Fish Physiology and Biochemistry vol. 9 no. 1 pp 51-62 (1991)
Kugler Publications, Amsterdam/Berkeley

Changes in gonadal hormones during oocyte development in the striped bass, *Morone saxatilis*

David L. Berlinsky and Jennifer L. Specker
Department of Zoology, University of RI, Kingston, Rhode Island 02881, U.S.A.

Keywords: striped bass, reproduction, steroid hormones, oocyte development

Accepted: May 25, 1990

Abstract

Wild striped bass, *Morone saxatilis*, were collected from coastal waters and spawning areas to describe the endocrine correlates of oocyte development in non-captive, migratory fish. The fish were classified according to their most advanced oocytes. Serum levels of estradiol (E_2), testosterone (T) and 17α-20β-dihydroxy-progesterone (DHP) were measured by radioimmunoassay (RIA). Females in the primary growth phase and early secondary growth phase (pre-vitellogenic) had low levels of plasma steroids, ovarian lipid content and gonadosomatic indices (GSIs). Significant increases in E_2, T, ovarian lipid content and GSIs occurred during the vitellogenic phase. Maximum levels of all reproductive parameters were found in prespawning fish sampled in the Hudson River. Mean levels of E_2, T, ovarian lipids and GSIs for these fish were 2.0 $\pm$ 0.5 ng/ml, 3.0 $\pm$ 0.3 ng/ml, 24 $\pm$ 1 mg/g, and 5.6 $\pm$ 0.3% (mean $\pm$ SEM), respectively. In fish induced to spawn with human chorionic gonadotropin (HCG), DHP levels (1.9 $\pm$ 0.4 ng/ml) were significantly elevated. Similar levels were found in two fish captured during the spawning season, suggesting that DHP may serve as the maturation-inducing steroid in this species.

Introduction

The striped bass, *M. saxatilis*, is an anadromous teleost indigenous to the Atlantic coast of North America. Like many teleosts from temperate waters, striped bass have an annual reproductive cycle with group synchronous ovarian development (Specker *et al.* 1987). The major part of oocyte growth occurs between November and May, although the exact timing varies (Merriman 1941; Jackson and Tiller 1952; Lewis 1962). The timing of spawning is related to latitude (Raney 1952; Nichols and Miller 1967). For instance, in the St. John's River of Florida, spawning may be initiated as early as February, whereas in the St. Lawrence River of Canada spawning does not begin until July (Setzler *et al.* 1980). The major spawning grounds on the Atlantic coast are tributaries of the Chesapeake Bay, the Hudson River and the Roanoke River in North Carolina (Raney 1952). Following spawning, striped bass undertake a feeding migration to coastal waters (McLaren *et al.* 1981).

The endocrine control of reproductive events in striped bass has received little attention. The objective of the present study was to describe the endocrine correlates of oocyte development in wild

Address for correspondence: Dr. Jennifer Specker, Department of Zoology, University of Rhode Island, Kingston, RI 02881-0816, U.S.A., 401, 792-2658.

Table 1. Season, location and method of capture of striped bass sampled from 1986–1988.

Sample designation	Season	Year	Location	Capture method
A	May-Jun.	1986–88	Rhode Island	Floating pound net
B	Sep-Nov.	1986–87	Rhode Island	Hook and line
C	Nov.	1987	Hudson River	Haul Seine
D	Dec.	1986	Chesapeake Bay	Gill net
E	Feb.	1988	Long Island Sound	Gill net
F	Mar.	1988	Chesapeake Bay	Gill net
G	May	1986–87	Hudson River	Haul Seine
H	May	1986	Verplanck hatchery	Gill net

striped bass. This study is part of our overall effort to assess the proportion of coastal migrants showing evidence of sexual maturity. Although most male striped bass spawn beginning in their third year, females mature anywhere from 3- to 8-yrs of age (see Specker *et al.* 1987). In addition to this inherent variation in the maturity status of the females we sampled, the stock composition of the coastal migrants changes with time (Fabrizio 1987a,b).

Materials and methods

Sampling

The sample date, location, and method of capture for the wild striped bass collected are shown on Table 1. Fish were stunned by a blow to the head and blood was collected by caudal puncture into nonheparinized syringes. Serum was separated by centrifugation and stored at −20°C for later hormone analysis. Body and gonad weights and fish fork-length were recorded for each fish. Gonadosomatic indices (GSIs) were calculated as (gonad weight/body weight) × 100.

Striped bass sampled at the Verplanck Hatchery (Designated H; Verplanck, New York) were injected with human chorionic gonadotropin (HCG) at a dose of 150 I.U./kg body weight upon capture. Blood samples were collected after mechanical expulsion of the ova.

Histology

Ovarian tissue for histological analysis was removed from the midlength of the ovary, fixed in Bouin's solution, dehydrated in an ethanol series and cleared in methyl salicylate prior to paraffin infiltration and embedding. The tissue was sectioned at 10 μm and stained with hematoxylin and eosin. Tissues were stained with alcian blue and metanil yellow to detect the presence of carbohydrates, specifically acid mucopolysaccharides, and with mercuric bromphenol blue to detect proteins (Humason 1979).

Sections of ovarian tissue were photographed using a Nikon S-U microscope equipped with a M-35 camera. Micrograph slides were projected onto a Scriptel glass digitizing tablet (Sigma Scan, Jandel) and the diameters of at least 50 oocytes which had been sectioned through the nucleus were measured in order to record the maximum oocyte diameter for each fish.

Oocytes were classified using criteria established previously for striped bass (Groman 1982; Specker *et al.* 1987). These criteria along with our new observations are described under Results. Females were categorized as immature if their ovaries contained nothing more advanced than primary growth (PG) oocytes. Females were classified as mature if their ovaries contained oocytes in the secondary growth phase as evidenced first by the appearance of droplets in the ooplasm (early SG) and later by the appearance of vesicles containing protein granules – secondary growth yolk granule stage or vitellogenic (VTG). Females were also considered

mature if their oocytes were in the final maturation (FM) or atretic (AT) stages.

