

DAILY TIME OF SPAWNING OF 12 FISHES IN THE PECONIC BAYS, NEW YORK

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ABSTRACT

Diel spawning periodicity occurs throughout the spawning season in 11 of 12 fishes studied in the Peconic Bays, New York. The bay anchovy, *Anchoa mitchilli*; Atlantic menhaden, *Brevoortia tyrannus*; northern and striped searobins, *Prionotus carolinus* and *P. evolans*; hogchoker, *Trinectes maculatus*; weakfish, *Cynoscion regalis*; windowpane flounder, *Scophthalmus aquosus*; and butterfish, *Pepilus triacanthus*, spawn primarily in the evening or at night. The tautog, *Tautoga onitis*, and cunner, *Tautoglabrus adspersus*, begin spawning in the afternoon and spawning continues into the night. Scup, *Stenotomus chrysops*, spawns in the morning, and Atlantic mackerel, *Scomber scombrus*, spawns throughout the day.

The prevalence of nocturnal spawners in the Peconic Bays is inconsistent with predictions of hypotheses attributing diel spawning periodicity to reproductive isolation and visual constraints. Some possible causes of diel spawning periodicity are reproductive synchronism between the sexes, deleterious effects of sunlight on embryogenesis, and parent or embryo predator avoidance.

In his review, Woodhead (1966) cited several references indicating that spawning occurs only in the evening or at night in some clupeids, gadids, pleuronectids, exocoetids, and mullets, and only during daylight hours in some gobies, blennies, and pomacentrids. Woodhead concluded: "There is relatively little direct information describing the spawning behaviour of marine fish, but such as is available suggests that spawning is restricted to a particular part of the day." Recent research generally supports that conclusion.

Simpson (1971) determined the time of day of spawning of four marine fishes from the occurrence of recently spawned eggs in plankton collections. His results showed spawning occurs in plaice, *Pleuronectes platessa*, between 1800 and 0700 h; sprat, *Sprattus sprattus*, between 2200 and 0600 h; pilchard, *Sardina pilchardus*, between 2000 and 0200 h; and throughout the day in dab, *Limanda limanda*, but most intensely between 2400 and 1200 h. Wicklund (1970) observed that natural spawning of small (total length <125 mm) cunner, *Tautoglabrus adspersus*, was restricted to between 1200 and 1700 h. A sevenfold difference in numbers of fish eggs in night vs. day plankton collections prompted Hobson and Chess (1978) to suggest that many reef fishes primarily spawn at night. Ten anchovy species in the Gulf of

Panama have daily spawning periods lasting about 3 h, and all spawn between about 1700 and 0430 h (Simpson 1959).

Accumulating evidence indicates that diel spawning periodicity is a common phenomenon in marine fishes. In this paper further information is presented on daily spawning times of 12 marine fishes from 10 families.

METHODS

From midspring to late fall 1972, 1973, and 1974 plankton collections were taken usually at 9-13 locations in the Peconic Bay area, Long Island, N.Y. (Figure 1). In 1972 and 1973 samples were taken on two consecutive days at intervals of 5-11 days. In 1974 samples were collected at monthly intervals. All collections were made during daylight hours from 0600 to 1735 h e.s.t. At least three vertical plankton-haul samples were taken from the bottom (or to a maximum depth of 12 m) to the surface at each location with a No. 3 (0.333 mm mesh) conical plankton net with a mouth area of 0.5 m². The plankton samples were killed and preserved in 4% seawater Formalin² and stored in 1 l glass jars. Surface water temperature and solar time of day (hours since sunrise; time of sunrise

