g., spawning site preference, spawning seasonality, lunar periodicity, and spawning behavior) appear to be a strategy to introduce gametes into an environment where predation is relatively less intense. However, the strategy must also assure that young juveniles are returned to suitable, but patchy, habitat for settlement.

INTRODUCTION

The Lutjanidae is a large family consisting of about 17 genera and 103 species (Anderson 1986) found in the warmer regions of the world's oceans. Most species inhabit marine waters to depths of about 550 m, but a few occur in estuaries, particularly as juveniles and sometimes as adults. The family is speciose, with tropical members inhabiting a wide depth range. Temperate regions usually accommodate only the deeper-dwelling species. Snappers are highly substrate oriented and are usually associated with reefs and rock outcroppings.

Snappers can reach large size (>100 cm total length (TL) and 40 kg) and are important food fish in many parts of the world. Worldwide landings are estimated to be about 60,000 metric tons (FAO 1984). Commercial, recreational, and artisanal fishermen land snappers with bottom longlines, hook and line, traps, spears, and occasionally bottom trawls.

Despite their importance, the biology of many species is not well known. This paper presents a review of the state of knowledge of the reproductive biology of the Lutjanidae, with some general conclusions regarding similarities and differences among species throughout the tropical and temperate regions of the world. In some cases, this has been possible, but in others, obscure and inconsistent methodology make any general conclusions tentative at best.

SEXUALITY

Available information suggests that lutjanids are gonochoristic. Following sexual differentiation, sex remains fixed throughout life. Although studies utilizing

histological techniques to examine the gonads are not numerous (Rodriguez Pino 1962; Alves 1971; Futch and Bruger 1976), only normal gonochoristic testicular and ovarian tissue features are reported. Standard histological evidence for hermaphroditism, including persistence of an ovarian lumen in the testis or testicular tissue embedded in the ovarian mass (Smith 1965; Fishelson 1975), has not been noted. Similarly, analyses of sex ratios in species from geographically diverse locations (Table 5.1) do not show a pattern of consistent variation in sex ratio with size that would suggest hermaphroditism (i.e., very high proportions of one sex at small size that gradually decrease with increasing size, eventually diminishing to near 0 (Wenner 1972)). Rather, the data show inconsistent variation of population and size-specific sex ratios. The more thorough studies, in which a wide range of sizes was sampled, suggest a tendency for females to be preponderant at larger sizes (Rodriguez Pino 1962; Erhardt 1977; Grimes and Huntsman 1980; Baez Hidalgo et al. 1982; Everson 1984). This predominance of females among large fish probably results from differential longevity of the sexes, as females have been shown to outlive males in at least a few species (Rodriguez Pino 1962; Grimes and Huntsman 1980). Also, if a species were hermaphroditic, both sexes should not be present at most ages. Rodriguez Pino (1962) has shown that Lutjanus synagris from Cuba has both males and females at every age up to 4 years, with only females present thereafter.

Sexual dimorphism is apparently rare among the Lutjanidae; it is reported in only two species (genus Pristipomoides) from the Indo-west Pacific (Kami 1973). The ventral lobe of the caudal fin of female P. auricilla from Guam is inconsistently tinged with yellow, but if tinged, never forms a distinct blotch. Large males (>270 mm fork length (FL)), however, usually have a distinct yellow blotch on the ventral lobe of the caudal fin. In P. filamentosus, males have dusky anal and pelvic fin membranes, and large specimens have a yellow-orange tinge between the first and second anal spines and last two rays. Occasionally, anal fins of large females are dusky, but never tinged in yellow-orange.

MATURITY

Review of the published literature concerning sexual maturity among the Lutjanidae (Table 5.2) showed that

TABLE 5.1
Sex ratio information on various lutjanid species arranged according to zoogeographic province. N = sample size, F = female, M = male, TL = total length, FL = fork Length, and SL = standard length

Species	Location	Population Ratio (F:M)	Ratio at Length	Reference
		Western Atlantic Species		
Rhomboplites aurorubens	North Carolina and South Carolina	1.6:1 (N = 874)	Size range 100-650 mm TL; biased in favor of F's above 150 mm, eventually reaching 100% F	Grimes 1976; Grimes and Huntsman 1980
	Puerto Rico	1:1.1 (N = 1,322)	About equal from 110 to 380 mm FL	Boardman and Weiler 1980
Lutjanus vivanus	Puerto Rico	1.3:1 (N = 3,235)	About 55-60% F from <210 to >530 mm FL	Boardman and Weiler 1980
	Jamaica	1:1.4 (N = 452)	Between 200 and 700 mm FL varies 25-60% with no pattern	Thompson and Munro 1974, 1983
	Virgin Islands	1:1.17 (N = 141)	No data	Sylvester et al. 1980
L. vivanus	Virgin Islands	1:1.04 (N = 265)	No data	Brownell and Rainey 1971
L. buccanella	Puerto Rico	1.8:1 (N = 672)	Between <140 and 500 mm FL decreases slowly from about 80 to 40% F	Boardman and Weiler 1980
	Virgin Islands	1:1.29 (N = 39)	No data	Sylvester et al. 1980
	Jamaica	1.5:1 (N = 756)	Between 190 and 510 mm FL decreases steadily from about 80 to 10% F	Thompson and Munro 1974, 1983
	Virgin Islands	1:1.2 (N = 91)	No data	Brownell and Rainey 1971
Apsilus dentatus	Jamaica	1:1.3 (N = 564)	Between 280 and 580 mm FL decreases steadily	Thompson and Munro 1974, 1983
L. apodus	Jamaica	1.03:1 (N = 75)	Between 200 and 500 mm FL varies between 33 and 75% F, with no pattern	Thompson and Munro 1974, 1983
Ocyurus chrysurus	Jamaica	1:1.3 (N = 695)	Between 200 and 580 mm FL varies erratically 10 to 60%, eventually attaining 100% F at large size	Thompson and Munro 1974, 1983

(Continued)

TABLE 5.1 (Cont.)

Species	Location	Population Ratio (F:M)	Ratio at Length	Reference
	Florida Keys	1:1.04 (N = 1,621)	No data	Collins and Finucane Unpub.
	Cuba	1:1.4 (N = 1,902)	No data	Piedra 1965
L. synagris	Trinidad	1.13:1 (trap) 1.6:1 (trawl) (N = ?)	No data	Manickchand-Dass In press
L. synagris	Cuba	1.3:1 (N = 1,640)	No data	Claro 1981
		1.9:1 (N = 1,441)	Between 80 and 420 mm FL 50% F initially, then 60-70% F to 300 mm, then 100% F	Rodriguez-Pino 1962
	Colombian Caribbean	1:1.3 (N = 2,472)	Size range 100-500 mm SL; about 40-60% F up to 400 mm, then increasing to 88% F above 400 mm	Erhardt 1977
L. griseus	Florida Keys	1:1.1 (N = 722)	No data	Starck and Schroeder 1970
	Florida Bay (Florida Everglades)	1.1:1 (N = 790)	No data	Croker 1962
L. griseus	Cuba	1.6:1 (N = 1,331)	Size range 140-530 mm FL; up to about 300 mm about 50% F, then slowly increases to 100% F by 450 mm	Baez Hidalgo et al. 1982
L. campechanus	Northwestern Gulf Campeche Banks	1:1.3 (N = ?) 1.1:1 (N = 555)	Size range 200-400 mm SL, M's predominate Size range 250-800 mm FL; 1:1 up to about 600 mm then % F increases	Moseley 1966 Camber 1955
	South Atlantic Bight and Northeastern Gulf of Mexico	1.1:1 (N = 1,245)	Size range 230-858 mm FL	Collins et al. Unpub.
	Northwestern Gulf of Mexico	1.01:1 (N = 1,129)	No data	Bradley and Bryan 1975
L. purpureus	Northeastern Brazil	1:1.04 (N = 1,085)	No data	Ivo 1973

(Continued)

TABLE 5.1 (Cont.)