Ovarian lipid content

Ovarian lipid levels were determined for fish in the primary growth, early secondary growth and vitellogenic stages of development. Fragments of ovarian tissue (1 g) were removed from the midlength of the ovary, minced with scissors and homogenized in 5 ml tap water with a Polytron tissue homogenizer (force 6). Lipids were then extracted in 10 ml ethyl ether (Fisher, reagent grade) by vortexing at high speed for 20 sec. The ether was decanted into previously weighed tubes (16 × 125 mm). The ether was evaporated with air and the procedure following homogenization was repeated twice. Lipid levels were calculated as the final weight of the glass tubes minus the tared weight. Values were expressed as mg/g of ovary.

Radioimmunoassay

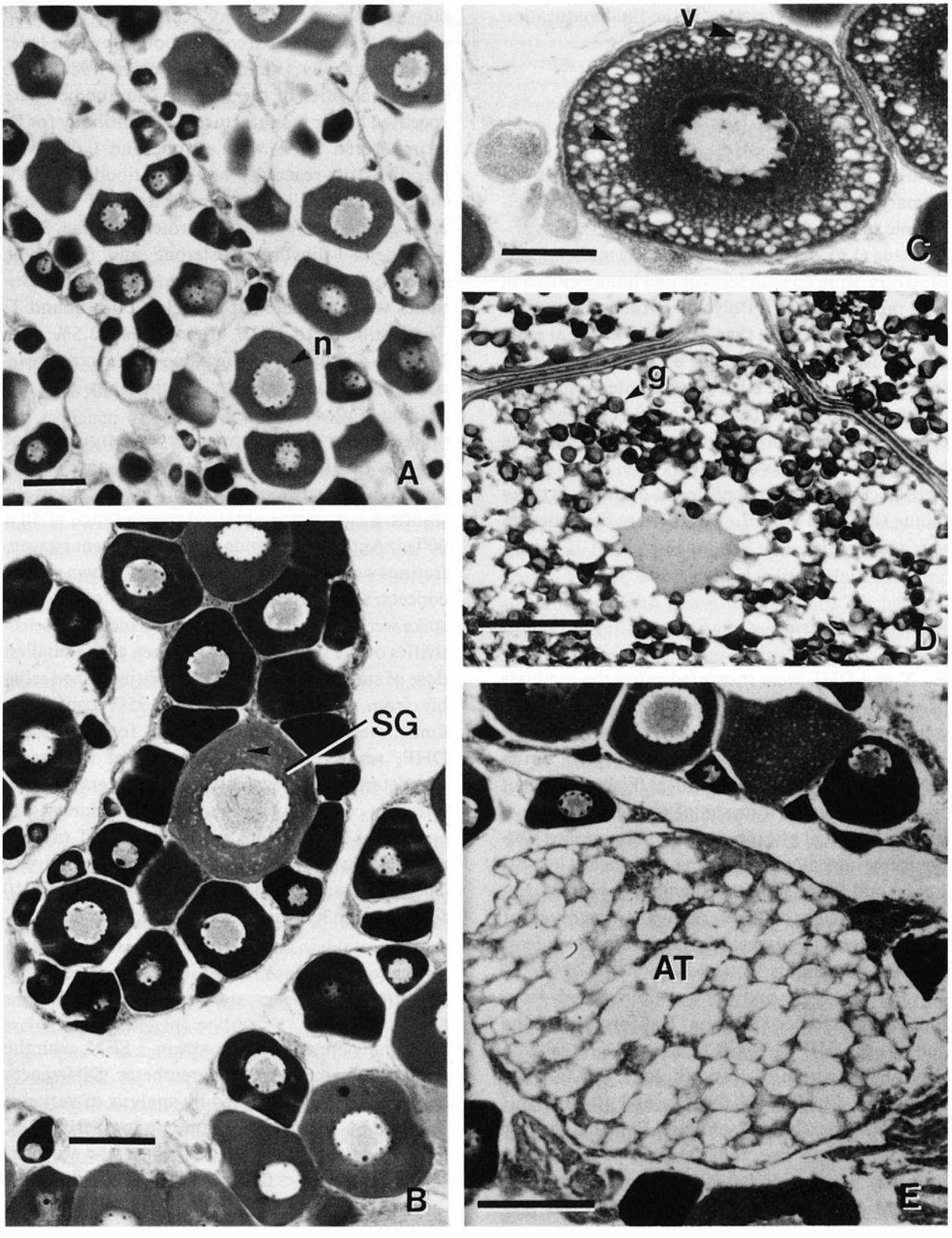
E_2, T and DHP were measured using the methods of Kagawa *et al.* (1981). Briefly, E_2, T and DHP were measured in sera by RIA following ether extraction. Steroids were extracted from serum (200 μl) twice with ethyl ether (Fisher, reagent grade), dried under a stream of nitrogen and resuspended in 200 μl phosphate buffer containing 10% bovine serum albumin (Sigma Chemical Co., St. Louis) and 0.1% sodium azide (assay buffer). Extraction efficiency as determined by recovery of tritiated steroids extracted from plasma was at least 90% for all steroids.

Antisera to E_2 and T were purchased from Endocrine Sciences (Tarzana, California) and the antisera to DHP was a gift from Dr. Y. Nagahama (National Institute of Basic Biology, Japan). Radiolabelled [2,4,6,7 H^3 (N)] E_2 and [1,2,6,7, H^3 (N)] T were purchased from New England Nuclear (Boston, Mass.) and radiolabelled 17α-hydroxyprogesterone was purchased from Amersham International (Arlington Heights, Ill.). DHP was prepared from 17α-hydroxyprogesterone by enzymatic conversion as described by Scott *et al.* (1982) and separated from the parent compound by thin layer chromatography (Vanderkraak *et al.* 1984). The cross-reactivities of the E_2 and T antibodies were specified by the manufacturer. The antibody for E_2 cross-reacted 1.3% with estrone and 0.6% with estriol. Cross-reactivity of this antibody was less than 0.1% with all other steroids tested. T antibody cross-reacted 20% with dihydrotestosterone, 3.6% with delta-1-dihydrotestosterone and 52% with delta-1-testosterone. These cross-reactivity estimates were calculated at a level of 50% bound T. The antibody to DHP cross-reacted 2.5% with 17α-20β-dihydroxy-5β-pregnane-3-one; cross-reactivity was less than 1% for all other steroids tested (Young *et al.* 1983).