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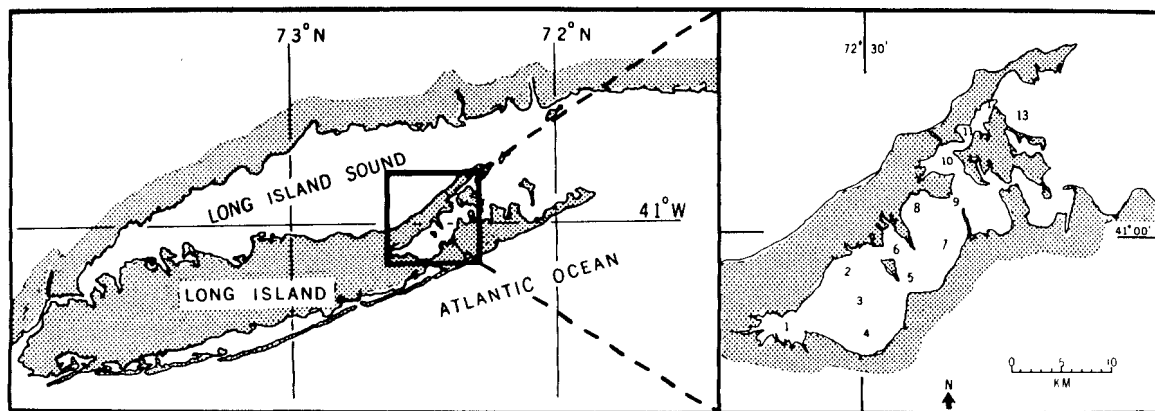


FIGURE 1.—Location of study site and 13 sampling stations in the Peconic Bays, Long Island, N.Y.

from National Ocean Survey 1971, 1972, 1973) of each collection were recorded. Since Peconic Bay waters are well mixed (Hardy 1976), the surface water temperatures were adequate indicators of temperatures of the water column and the natural incubation temperatures of recently spawned fish eggs (see Discussion section).

Over the 3-yr period more than 2,600 samples were collected and processed. Plankton samples were split into manageable subsamples and their entire contents were viewed under a stereomicroscope. Fish eggs were separated, identified to species, staged (Table 1), and counted. Developmental stages in Table 1 are approximately equal in duration when fish embryos are reared at constant temperatures (Ferraro 1980). References used for fish egg identification included: Kuntz (1915), Kuntz and Radcliffe (1917), Hildebrand and Cable (1930, 1934), Merriman and Sclar (1952), Wheatland (1956), Richards (1959), Mansueti and Hardy (1967), Williams (1967), Austin (1973), Berrien (1975), and Colton and Marak³.

Estimates of time of day of spawning for each species in a sample were determined by estimating the mean age of fish eggs <24 h old using embryo age prediction equations for Atlantic menhaden, *Brevoortia tyrannus*, in Ferraro (1980), below:

$$\log_{10} B = -0.193 + 17.193 T^{-1} + 34.090 T^{-2} - 461.276 T^{-3} \quad (1)$$

³Colton, J. B., Jr., and R. R. Marak. 1969. Guide to identifying the common planktonic fish eggs and larvae of Continental Shelf waters, Cape Sable to Block Island. Bur. Commer. Fish. Lab., Woods Hole, Mass., Lab. Ref. No. 69-9, 43 p.

TABLE 1.—Fish embryo stages of development.

Stage	Description
1	Fertilized eggs prior to cell division to 8-cell stage
2	Eight-cell stage to completion of blastodisc formation
3	Blastodisc formation to germ ring ½ way around egg
4	Germ ring ½ way around egg to just prior to blastopore closure
5	Blastopore closure to tail bud beginning to separate from the yolk
6	Tail bud free of yolk to caudal ¼ of body free of the yolk
7	Caudal ¼ of body free of yolk to caudal ¼th of body free of yolk
8	Caudal ¼th of body free of yolk to fin fold moderately wide and tail portion of embryo rotated out of embryonic axis and tail approaching head
9	Tip of tail approaching head to hatching

and,

$$A = B (S - 1) \quad (2)$$

where B = development time (hours) per stage of development
 T = temperature (in degrees Celsius)
 S = stage of development (Table 1)
 A = mean age (in hours)

and subtracting these values from the time the samples were collected in the field. (Field data on differences in development stages of embryos from consecutive day classes indicated that the *B. tyrannus* embryo age equations introduced little or no error when estimating embryo ages of <24 h of most of the species in this study (see Results).)

RESULTS

Discrete day classes of fish eggs of most species were identified in the field samples. Fish eggs were present in samples at distinct morphological stages of development while other morphological

stages were completely absent. Spring spawners typically had polymodal embryonic stage frequency distributions with one or more embryonic stages absent between adjacent modes. As water in the Peconic Bays warmed, the number of modes in the embryo stage frequency distribution decreased such that by midsummer the distribution was unimodal. Also, as water temperature increased the most recently spawned eggs of most fishes were found at consistently later stages of development.