Species	Location	Population Ratio (F:M)	Ratio at Length	Reference
		Indo-West Pacific Species		
L. vaigiensis	Society Islands	1.7:1 (N = 56)	No data	Randall and Brock 1960
	Gulf of Aden	1:3.8 (N = 19)	Size range 225-315 mm SL	Druzhinin and Filatova 1980
L. sebae	Gulf of Aden	1:1.04 (N = 100)	Size range 215-745 mm SL	Druzhinin and Filatova 1980
L. rivulatus	Gulf of Aden	1.1:1 (N = 13)	Size range 555-715 mm SL	Druzhinin and Filatova 1980
L. lineolatus	Gulf of Aden	1.8:1 (N = 56)	Size range 175-325 mm SL	Druzhinin and Filatova 1980
L. kasmira	Gulf of Aden	1:1.5 (N = 5)	Size range 135-195 mm SL	Druzhinin and Filatova 1980
L. kasmira	Andaman Sea	1:1.16 (N = 1,122)	<99 mm TL M's predominate; 100-169 mm F's dominant; >170 mm M's dominant; above 230 mm no F's	Rangarajan 1971
L. gibbus	Gulf of Aden	1:1.5 (N = 32)	Size range 265-475 mm SL	Druzhinin and Filatova 1980
L. duodecim-lineatus	Gulf of Aden	1.9:1 (N = 77)	Size range 225-365 mm SL	Druzhinin and Filatova 1980
L. fulviflamma	New Caledonia	1.1:1 (N = 68)	Size range 100-300 mm SL; about 50% F to 260 mm when increases to 100% F	Loubens 1980
	East Africa	2.04:1 (N = 76)	Size range 51-220 mm SL	Talbot 1960
L. quinquelineatus	Caledonia (N = 190)	1:1.2	Size range 100-219 mm SL; in favor of M's throughout	Loubens 1980
L. vitta	New Caledonia	1:1.1 (N = 147)	Size range 100->300 mm SL; about 40% F decreasing to 9% F by >300 mm	Loubens 1980
L. amabilis	New Caledonia	1:1.6 (N = 282)	Size range <200-520 mm SL; 40% F gradually becoming 0%	Loubens 1980
L. johni	Andaman Sea	1:1.4 (N = ?)	No data	Druzhinin 1970

(Continued)

TABLE 5.1 (Cont.)

Species	Location	Population Ratio (F:M)	Ratio at Length	Reference
L. malabaricus	Andaman Sea	1.2:1 (N = ?)	No data	Druzhinin 1970
L. malabaricus	Vanuatu, New Hebrides	2.7:1 (N = 78)	No data	Brouard and Grandperrin 1984
P. multidens	Andaman Sea/ South China Sea	1.2:1 (N = 301)	Size range about 200-600 mm SL	Min et al. 1977
	Vanuatu, New Hebrides	1.4:1 (N = 382)	No data	Brouard and Grandperrin 1984
P. typus	Andaman Sea/ South China Sea	1:1.4 (N = 730)	Size range about 200-600 mm SL	Min et al. 1977
P. filamentosus	Andaman Sea/ South China Sea	1.3:1 (N = 677)	Size range about 200-700 mm SL	Min et al. 1977
	Guam	1:1.4 (N = 183)	Size range 179-600 mm SL	Kami 1973
	Hawaiian Islands	1:1.02 (N = 449)		Ralston 1981
P. auricilla	Guam (N = 384)	1.3:1 mm SL	Size range 200-410	Kami 1973
P. sieboldii	Guam	1:1.1 (N = 110)	Size range 170-350 mm SL	Kami 1973
P. flavipinnis	Guam	1.1:1 (N = 180)	Size range 167-427 mm SL	Kami 1973
	Vanuatu, New Hebrides	1.26:1 (N = 165)	No data	Brouard and Grandperrin 1984
E. carbunculus	Vanuatu, New Hebrides	2.04:1 (N = 137)	No data	Brouard and Grandperrin 1984
	Hawaiian Islands	2.02:1 (N = 833)	Size range about 275-625 mm FL; biased in favor F's above 350 mm FL, eventually reaching >90% F's	Everson 1984
E. coruscans	Vanuatu, New Hebrides	1.7:1 (N = 135)	No data	Brouard and Grandperrin 1984

TABLE 5.2
Length at first sexual maturity and maximum length in the population for selected Lutjanidae according to location and sex. Length at maturity was determined by visual staging of gonads. Maximum length is as reported for that population except as noted

Species	Location	Sex	Length (mm) at First Maturity	Maximum Length in Population	Percent of Maximum Length at First Maturity	Reference
			Western Atlantic Species			
Rhomboplites aurorubens	North Carolina and South Carolina	F	186 TL	627 TL	29.6	Grimes 1976; Grimes and Huntsman 1980
	Puerto Rico	M	140 FL	380 FL	36.8	Boardman and Weiler 1980
		F	170 FL		44.7	
Lutjanus synagris	Cuba	M	91[a]	300	22.8	Reshetnikov and Claro 1976
		F	91	400	22.8	
	Trinidad	M	225 TL	485 TL	46.4	Manickchand-Dass In press
		F	230 TL	431 TL	47.4	
	Cuba	M	85 FL	275 FL	30.9	Rodriguez-Pino 1962
		F	85 FL	310 FL	27.4	
L. synagris	Jamaica	M	183 FL	410 FL	44.6	Thompson and Munro 1974, 1983
		F	176 FL	410 FL	42.9	
Ocyurus chrysurus	Jamaica	M	260 FL	550 FL	47.3	Thompson and Munro 1974, 1983
		F	290 FL	560 FL	51.7	
	Florida Keys	F	200 FL	567 FL	35.3	Collins and Finucane Unpub.
L. griseus	Florida Keys	M	185 SL	489 SL	37.8	Starck and Schroeder 1970
		F	195 SL	489 SL	39.8	
	Cuba	M	245 FL	525 FL	46.7	Baez Hidalgo et al. 1982
		F	325 FL	525 FL	61.9	
L. campechanus	U.S. South Atlantic Bight and Gulf of Mexico	M	325 FL			
		F	325 FL	970 FL[b]	33.5	Collins et al. Unpub.
	Southwest Florida	M, F	334 FL	941 FL	35.5	Futch and Bruger 1976
	Campeche Banks	M, F	310 FL	778 FL	39.8	Camber 1955
	Northwestern Gulf of Mexico	M	230 FL	850 FL	27.1	Bradley and Bryan 1975
		F	255 FL	850 FL	30.0	
L. purpureus	Northeastern Brazil	M	400 TL	825 TL[c]	48.5	Alves 1971
		F	420 FL	825 TL	50.9	Gesteira and Ivo 1973

(Continued)

TABLE 5.2 (Cont.)

Species	Location	Sex	Length (mm) at First Maturity	Maximum Length in Population	Percent of Maximum Length at First Maturity	Reference
L. vivanus	Virgin Islands	M F	270 FL 240 FL	660 FL 660 FL	40.9 36.4	Brownell and Rainey 1971
L. vivanus	Jamaica	M F	525 FL 575 FL	720 FL 680 FL	72.9 84.5	Thompson and Munro 1974, 1983
	North Carolina and South Carolina	M F	270 TL 240 FL	660 TL 660 TL	40.9 36.4	Grimes et al. 1977
L. buccanella	Jamaica	M	260 FL 240 FL	490 FL 490 FL	53.1 48.9	Thompson and Munro 1974, 1983
	North Carolina and South Carolina	F	350 TL	627 TL	55.8	Grimes et al. 1977
	Virgin Islands	M F	380 FL 180 FL	540 FL	70.3 33.3	Brownell and Rainey 1971
L. apodus	Jamaica	M F	250 FL 250 FL	570 FL 570 FL	43.8 43.8	Thompson and Munro 1974, 1983
L. jocu	Jamaica	F	323 FL	720 FL	44.9	Thompson and Munro 1974, 1983
L. analis	Cuba	M, F	402 FL	690 FL	58.3	Rojas 1960
Apsilus dentatus	Jamaica	M F	440 FL 400 FL	560 FL 540 FL	78.6 74.1	Thompson and Munro 1974, 1983
Pristipomoides macropthalmus	Jamaica	F	180 FL	350 FL	51.4	Thompson and Munro 1974, 1983
P. macropthalmus	Virgin Islands	M, F	230 FL	430 FL	53.5	Brownell and Rainey 1971
			Indo-West Pacific Species			
L. bohar	East Africa	M, F	450 SL	660 SL	68.2	Talbot 1960
L. sebae	East Africa	M, F	490 SL	665 SL	73.7	Talbot 1960
L. amabilis	New Caledonia	M F	186 SL 191 SL	442 SL 382 SL	42.1 50	Loubens 1980
L. fulviflamma	New Caledonia	M F	185 SL 172 SL	258 SL 285 SL	71.7 60.4	Loubens 1980
	East Africa	M F	145 SL 160 SL	220 SL 220 SL	65.9 72.7	Talbot 1960

(Continued)

TABLE 5.2 (Cont.)