Parallelism was determined by measurements of aliquots of different volumes of the same plasma pools. A linear response which was parallel to the standard curves was obtained over a range of 50–200 μl. Authentic steroids in three different concentrations were added to serum pools of known steroid concentrations and recoveries >90% of the cold spike were obtained for all three steroids. The sensitivities of the standard curves, taken as the smallest dose of standard which could be distinguished reliably from the buffer blank with 95% confidence limits, were 15, 30 and 30 pg/ml for E_2, T, and DHP, respectively. The precision of the assays was determined by calculating the interassay and intrassay coefficients of variation. The inter-assay coefficient of variations for E_2 (n = 6), T (n = 8) and DHP (n = 6) were 7, 12 and 13%, respectively. The intra-assay coefficients of variations (n = 10 for all) were 3, 9 and 11%, respectively.

Statistics

The results are expressed as mean ± SEM, with the number of samples (n) in parentheses. Differences between means were tested by analysis of variance followed by Tukey's HSD multiple comparison test (Sokal and Rolf 1981). Significance was accepted for all tests at $p < 0.05$.


n
A
v
C
g
D
SG
B
AT
E

Results

Reproductive characteristics of the fish are summarized by reproductive stage. Figure 1 shows photomicrographs of ovaries in each developmental stage. Figures 2 and 3 show comparisons of serum levels of E_2, T, and DHP, and ovarian lipids and gonadosomatic indices of immature fish (PG) and of mature fish in early secondary growth (SG), vitellogenic (VTG), final maturation (FM) and atretic (AT) stages. Figure 4 is a composite illustrating differences in reproductive parameters between immature and mature fish at various times during the reproductive cycle. It should be noted that these data are from different years and from fish in different locations. Table 2 indicates sample sizes, body weight and length, gonad weight and the maximum oocyte diameter of the females shown in Figures 2–4.

Oocyte histology: Classification of females

Figure 1 illustrates various stages of oocyte development. Primary growth oocytes had a maximum diameter of 150 μm with uniformly staining ooplasm (Fig. 1A). The ooplasm of the largest primary growth oocytes stains less basophilically. These primary growth oocytes are present in all striped bass ovaries. Oocytes entering the secondary growth phase were characterized by the presence of translucent spheres in the periphery of the ooplasm. The smallest secondary growth oocytes were 120 μm, but most entered this phase at diameters of about 150 μm (Fig. 1B). Oocytes in this previtellogenic secondary growth phase have been referred to as early yolk vesicle or cortical alveoli stage oocytes (Groman 1982; Specker *et al.* 1987). However, in the striped bass, the contents of the first spheres do not stain with alcian blue, thus they are probably not true cortical alveoli. The contents of these vesicles did not stain with any we used and appear to have been dissolved during fixation and embedding; thus, we suspect that the very first spheres or vesicles contain lipid as in the related bass, *Dicentrarchus labrax* (Mayer *et al.* 1988). These spheres increased in number and were scattered throughout the ooplasm until the oocytes attained diameters of approximately 300 μm (Fig. 1B, C).

Oocytes that stained positively with alcian blue, suggesting the presence of vitellogenin, had diameters that were greater than approximately 300 μm (Fig. 1C). Oocytes which had entered the vitellogenic stage of development were also characterized by the presence of yolk globules. These appeared as spheres located initially around the periphery of the ooplasm which stained with metanil yellow. As the vitellogenic phase progressed (oocyte diameters ≥ 500 μm) these yolk globules were found throughout the ooplasm, increased in size and finally fused into large polygonal masses (Fig. 1D).

The highly developed oocytes sampled from fish during the spawning season (oocyte diameters 0.8–1.0 mm) were difficult to section in some cases, as the ooplasm became brittle and porous during fixa-

Fig. 1. Histological characteristics of striped bass ovaries in the reproductive phases identified in this report. The fish in panels A, B and E were collected off Rhode Island in May and June; the fish in panel C was collected off Rhode Island in October; and the fish in panel D was collected on the spawning grounds of the Hudson River in May. Bar in lower left represents 100 μm in all panels. (*A*) Ovarian section from an immature striped bass showing primary growth oocytes ranging in diameter from about 10 μm to 130 μm. Several nucleoli (n) may be seen near the nuclear membrane in the most advanced primary growth oocytes. Note uniform staining of ooplasm in all oocytes. Hematoxylin and eosin. (*B*) Ovarian section from a striped bass entering secondary growth. The ooplasm of the single early secondary growth (SG) oocyte (160 μm) no longer stains uniformly due to the inclusion of putative lipid droplets (arrow). Note the ooplasm of the larger primary growth oocytes stains less basophilically than that of the smaller primary growth oocytes. Hematoxylin and eosin. (*C*) Ovarian section from a striped bass entering vitellogenesis (cell is 300 μm in diameter). Oocytes in this stage contain larger translucent spheres than those in early secondary growth (arrow). Also present in these oocytes are a second type of vesicle (v) containing putative vitellogenin which stains positively with alcian blue. Alcian blue and metanil yellow. (*D*) Ovarian section from a striped bass in a later vitellogenic phase (cells almost 500 μm in diameter). Oocytes in this stage contain yolk globules (g) which do not incorporate alcian blue. Alcian blue and metanil yellow. (*E*) Ovarian section from a striped bass demonstrating atretic oocytes (AT). Note atretic oocytes do not contain yolk globules seen in vitellogenic oocytes. Hematoxylin and eosin.

