Lipid Dynamics in Relation to the Annual Reproductive Cycle in Yellowtail Rockfish (*Sebastes flavidus*)

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MacFarlane, R. B., E. C. Norton, and M. J. Bowers. 1993. Lipid dynamics in relation to the annual reproductive cycle in yellowtail rockfish (*Sebastes flavidus*). Can. J. Fish. Aquat. Sci. 50: 391–401.

In yellowtail rockfish (*Sebastes flavidus*), lipids that accumulated in mesenteries and liver during the summer and early fall upwelling were subsequently translocated to developing ovaries during late fall and winter. Tissue and serum lipids were assessed by stage of ovary maturation from fish collected monthly over six annual reproductive cycles (1985–91) from Cordell Bank, a seamount off central California. Lipids were primarily transported to ovaries prior to fertilization. Energetic lipids (triglycerides, nonesterified fatty acids) were maximal in serum during yolk accumulation stages and declined significantly during embryonic stages. Between fertilization and parturition, lipid and protein content of ovaries declined by about 21%, a value approaching the minimum for lecithotrophy (i.e. ovoviviparity). During gestation, however, serum phospholipids and calcium (vitellogenin surrogate) were significantly elevated relative to male levels, suggesting matrotrophic contributions. A reproductive mode that is primarily lecithotrophic but supplemented by maternal inputs during embryogenesis would be beneficial to viviparous fishes of the California coast. This strategy may optimize reproduction by coupling the disparate times of food abundance and gestation, yet allow for provision of nutrients late in the reproductive cycle should they be available.

Chez le sébaste à queue jaune (*Sebastes flavidus*), les lipides qui se sont accumulés dans le mésentère et le foie au cours de l'été et lors de l'upwelling tôt en automne, ont par la suite été transportés jusqu'aux ovaires en développement au cours de la fin de l'automne et en hiver. Les lipides contenus dans les tissus et le sérum ont été dosés en fonction des étapes de maturation de l'ovaire chez des poissons prélevés chaque mois pendant six cycles reproductifs annuels (1985–1991) et qui provenaient de Cordell Bank, un mont sous-marin situé au large de la partie centrale de la Californie. Les lipides ont d'abord été transportés jusqu'aux ovaires avant la fécondation. La concentration en lipides calorigènes (triglycérides, acides gras non estérifiés) était maximale dans le sérum au cours des étapes d'accumulation du vitellus et diminuait sensiblement au cours des stades embryonnaires. Entre la fécondation et la ponte, la teneur en lipides et en protéines des ovaires a diminué d'environ 21 %; cette valeur confine au minimum requis pour définir la lécithotrophie (c.-à-d. ovoviviparité). Cependant, pendant la maturation des oeufs dans l'organisme, la concentration en calcium et en phospholipides sériques (substitut de la vitellogénine) a été significativement élevée par rapport à la teneur observée chez les mâles, ce qui nous amène à envisager des contributions caractéristiques du système reproducteur de la femelle. Un mode de reproduction qui est avant tout lécithotrophe, mais qui est complété par des apports maternels durant l'embryogenèse présenterait un avantage pour les poissons vivipares de la côte de la reproduction en permettant de faire le pont entre des époques différentes d'abondance des aliments et d'embryogenèse, mais en assurant la disponibilité d'éléments nutritifs tard dans le cycle de la reproduction.

Received February 24, 1992
Accepted August 6, 1992
(JB417)

Reçu le 24 février 1992
Accepté le 6 août 1992

The coastal region of California is subject to variable seasonal upwelling (Boje and Tomczak 1978). Upwelling onset, duration, and intensity, and perhaps advection by the California Current (Bernal and McGowan 1981), modulate the trophodynamics of coastal fish communities (Hobson and Chess 1988). The nutritional state of many fish species within this system is tied to the temporal pattern of productivity produced by these influences.

Rockfish (*Sebastes*) are dominant components of fish communities within the California upwelling region. These viviparous species respond to changes in environmental conditions by annually and interannually varying the accumulation of lipids. Lipid accumulation may influence reproduction (Larson 1991), but Guillemot et al. (1985) interpreted seasonal (i.e. quarterly) changes in mesenteric fat volume in four species of rockfish as having little or no reproductive function. They conjectured that since there was overlap in fat and gonad cycles, lipid reserves acquired in the summer and fall were used primarily for adult maintenance functions during the winter. Yet, yellowtail rockfish (*Sebastes flavidus*), one of the species assessed by Guillemot et al. (1985), had impaired reproduction that corresponded to low fat deposits during the 1983 El Niño (Lenarz and Wyllie Echeverria 1986).

In marine fishes, lipids are the major source of nutrition (Sargent 1976; Sargent et al. 1989). When maternal diets are deficient, insufficient transfer of lipids to developing ovaries may reduce fecundity and the viability of the progeny (Watanabe 1985; Luquet and Watanabe 1986; Heming and Buddington 1988). Indeed, fluctuations in the quantity and/or quality of larvae released due to variations in food availability are potential contributors to the significant interannual variability of recruitment strength found in rockfish (Moser and Boehlert 1991).

Despite the apparent importance of lipids to ovarian development, data exist primarily for oviparous teleosts. Information is limited temporally, or by lipid components and tis-

sues assayed (Luquet and Watanabe 1986; Kjorsvik et al. 1990). Even less information is available for viviparous teleosts (e.g. see Pekkarinen and Kristoffersson 1975; Korsgaard and Petersen 1979). For species of the genus *Sebastes*, nothing is known of lipid dynamics beyond mesenteric fat variations.

Since April 1985, we have studied the reproductive biology of a population of *S. flavidus* living on Cordell Bank, a seamount off the central coast of California. This paper presents the results of our investigation of lipid dynamics in yellowtail rockfish during the annual reproductive cycle. Lipids in serum, gonad, liver, mesenteries, and muscle tissues were evaluated temporally and by stage of ovarian maturation to elucidate the relationship of lipid components to specific oocyte and embryonic developmental stages.

Materials and Methods

Adult yellowtail rockfish were obtained by hook and line at depths ranging from 50 to 150 m from Cordell Bank, a seamount 37 km west of Pt. Reyes, California. Specimens were collected monthly from April 1985 through March 1991, except for June 1985 and November 1986 (rough sea conditions) and several months between May 1988 and November 1989 (operational research constraints). Approximately 10 females and 5 males were examined monthly from May 1987 to the end of the study; prior to May 1987, only females were assessed.