Species	Location	Sex	Length (mm) at First Maturity	Maximum Length in Population	Percent of Maximum Length at First Maturity	Reference
L. quinquelineatus	New Caledonia	M	112 SL	189 SL	59.3	Loubens 1980
		F	113 SL	195 SL	57.9	
L. vitta	New Caledonia	M	128 SL	312 SL	41.0	Loubens 1980
		F	138 SL	264 SL	52.3	
L. rivulatus	East Africa	M	450 SL	640 SL	70.3	Talbot 1960
L. gibbus	East Africa	M	240 SL	355 SL	67.6	Talbot 1960
		F	223 SL	355 SL	62.8	
L. sanguineus	East Africa	M	480 SL	650 SL	73.8	Talbot 1960
		F	505 SL	650 SL	77.7	
L. kasmira	East Africa	M	155 SL	205 SL	75.6	Talbot 1960
		F	125 SL	205 SL	60.9	
L. monostigma	East Africa	M	350 SL	420 SL	Insufficient data	Talbot 1960
L. argentimaculatus	East Africa	M	350 SL	630 SL	Insufficient data	Talbot 1960
Aprion virescens	East Africa	M	410 SL	800 SL	51.3	Talbot 1960
		F	465 SL	800 SL	58.1	
L. johni	Andaman Sea	M	301	913	32.9	Druzhinin 1970
		F	291		31.9	
L. ehrenbergi	East Africa	F	75 SL	228 SL[d]	32.9	Talbot 1960
L. vaigiensis	East Africa	M	190 SL	250 SL	76.6	Talbot 1960
P. filamentosus	Hawaiian Islands	F	456 FL	947 SL	48.1	Kikkawa 1984
P. multidens	South China Sea/ Andaman Sea	F	350 SL	700 SL	50	Min et al. 1977
P. multidens	South China Sea/ Andaman Sea	F	450 SL	680 SL	66.2	Min et al. 1977
P. typus	South China Sea/ Andaman Sea	F	280 SL	620 SL	45.2	Min et al. 1977
Etelis carbunculus	Hawaiian Islands	F	298 FL	650 FL	45.8	Everson 1984

[a]Length measurement not reported
[b]From Nelson and Manooch 1982
[c]Length from Ivo 1973
[d]From Druzhinin 1970, measurement not specified
[e]Not included in the statistical analysis

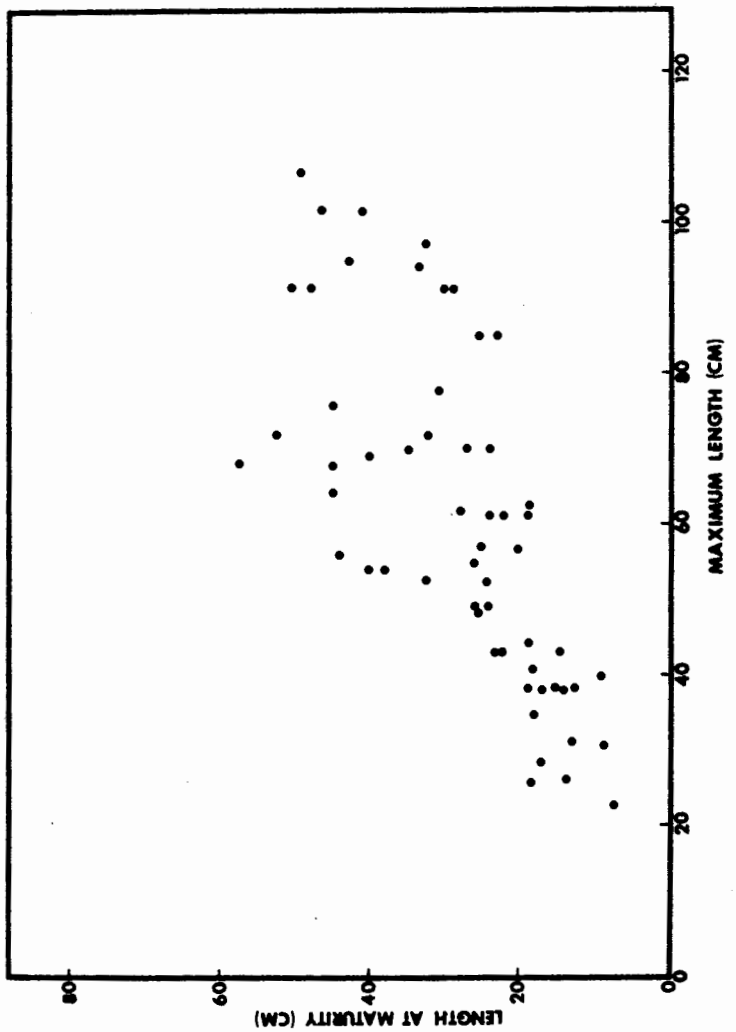

Figure 5.1 The relationship between length at sexual maturity and the maximum length attained in 57 lutjanid populations.

length at maturity ranges from 23 to 84% of the maximum length reported, that the relationship between maturity length and maximum length is linear (Figure 5.1), and that males mature at a slightly smaller size than females.

I used analysis of covariance to test the data in Table 5.2 for differences in size of maturity between (1) continental and insular habitats, (2) zoogeographic provinces, and (3) habitat depth. Because maturity length increases linearly with the maximum length reported for the population (Figure 5.1), the latter was used as a covariate to adjust the analysis for the possibility of different maximum sizes in the various species and populations.

There are consistent differences in the percentage of maximum length at which maturity is attained between continental and insular members of the fauna, as well as between deep (>91 m) and shallow (<91 m) components (Table 5.3). However, there are no apparent differences in relative size of maturity between western Atlantic and Indo-west Pacific lutjanids. Species and populations associated with islands mature at relatively larger size than those associated with continents (51 and 41% of maximum length, respectively). Similarly, populations and species associated with deep habitats mature at 49% of their maximum length, as compared to 43% for shallow species and populations (Table 5.3). Analysis of covariance testing for differences in length at maturity with regard to insular and continental habitats and habitat depth were significant ($P<0.01$), and there were no significant interactions (Table 5.4). Although an effect due to zoogeographic province was evident at the $P = 0.05$ level of significance, it was not as clear an effect as depth and habitat type.