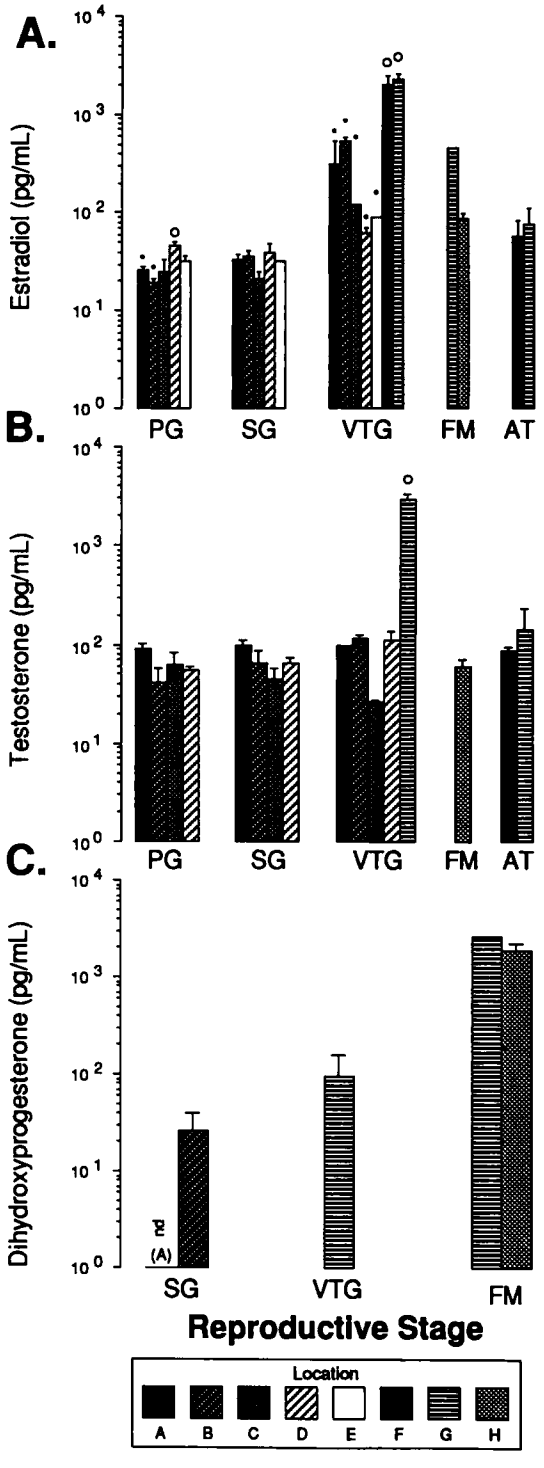


Fig. 2. Comparison of serum levels of estradiol (panel A), testosterone (panel B) and dihydroxyprogesterone (panel C) in female striped bass in various reproductive phases. Phases are: Primary Growth (PG), early Secondary Growth (SG), Vitellogenic (VTG), Final Maturation (FM), and Atretic (AT). Means

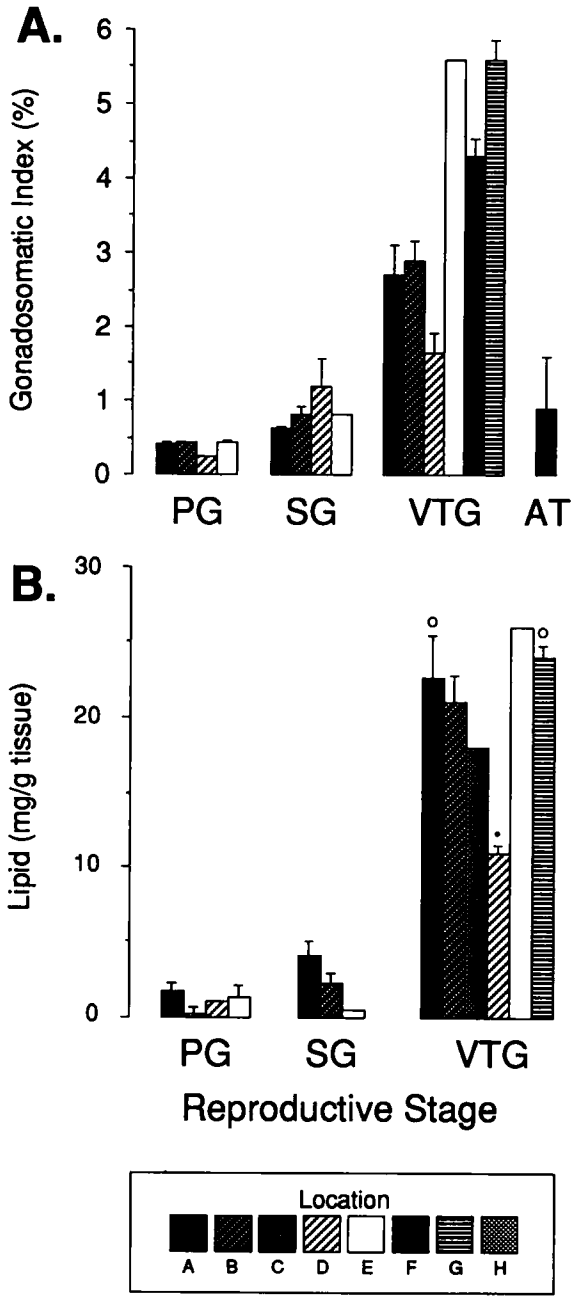


Fig. 3. Comparison of gonadosomatic indices (panel A) and ovarian lipid content (panel B) in female striped bass in various reproductive phases. Phases are: Primary Growth (PG), early Secondary Growth (SG), Vitellogenic (VTG), Final Maturation (FM), and Atretic (AT). Sampling locations are given in Table 1.

←

with different symbols are significantly different from each other ($p < 0.05$) within reproductive stage. Sampling locations are shown in Table 1.