Immediately after capture, blood was obtained by cardiac puncture using sterile Vacutainers without anticoagulant and allowed to clot before centrifugation for serum isolation. Fish were held on ice until examination, dissection, and tissue subsampling were performed (within 24 h). Following morphometric determinations, liver, gonad, and muscle samples were frozen at −70°C for later lipid analysis. Ovary sections were excised and fixed in 10% neutral buffered formalin for histological preparation. Paraffin-embedded, hematoxylin-, and eosin-stained sections of oocytes and embryos were categorized into one of nine stages of development according to the following ovary maturation stage (OMS) classification scheme (Bowers 1992):

OMS	State of development
1	Recovery (early recrudescence)
2	Early yolk accumulation
3	Late yolk accumulation
4	Migratory nucleus
5	Ovulation and fertilization
6	Early-celled embryo
7	Embryonic body
8	Eyed larvae
9	Spent

We recorded each specimen's sex, standard length, and total weight and the weights of liver, gonad, and mesenteric fat. We calculated each tissue's relative weight index (i.e. liver somatic (LSI), gonadosomatic (GSI), and mesenteric fat index (MFI), respectively) as (tissue weight/body weight) × 100. The age of each fish was determined by counting annual growth increments of otoliths using routine break-and-burn techniques.

Serum triacylglycerols (triglycerides), total cholesterol, and calcium were measured by a computerized Technicon sequential multiple analyzer (SMAC) according to the procedures supplied by the manufacturer (Technicon Instruments Corp., Tarrytown, NY). Serum calcium concentrations were used as an indicator of serum vitellogenin (Tinsley 1985). Calcium is stoichiometrically incorporated into vitellogenin and correlates with ovarian but not testicular maturation (Ng and Idler 1983; Mommsen and Walsh 1988). References to vitellogenin in this paper are based on serum calcium determinations. Serum phospholipids and nonesterified fatty acids were quantified by in vitro enzymatic colorimetric methods using test kits purchased from Wako Pure Chemical Industries, Ltd., Osaka, Japan.

Total lipids were extracted in duplicate from 1–2 g of liver, gonad, and muscle tissues by the biphasic method of Bligh and Dyer (1959) following homogenization using a Polytron (Brinkmann Instruments Co., Westbury, NY). After December 1988, a different extraction technique was used. Frozen tissue samples were minced into thin 2-mm slices and extracted in sufficient chloroform–methanol (2:1, v/v) to achieve a final concentration of about 30 μg/μL. Lipids were extracted for 24 h with occasional stirring; subsequently, an additional 5.0 mL of solvent was added and extraction continued for another 24 h. Triplicate determinations of three separate livers revealed no significant differences in mean lipid concentrations between the two extraction techniques (ANOVA, $P = 0.31$).

Total lipids were quantified by thin layer chromatography combined with flame ionization detection (TLC-FID) using an Iatroscan TH-10 Mark III (Iatron Laboratories Inc., Tokyo, Japan) interfaced with T Datascan software (RSS Inc., Costa Mesa, CA). Triplicate 1.0-μL aliquots were spotted on Chromarods S-III, dried, and scanned at 3.1 mm/s, hydrogen pressure of 0.95 kg/cm^2, and air flow of 2000 mL/min. Chromarods were stored desiccated, cleaned with 9 N H_2SO_4, rinsed with Milli-Q water, and activated by two passes through the FID. Peak areas were converted to lipid weight by comparison with external standard curves created from dilutions of gravimetrically measured lipid extracts from *S. flavidus* livers.

Ovary protein concentrations were analyzed by the Lowry method using bovine serum albumin standards (Lowry et al. 1951).

Temporal variations of lipids and lipid concentration relationships to stage of ovarian maturation were analyzed by general linear model (GLM) ANOVA procedures within SAS computer software (SAS Institute Inc., Cary, NC). If age or length was related to a variable's value, this effect was removed using the ANCOVA option in the GLM procedure. Comparisons between means were accomplished by Tukey's Studentized range (HSD) test, which controls the maximum experimentwise error rate, and paired *t*-tests.

To assess the change in weights of ovary lipid and protein according to OMS, these variables were adjusted for differences in female size by ANCOVA within the GLM procedure in SAS. The natural logarithm of standard length was used as the covariate, since it stabilizes the variance among means and approximates the relationship between body weight and length. Total body weight varies in relation to length due to increasing ovary weight during reproductive development. Therefore, it cannot be used as a covariate to improve the precision of determining the relationship between tissue component quantity and OMS independent of fish size.

Results

Temporal Variations

Fluctuations of lipids during the annual reproductive cycle were evaluated on specimens collected monthly between May 1987 and April 1988 (Table 1). This interval covered one reproductive cycle starting from the onset of ovarian

TABLE 1. Mean (±SE) standard lengths and ages of *S. flavidus* assessed during the reproductive cycle in 1987–88. Means among months within the same sex are significantly different: *$P < 0.05$; **$P < 0.001$.

	Females			Males		
Month	Standard length (cm)	Age (yr)	*n*	Standard length (cm)	Age (yr)	*n*
May	33.0 ± 0.1	8 ± 1	6	37.2 ± 0.6	26 ± 6	4
June	37.2 ± 1.4	16 ± 3	8	35.1 ± 0.7	13 ± 2	7
July	41.2 ± 0.9	20 ± 2	11	37.4 ± 1.7	15 ± 3	4
August	38.3 ± 0.8	18 ± 2	10	35.0 ± 0.8	17 ± 3	5
September	35.5 ± 1.2	13 ± 3	10	32.0	8	1
October	37.9 ± 1.0	18 ± 2	10	34.6 ± 0.8	14 ± 3	5
November	37.6 ± 1.1	18 ± 2	10	37.1 ± 0.9	17 ± 3	4
December	36.6 ± 1.1	16 ± 2	10	34.7 ± 1.0	19 ± 3	5
January	37.0 ± 1.9	14 ± 3	7	35.7 ± 0.6	16 ± 2	6
February	32.5 ± 1.2	11 ± 2	8	33.3 ± 0.6	15 ± 2	7
March	38.2 ± 1.0	20 ± 3	10	34.5 ± 1.5	17 ± 5	5
April	36.8 ± 1.4	14 ± 2	8	36.0 ± 0.8	22 ± 5	5
Total	37.0 ± 0.4**	16 ± 1*	108	35.3 ± 0.3*	17 ± 1	58

recrudescence in May and terminating with parturition of larvae in February and March. Data from fish collected in April reveal the start of the next cycle. Since the male reproductive cycle precedes that of the female, data from males were used to assess changes in females specific to the cycle of ovarian development. Significant differences among monthly mean length or age were not important for analysis of lipid variables during the 12 mo assessed. Only GSI and MFI varied significantly with length; no variables were affected by age differences.

The gonadal cycles of females and males are not synchronous in *S. flavidus* (Fig. 1). Maximum testicular size was in August when copulation occurred whereas ovaries did not enlarge until November. Histologically, initial yolk accumulation become apparent in July and persisted for at least 6 mo.

Mesenteric fat and liver mass increased significantly ($P < 0.0001$) until August and remained elevated through November in females (Fig. 1). Whereas liver mass increased evenly in both sexes, females gained greater amounts of fat in their intestinal mesenteries than males from August through November ($P < 0.05$). As ovaries matured through fertilization, embryogenesis, and parturition, liver mass and mesenteric fat declined. These somatic trends also occurred in males during this interval.