I speculate that these differences in length at first maturity with regard to habitat depth and habitat type may be due to differences in the richness of food resources in insular versus continental and deep versus shallow habitats, coupled with the fact that sexual maturity in fish largely depends upon the allocation of energy between somatic and reproductive growth (Roff 1983). Fish have evolved a life history with an optimal balance between (1) rapid somatic growth to minimize predation while small and vulnerable, and (2) earliest possible reproduction to maximize the contribution of progeny to future generations. In young fish, energy resources are allocated more to somatic than gonadal growth, to obtain some minimum size where reproduction is physiologically possible and

TABLE 5.3
Length at maturity (MATLEN) and maximum length (MAXLEN) of selected lutjanid populations according to habitat type (insular or continental), zoogeographic province (western Atlantic or Indo-west Pacific), and habitat depth (deep ≥91 m or shallow ≤91 m). The % MAXLEN is the average percentage of maximum length at which sexual maturity occurs (SD = standard deviation)

		N	Mean	SD	Maximum	Minimum	% MAXLEN
Insular	MATLEN	38	245.6	120.5	575.0	85.0	51
	MAXLEN	38	477.0	164.3	947.0	189.0	
Continental	MATLEN	36	301.0	117.1	505.0	75.0	43
	MAXLEN	36	708.1	208.1	1066.0	228.0	
Western Atlantic	MATLEN	43	268.6	108.0	575.0	85.0	46
	MAXLEN	43	581.6	166.7	970.0	275.0	
Indo-west Pacific	MATLEN	31	277.9	139.4	505.0	75.0	46
	MAXLEN	31	600.3	278.6	1066.0	189.0	
Deep (≥91 m)	MATLEN	33	333.7	118.2	575.0	140.0	49
	MAXLEN	33	682.3	185.7	1066.0	350.0	
Shallow (≤91 m)	MATLEN	41	223.3	100.6	465.0	75.0	43
	MAXLEN	41	514.7	217.1	1015.0	189.0	

TABLE 5.4
Analysis of covariance of length at sexual maturity according to habitat type (insular or continental), zoogeographic province (western Atlantic or Indo-west Pacific), water depth (deep ≥91 m or shallow ≤91 m). Maximum length in the population is the covariate. All possible interactions between the main effects (i.e., habitat type, zoogeographic province, and habitat depth) and the covariate were tested, found nonsignificant, and dropped from the final model (df = degrees of freedom)

Effect	Sum of Squares	Mean Square	F-Value	df	P
Covariate	440732		85.01	1	0.0000
Overall	577.2		0.11	1	0.7396
Habitat type	59008		11.38	1	0.0012
Zoogeographic province	29385.8		5.67	1	0.0200
Habitat depth	43992.4		8.49	1	0.0048
Error	357745.8	5184.7			

the level of predation acceptable (Iles 1974; Roff 1982, 1983). Furthermore, fish growth is indeterminate, and maximum size is controlled (within genetic limitations) by food availability. Therefore, it may be that fish from relatively resource rich environments mature at a smaller proportion of final size than do fish from a poorer environment.

Habitats associated with continental margins and shallow depths are relatively rich in comparison to insular and deep habitats. Higher biological production is usually associated with large land masses for several reasons, such as opportunities for upwelling near continents (Cushing 1975), runoff of nutrient material into coastal waters (Gross 1972), and a greater amount of shallow continental shelf area providing habitat. Similarly, decreasing biological production is associated with increasing depth, primarily due to lower ambient light levels supporting primary production. A consequence of high production may be a greater food supply for the large predaceous fishes (e.g., lutjanids) in the community.

Another hypothesis to explain the effect of habitat on size at maturity relates to the physiological costs of reproduction over short versus long spawning seasons. Selection may have favored larger maturing fish on islands because the cost of spawning year round may be higher than the cost of more restricted spawning, as is typical of continental stocks. If true, maturation may be delayed until fish are able to sustain such costs. This explanation does not work as well for fish from deep versus shallow habitats, although the former do tend towards a less temporally restricted spawning season (see Seasonality section).

SEASONALITY

Numerous references to the seasonality of snapper reproduction suggest two fairly distinct seasonal patterns: (1) a restricted season (centered around summer) and (2) more or less continuous year-round spawning with peaks of reproductive activity in the spring and fall (Table 5.5). The pattern seems to depend more upon whether a population is found along a continental margin or on oceanic islands than upon latitude. Restricted spawning is more characteristic of continental species and populations, regardless of latitude. For example, continental populations (North Carolina, South

TABLE 5.5
Spawning seasons of selected Lutjanidae according to location and zoogeographic province. An X indicates ripe females were collected, XX indicates a peak spawning month, and dashed lines mean the author stated that spawning was continuous, or other types of analyses indicate spawning over the dashed period. Types of analyses are as follows: GSI = gonosomatic index, OD = ovum diameter distribution, VS = visual maturity staging, HS = histological sections, L = larval distribution, J = juvenile distribution, GW = gonad weights, MS = microscopic staging, and SR = sex ratio

Species	Location	Months: J	F	M	A	M	J	J	A	S	O	N	D	Analysis	Reference
		Western Atlantic Species													
Apsilus dentatus	Jamaica	X	--	XX	-X	--	XX	-X	----	-X	--	X	--	XX	VS	Munro et al. 1973
	Northeastern Caribbean, including Virgin Islands	X	X	X							X				VS	Erdman 1976
Lutjanus analis	Northeastern Caribbean, including Virgin Islands		X												VS	Erdman 1976

(Continued)

TABLE 5.5 (Cont.)

Species	Location	Months J	F	M	A	M	J	J	A	S	O	N	D	Analysis	Reference
L. apodus	Jamaica				X	X	X	X						VS	Munro et al. 1973
	Jamaica		X	X	X	X	X		X	X	X	X		VS	Thompson and Munro 1974, 1983
	Northeastern Caribbean, including Virgin Islands			X										VS	Erdman 1976
L. buccanella	Northeastern Caribbean including Virgin Islands		X		X					X				VS	Erdman 1976
	Jamaica		X	-----	XX	-X			X	--XX	----	X		VS	Thompson and Munro 1974, 1983
	Jamaica		X	--X	--XX	-X	--------		X	--XX	----	X		VS	Munro et al. 1973
	Puerto Rico	X	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	X	VS	Boardman and Weiler 1980
L. campechanus	Southwest Florida							---XX	-XX--					HS	Futch and Bruger 1976
	Northwestern Gulf of Mexico (Texas)						------XX--							VS, J	Moseley 1966
	Southeastern U.S. (North Carolina-East Florida)					X--X	--X	--X	--X					VS, GSI, MS	Collins et al. Unpub.
	Northwestern Gulf of Mexico (Texas)					X--XX	-XX	-X	--X	--X	--X	--X		VS, J	Bradley and Bryan 1975
	Campeche Banks, Mexico							XX-XX	----X					VS	Camber 1955
	Northwestern Gulf of Mexico (Texas)					X----------								VS, J	Baughman 1943
	North Carolina and South Carolina						--------							VS	Grimes et al. 1977

(Continued)

TABLE 5.5 (Cont.)

Species	Location	Months												Analysis	Reference
		J	F	M	A	M	J	J	A	S	O	N	D		
L. griseus	Northeastern Caribbean, including Virgin Islands					X			X	X				VS	Erdman 1976
	Venezuela						---	X	--X	---				VS, GSI	Campos and Bashirullah 1975
	Cuba					X	---	X	--X	X				VS, GSI	Baez Hidalgo et al. 1982
	Florida Keys						X--	X	--X	--X				VS, J, GW	Starck and Schroeder 1970
L. iocu	Jamaica			X										VS	Munro et al. 1973
	Jamaica			X								X		VS	Thompson and Munro 1974, 1983
	Northeastern Caribbean, including Virgin Islands			X										VS	Erdman 1976
L. mahogoni	Northeastern Caribbean, including Virgin Islands								X					VS	Erdman 1976
L. purpureus	Northeastern Brazil	X	--X	--X	--X						X	--X	--X	VS, GW	Gesteira and Ivo 1973
	Northeastern Brazil	X	--X	--X	--X	X							X	VS	Fonteles-Filho 1970, 1972
	Northeastern Brazil	X	X	X	X									VS	Ivo 1973
		----------								----------				GW	De Moraes and DosSantos 1969
L. synagris	Northeastern Caribbean, including Virgin Islands			XX	-X	--X	-----		X	------				VS	Erdman 1976
	Jamaica		X	X										VS	Munro et al. 1973

(Continued)

TABLE 5.5 (Cont.)