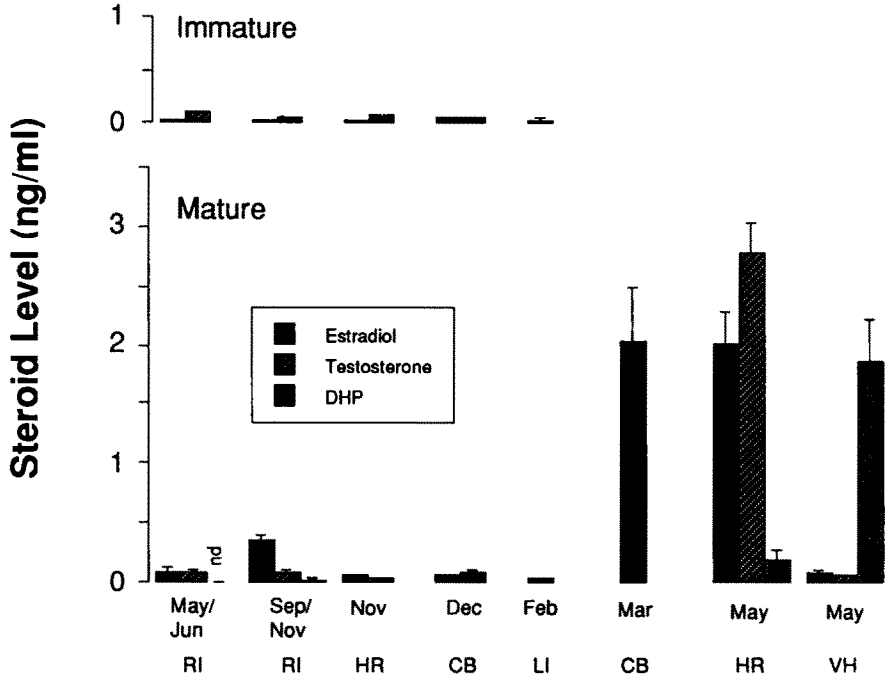


Fig. 4. Composite of seasonal changes in serum steroid levels in immature and mature striped bass sampled from various locations (RI = Rhode Island; HR = Hudson River; CB = Chesapeake Bay; LI = Long Island; VH = Verplanck Hatchery). nd = not detectable.

Table 2. Characteristics of striped bass by reproductive stage and sample.

Sample and month	Stage	Sample number	Fork length (mm)	Fish wt. (kg)	Gonad wt. (g)	Maximum oocyte diameter (μm)
A:	PG	51	469 ± 6	1.4 ± 0.1	6.6 ± 0.8	105 ± 2
May/Jun.	SG	30	612 ± 22	3.7 ± 0.5	32.6 ± 6.2	201 ± 6
	VTG	8	633 ± 26	3.8 ± 0.7	86.5 ± 16	405 ± 24
	AT	17	684 ± 36	4.6 ± 0.8	46.7 ± 11.7	
B:	PG	5	533 ± 9	2.0 ± 0.1	10.1 ± 0.61	114 ± 3
Sep/Nov.	SG	19	624 ± 29	3.4 ± 0.7	29.0 ± 11.8	188 ± 8
	VTG	18	947 ± 44	12.8 ± 1.4	391 ± 64	334 ± 30
C:	PG	6	538 ± 26	2.1 ± 0.3	7.9 ± 2.7	140 ± 5
Nov.	SG	5	634 ± 71	3.9 ± 1.4	47.7 ± 23.3	255 ± 45
	VTG	3	690 ± 31	4.6 ± 0.6	54.8 ± 8.5	360 ± 10
D:	PG	12	373 ± 10	0.8 ± 0.1	2.2 ± 0.3	95 ± 3
Dec.	SG	3	571 ± 16	2.3 ± 0.6	36.2 ± 18	220 ± 8
	VTG	8	551 ± 19	2.5 ± 0.3	41.7 ± 6.5	360 ± 32
E:	PG	11	519 ± 29	1.7 ± 0.3	10.5 ± 3.2	105 ± 5
Feb.	SG	2	547, 554	1.8, 2.0	10.4, 20.4	205, 215
	VTG	1	619	2.7	153	600
F:	VTG	6	596 ± 30	3.3 ± 0.7	162 ± 39	403 ± 16
Mar.						

Table 2. Continued.

Sample and month	Stage	Sample number	Fork length (mm)	Fish wt. (kg)	Gonad wt. (g)	Maximum oocyte diameter (μm)
G: May	VTG	41	690 ± 9	5.1 ± 0.2	317 ± 20	810 ± 54
	FM	2	680, 688	5.0, 5.1	509, 709	
	AT	3	706 ± 64	4.9 ± 1.0	36.8 (1)	
H: May	FM	11	827 ± 28	6.9 ± 0.6	not measured	920 ± 46

Data are shown as mean ± SEM.

tion. The resulting loss of histological details did not permit distinction between oocytes in the terminal stages of vitellogenesis and those in the final maturation stage. Fish which had recently spawned could be identified by the presence of atretic oocytes (Fig. 1E). These oocytes were of ovulatory size (1.0 mm), but no nuclei were present in serial sections, indicating degradation had begun. These follicles could be distinguished from those in the final maturation stage of development which had undergone germinal vesicle breakdown, as the latter still retained yolk globules and remnants of nuclear material.

Immature females: Primary growth oocytes

Fish classified as immature were observed throughout the year except on the spawning grounds during the spawning season. Plasma levels of E_2 and T were low (< 100 pg) throughout the year. Immature fish sampled in Maryland during December had elevated levels of E_2 (46 ± 5 pg/ml, n = 11) relative to fish sampled in Rhode Island waters during the spring (26 ± 3 pg/ml, n = 51) or fall (20 ± 2 pg/ml, n = 5). No differences were found in T or ovarian lipid levels between sampling dates or locations. Mean T and ovarian lipid levels were 68 ± 11 pg/ml (n = 29) and 1.0 ± 0.6 mg/g (n = 17), respectively.

Maturing females: Secondary growth oocytes

Early secondary growth (SG)

Fish with oocytes entering secondary growth phase of development were also found during all sampling periods. The reproductive parameters measured for these fish were low throughout the year in all sampling locations. Plasma E_2 and T concentrations and ovarian lipid content averaged 33 ± 6 pg/ml (n = 19), 81 ± 14 pg/ml (n = 30) and 1.5 ± 0.3 mg/g (n = 68), respectively. No differences were found between these levels and those measured in immature fish at any sampling period. However, the lipid content of ovaries from striped bass caught off Rhode Island was on average three times higher in those entering early secondary growth compared to those still in primary growth phase. Mean GSI was less than 1.0% for all sampling locations, except Maryland-December had a mean GSI of 1.2 ± 0.4% (n = 3).