Indirect evidence from field data indicated that embryonic development rates of most species in this study were similar. Tests of differences between modes of embryo development stages representing two consecutive day classes from field samples at 17° C by a posteriori sums of squares simultaneous testing procedure (Sokal and Rohlf 1969) indicated no significant difference ($P > 0.05$) in embryonic growth per day of *B. tyrannus*; bay anchovy, *Anchoa mitchilli*; tautog, *Tautoga onitis*; *Tautogolabrus adspersus*; and searobins, *Prionotus* spp. Also, age differences between day classes of fish embryos in field samples at temperatures between 15.0° and 17.5° C were calculated using the *B. tyrannus* embryo age prediction Equations (1) and (2). The results (Table 2) showed that the *B. tyrannus* equations gave good predictions of the expected age difference between embryo day classes for most of the species in this study.

With the exceptions of scup, *Stenotomus chrysops*; Atlantic mackerel, *Scomber scombrus*; and to a lesser extent *Tautoga onitis* and *Tautogolabrus adspersus* very few early-cleavage stage eggs were collected in our daytime sampling program.

TABLE 2.—Mean age differences (\bar{x} , in hours) of fish embryos representing two consecutive day classes in field samples at temperatures¹ between 15.0° and 17.5° C determined by development stage differences between day classes and embryo age prediction equations for *Brevoortia tyrannus*. The expected age difference is 24 h.

Species	Number of samples	$\bar{x} \pm SE$
<i>Brevoortia tyrannus</i>	124	25.6 ± 0.40
<i>Anchoa mitchilli</i>	53	21.8 ± 0.31
<i>Stenotomus chrysops</i>	20	20.5 ± 0.48
<i>Cynoscion regalis</i>	15	25.4 ± 1.21
<i>Tautoga onitis</i>	101	24.9 ± 0.43
<i>Tautogolabrus adspersus</i>	53	23.6 ± 0.77
<i>Peprilus triacanthus</i>	4	24.2 ± 1.57
<i>Prionotus</i> spp.	64	22.0 ± 0.39
<i>Scophthalmus aquosus</i>	7	22.0 ± 3.16

¹Range of temperatures chosen were temperatures at which at least two fish embryo day classes would be present.

Mean daily spawning times of fishes were calculated from hourly time of spawning frequency distributions of sample estimates of spawning time (Table 3). The 1974 data were used to compute estimated spawning times of *Stenotomus chrysops*; weakfish, *Cynoscion regalis*; window-pane flounder, *Scophthalmus aquosus*; and butterfish, *Peprilus triacanthus*, and only 1973 data were used to compute the spawning time of the hogchoker, *Trinectes maculatus*. Time of spawning estimates were similar for species where data were available for 2 yr. Histograms of relative frequency distributions of sample estimates of spawning time are presented for 1973 data on *Anchoa mitchilli*; *Brevoortia tyrannus*; *Tautoga onitis*; *Tautogolabrus adspersus*; northern and striped searobins, *Prionotus carolinus* and *P. evolans* (note: the searobins are considered together because their embryos can not be reliably distinguished); and *Trinectes maculatus* in Figure 2. In summary, the results show that *A. mitchilli*, *B. tyrannus*, *P. carolinus*, *P. evolans*, *T. maculatus*, *C. regalis*, *S. aquosus*, and *Peprilus triacanthus* spawn primarily in the evening or at night; *Tautoga onitis* and *Tautogolabrus adspersus* spawn in the afternoon and at night; and *Stenotomus chrysops* spawns in the morning.

There was no evidence of diel spawning periodicity by Atlantic mackerel. Typically, all developmental stages (Table 1) were present in samples containing Atlantic mackerel eggs. The only general trend in the Atlantic mackerel egg data was a decrease in numbers of later developmental stages, presumably due to dispersion or egg mortality.

TABLE 3.—Mean daily spawning times (\overline{DST} , in hours after sunrise) of fishes calculated from hourly frequency distributions of sample estimates of spawning time. Estimated ages of fish eggs < 24 h old in field samples were subtracted from their time of collection to obtain sample estimates of spawning time.