Species	Location	Months												Analysis	Reference
		J	F	M	A	M	J	J	A	S	O	N	D		
	Trinidad	X	--	X	--	XX	-	X	--	X	--	X	--	VS, J	Manickchand-Dass In press
	Cuba			X	--	X	--	XX	-	X	--	X	--	VS, HS	Rodriguez-Pino 1962
	Colombian Caribbean	X	--	X	--	XX	-	XX	X	X	X	X	X	VS	Erhardt 1977
	Cuba					X	X	X	X	X				VS, GSI	Reshetnikov and Claro 1976
L. vivanus	Puerto Rico	X	-	-	-	-	-	-	-	-	-	-	X	VS	Boardman and Weiler 1980
	Jamaica			XX	-	X	--	X	-	-	-	X	--	VS	Munro et al. 1973
	Northeastern Caribbean, including Virgin Islands		X			X				X		X		VS	Erdman 1976
	North Carolina and South Carolina						X	--	X	--	X				Grimes et al. 1977
Ocyurus chrysurus	Jamaica	XX	-	XX	-	XX	-	X	--	X	--	X	--	VS	Thompson and Munro 1974, 1983
	Northeastern Caribbean, including Virgin Islands		X		XX	XX	XX	X			XX			VS	Erdman 1976
	Jamaica		-	-	XX	-	-	-	-	X	--	X	-	VS	Munro et al. 1973
	Florida Keys	X		X	--	XX	-	XX	-	XX	-	XX	X	VS, MS, GSI	Collins and Finucane Unpub.
	Cuba			X	--	X	--	XX	-	XX	-	X	--	VS	Piedra 1965
Rhomboplites aurorubens	North Carolina and South Carolina					X	--	X	--	X	--	X	--	GSI, OD, VS	Grimes 1976 Grimes and Huntsman 1980
	Northeastern Caribbean, including Virgin Islands		X	-	-	-	-	X	--	X				VS	Erdman 1976

(Continued)

TABLE 5.5 (Cont.)

Species	Location	Months												Analysis	Reference
		J	F	M	A	M	J	J	A	S	O	N	D		
	Puerto Rico	X----------											X[a]	VS	Boardman and Weiler 1980
	Jamaica											X[b]			Munro et al. 1973
	North Carolina, South Carolina, Georgia								X--X[c]					L	Powles and Stender 1976
	Georgia							X--X						L	Fahay 1975
	Tortugas, Fla.							X[b]						VS	Longley and Hildebrand 1941
	Indo-West Pacific Species														
Aphareus rutilans	Vanuatu, New Hebrides	X	X		X	X				X	X	XX	XX	GSI, VS	Brouard and Grandperrin 1984
Aprion virescens	East Africa	X--X										---X		VS	Talbot 1960
	East Africa	X									X[d]			VS	Nzioka 1979
Etelis carbunculus	Vanuatu, New Hebrides			X	X	X		X	X		X	XX	X	GSI, VS	Brouard and Grandperrin 1984
	Hawaiian Islands						X--X--X							VS, GSI, OD, MS	Everson 1984
E. coruscans	Vanuatu, New Hebrides	X		XX	XX	XX		X	X	X	X	X	XX	GSI, VS	Brouard and Grandperrin 1984
L. amabilis	New Caledonia	XX-X							X--X--X--XX-XX					VS, GSI	Loubens 1980
L. argentimaculatus	East Africa											X		VS	Talbot 1960
L. bohar	East Africa	---X--X---------X---------X------X---												VS	Talbot 1960
	East Africa	X								X	XX			VS	Nzioka 1979
L. duodecimlineatus	Gulf of Aden			X										VS	Druzhinin and Filatova 1980
L. fulviflamma	New Caledonia	---X--								-X------X-				VS, GSI	Loubens 1980
	East Africa	------X							X-----X-----X-					VS	Talbot 1960

TABLE 5.5 (Cont.)

Species	Location	Months												Analysis	Reference
		J	F	M	A	M	J	J	A	S	O	N	D		
	East Africa								X	X			XX	VS	Nzioka 1979
L. gibbus	East Africa	------		X						X	-----	X	--X	VS	Talbot 1960
	East Africa	X	X								XX[b]			VS	Nzioka 1979
L. johni	Andaman Sea									X				VS	Druzhinin 1970
L. kasmira	East Africa			X								X		VS	Talbot 1960
	Andaman Sea	X	X	X						X	X	XX	XX	VS, GSI	Rangarajan 1971
	East Africa	X[d]												VS	Nzioka 1979
	Western Samoa			X	X	X	X	X	X	X	X	X	X	GSI, VS, SR	Mizenko 1984
L. lineolatus	Gulf of Aden			X										VS	Druzhinin and Filatova 1980
	East Africa											X[d]		VS	Nzioka 1979
L. malabaricus	Andaman Sea									X				VS	Druzhinin 1970
	Vanuatu, New Hebrides	XX	X	X		X	X	X			X	XX	XX		Brouard and Grandperrin 1984
L. monostigma	East Africa		X									X		VS	Talbot 1960
L. quinque-lineatus	New Caledonia	XX-	X	-----	X						X--	XX-	XX	VS	Loubens 1980
L. rivulatus	East Africa	---X		--X	--X				X			X--	X	VS	Talbot 1960
	Gulf of Aden			X[b]										VS	Druzhinin and Filatova 1980
	East Africa	X	X								XX		X[d]	VS	Nzioka 1979
L. rufolineatus	Western Samoa			XX	XX	XX	XX	X	X	X	X	X	X	GSI, VS, SR	Mizenko 1984
L. sanguineus	East Africa			X	X				X	X		X		VS	Talbot 1960
	East Africa			X						X	XX		X[d]	VS	Nzioka 1979
L. sebae	Gulf of Aden			X										VS	Druzhinin and Filatova 1980

(Continued)

TABLE 5.5 (Cont.)

Species	Location	Months												Analysis	Reference
		J	F	M	A	M	J	J	A	S	O	N	D		
	East Africa	X	--	X	--	X						X	-- X	VS	Talbot 1960
	East Africa	X	X								X[d]			VS	Nzioka 1979
L. vaigiensis	Society Islands	X	X	X							X	X	X[b]	VS	Randall and Brock 1960
	Gulf of Aden			X[b]										VS	Druzhinin and Filatova 1980
L. vitta	New Caledonia	XX	-XX	----	X			X	--	X	--	XX	-XX-XX	VS, GSI	Loubens 1980
Pristipomoides argyrogrammicus	East Africa							X		X	X		X[d]	VS	Nzioka 1979
P. filamentosus	Hawaiian Islands			X	X	XX	XX	XX	XX	XX	X	X	X	VS, GSI	Ralston 1981
	Hawaiian Islands								X	X	X			VS, GSI	Kikkawa 1984
	South China Sea and adjacent waters				X									GSI	Min et al. 1977
P. flavipinnis	Vanuatu, New Hebrides	XX	XX	X	X	X	X	X	X	X	X	X	XX	GSI, VS	Brouard and Grandperrin 1984
P. multidens	South China Sea and adjacent waters					X			X					GSI	Min et al. 1977
	Vanuatu, New Hebrides	XX	X	X	X	X	X	X	X	X	X	X	XX	VS, GSI	Brouard and Grandperrin 1984
	Western Samoa	X	X	X			X	X	X	X	X	X	X	GSI, VS, SR	Mizenko 1984
P. typus	South China Sea and adjacent waters			X		X			X					GSI	Min et al. 1977

[a]Monthly data not given
[b]Only months the species were collected
[c]Only summer months sampled
[d]No samples March-July

Carolina, Florida Keys) of Rhomboplites aurorubens, L. vivanus, and Ocyurus chrysurus are restricted spawners, while their insular counterparts (i.e., populations in Puerto Rico, Jamaica, and the northeastern Caribbean including the Virgin Islands) spawn year round. Strictly continental species such as L. campechanus from southeastern North America and Campeche Bank, Mexico, and L. purpureus from northeastern Brazil (3°-5° S) display the restricted pattern. Tropical East African populations (Tanzania and Kenya, 3°-7° S) of L. sebae, L. fulviflamma, L. rivulatus, L. gibbus, L. sanguineus, L. kasmira, L. monostigma, and Aprion virescens display the restricted continental pattern, as do Pristipomoides multidens and P. typus from the South China Sea and adjacent waters (20° N). Conversely, insular populations of L. kasmira (Western Samoa), L. malabaricus (New Hebrides), P. multidens (Western Samoa and New Hebrides), Etelis carbunculus (New Hebrides), E. coruscans (New Hebrides), Aphareus rutilans (New Hebrides), and L. rufolineatus (Western Samoa) do some spawning year round with peak activity during late spring, summer, and fall.