Serum levels of triglycerides, nonesterified fatty acids (NEFA), and phospholipids were similar in females and males during the summer and early fall months except for September (Fig. 2). The mean triglyceride level in female serum in September (1979 ± 152 mg/dL) was more than twice the highest level recorded during the 6 yr of the study and should be considered anomalous. This was also true for NEFA in females. Serum cholesterol levels were indistinguishable between the sexes for the entire reproductive cycle except in August ($P < 0.05$).

During the winter months spanning late yolk accumulation and embryonic stages, serum lipids (except cholesterol) in females were significantly elevated over those in males ($P < 0.05$) (Fig. 2). In October, serum calcium levels in females (indicative of vitellogenin transport) became increasingly greater than in males ($P < 0.05$), attained maximal differences in December ($P < 0.0001$), and returned to the same levels in March, following parturition (Fig. 2).

Total lipid concentrations in liver were similar throughout the year in females and males (Fig. 3). Liver lipid fluctuated considerably during the reproductive cycle. In females, maximal concentrations occurred in August and declined to minimal values during January–March when parturition was completed.

During the annual cycle, lipid concentrations were elevated in ovaries from October through February($P < 0.001$), concurrent with increased ovary size (Fig. 3). Although concentrations of lipids in ovaries in April and in testes in June and January were high, the quantities were very low due to small gonad sizes. Testes lipids were below detection (5 μg) in February and March.

Muscle tissue contained relatively low concentrations of lipids in *S. flavidus* during the year (Fig. 3). Profiles of lipid concentration in muscle revealed no significant differences between the sexes throughout the reproductive cycle. There was little variation in lipid concentration of muscle between months.

Variation in Maturation Stage

Although ovarian development is synchronous within a female, a range of OMS may exist at one time within the *S. flavidus* population. This is particularly the case during embryonic stages, since gestation lasts only about 30 d. Consequently, analyses by month do not reveal lipid levels during each OMS precisely. Therefore, changes in lipid concentrations by OMS were analyzed for the entire data set (April 1985 – March 1991). The mean length and age of fish analyzed for each OMS are presented in Table 2.

There was an inverse relationship between liver or mesenteric fat tissue amounts and the size of ovaries (Fig. 4). Liver and mesenteric fat increased significantly ($P < 0.05$) during early yolk accumulation (OMS 2) and declined ($P < 0.05$) during later oocyte and embryonic stages. Ovaries attained their largest size at the most advanced embryo stage, eyed larvae (OMS 8), when liver and mesenteric fat were minimal.

Serum lipid concentrations, as well as vitellogenin (measured as Ca^{2+}), in adult females were significantly different among OMS ($P < 0.0001$ for all variables) (Fig. 5). Triglycerides were greater in maternal serum during oocyte stages than during embryonic stages ($P < 0.05$). The NEFA were more

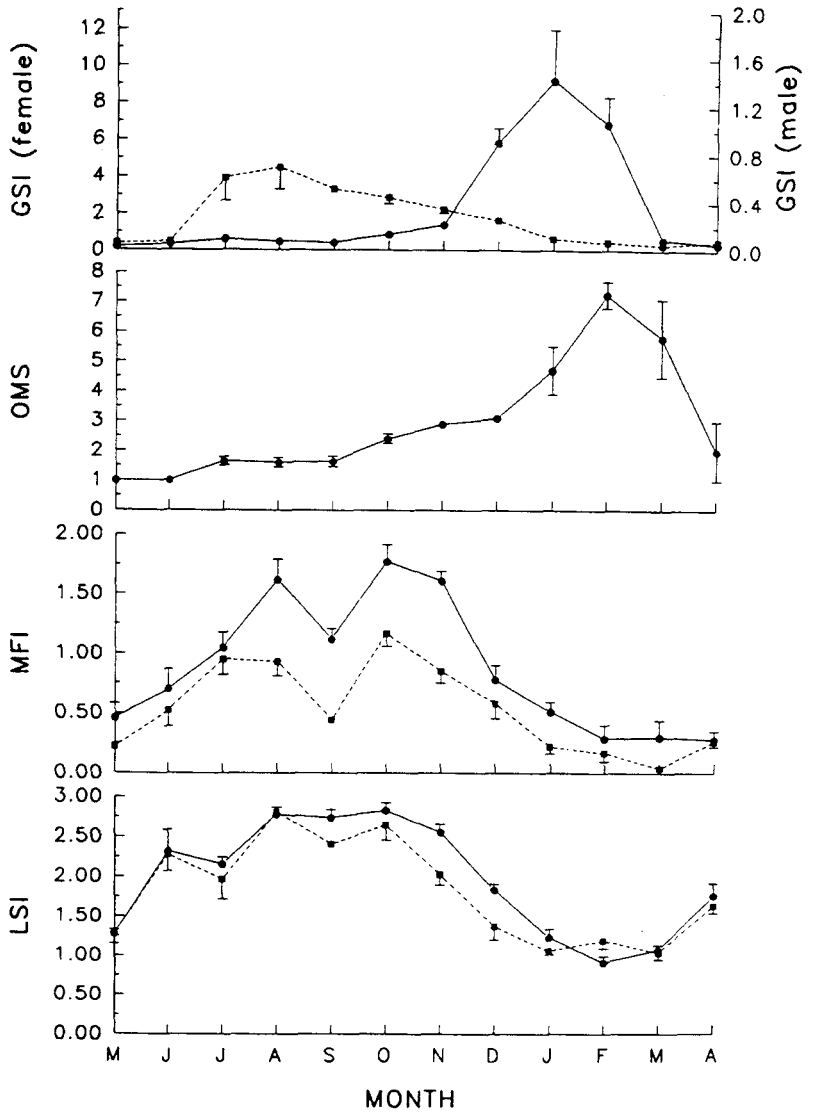

FIG. 1. Monthly variation of relative GSI, OMS, MFI, and LSI in *S. flavidus* for one reproductive cycle, May 1987 – April 1988. Values are means ± SE. Solid line, females; broken line, males.

variable than triglycerides but declined during embryonic stages as well ($P < 0.05$).

Cholesterol and phospholipids, which function predominantly as structural components, had somewhat different profiles in maternal serum relative to OMS than triglycerides or NEFA. Both lipid classes were significantly elevated ($P < 0.05$) during early-celled and embryonic body stages (OMS 6 and 7) compared with values during ovulation/fertilization (OMS 5) and eyed larvae (OMS 8) stages.

Serum calcium concentrations were statistically similar during OMS 3–8 but greater than during OMS 1, 2, and 9 ($P< 0.05$).

Tissue lipids were analyzed in fewer females (liver and ovary, $n = 284$; muscle, $n = 67$) than were analyzed for serum lipids and were randomly chosen from monthly collections (Fig. 6). Liver lipid, greatest in OMS 2, decreased significantly during gestation ($P < 0.05$). Lipid levels in muscle were low and not significantly different among OMS ($P = 0.20$). The greatest increases in lipid concentrations in ovaries occurred during OMS 3 and 4 (late yolk accumulation and migratory nucleus). Ovary lipids declined during gestational stages (OMS 5–8; $P < 0.05$).