Vitellogenesis (VTG)

Striped bass sampled on the spawning grounds during the spring months demonstrated the highest degree of reproductive development. Plasma E_2 levels of striped bass sampled in the Hudson River (May) and Maryland (March) averaged 2220 ± 318 pg/ml (n = 41) and 2037 ± 465 pg/ml (n = 6), respectively. Statistical differences were observed for E_2 between these periods and all other sampling periods (364 ± 83 pg/ml, n = 31). Plasma E_2 levels measured in fish sampled at all locations except Maryland-December were different from those measured in fish with oocytes in primary growth and early secondary growth phase. T production paralleled that of E_2 throughout the year. A mean level of 2981 ± 272 pg/ml (n = 26) was recorded for fish sampled on the Hudson River spawning grounds during May. This level differed from levels

measured at all other locations (102 ± 14 pg/ml, n = 17). GSIs for vitellogenic fish were always greater than 1.0% and a maximum of 10.2% was recorded for one fish. Striped bass sampled on the Hudson River spawning grounds had GSIs which averaged 5.6 ± 0.3% (n = 41). Ovarian lipid levels for fish in the vitellogenic phase were different in all sampling periods from those in the primary growth and early secondary growth phases. Ovarian lipid levels from fish sampled during the spring months in Rhode Island (22 ± 4 mg/g, n = 10) and from the Hudson River spawning grounds (24 ± 1 mg/g, n = 6) were different from those in Maryland in December (11 ± 1 mg/g, n = 5).

Final maturation (FM)

Striped bass sampled at the Verplanck Hatchery following HCG injection had plasma E_2, T and DHP levels of 86 ± 11 pg/ml (n = 10), 61 ± 9 pg/ml (n = 10) and 1872 ± 352 pg/ml (n = 11), respectively. DHP levels were low or nondetectable in fish sampled in other developmental stages. Two fish sampled in the Hudson River during the spawning season 1986 had DHP levels which were not different from those sampled at the Verplanck Hatchery. These fish were judged, *a posteriori*, to be in the final maturation stage.

Summary of results

Immature striped bass were defined as those whose oocytes had not progressed beyond the primary growth phase. These fish had low plasma E_2 and T levels (≤100 pg/ml), GSIs (≤1.0%) and ovarian lipid levels (≤2 mg/g) (see Figs. 2 and 3). No differences were found in plasma steroid hormone levels or ovarian lipid content between immature fish and those which had entered early secondary growth phase. However, striped bass that had entered the vitellogenic phase had elevated plasma E_2, T, ovarian lipid levels and GSIs. Maximum levels of all reproductive characteristics were found in prespawning fish sampled in the Hudson River. Mean plasma levels of E_2 and T, ovarian lipid levels and GSIs for these fish were 2037 ± 465 pg/ml, 2981 ± 272 pg/ml, 24 ± 1 mg/g, and 5.6 ± 0.3% respectively. Striped bass injected with HCG at the hatchery, and thus judged to be in the final maturation stage, had elevated plasma levels of DHP (1872 ± 352 pg/ml), whereas both plasma E_2 and T levels were lower than in mature females caught in the Hudson River in the same month.

Discussion

This study describes the endocrine changes which occur during oocyte development in the female striped bass. Mature striped bass sampled in coastal waters soon after returning from their spawning migration were undergoing gonadal recrudescence by May. The ovaries contained oocytes which had entered early secondary growth as indicated by translucent inclusions in the ooplasm. Vitellogenesis was underway by November in the largest females. The transition into final maturation occurred very close to the time of spawning. These aspects of reproductive development in wild striped bass are described and compared to reported changes occurring in other teleost species. Histological aspects of striped bass oocyte development closely resemble those described for the bass, *D. labrax* (Mayer *et al.* 1988).

Pre-vitellogenic females had low steroid levels, GSIs and ovarian lipid levels. This is in agreement with findings in other teleost species (Wingfield and Crim 1977; Pankhurst and Conroy 1987). Vitellogenic females had elevated plasma E_2 levels. The most advanced stages of vitellogenesis were observed in fish sampled in the Hudson River during the spawning season. However, striped bass with well-developed vitellogenic oocytes were caught in coastal Rhode Island waters during the fall and spring months, including June. Since spawning occurred during May, these fish either failed to spawn that season or were preparing to spawn in a location other than the major spawning areas. It has been suggested that striped bass spawn in rivers along the Atlantic coast other than those associated with the major spawning areas (Raney 1952), including river systems in Canada (Leim and Scott 1968).

Vitellogenesis was accompanied by increased

plasma E_2 levels as in other teleosts (Ng and Idler 1983; Sellman and Wallace 1986). Striped bass sampled in Rhode Island during November were of two distinct sizes. Large fish (>12 kg) were sampled from waters near Block Island, Rhode Island. Of these 19 fish, 18 were in the vitellogenic stage of development and one was only as far as early secondary growth. The small fish (<5 kg) sampled at this time of year closer to the shore were in primary growth or early secondary growth phase. Greeley *et al.* (1987) have also observed an influence of fish size on the timing of ovarian development in striped mullet. Fish >32 cm were found to enter vitellogenesis two months earlier than smaller fish in their study.

The highest E_2 levels observed in this study were approximately 3 ng/ml and were observed in prespawning fish. This is at the lower end of the spectrum of values reported for other species, but is similar to plasma levels reported in the striped mullet (Dindo and Macgregor 1981) and the king mackerel (Macgregor *et al.* 1981). E_2 levels reported for various species show a wide range with maximum values of less than 1 ng/ml found in the orange roughy, blue cod and bluefish (Macgregor *et al.* 1981; Pankhurst and Conroy 1987, 1988) to over 50 ng/ml in some salmonid species such as brook trout and rainbow trout (Scott *et al.* 1983; Tam *et al.* 1986). This variation between species in steroid concentrations may be due in part to differences in sampling procedure. The stress of capture has been shown to decrease plasma levels of reproductive steroids in the brown trout, *Salmo trutta*, (Pickering *et al.* 1987) and dogfish, *Scyliorhinus canicula* (Jenkins and Dodd 1982). Furthermore, Safford and Thomas (1987) demonstrated that different methods of capture could influence gonadal steroid levels to different degrees. One of us found no statistical differences between plasma T levels of male fish captured by haul seine or gill net during a period of active steroidogenesis (Berlinsky 1989).