Several populations of lutjanids do not conform to this pattern. For example, snappers associated with large tropical islands such as Cuba (L. synagris, L. griseus, and O. chrysurus) and New Caledonia (L. amabilis and L. fulviflamma) do not display the typical insular pattern; they exhibit the continental pattern of restricted spawning. Lutjanus kasmira from the Andaman Sea and Etelis carbunculus from the Hawaiian Islands also do not conform to the pattern, as they are a continental population that spawns during fall and winter, and an insular population with restricted summer spawning, respectively.

The cause for the two patterns is not obvious. Presumably the patterns are adaptive and have survival value to their respective populations. Cushing (1975) and others have suggested that spawning cycles are timed to coincide with peaks in production cycles that provide food for the larvae. Nzioka (1979) suggested that peak spawning occurs among continental East African lutjanids at the time of highest productivity during the southeast monsoon, which speeds up the East African current, lowers the thermocline, and promotes vertical mixing. This also coincides with a period of low, but increasing, rainfall for that region (Dar es Salaam, Tanzania; Ruffner and Bair 1981). Lutjanus purpureus, a continental species from notheastern Brazil, also spawns during the season of lowest rainfall (Recife, Brazil; Ruffner and Bair 1981).

Similarly, L. kasmira in the Andaman Sea off Burma spawn during winter when rainfall is much lower than summer (Moidmein, Burma; Ruffner and Bair 1981). Continental snapper populations along the east coast of North America, from Venezuela and Campeche Banks, Mexico, spawn coincident with high summer rainfall (Wilmington, North Carolina; Miami, Florida; Pensacola, Florida; Caracas, Venezuela; and Mérida, Mexico; Ruffner and Bair 1981), warmest water temperatures, and peak production. Perhaps continental spawning is timed to introduce larvae into local production cycles created by oceanographic and meteorological conditions of high rainfall and subsequent nutrient runoff.

Populations on the large islands of Cuba and New Caledonia also reproduce during highest summer and fall rainfall (Havana, Cuba and Noumea, New Caledonia; Ruffner and Bair 1981). Perhaps these two large islands have the equivalent of continental production cycles, with peaks coincident with high rainfall.

Most island populations are in tropical and warm temperate areas where production is typically continuous and of low amplitude (Cushing 1975), and snapper reproduction there occurs more or less year round. Perhaps this is because there is no feeding advantage to be gained by restricting the spawning season, but predation can be avoided by spawning over an extended period. In contrast to continental and large island populations, reproductive cycles on islands are apparently not correlated with rainfall. In Trinidad, L. synagris spawn all year but peak during the dry spring (Manickchand-Dass In press). In contrast, peak spawning of many Indo-west Pacific island populations is reported to occur in late spring and summer when rainfall is frequently high (e.g., Guam, Mariana Islands, and Pago Pago, American Samoa (Ruffner and Bair 1981)).

The view that spawning in continental snapper populations may be timed to coincide with production cycles, while those associated with small islands reproduce year round because of low amplitude cycles, has support in the literature. Cushing (1975) has enunciated a very similar idea, based upon latitude, that summer spawning may be characteristic of fishes in low latitude steady-state production cycles, whereas spring and autumn spawning may be characteristic of the discontinuous high-amplitude production cycles of high latitudes. Lambert and Ware (1984) described reproductive strategies and suggested that pelagic and demersal spawning fish respond to the

major problems facing their larvae, i.e., finding food and avoiding predation, in different ways. Pelagic spawners use an "all at once" strategy to introduce larvae into a rich food supply so that they may grow rapidly and escape predators, which are swamped by great larval abundance. Demersal spawners "bet hedge" and produce slow-growing larvae in batches over an extended period. This insures a more even distribution of scarce food to the larvae and is a hedge against predation. Lutjanid reproductive strategies may fit the Lambert and Ware (1984) scheme because they are fast growing (Richards 1982) and are produced in batches (see Spawning section below) over an extended period. If food for larvae is more abundant during a season, then reproduction will be more seasonal (continental populations). If production is low and continuous (islands) and food is always scarce, then spawning will be continuous and in small batches as a hedge against predation.

SPAWNING

There is consistent evidence that lutjanids are batch spawners. Distributions of ovum diameters from the western Atlantic species L. synagris (Erhardt 1977), L. purpureus (De Moraes 1970), L. griseus (Campos and Bashirullah 1975), and R. aurorubens (Grimes and Huntsman 1980); and the Indo-west Pacific species P. multidens and P. typus (Min et al. 1977; Kikkawa 1984), L. kasmira (Rangarajan 1971), and E. carbunculus (Everson 1984) all show marked polymodality, a characteristic generally taken to indicate multiple or serial spawnings by individual females during the reproductive season. Striking variation in ovary lengths and weights of L. griseus during the reproductive season indicated batch spawning to Starck and Schroeder (1970). Similarly, marked variations in gonosomatic indices (ovary weight/TL^3) of fish sampled during the spawning season were interpreted to indicate serial spawning in R. aurorubens (Grimes and Huntsman 1980), and Ralston (1981) suggested that the low standing reproductive investment of P. filamentosus (ovaries of ripe females about 4% of body weight) made it likely the species was a multiple spawner. Everson (1984) found spawned-out ovaries only at the end of the spawning season, indicating fractional spawning in E. carbunculus. Grimes and Huntsman (1980) and Everson (1984) also found ovaries containing ova in various developmental stages in

R. aurorubens and E. carbunculus, which further suggested fractional spawning.

Large females may spawn longer and perhaps more times than small females. Grimes and Huntsman (1980) reported that the gonosomatic indices of large female R. aurorubens were high earlier and longer during the spawning season, and Starck and Schroeder (1970) observed that large fish with well-developed gonads remained on the reef longer than small ones, and thus probably spawned more often. Everson (1984) found that large E. carbunculus matured earlier in the reproductive season and remained in spawning condition longer than small fish.

The number of batches of eggs produced each spawning season has not been conclusively determined. Arnold et al. (1978) and Suzuki and Hioki (1979) reported several spawnings of captive L. campechanus and L. kasmira over periods of 1 month and 3 weeks, respectively. Each spawning of L. campechanus consisted of a "few thousand" small (0.8 mm diameter), nearly transparent eggs. It is not known, of course, if these spawnings corresponded to one or more size modes of developing ova, or how the artificial conditions affected events.

Most authors (cited above) report two or three distinct modes of developing ova from ripe females, but how the number of modes relates to the actual number of spawnings is not clear because the process of recruitment of developing ova from the undifferentiated oocyte pool is undescribed. Reshetnikov and Claro (1976) reported that L. synagris females spawned two to three batches of eggs in a spawning season, based upon temporal variation in gonosomatic index for the same school of fish. The data supporting this conclusion, however, are equivocal.

The timing of reproduction almost certainly involves a number of environmental cues, for example, temperature, photoperiod, and the lunar cycle. Temperature and photoperiod influence the overall seasonality of reproduction, at least for some lutjanids. Grimes and Huntsman (1980) showed that increasing gonad development and preparation for spawning in R. aurorubens was correlated with increasing water temperature and photoperiod off southeastern North America (North Carolina). Similarly, E. carbunculus spawned in the Hawaiian Islands when water temperature and photoperiod were near the seasonal peak (Everson 1984). Ripe R. aurorubens were found off North Carolina when water temperature in the habitat was 20.6°-24.8° C and photoperiod 13.5-14.5 h. When Arnold et al. (1978) spawned L. campechanus in captivity, they simulated

normal temperature and photoperiod conditions for the northwestern Gulf of Mexico (Port Aransas, Texas). Natural spawning occurred under conditions of 15 h light and 23°-25° C.