The quantities of lipid and protein in ovaries attained maxima at the start of embryogenesis and experienced net declines

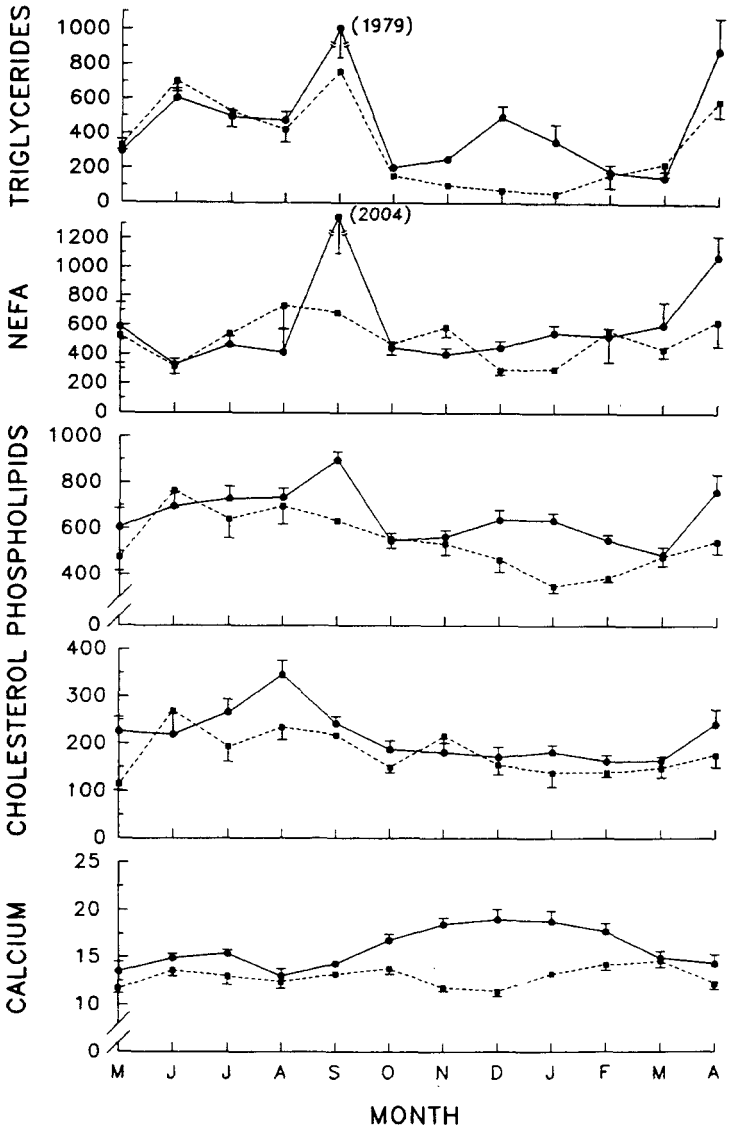

FIG. 2. Changes in serum triglycerides, NEFA, phospholipids, cholesterol, and calcium (vitellogenin surrogate) in *S. flavidus* during one reproductive cycle. Values are means ± SE in mg/dL except NEFA (μEq/L). Solid line, females; broken line, males.

through gestation (Fig. 7a). When lipid and protein quantities were converted to energy values, using factors of 39.6 and 20.1 kJ/g, respectively (Brett and Groves 1979), it became evident that maximum energy was sequestered in ovaries during OMS 6 (early-celled) or the start of embryogenesis (Fig. 7b). Greater energy was in the form of lipid during embryonic development whereas protein dominated quantitatively. Since OMS 5 (ovulation/fertilization) is an event rather than a developmental interval, and occurs during a very short time span, only three females' ovaries were assayed in this stage; therefore, the decline in lipid apparent in Fig. 7 is probably unrepresentative of that portion of the reproductive sequence.

Discussion

Female yellowtail rockfish accumulate greater quantities of lipids in mesenteric depots than males during the active feeding period of summer and fall. Presumably this is advantageous to the maternal role in viviparity during the winter when food is

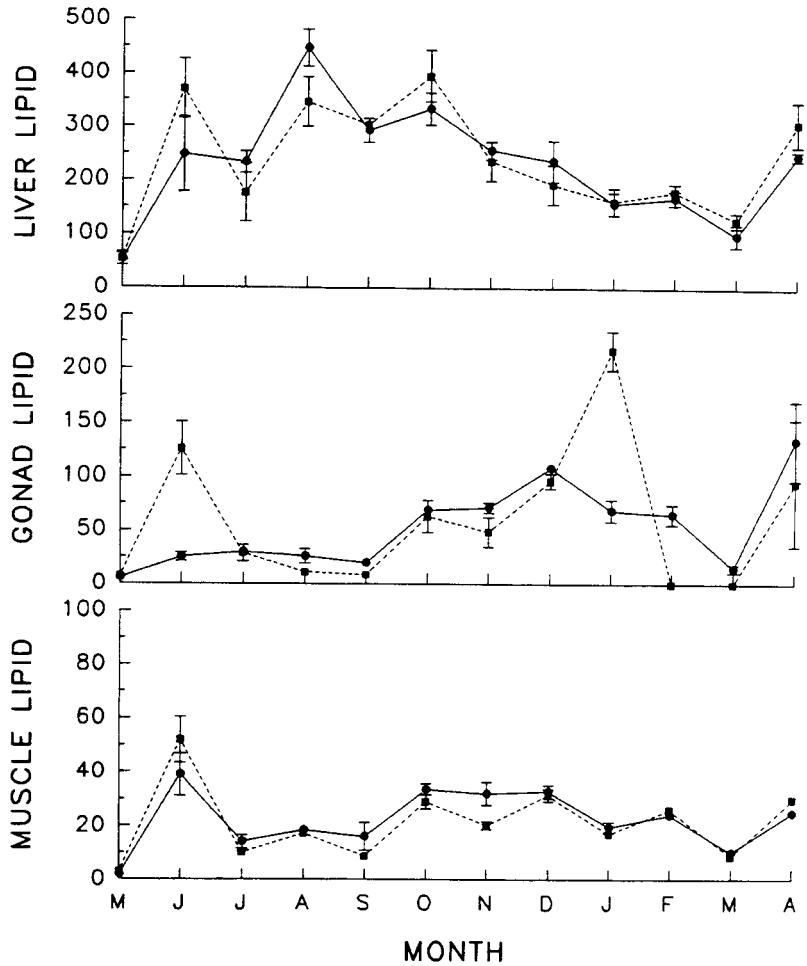

FIG. 3. Monthly concentration of total lipid in liver, gonad, and muscle of *S. flavidus* during one reproductive cycle. Values are means ± SE in mg/g fresh weight. Solid line, females; broken line, males.

TABLE 2. Mean (± SE) standard lengths and ages of female *S. flavidus* assessed by OMS. Females collected from April 1985 to March 1991. Means among stages are significantly different: $^{**}P < 0.001$.