T serves as a precursor for E_2 synthesis and may also have additional unrelated functions in teleosts (Scott *et al.* 1984). T and E_2 levels typically fall during the final maturation stage as the shift in steroidogenesis favors the production of DHP (Scott *et al.* 1984; Pankhurst and Conroy 1987). The shift is believed to result from a gonadotropin surge (Scott *et al.* 1983). Striped bass also demonstrate this sequential pattern of steroid hormone synthesis. HCG-injected fish which had completed final maturation and spawned had higher DHP and lower E_2 and T levels than fish in the advanced stages of vitellogenesis. A similar hormone profile was observed in two fish sampled on the Hudson River spawning grounds during the spawning season. These fish were believed to be in the final maturation stage based on steroid hormone profiles. The drop in T production does not appear to be a prerequisite for final maturation however, since Fitzpatrick *et al.* (1986) found that T and 11-ketotestosterone levels remained elevated throughout the final maturation period in coho salmon.

DHP levels have been measured in captive striped bass during the final maturation period (Thomas 1988), however, it remains unclear specifically how far in advance of spawning DHP levels rise. Since only 2 of 41 wild striped bass sampled during the spawning season showed elevated DHP levels, it appears the shift in steroidogenesis towards DHP production occurred very close to the time of actual spawning. Gonadotropin levels peak shortly before spawning in many teleost species (Peter 1981; Stacey *et al.* 1984). Evidence suggests that the gonadotropin surge is required for the shift in steroidogenesis necessary for DHP production (Scott *et al.* 1983). More work is necessary to establish DHP as important for final maturation in striped bass as it is in some other teleosts (Nagahama and Adachi 1985; Nagahama 1987).

In conclusion, the endocrine correlates of oocyte development in this temperate species exhibiting group synchronous ovarian development resemble those of other temperate fishes. The striped bass containing oocytes in primary growth and early secondary growth phases had low levels of steroid hormones and low GSIs. Plasma E_2 levels were elevated in vitellogenic fish and reached peak levels during the prespawning period. During the periovulatory period plasma E_2 levels declined as steroid pathways shifted toward DHP production. Thus, the most sensitive indicator for sexual maturity in the female striped bass is the appearance of the first inclusions, probably lipid droplets, in the

ooplasm of oocytes being recruited into secondary growth. Fish in the vitellogenic phase and beyond are equally distinguishable by oocyte histology, plasma E_2 levels, and GSI. Further work is needed to determine the duration of each phase of oocyte development and whether other gonadal steroids play important roles.

Acknowledgements

This study was supported by the National Marine Fisheries Service (Grant NA87EA-D-00022), the NOAA National Sea Grant Program (Grant NA85AA-D-SG094), and through a Hudson River Foundation Fellowship to D.L.B. The U.S. Government is authorized to produce and distribute reprints for government purposes notwithstanding any copyright notation that may appear herein. We thank John F. O'Brien, Rode Island Division of Fish and Wildlife, for coordinating collection of fish and providing valuable insight. We wish to thank Andy Kahnle, Byron Young and associates (New York Department of Environmental Conservation); Steve Early (Maryland Department of Natural Resources); Bill Dey and Bruce Freidmann (EA S&T, Verplanck, New York); Charlie Wooley (USFWS); and Tom Hoxsie (Pt. Judith, Rhode Island) for assistance in sample collection. Steve Parker and Tim Whitesel provided important help at all stages of the study. We thank Drs. Carl Schreck, A.P. Scott, and Harold Bibb for their expertise and Kenneth Davignon for the illustrations.

References cited

Berlinsky, D.L. 1989. Changes in steroid hormones during oocyte development in the striped bass, *Morone saxatilis*. Ph.D. Dissertation. University of Rhode Island, U.S.A.

Dindo, J.J. and MacGregor, R. 1981. Annual cycle of serum gonadal steroids and serum lipids in striped mullet. Trans. Am. Fish. Soc. 110: 403–409.

Fabrizio, M.C. 1987a. Contribution of Chesapeake Bay and Hudson River stocks of striped bass to Rhode Island coastal waters as estimated by isoelectric focusing of eye lens proteins. Trans. Am. Fish. Soc. 116: 588–593.

Fabrizio, M.C. 1987b. Growth-invariant discrimination and classification of striped bass stocks by morphometric and electrophoretic methods. Trans. Am. Fish. Soc. 116: 728–736.

Fitzpatrick, M.S., Van Der Kraak, G. and Schreck, C.B. 1986. Profiles of plasma sex steroids and gonadotropin in coho salmon, *Oncorhynchus kisutch*, during final maturation. Gen. Comp. Endocrinol. 62: 437–451.

Greeley, M.S., Calder, D.R. and Wallace, R.W. 1987. Oocyte growth and development in the striped mullet, *Mugil cephalus* during seasonal recrudescence: Relationship to fecundity and size at maturity. Fish Bull. 85: 187–200.

Groman, D.B. 1982. Histology of the Striped Bass. American Fisheries Society Monograph 3. Bethesda, Maryland.

Humasun, G.L. 1979. Animal Tissue Techniques. H.H. Freeman Co., San Francisco.

Jackson, H.W. and Tiller, R.E. 1952. Preliminary observations on spawning potential in the striped bass (*Roccus saxatilis* Walbaum). Maryland Dept. Res. Educ., Publ. No. 93.

Jenkins, N. and Dodd, J.M. 1982. Some effects of trawling stress and captivity on testosterone and estradiol-17β in the female dogfish, *Scyliorhinus canicula*. Gen. Comp. Endocrinol. 46: 394.

Kagawa, H., Takano, K. and Nagahama, Y. 1981. Correlation of plasma estradiol-17β and progesterone levels with ultrastructure and histochemistry of ovarian follicles in the white-spotted char, *Salvelinus leucomaeni*. Cell Tiss. Res. 218: 315–329.

Leim, A.H. and Scott, W.B. 1968. Fishes of the Atlantic Coast of Canada Bull. Fish. Res. Bd. Can. #155.

Lewis, R.M. 1962. Sexual maturity as determined by ovum diameters in striped bass from North Carolina. Trans. Am. Fish. Soc. 91: 279–282.

MacGregor, R., Dindo, J.J. and Finucane, J.H. 1981. Changes in serum androgens and estrogens during spawning in bluefish, *Pomatomus salator* and king mackerel, *Scomberomorus cavalla*. Can. J. Zool. 59: 1749–1754.

Mayer, I., Shackley, S.E. and Ryland, J.S. 1988. Aspects of the reproductive biology of the bass, *Dicentrarchus labrax* L. I An histological and histochemical study of oocyte development. J. Fish Biol. 33: 609–622.