Species	Year	N	$\overline{DST} \pm SE$
<i>Brevoortia tyrannus</i>	1972	198	16.36 ± 0.175
	1973	370	17.84 ± 0.168
<i>Anchoa mitchilli</i>	1972	455	16.09 ± 0.103
	1973	693	16.78 ± 0.078
<i>Stenotomus chrysops</i>	1974	32	5.28 ± 0.276
	1974	74	17.45 ± 0.407
<i>Cynoscion regalis</i>	1972	160	15.52 ± 0.200
	1973	447	17.62 ± 0.126
<i>Tautoga onitis</i>	1972	101	15.40 ± 0.343
	1973	322	15.98 ± 0.215
<i>Peprilus triacanthus</i>	1974	22	18.55 ± 0.881
	1972	174	19.19 ± 0.307
<i>Prionotus</i> spp.	1973	330	19.15 ± 0.197
	1974	38	16.68 ± 0.607
<i>Trinectes maculatus</i>	1973	132	16.55 ± 0.110

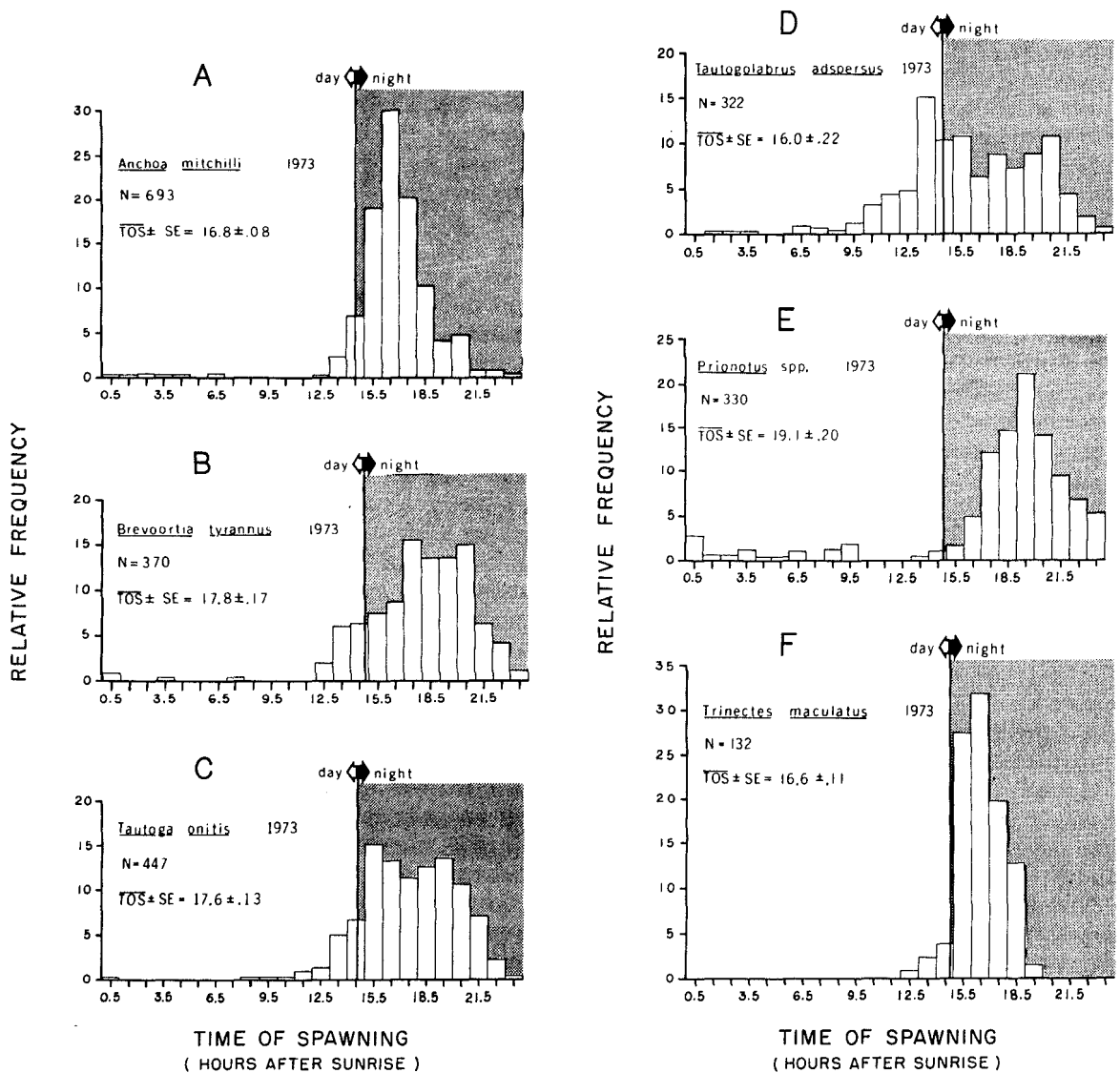


FIGURE 2.—Relative frequency distributions of estimated spawning times (TOS) of (A) *Anchoa mitchilli*, (B) *Brevoortia tyrannus*, (C) *Tautoga onitis*, (D) *Tautogolabrus adspersus*, (E) *Prionotus* spp., and (F) *Trinectes maculatus*, determined by subtracting estimated mean ages of fish eggs <24 h old from their time of collection in 1973 samples. Mean day length during spawning seasons is indicated.

DISCUSSION

Direct observation of fish spawning at sea is rare, and aquarium observations may not be characteristic of natural spawning or may be difficult or impractical to implement for logistic reasons. Since embryogenesis begins at spawning in most marine teleosts, the time of day spawning occurs can be determined indirectly from the age of embryos captured at sea. Several investigators, including Ahlstrom (1943), Gamulin and Hure

(1956), and Simpson (1971), collected plankton samples throughout the day and determined spawning times of fishes from the occurrence of recently spawned eggs. Under certain circumstances (when field temperatures are fairly constant and there is little translocation of eggs) and with knowledge of embryonic development rates, however, spawning times can be back calculated by subtracting age of fish embryos from their time of collection. The method of estimating spawning time of fishes in this paper utilizes field

data commonly obtained in ichthyoplankton research and does not require a continuous field sampling program.

Factors influencing the accuracy of estimated spawning times of fishes in this paper are intraspecific and interspecific differences in development rates of fish embryos and temperature effects on embryo stage (Table 1) duration. Intraspecific differences in development rates are likely to introduce only small and unbiased error in spawning time estimates since incubation times from which age estimates