OMS	Description	Standard length (cm)	Age (yr)	*n*
1	Recovery	37.2 ± 0.3	16 ± 1	166
2	Early yolk	38.5 ± 0.3	17 ± 1	94
3	Late yolk	38.4 ± 0.3	18 ± 1	156
4	Migratory nucleus	36.8 ± 0.6	16 ± 1	42
5	Ovulation/fertilization	33.3 ± 0.7	11 ± 2	3
6	Early-celled embryo	34.7 ± 0.8	13 ± 2	12
7	Embryonic body	37.0 ± 0.9	19 ± 2	30
8	Eyed larvae	36.1 ± 1.4	15 ± 2	12
9	Spent	36.5 ± 0.6	17 ± 1	48
Total		37.5 ± 0.2**	17 ± 1	563

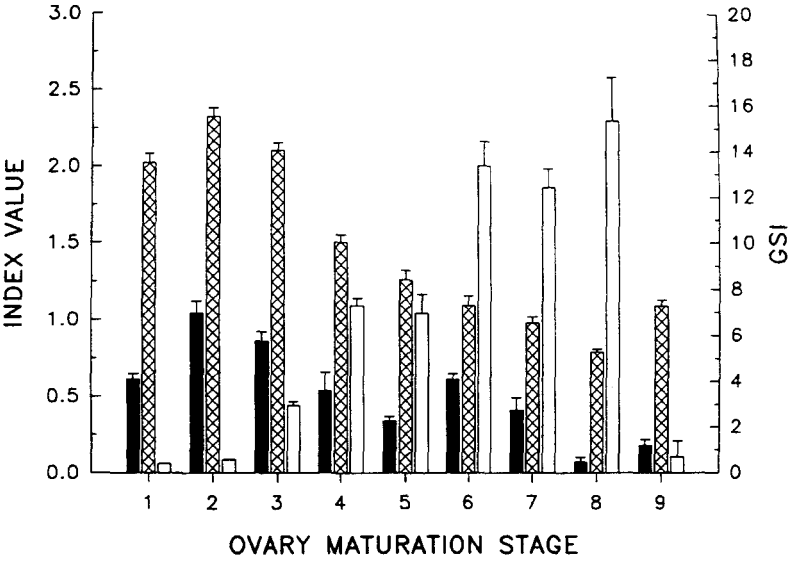

FIG. 4. Mean (+SE) values of LSI, MFI, and GSI by OMS of adult female *S. flavidus* from Cordell Bank, CA, collected between April 1985 and April 1991 (six reproductive cycles). MFI (solid bars) and LSI (cross-hatched bars) on left ordinate; GSI (open bars) on right ordinate. OMS: 1, recovering; 2, early yolk; 3, late yolk; 4, migratory nucleus; 5, ovulation/fertilization; 6, early-celled embryo; 7, embryonic body; 8, eyed larvae; 9, spent.

typically scarce on the central California coast (Bolin and Abbott 1963; Brinton 1976; Hobson and Chess 1988).

Lipids declined in mesenteries and liver as oocytes progressed from yolk accumulation through embryogenesis. During these stages, elevated lipid concentrations in maternal serum, relative to those of males, indicate that at least part of this transport was for female reproductive-specific purposes. Due to the increased body size of pregnant females, some of the mobilized triglycerides may be required for increased energy demands of functions such as locomotion and ion regulation, but the data suggest that a substantial portion was incorporated into developing ovaries. It is doubtful that energy costs of locomotion are high. Yellowtail rockfish are largely quiescent and do not migrate to any great extent (Carlson and Haight 1972; Carlson and Barr 1977). Further, serum glucose is quite low in *S. flavidus* (14.2 ± 0.5 mg/dL, n = 487), indicative of an inactive lifestyle (Love 1980).

Guillemot et al. (1985) measured changes in mesenteric fat volume across the annual reproductive cycle for several species of *Sebastes*, including *S. flavidus*. They described a pattern of fat accumulation similar to our results, but interpreted the data differently. They concluded that fat accumulation coincided with gametogenesis, and thus served primarily adult maintenance functions. Such a conclusion may have resulted from pooling data from several locations into yearly quarters. Our results, using monthly measurements and analysis by stage of ovarian maturation, clearly show an inverse relationship between liver and mesenteric fat quantity and ovarian development. Our data indicate that lipid stores acquired during the feeding period are destined for energy-requiring functions and structural proliferation in ovaries as well as for maintenance expenses of the adult during the poor feeding conditions of winter.

Viviparity in fishes can range from strict lecithotrophy, where embryonic nutrition is provided exclusively by energy reserves deposited during oogenesis, to extreme matrotrophy, where maternally contributed nutrients are provided only during gestation (Wourms 1981). Historically, members of the genus *Sebastes* have been considered lecithotrophic (Wourms 1991); however, recent evidence has suggested that this may not be the case for all rockfish species. Energy balance estimates (Boehlert and Yoklavich 1984; Boehlert et al. 1986; Dygert and Gunderson 1991) and in vitro incorporation of labeled glycine by embryos (Yoklavich and Boehlert 1991) indicated possible matrotrophy in several rockfish species.

Using conventional criteria to discriminate between lecithotrophic and matrotrophic viviparity, *S. flavidus* appear to be on the more lecithotrophic end of the continuum, with possible matrotrophic contributions of lipids intended for primarily structural functions. If one calculates the change in lipid and protein content in ovaries from fertilization to eyed larvae stage (i.e. just prior to parturition) for yellowtail rockfish, there is an estimated 21% reduction in weight and 16% energy loss. Net weight losses of 25–35% suggest no maternal nutrient inputs during gestation (i.e. lecithotrophy) whereas weight changes ranging from slight losses (e.g. to 10%) to net increases indicate matrotrophy (Wourms et al. 1988).

Respirometry and calorimetry measurements on three species of rockfishes, *S. melanops*, *S. schlegeli*, and *S. caurinus*, suggested some maternal transfer of energy during gestation where weight changes were −11, +22, and −21%, respectively (Boehlert and Yoklavich 1984; Boehlert et al. 1986; Dygert and Gunderson 1991). The comparable energy losses, based on calorimetry data, for the three rockfish species were 20, 7, and 34%, respectively. Our method of assessing changes in organic weight and energy content during ovarian matura-