McLaren, J.B., Cooper, J.C., Hoff T.B. and Lander, V. 1981. Movements of Hudson River striped bass. Trans. Am. Fish. Soc. 110: 158–167.

Merriman, D. 1941. Studies of the striped bass (*Roccus saxatilis*) of the Atlantic coast. U.S. Fish and Wildl. Serv. Fishery Bull. 50: 1–77.

Nagahama, Y. and Adachi, S. 1985. Identification of maturation-inducing steroid in a teleost, the Amago salmon (*Oncorhynchus rhodurus*). Dev. Biol. 10: 428–435.

Nagahama, Y. 1987. 17α,20β-Dihydroxy-4-pregnen-3-one: A teleost maturation-inducing hormone. Develop. Growth Differ. 29: 1–12.

Nichols, P.V. and Miller, R.V. 1967. Seasonal movements of striped bass, *Roccus saxatilis* tagged and released in the Potomac River Maryland, 1959–1961. Ches. Sci. 8: 102–124.

Ng, T.B. and Idler, D.R. 1983. Yolk formation and differentiation in teleosts. *In* Fish Physiology. Vol. IX A, pp. 373–397.

Edited by W.S. Hoar, D.J. Randall and E.M. Donaldson. Academic Press, New York.

Pankhurst, N.W. and Conroy, A.M. 1987. Seasonal changes in reproductive condition and plasma levels of sex steroids in the blue cod, *Parapercis colias* (Bloch and Schneider) (Mugiloididae). Fish Physiol. Biochem. 4: 15–26.

Pankhurst, N.W. and Conroy, A.M. 1988. Endocrine changes during gonadal maturation and spawning in the orange roughy, *Hoplostethus atlanticus* Collett. Gen. Comp. Endocrinol. 70: 262–273.

Peter, R.E. 1981. Gonadotropin secretion during the reproductive cycles of teleosts: influence of environmental factors. Gen. Comp. Endocrinol. 45: 294–305.

Pickering, A.D., Pottinger, T.G., Carragher, J. and Sumpter, J.P. 1987. The effects of acute and chronic stress on the levels of reproductive hormones in the plasma of mature male brown trout, *Salmo trutta* L. Gen. Comp. Endocrinol. 61: 120–126.

Raney, E.C. 1952. The life history of the striped bass, *Roccus saxatilis* (Walbaum). Bull. Bingham Oceanographic Colln. Yale University 14: 5–97.

Safford, S.E. and Thomas, P. 1987. Effects of capture and handling on circulating levels of gonadal steroids and cortisol in the spotted seatrout, *Cynoscion nebulosus*. Proc. Third Intl. Sym. Reprod. Physiol. Fish. St. John's, Newfoundland, Canada. Abstract, p. 312.

Scott, A.P., Sheldrick, E.L. and Flint, A.P.F. 1982. Measurement of 17α-20β-dihydroxy-4-pregnen-3-one in the plasma of rainbow trout (*Salmo gairdneri* Richardson): seasonal changes and response to salmon pituitary extract. Gen. Comp. Endocrinol. 46: 444–451.

Scott, A.P., Sumpter, J.P. and Hardiman, P.A. 1983. Hormone changes during ovulation in the rainbow trout (*Salmo gairdneri* Richardson). Gen. Comp. Endocrinol. 49: 128–134.

Scott, A.P., MacKenzie, D.S. and Stacey, N.E. 1984. Endocrine changes during natural spawning in the white sucker, *Catostomus commersoni* II. Steroid Hormones. Gen. Comp. Endocrinol. 56: 349–359.

Selman, K. and Wallace, R.A. 1986. Oogenesis in *Fundulus heteroclitus* IV. Yolk vesicle formation. J. Exp. Zool. 239: 277–288.

Setzler, E.M., Boynton, W.R., Wood, K.V., Zion, H.H., Lubers, L., Mountford, N.K., Pulles, P. and Tucker, L. 1980. Synopsis of biological data on striped bass, *Morone saxatilis* (Walbaum). NOAA Tech. Report FAO Synopsis No. 121.

Sokal, R.R. and Rohlf, F.J. 1981. Biometry. The Principles and Practice of Statistics in Biological Research. W.H. Freeman and Co., San Francisco.

Specker, J.L., Berlinsky, D.L., Bibb, H.D. and O'Brien, J. 1987. Oocyte development in striped bass: Factors influencing estimates of age at maturity. Trans. Am. Fish. Soc. 1: 162–174.

Stacey, N.E., MacKenzie, D.S. Marchant, T.A. and Kyle, A.L. 1984. Endocrine changes during natural spawning in the white sucker, *Catostomus commersoni* I. Gonadotropin, growth hormone and thyroid hormones. Gen. Comp. Endocrinol. 56: 333–348.

Tam, W.H., Roy, J.J. and Makaran, R. 1986. Ovarian cycle and plasma concentrations of estrogen and vitellogenin in brook trout, *Salvelinus fontinalis*. Can. J. Zool. 64: 744–751.

Thomas, P. 1988. Changes in the plasma levels of maturation inducing steroids in several perciform fishes during induced ovulation. Am. Zool. 28: 53.

Van Der Kraak, G., Dye, H.M. and Donaldson, E.M. 1984. Effects of LH-RH and des-Gly^{10}[D-Ala^{6}]LH-RH-ethylamide on plasma gonadotropin levels and oocyte maturation in adult female coho salmon (*Oncorhynchus kisutch*). Gen. Comp. Endocrinol. 49: 470–476.

Wallace, R.A. and Selman, K. 1981. Cellular and dynamic aspects of oocyte growth in teleosts. Am. Zool. 57: 617–626.

Wingfield, J.C. and Crimm, A.S. 1977. Seasonal changes in plasma cortisol, testosterone and estradiol 17-β in the plaice, *Pleuronectes platessa*. Gen. Comp. Endocrinol. 31: 1–11.

Young, G., Crim, L.W., Kagawa, H., Kambegawa, K. and Nagahama, Y. 1983. Plasma 17α-20β-dihydroxy-4-pregnene-3-one during sexual maturation of amago salmon (*Oncorhynchus rhodus*): Correlation with plasma gonadotropin and *in vitro* production by ovarian follicles. Gen. Comp. Endocrinol. 51: 96–105.