are made are short (<24 h) and mean stages of development of all embryos of a species (<24 h old) in a sample are used in the embryo age calculation. Interspecific differences in development rates of most species in this study are also probably small (see Results). A maximum standard deviation of 2.3 h can be expected in spawning time estimates due to the influence of temperature on embryo stage duration because most fish eggs were collected in water temperatures above 15° C (Ferraro 1980). Surface water temperatures at the time of field collection were probably adequate indicators of natural incubation temperatures of recently spawned eggs since there is little, if any, vertical thermal stratification in the Peconic Bays and surface water temperature at a particular location generally fluctuates by <1° C during a tidal cycle (Hardy 1976).

Based on the occurrence of recently spawned eggs in plankton collections at Beaufort, N.C., Kuntz (1915) and Hildebrand and Cable (1930) concluded that *A. mitchilli* spawned between 1800 and 2100 h (13-16 h after sunrise), and Hildebrand and Cable (1938) concluded that *Trinectes maculatus* spawned between 1800 and 2000 h (13.5-15.5 h after sunrise). Those observations coincide with the onset of spawning estimated for *A. mitchilli* and *T. maculatus* in this paper. Reintjes' (1968) conclusion that *B. tyrannus* spawns at night, Welsh and Breder's (1924) conclusion that *C. regalis* spawns in the evening and at night, and Sette's (1943) calculations showing *Scomber scombrus* spawns throughout the day were confirmed in this research. Wicklund's (1970) observations on the spawning of cunner overlap but have a much shorter duration than that indicated for cunner in Figure 2D. Wicklund (1970) only observed spawning by small (total length <125 mm) cunners between 1200 and 1700 h (7-12 h after sunrise); he never observed larger cunners spawning although they were present and defended territories in his study area. Olla and

Samet (1977) noted that tautog in laboratory aquaria spawned almost exclusively between 1330 and 1600 h (7.5-10 h after sunrise). Their experimental fish, however, had been exposed to unnatural photoperiod and temperatures and spawned about 2 mo earlier than tautog normally spawn in nature. Recently spawned eggs in plankton collections indicated that some tautog spawn in the afternoon (8-10 h after sunrise) in the Peconic Bays, but the bulk of tautog spawning appears to take place later in the evening and at night.