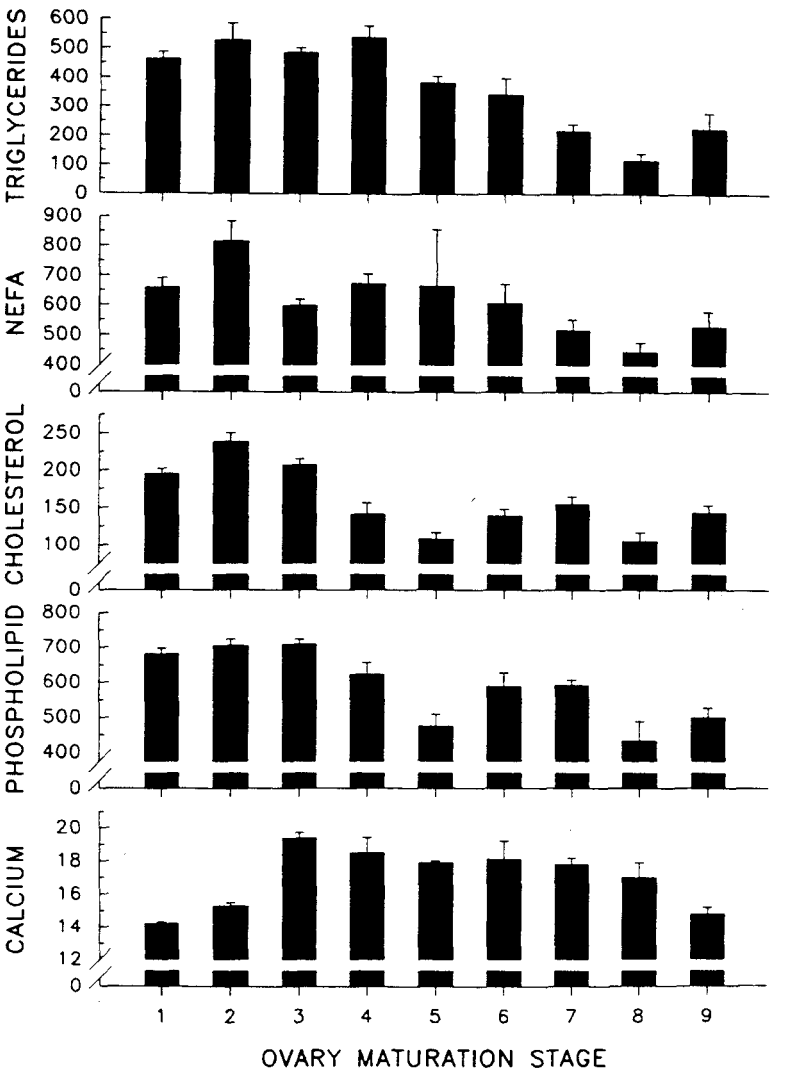

FIG. 5. Variation in serum lipids and calcium (vitellogenin surrogate) by OMS in adult female *S. flavidus* from April 1985 through April 1991. Values are means + SE in mg/dL for all variables except NEFA (μEq/L). See legend of Fig. 4 for OMS key.

tion, independent of calorimetry and respirometry, established *S. flavidus* values within the ranges established for other rockfish species considered to have some degree of matrotrophy (Wourms 1991).

Levels of phospholipids, cholesterol, and calcium (indicative of vitellogenin in females) in maternal *S. flavidus* serum during gestation were high relative to values found in male serum during the same period. This indicates matrotrophic contributions to embryonic nutrition in *S. flavidus*. For instance, lipids, particularly phospholipids, were increased in serum of the matrotrophic blenny *Zoarces viviparus* (Korsgaard and Petersen 1979) and the embiotocid *Cymatogaster aggregata* (deVlaming et al. 1983) during gestation.

If elevated serum calcium in yellowtail rockfish reflects vitellogenin levels, as found in other fish species (Oguri and Takada 1967; Yaron et al. 1977; Elliot et al. 1979; Hori et al. 1979), then vitellogenin transport during embryogenesis contrasts with data from a western Pacific congener, *Sebastes taczanowski* (Takemura et al. 1991). Vitellogenin did not occur in maternal serum of *S. taczanowski* during gestation. However, another viviparous teleost, *Gambusia affinis*, previously considered lecithotrophic (Wourms et al. 1988), has been shown to circulate vitellogenin during pregnancy (R. A. Wallace, C. V. Whitney Laboratory, St. Augustine, FL, pers. comm.).

A reproductive strategy of primarily lecithotrophic viviparity, supplemented by matrotrophy of certain components,

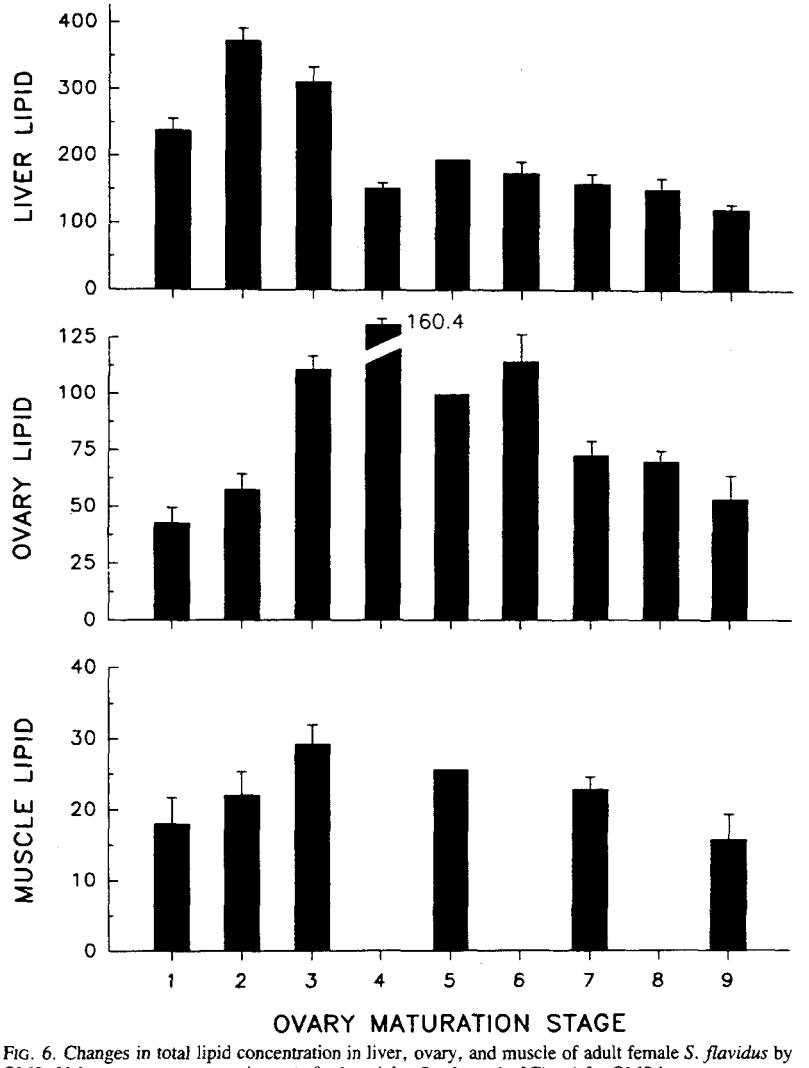

FIG. 6. Changes in total lipid concentration in liver, ovary, and muscle of adult female *S. flavidus* by OMS. Values are means + SE in mg/g fresh weight. See legend of Fig. 4 for OMS key.

would be beneficial to *S. flavidus*. Species inhabiting Pacific coastal areas of temperate North America must adapt to cycles of physical factors (e.g. temperature, currents) and biotic productivity dominated by upwelling of deep ocean water (Boje and Tomczak 1978). In most years, upwelling and associated productivity begin in March or April off central California (Bakun et al. 1974; Cushing 1978). During winter, when *S. flavidus* reproduce, upwelling is usually greatly reduced leading to scarce food supplies, although upwelling and productivity during this period do occur in some years (e.g. Bakun 1975). Supplemental matrotrophic processes would allow utilization of environmental productivity for reproduction during this time. Being primarily lecithotrophic, however, females can accumulate lipid reserves during the summer and early fall when prey is predictably abundant to support reproduction during the winter. Thus, *S. flavidus* employ lecithotrophy as an adaptive strategy in a predictable, yet cyclic environment to couple disparate time intervals of food abundance and reproductive development. This contrasts with other situations where lecithotrophy may be advantageous, such as with *Poeciliopsis*, where unpredictable environmental conditions and food supply are encountered (Thibault and Schultz 1978).