Lunar cycling of spawning activity appears to be common among reef fishes (Johannes 1978; Lobel 1978; May et al. 1979; McFarland 1982), apparently acting to align spawning precisely with tidal conditions favoring survival. The Lutjanidae are no exception. Based upon a visual determination of maturation stages for gonads, Randall and Brock (1960) reported spawning near full moon for L. vaigiensis in the Society Islands. Starck and Schroeder (1970) drew the same conclusion for L. griseus by observing variation in gonad lengths and weights. Occurrence of ripe gonads and regular cycling in gonosomatic index (gonad weight/body weight) indicated to Mizenko (1984) that L. kasmira, L. rufolineatus, and P. multidens spawned at or near full moon on Western Samoan reefs. Reshetnikov and Claro (1976) also reported that spawning of L. synagris in Cuba always coincided with full moon. The fact that Suzuki and Hioki (1979) had successive spawnings of aquarium-maintained L. kasmira on dates corresponding to new and full moon provides additional evidence for lunar spawning periodicity. Although Grimes and Huntsman (1980) could not demonstrate lunar reproductive cycling in R. aurorubens, very similar reproductive condition (gonosomatic index) of fish caught from the same school suggested that reproduction was synchronized within the school.

Spawning of lutjanids has seldom been observed. Wiklund (1969) gave the following account of L. synagris spawning off southeast Florida. Courtship behavior began during the crepuscular period (1930-2000 h) when fish began to aggregate near the bottom in groups of 5-10 fish and to chase each other. Most members of the group (males) pursued a single lighter-colored female, and different males nuzzled the vent of the female. The group became more condensed and very active while moving slowly off the bottom. At about 2 m (7 ft) off the bottom the fish became extremely active, then swam suddenly in all directions depositing eggs and milt in the water column. The spawning was completed before dark.

Both L. campechanus (from the Gulf of Mexico) and L. kasmira (from Japan) have spawned in captivity (Arnold et al. 1978; Suzuki and Hioki 1979). The red coloration of L. campechanus became noticeably deeper and more vivid, and males nudged the bellies of females. In L. kasmira, courtship behavior began among a small group of males and females hovering near the bottom at 1800 to 1900, approximately 2 h before spawning. Pairs swam together in upward spirals with males pecking and pushing the bellies of females with their snouts. Spiral ascending movements became more rapid and reached higher in the water column, and were repeated 20-30 times over 2 h. Finally, spawning occurred simultaneously among 10 or more fish spiraling upward together, releasing their gametes just below the surface.

FECUNDITY

Information in the published literature concerning fecundity is fraught with inconsistency, and little analysis was possible (Table 5.6). The data allow only the general, and obvious, conclusion that the Lutjanidae are highly fecund.

Maximum and minimum fecundity values reported for the various species of Lutjanidae varied by about two orders of magnitude. For example, maximum fecundity ranged from 9.3×10^6 ova for L. campechanus from the South Atlantic Bight and Gulf of Mexico of North America to 2.03×10^5 ova for L. buccanella from the Virgin Islands. Minimum values for ripe females were similarly variable among species (1.8×10^6 ova in L. griseus from Venezuela to 8.17×10^3 ova in R. aurorubens from the North American South Atlantic Bight).

Fecundity estimates for the same species from different locations were also quite variable but were within the same order of magnitude. For example, maximum fecundity of L. synagris from northeastern Brazil was estimated to be 2.28×10^5 for a 494 mm TL female, while similar-sized animals from Trinidad (419 mm TL) and the Colombian Caribbean (420 mm TL) had estimates of 5.95×10^5 and 2.67×10^5, respectively.

Fecundity is usually an exponential function of body size, so if there were a consistent relationship between body size (e.g., weight) and fecundity among the lutjanid species, it would be indicated by the consistency of exponents in predictive equations. No such relationship is obvious, but the available data are clearly inadequate to properly address the question. Consistency in the relationship between fecundity and body size was also examined by calculating maximum and minimum relative fecundity (ova per gram of body weight, Table 5.6).

TABLE 5.6
Fecundity (F) of selected Lutjanidae. Lengths are in millimeters, weight in grams, and fecundity per gram body weight is in parentheses. TL = total length, FL = fork length, SL = standard length

Species	Location	Maximum F (10^5)	Length/Weight at Maximum F	Minimum F (10^4)	Length/Weight at Minimum F	Reference
			Western Atlantic Species			
Rhomboplites aurorubens	North Carolina and South Carolina	17.8 (776/g)	557 TL/2,293 g	0.817	229 TL/139 g	Grimes 1976; Grimes and Huntsman 1980
Lutjanus vivanus	Virgin Islands	2.99	630[a]	0.90	265[a]	Sylvester et al. 1980
L. buccanella	Virgin Islands	2.03	445[a]	1.15	290[a]	Sylvester et al. 1980
L. purpureus	Northeastern Brazil	9.0 (153/g)	780 TL/5,850 g	9.0	460 TL	Gesteira and Ivo 1973
L. synagris	Northeastern Brazil	2.28	494 TL	2.0	244 TL	Gesteira and Rocha 1976
	Trinidad	5.95	419 TL	2.87	294 TL	Manickchand-Dass In press
	Cuba	9.94 (1,875/g)	310 FL/530 g	34.7 (1,000/g)	225 FL/180 g	Rodriguez-Pino 1962
	Colombian Caribbean	2.67 (213/g)	420 TL/1,250 g	4.12 (206/g)	250 TL/200 g	Erhardt 1977
L. campechanus	South Atlantic Bight and Gulf of Mexico	93.2 (746/g)	605 FL/12,485 g	4.4 (4/g)	420 FL/1,100 g	Collins et al. Unpub.
L. griseus	Venezuela	58.4 (1,390/g)	660 TL/4,200 g	180.0 (1,440/g)	468 TL/1,250 g	Campos and Bashirullah 1975
	Florida Keys	5.48	354 SL			Starck and Schroeder 1970
L. analis	Colombian Caribbean	3.73 (162/g)	520 TL/2,300 g	13.8 (345/g)	320 TL/400 g	Erhardt and Meinel 1977
	Cuba	13.7 (603/g)	512 FL/2,270 g			Rojas 1960
Ocyurus chrysurus	Florida Keys	13.9 (779/g)	480 FL/1,784 g	3.8 (208/g)	212 FL/182 g	Collins and Finucane Unpub.
	Cuba	6.19 (672/g)	382 FL/920 g	9.97 (216/g)	302 FL/460 g	Piedra 1965

TABLE 5.6 (Cont.)

Species	Location	Maximum F (10^5)	Length/Weight at Maximum F	Minimum F (10^4)	Length/Weight at Minimum F	Reference
		Indo-West Pacific Species				
Pristipomoides multidens	South China Sea/Andaman Sea	27.7 (769/g)	555 SL/3,600 g	49.0 (168/g)	484 SL/2,900 g	Min et al. 1977
P. typus	South China Sea/Andaman Sea	20.7 (828/g)	478 SL/2,500 g	76.0 (690/g)	356 SL/1,100 g	Min et al. 1977
P. filamentosus	South China Sea/Andaman Sea	21.4 (1,177/g)	425 SL/1,817 g	140.0 (1,125/g)	374 SL/1,244 g	Min et al. 1977
Etelis carbunculus	Hawaiian Islands	13.3 (534/g)	508 FL/2,490 g	34.9 (360/g)	383 FL/970 g	Everson 1984

[a]Length measurement unspecified

Maximum values ranged from 1,875 ova per gram for *L. synagris* from Cuba to 153 ova per gram for *L. purpureus* from northeastern Brazil. Minimum values were similarly variable (1,900 ova per gram for *L. synagris* from Cuba to 60 per gram for *R. aurorubens* from the North American South Atlantic Bight).