A systematic division of fishes in the Peconic Bays and a summary of their spawning times is presented in Table 4. Only Atlantic mackerel showed no indication of diel spawning periodicity, and only scup spawned exclusively during daylight hours. The remaining species spawned primarily during the evening or at night. Nothing exceptional is known about the adult habits or embryos of Atlantic mackerel or scup to suggest why their spawning times are different from the other species. There appears to be no connection between bathymetric distributions of embryos of some of the species (Williams 1968) and spawning time. There was no evidence of constancy in spawning time above the family level. Solar spawning times of most species, though, were consistent throughout the spawning season and in samples collected at different locations, indicating seasonal and local differences in ecologic factors (e.g., temperature, salinity, water depth, tide) had no effect on daily spawning time.

The tendency of marine teleosts with planktonic eggs to spawn in the evening or at night is evident in a listing (Table 5) of some species known or suspected of diel spawning periodicity. There is

TABLE 4.—Systematic division and summary of spawning times (hours after sunrise) of fishes in the Peconic Bays, N.Y. Spawning is indicated by +.

Taxa	Species	Spawning time			
		0-6	6-12	12-18	18-24
Clupeiformes:					
	<i>Brevoortia tyrannus</i>			+	+
	<i>Anchoa mitchilli</i>			+	+
Perciformes:					
	<i>Stenotomus chrysops</i>	+			
	<i>Cynoscion regalis</i>			+	+
	<i>Tautoga onitis</i>		+	+	+
	<i>Tautogolabrus adspersus</i>		+	+	+
	<i>Scomber scombrus</i>	+	+	+	+
	<i>Peprilus triacanthus</i>			+	+
	<i>Prionotus carolinus</i>			+	+
	<i>Prionotus evolans</i>			+	+
Pleuronectiformes:					
	<i>Scophthalmus aquosus</i>			+	+
	<i>Trinectes maculatus</i>			+	

TABLE 5.—Some marine teleosts which spawn planktonic eggs and are known or suspected of spawning only at particular times of the day.