It is interesting that *S. flavidus*, a relatively fecund viviparous species with a long life span, would seem to adopt a reproductive nutritional strategy of committing lipids to ovarian development so early in the cycle (2–3 mo prior to fertilization) and not later when adequate nutrition and energy for female sustenance can be ensured. Poor nutrition and energy reserves can lead to increased susceptibility to disease and parasites (Ghittino 1989). Most viviparous species have small broods

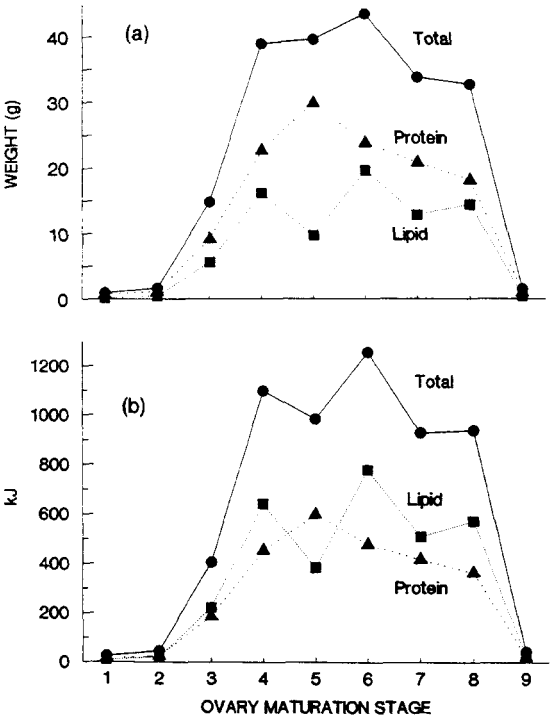

FIG. 7. Profiles of (a) quantities and (b) energy content of total organic weight, lipid, and protein in ovaries of standard female *S. flavidus* by OMS. Values are means adjusted for variation of size (ln (standard length)) by ANCOVA of females obtained from April 1985 through April 1991.

(Wourms et al. 1988 whereas yellowtail rockfish fecundity approximates 1×10^6/female with a reproductive life span to 45 yr (Eldridge et al. 1991). In lean feeding years, retaining lipids in mesenteries and other tissues until fertilization or later would increase the prospects of maternal survival and greater production of progeny in future, more optimal years, perhaps at the expense of the present year-class. If inadequate energy reserves are available, some of the intraovarian embryos may subsist on nutrients from other resorbing embryos, as proposed by Boehlert et al. (1986) for *S. schlegeli*, and contribute to a smaller year-class. Year-class strength is highly variable in *Sebastes* populations on the west coast of North America and may be due, in part, to lower reproductive success of adult populations during years of lower food supply (Moser and Boehlert 1991).

Acknowledgments

We thank J. A. Whipple, M. B. Eldridge, and B. M. Jarvis for providing morphometric and mesenteric fat data and R. Powers and his crew for their cooperation and assistance in locating and capturing specimens.

References

BAKUN, A. 1975. Daily and weekly upwelling indices, west coast of North America, 1967–73. U.S. Dep. Commer. NOAA Tech. Rep. NMFS SSRF-693: 114 p.

BAKUN, A. D., D. R. MCLAIN, AND F. V. MAYO. 1974. The mean annual cycle of coastal upwelling off western North America as observed from surface measurements. Fish. Bull. U.S. 72: 843–844.

BERNAL, P. A., AND J. A. MCGOWAN. 1981. Advection and upwelling in the California Current, p. 381–399. *In* F. A. Richards [ed.] Coastal upwelling. American Geophysical Union, Washington, DC.

BLIGH, E. G., AND W. G. DYER. 1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. 37: 911–917.

BOEHLERT, G. W., M. KUSAKARI, M. SHIMIZU, AND J. YAMADA. 1986. Energetics during embryonic development in kurosoi, *Sebastes schlegeli* Hilgendorf. J. Exp. Mar. Biol. Ecol. 101: 239–256.

BOEHLERT, G. W., AND M. M. YOKLAVICH. 1984. Reproduction, embryonic energetics, and the maternal–fetal relationship in the viviparous genus *Sebastes* (Pisces: Scorpaenidae). Biol. Bull. 167: 354–370.

BOJE, R., AND M. TOMCZAK [ED.] 1978. Upwelling systems. Springer-Verlag, Berlin, Germany. 303 p.

BOLIN, R. L., AND D. P. ABBOTT. 1963 Studies on the marine climate and phytoplankton of the central coastal area of California, 1954–1960. CALCOFI Rep. 9: 23–45.

BOWERS, M. J. 1992. Annual reproductive cycle of oocytes and embryos of yellowtail rockfish, *Sebastes flavidus* (Family Scorpaenidae). Fish. Bull. U.S. (In press)

BRETT, J. R., AND T. D. D. GROVES. 1979. Physiological energetics, p. 280–352. *In* W. S. Hoar, D. J. Randall, and J. R. Brett [ed.] Fish physiology. Vol. VIII. Bioenergetics and growth. Academic Press, New York, NY.

BRINTON, E. 1976. Population biology of *Euphausia pacifica* off southern California. Fish. Bull. U.S. 74: 733–762.

CARLSON, H. R., AND L. BARR. 1977. Seasonal changes in spatial distribution and activity of two species of Pacific rockfishes, *Sebastes flavidus* and *S. ciliatus*, in Lynn Canal, southeastern Alaska. Mar. Fish. Rev. 39: 23–24.

CARLSON, H. R., AND R. E. HAIGHT. 1972. Evidence for a home site and homing of adult yellowtail rockfish, *Sebastes flavidus*. J. Fish. Res. Board Can. 29: 1011–1014.

CUSHING, D. 1978. Upper trophic levels in upwelling areas, p. 101–110. *In* R. Boje and M. Tomczak [ed.] Upwelling ecosystems. Springer-Verlag, Berlin, Germany.

DEVLAMING, V., D. BALTZ, S. ANDERSON, R. FITZGERALD, G. DELAHUNTY, AND M. BARKLEY. 1983. Aspects of embryo nutrition and excretion among viviparous embiotocid teleosts: potential endocrine involvements. Comp. Biochem. Physiol. 76A: 189–198.