It seems likely that the large variation in the fecundity results is mostly due to inconsistency of method. The major methodological problem is in determining which ova to count in serial spawners, which have several more or less distinct groups of developing ova. It is difficult to distinguish small developing ova from primary oocytes on the basis of size alone. How does one easily determine if the developing ova present are all that will develop during the current reproductive season, or if more ova will be recruited later from the undifferentiated oocyte pool? Also, the fraction of the ovarian egg complement actually spawned is usually unknown. Another potential source of error in estimating the fecundity of fractional spawners is using sample ovaries from fish that have partially spawned. This results in underestimation and can be avoided by careful selection of ovarian samples early in the spawning season before any spawning takes place. However, in populations that spawn year round, or nearly so, this may be difficult.

Although problems of accurately estimating batch and total fecundity have been addressed by De Silva (1973), Macer (1974), Hunter and Goldberg (1979), Gale and Deutsch (1985), and others, no clear and simple methods to resolve them have been presented. The egg production process and its relation to body size, fecundity estimation, realized fertility, and other problem areas need thorough study.

REPRODUCTIVE STRATEGY

Lutjanids, like most species that reach large sizes and are abundant enough to support fisheries, would be considered r-strategists in the general parlance of life history tactics. They are highly fecund (see Fecundity section) broadcast spawners (see Spawning section) that produce fairly typical pelagic eggs (approximately 0.8 mm in diameter) and dispersive pelagic larvae (*L. synagris*, Borrero et al. 1978; *L. griseus*, Damas et al. 1978, Richards and Saksena 1980; *L. campechanus*, Arnold et al. 1978, Collins et al. 1980, Rabalais et al. 1980, and Minton et al. 1983; *R. aurorubens*, La Roche 1977; *L.*

kasmira, Suzuki and Hioki 1979). However, lutjanids, like many other reef fishes, have evolved a number of reproductive mechanisms that help insure survival in a temporally constant, but patchy, habitat where predation is an important structuring force. In fact, Johannes (1978) has convincingly argued that predation is an overriding selective factor in the life history of most reef fish. He suggests that many aspects of reproduction, such as spawning site preference; seasonality, frequency and duration of spawning; and lunar and diel spawning periodicity, are all adaptations to reduce predation on the young.

The reproductive seasonality of lutjanids, as described earlier, displays two more or less distinct patterns, irrespective of latitude: (1) insular or year round, usually with spring and fall peaks, and (2) a continental or a restricted (centered around summer) spawning season. Johannes (1978) suggested that spawning seasonality of coastal marine tropical fishes is timed to coincide with periods when wind and current speed are at a minimum, to reduce loss of pelagic larvae from the patchy habitats of reef environments. Reshetnikov and Claro (1976) suggested that spawning is timed to coincide with periods of high rainfall, when increased runoff introduces nutrients into coastal waters and supports greater food production for early life stages. Periods of highest rainfall and reproductive activity are correlated for some continental and large island lutjanid populations, but the relationship is inconsistent for small islands (see Seasonality section). The hypothesis that spawning is timed to coincide with greater food availability is not supported, at least for small islands, by findings that show spawning intensity and larval fish density are not correlated with plankton density or productivity around Hawaii and Jamaica (Munro et al. 1973; Miller 1974).

Clearly the Lutjanidae are batch or serial spawners (see Spawning section). Johannes (1978) has suggested that batch reproduction over an extended period might increase recruitment under circumstances where random factors determine the availability of space suitable for settling by recruits (Sale 1978). However, McFarland (1982) has shown that recruitment of French grunts (Haemulon flavolineatum) is tightly coupled to lunar and tidal events, and there is order in the occupation of space because the same species repeatedly occupies the same settlement sites. A more plausible advantage for batch reproduction is offered by Lambert and Ware (1984), who suggested that batch spawning is a hedge against egg and larval predation and has the additional advantage of affording a more equitable distribution of scarce food.

Johannes (1978) speculated that spawning site preference, diel periodicity of spawning, and patterns of spawning behavior are also adaptations to reduce predation. He theorized that spawning offshore near the outer reef introduces gametes into more predator-free offshore waters, while nocturnal spawning reduces the threat of visually orienting predators to both gametes and spawning adults. The upward spawning rush described during the spawning ritual of many reef fish is also thought to help distribute gametes out of reach of benthic predators. The little information available on the Lutjanidae regarding site selection and spawning behavior indicates that they are typical of reef fish. Croker (1962) and Starck and Schroeder (1970) reported that L. griseus spawns on the outer reef. The upward spawning rush, culminating in the release of gametes, has been reported to occur at night for both L. synagris and L. kasmira (Wiklund 1969; Suzuki and Hioki 1979).

Many reef fish spawn according to a lunar rhythm on or around new or full moon (Johannes 1978; Lobel 1978; McFarland 1982), as if taking advantage of maximum tidal flows to flush propagules offshore to a more predator-free environment and ultimately to return them to inshore juvenile settlement sites (McFarland 1982). Lunar cycling of spawning is evidently the rule among the Lutjanidae (see Spawning section).

If spawning site preference, spawning seasonality, lunar and diel periodicity, etc., among the lutjanids are indeed adaptations to get propagules offshore to more predator-free waters, then egg and larval development rates should be rapid so that the young would not be swept away by oceanic currents before their development allowed return to suitable settlement sites by tidal flow. For example, McFarland (1982) demonstrated that H. flavolineatum spawn at about new or full moon and the larvae develop rapidly, returning to settle as juveniles 14 days later on the next spring tide. Data relevant to the length of the planktonic larval period of snapper are meager, but do suggest a similar rapid development rate. Fertilized eggs of L. synagris (Borrero et al. 1978), L. griseus (Damas et al. 1978), L. campechanus (Arnold et al. 1978; Rabalais et al. 1980; Minton et al. 1983) and L. kasmira (Suzuki and Hioki 1979) hatch in 19, 18, 20, and 18 h at ambient seawater temperatures; and the yolk is absorbed in 40-50,

45, 48, and 72 h. First feeding of larval L. campechanus (Rabalais et al. 1980) and L. kasmira (Suzuki and Hioki 1979) occurred 72 h after hatching. The total duration of the planktonic larval phase is unknown, however.

SUMMARY

The Lutjanidae are gonochoristic. Histological studies have not revealed cellular or gross structural evidence to indicate hermaphroditism. Population sex ratios may be slightly unequal and skewed in favor of one sex at larger size. Evidence suggests, however, that skewed sex ratios probably result from differential growth and mortality between the sexes.

Sexual maturation evidently occurs at a slightly smaller size in males than females, and on average at about 40-50% of maximum length for both sexes. Populations and species associated with islands mature at about 51% of their maximum length, while the figure for continental stocks is 43%. Members of the deep reef fauna (>91 m) mature at an average of 49% of maximum length, and shallow forms (<91 m) at 43%.

Like most broadcast spawners, the Lutjanidae are highly fecund, with large females (approximately 100 cm) producing up to 5-7 x 10^6 ova. However, because they are batch spawners with several size modes of developing ova simultaneously present in ovaries, it has been difficult to realistically estimate total egg production for one spawning season.

Two patterns of reproductive seasonality emerge. Continental populations and species have a spawning season which is typically centered around summer, while populations and species associated with small oceanic islands reproduce year round with pulses of activity in the spring and fall.

Spawning evidently occurs at night near open water and is timed to coincide with spring tides at new and full moons. Distinct courtship behavior culminates in an upward spiral swim toward the surface when gametes are released. Individual fish are believed to spawn more than once during a reproductive season (batch spawning).

Predation is apparently a strong selective factor for reef fish; therefore, many aspects of the reproductive biology of the lutjanids appear as adaptations to introduce gametes into an environment where predation is reduced. At the same time, these adaptations must assure that young juveniles are returned to a suitable, but highly patchy, habitat for settlement.

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