Family and species	Spawning time	Reference
Ophichthidae:		
<i>Pisodonophis cruentifer</i>	Night	Naplin and Obenchain (1980)
Clupeidae:		
<i>Etrumeus teres</i>	Night	Houde (1977)
<i>Sardinella melanosticta</i>	Night	Kamiya (1925)
<i>Sardinops sagax</i>	Evening	Ahlstrom (1943)
<i>Sardinia pilchardus</i>	Evening and night	Gamulin and Hure (1956); Simpson (1971)
<i>Sprattus sprattus</i>	Night	Simpson (1971)
Engraulidae:		
<i>Anchoa hepsetus</i>	Evening and night	Hildebrand and Cable (1930)
<i>A. mitchilli</i>	Evening and night	Kuntz (1915); Hildebrand and Cable (1930)
<i>Cetengraulis mysticetus</i>	Night	Simpson (1959)
<i>Engraulis eurystole</i>	Evening	Kuntz and Radcliffe (1917)
<i>E. mordax</i>	Night	Bolin (1936)
<i>Engraulis</i> spp.	Evening	Delsman (1929)
<i>Stolephorus purpureus</i>	Night	Yamashita (1951)
<i>Stolephorus</i> spp.	Night	Delsman (1931)
Antennariidae:		
<i>Histrio histrio</i>	Afternoon and evening	Walters (pers. commun. in Breder and Rosen 1966)
Gadidae:		
<i>Enchelyopus cimbrius</i>	Morning	Battle (1930)
<i>Gadus morhua</i>	Evening and night	Brawn (1961); Breder and Rosen (1966)
<i>Merluccius merluccius</i>	Morning	Storrow (1913)
Pomatidae:		
<i>Pomatomus saltatrix</i>	Evening	Norcross et al. (1974)
Carangidae:		
<i>Caranx kurra</i>	Night	Delsman (1926)
<i>C. macrosoma</i>	Night	Delsman (1926)
<i>C. crumenophthalmus</i>	Night	Delsman (1926)
Pomadasyidae:		
<i>Orthopristis chrysoptera</i>	Evening	Hildebrand and Cable (1930)
Sciaenidae:		
<i>Bairdiella chrysura</i>	Evening	Kuntz (1915)
<i>Cynoscion nebulosus</i>	Night	Tabb (1966)
<i>C. regalis</i>	Evening and night	Welsh and Breder (1924)
Labridae:		
<i>Tautoga onitis</i>	Afternoon	Olla and Sarnet (1977)
<i>Tautoglabrus adspersus</i>	Afternoon	Wicklund (1970)
Scaridae:		
<i>Scarus croicensis</i>	Afternoon	Colin (1978)
<i>Sparisoma rubripinne</i>	Afternoon	Randall and Randall (1963)
Mugilidae:		
<i>Mugil cephalus</i>	Night	Arnold and Thompson (1958)
<i>M. curema</i>	Night	Anderson (1957)
Scomberidae:		
<i>Scomber japonicus</i>	Night	Kamiya (1925)
<i>Scomberomorus maculatus</i>	Evening and night	Ryder (1882); Rathbun (1894); Smith (1907)
Pleuronectidae:		
<i>Hippoglossus hippoglossus</i>	Night	Nordg�ard (1929)
<i>Pleuronectes platessa</i>	Night	Forster (1953); Simpson (1971)
<i>Pelotretis flavilatus</i>	Night	Thomson and Anderton (1921)
<i>Colistium nudipinnis</i>	Night	Thomson and Anderton (1921)
<i>C. guntheri</i>	Night	Thomson and Anderton (1921)
<i>Peltorhamphus novaezeelandiae</i>	Night	Thomson and Anderton (1921)
<i>Rhombosolea plebeia</i>	Night	Thomson and Anderton (1921)
<i>R. tapirina</i>	Night	Thomson and Anderton (1921)
Soleidae:		
<i>Trinectes maculatus</i>	Evening	Hildebrand and Cable (1938)

diel and lunar spawning periodicity in some coral reef fishes (e.g., Lobel 1978; Johannes 1978; May et al. 1979). References cited in Breder and Rosen (1966) indicate that at least 70 freshwater and marine teleosts with demersal or attached eggs may spawn or oviposit at particular times of the day. Even though many of the data are only suggestive, there are indications that diel spawning periodicity may be a common and widespread phenomenon among fishes.

Diel spawning periodicity in fishes may be due

to physiological constraints or may be adaptive. Woodhead (1966) and Blaxter (1965, 1970) pointed out that light may restrict spawning to a particular time of day, especially in species where vision is important in sexual displays, courtship, and pairing. Woodhead (1966) noted, however, that species which require daylight for courtship might still spawn or oviposit at other times of the day. Obviously, nocturnal spawners are not light limited. If adaptive, the value of reproductive periodicity may be found in the synchronization of reproduc-

tion with the biotic or abiotic environment (Nikolsky 1963; Aschoff 1964; Schwassman 1969). The annual spawning cycle of fishes which may be timed to coincide with the annual production cycle, or a period of low predation, etc. (Nikolsky 1963; Cushing 1969; Hoar 1969), may be the coarse adjustment, and diel spawning time the fine tuning adjustment to temporally changing environmental conditions.

Spawning periodicity may be important in synchronizing reproduction between the sexes (Aschoff 1964; Marshall 1967). The precise daily timing of reproduction may be particularly important in species which engage in mass spawnings. An extreme example are the lancelets (e.g., *Branchiostoma lanceolatum*) which, according to Breder and Rosen (1966), release eggs and sperm into the water at sunset for chance fertilization. Temporally synchronizing spawning in pairing species presumably is more efficient and may optimize the number of receptive encounters.

Marshall (1967) suggested diel spawning periodicity might serve to increase reproductive isolation between related and morphologically similar species. Reproductive isolation may be important in a species-rich habitat such as a coral reef, but many temperate water marine fishes apparently spawn at or about the same time, i.e., in the evening and at night (Tables 4, 5).