DYGERT, P. H., AND D. R. GUNDERSON. 1991. Energy utilization by embryos during gestation in viviparous copper rockfish, *Sebastes caurinus*. Environ. Biol. Fishes. 30: 165–171.

ELDRIDGE, M. B., J. A. WHIPPLE, M. J. BOWERS, B. M. JARVIS, AND J. GOLD. 1991. Reproductive performance of yellowtail rockfish, *Sebastes flavidus*. Environ. Biol. Fishes 30: 91–102.

ELLIOT, J. A. K., N. R. BROMAGE, AND C. WHITEHEAD. 1979. Effects of estradiol-17β on serum calcium and vitellogenin levels in rainbow trout. J. Endocrinol. 83: 54P–55P.

GHITTINO, P. 1989. Nutrition and fish diseases, p. 682–713. *In* J. E. Halver [ed.] Fish nutrition. Academic Press, San Diego, CA.

GUILLEMOT, P. J., R. J. LARSON, AND W. H. LENARZ. 1985. Seasonal cycles of fat and gonad volume in five species of northern California rockfish (Scorpaenidae: *Sebastes*). Fish. Bull. U.S. 83: 299–311.

HEMING, T. A., AND R. K. BUDDINGTON. 1988. Yolk absorption in embryonic and larval fishes, p. 407–446. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol. XIA. The physiology of developing fish. Academic Press, San Diego, CA.

HOBSON, E. S., AND J. R. CHESS. 1988. Trophic relations of the blue rockfish, *Sebastes mystinus*, in a coastal upwelling system of northern California. Fish. Bull. U.S. 86:715–743.

HORI, S. H., T. KODAMA, AND K. TANAHASHI. 1979. Induction of vitellogenin synthesis in goldfish by massive doses of androgen. Gen. Comp. Endocrinol. 37: 306–320.

KJORSVIK, E., A. MANGOR-JENSEN, AND I. HOLMEFJORD. 1990. Egg quality in fishes. Adv. Mar. Biol. 26: 71–113.

KORSGAARD, B., AND I. PETERSEN. 1979. Vitellogenin, lipid and carbohydrate metabolism during vitellogenesis and pregnancy, and after hormonal injection in the blenny *Zoarces viviparus* (L.). Comp. Biochem. Physiol. 63B: 245–251.

LARSON, R. J. 1991. Seasonal cycles of reserves in relation to reproduction in *Sebastes*. Environ. Biol. Fishes 30: 57–70.

LENARZ, W. H., AND T. WYLLIE ECHEVERRIA. 1986. Comparison of visceral fat and gonadal volumes of yellowtail rockfish, *Sebastes flavidus*, during a normal year and a year of El Niño conditions. Fish. Bull. U.S. 84: 743–745.

LOVE, R. M. 1980. The chemical biology of fishes. Vol. 2. Advances 1968–1977. Academic Press, New York, NY. 943 p.

LOWRY, O. H., N. J. ROSEBROUGH, A. L. FARR, AND R. J. RANDALL. 1951. Protein measurement with the folin phenol reagent. J. Biol. Chem. 193: 265–275.

LUQUET, P., AND T. WATANABE. 1986. Interaction "nutrition–reproduction" in fish. Fish Physiol. Biochem. 2: 121–129.

MOMMSEN, T. P., AND P. J. WALSH. 1988. Vitellogenesis and oocyte assembly, p. 347–406. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol. XIA. The physiology of developing fish. Academic Press, San Diego, CA.

MOSER, H. G., AND G. W. BOEHLERT. 1991. Ecology of pelagic larvae and juveniles of the genus *Sebastes*. Environ. Biol. Fishes. 30: 203–224.

NG, T. B., AND D. R. IDLER. 1983. Yolk formation and differentiation in teleost fishes, p. 373–404. *In* W. S. Hoar, D. J. Randall, and E. M. Donaldson [ed.] Fish physiology. Vol. IXA. Reproduction. Academic Press, New York, NY.

OGURI, M., AND N. TAKADA. 1967. Serum calcium and magnesium levels of goldfish, with special reference to the gonadal maturation. Bull. Jpn. Soc. Sci. Fish. 33: 161–166.

PEKKARINEN, M., AND R. KRISTOFFERSSON. 1975. Seasonal changes in concentrations of plasma lipids in the brackish-water eelpout, *Zoarces viviparus* (L.). Ann. Zool. Fenn. 12: 260–262.

SARGENT, J. R. 1976. The structure, metabolism and function of lipids in marine organisms, p. 149–212. *IN* D. C. Malins [ed.] Biochemical and biophysical perspectives in marine biology. Vol. 3. Academic Press, London.

SARGENT, J., R. J. HENDERSON, AND D. R. TOCHER. 1989. The lipids, p. 154–218. *In* J. E. Halver [ed.] Fish nutrition. 2nd ed. Academic Press, San Diego, CA.

TAKEMURA, A., A. HARA, AND K. TAKANO. 1991. Immunochemical identification and partial characterization of female-specific serum proteins in white-edged rockfish, *Sebastes taczanowskii*. Environ. Biol. Fishes 30: 49–56.

THIBAULT, R. E., AND R. J. SCHULTZ. 1978. Reproductive adaptations among viviparous fishes (Cyprinodontiformes: Poeciliidae). Evolution (Laurence, KA) 32: 320–333.

TINSLEY, D. 1985. A comparison of plasma levels of phosphoprotein, total protein and calcium as indirect indices of exogenous vitellogenesis in the crucian carp, *Carassius carassius* (L.). Comp. Biochem. Physiol. 80B: 913–916.

WATANABE, T. 1985. Importance of the study of broodstock nutrition for further development of aquaculture, p. 395–414. *In* C. B. Cowey, A. M. Mackie, and J. G. Bell [ed.] Nutrition and feeding in fish. Academic Press, London.

WOURMS, J. P. 1981. Viviparity: the maternal–fetal relationship in fishes. Am. Zool. 21: 473–515.

1991. Reproduction and development of *Sebastes* in the context of the evolution of piscine viviparity. Environ. Biol. Fishes 30: 111–126.

WOURMS, J. P., B. D. GROVE, AND J. LOMBARDI. 1988. The maternal–embryonic relationship in viviparous fishes, p. 1–134. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol. XIB. The physiology of developing fish. Academic Press, San Diego, CA.

YARON, Z., A. TERKATIN-SHIMONY, Y. SHAHAM, AND H. SALZER. 1977. Occurrence and biological activity of estradiol-17β in the intact and ovariectomized *Tilapia aurea* (Cichlidae, Teleostei). Gen. Comp. Endocrinol. 33: 45–52.

YOKLAVICH, M. M., AND G. W. BOEHLERT. 1991. Uptake and utilization of ^{14}C-glycine by embryos of *Sebastes melanops*. Environ. Biol. Fishes 30: 147–153.