Diel spawning periodicity could be an adaptive behavior of fishes to avoid high incident solar radiation during a very sensitive period of embryonic development. Bell and Hoar (1950) and Eisler (1958, 1961) demonstrated the lethal and deleterious effects of light on salmonid embryos, especially during early embryogenesis; and Marinaro and Bernard (1966) demonstrated lethal effects of light, particularly ultraviolet light, on some marine planktonic fish embryos. Perlmutter (1961) and Breder (1962) believed that some characteristics of fish eggs (e.g., transparency, oil droplets, melanophores) were physiological adaptations to minimize deleterious effects of light on fish embryos, and Perlmutter (1961) listed several spawning behaviors of fishes which he thought were adaptations to avoid or minimize exposure of embryos to light. If light is especially harmful to recently fertilized fish eggs, nocturnal spawning could be an adaptive behavior to avoid light during early embryonic development. However, an explanation is then necessary for why light is not a factor for diurnal spawners such as Atlantic mackerel and scup.

Nikolsky (1963) suggested that some fishes spawn at times of day when spawning adults or their eggs will be least susceptible to predation. The "exhausted" condition of some fishes that have recently spawned (Brawn 1961; Breder and Rosen 1966) and evidence of increased vulnerability of some spawning fishes to trawling (Mohr, in Blaxter 1965) tend to support the idea that spawning time may be an adaptation to minimize losses due to predation on the parents. Visual predators, predators with diurnal feeding patterns, or predators which undergo diurnal vertical migrations (e.g., ctenophores; Hirota 1974) could subject planktonic fish embryos to different levels of predation over a diurnal cycle. Synchronizing daily spawning time to coincide with a period of low fish embryo predation minimizes fish embryo mortality due to predation. If a fish embryo predator had a diurnal predation cycle of 12 h high and 12 h low predation, Figure 3 shows that a fish spawning at the beginning of a low predation period ensures 50% or more of the embryo incubation time of its progeny will be spent at the low predation level. Qualitatively the results would be the same if changes in predation were gradual and periods of high and low predation were of different durations. Figure 3 also shows that if predation cycles cause diel spawning periodicity, selection for diel spawning periodicity is potentially greater when embryo incubation times are short.

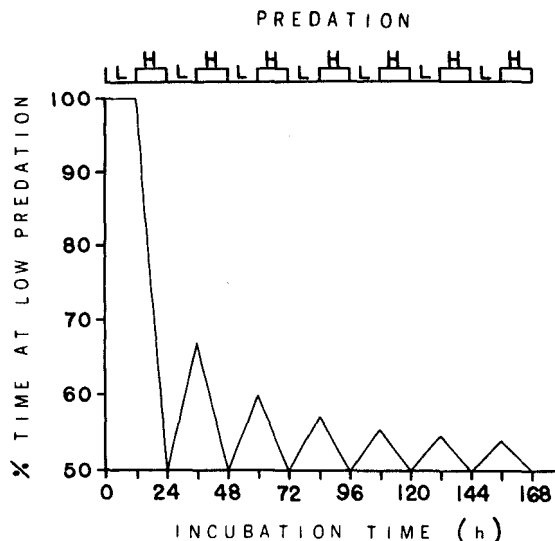


FIGURE 3.—Relationship between percentage of time spent at low predation when spawning occurs at the beginning of a period of low predation and total incubation time of embryos, assuming 12 h alternating periods of low (L) and high (H) predation.

The physiological or adaptive cause(s) of diel spawning periodicity in fishes may become clear as data on its occurrence accumulates or by experiments. Effects of natural maximum solar radiation at the sea surface on different development stages of marine planktonic fish embryos should be studied experimentally. Field studies on fish embryo mortality at different times of day, and studies on feeding patterns of major fish embryo predators and adult fish predators during the spawning season could help elucidate or eliminate some of the factors suspected of causing diel spawning periodicity. If correct, one of the implicit consequences of the diurnal predation cycle hypothesis is that diel spawning periodicity should be more common in fishes with short embryo incubation times (Figure 3), and this prediction should be tested. Additional data on diel spawning periodicity in fishes and studies such as those listed above should ultimately provide important insights into fish physiology, reproductive biology, and ecology.

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