Nutritional dynamics during embryonic development in the viviparous genus *Sebastes* and their application to the assessment of reproductive success

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Abstract.—Concentrations of lipids and protein were measured in embryos during gestation in two species of viviparous rockfishes off the central California coast. Total lipids and protein declined linearly through embryonic maturation in semipelagic yellowtail rockfish, *Sebastes flavidus*, and pelagic shortbelly rockfish, *Sebastes jordani*. Energetically, lipids were the predominant source of energy for embryonic development in both species, but lipid and protein catabolism was significantly greater for yellowtail rockfish. Total lipids, protein, and lipid class composition were measured during embryonic maturation in three populations of shortbelly rockfish, located at Ascension, Pioneer, and Bodega submarine canyons, to determine intraspecific variability of nutritional dynamics. Triacylglycerols and polar lipids (mostly phospholipids), the predominant lipid classes in all maturation stages, were depleted through embryonic development. Steryl or wax esters and cholesterol also declined, but were in much lower concentrations. The goodness-of-fit of linear regressions for protein, total lipid, and lipid classes by stage of embryonic maturation allowed estimations of their concentrations at birth, thus providing a measure of nutritional condition, or qualitative reproductive success. Analyses determined that there were significant differences in metabolism and estimated concentrations at birth of nutrients between the two species and among the shortbelly rockfish populations, indicating differential potential for survival during early planktonic life stages until favorable feeding conditions occur. Results suggest that the contribution of individual populations to the diversity of metapopulations or year classes may be influenced by the nutritional condition of larvae at birth.

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Variability of annual recruitment to marine fish stocks has been attributed to several factors, including the quantity and quality of progeny produced and the influences of environmental conditions on subsequent survival. Although either factor could be effective alone, at times they may interact. Poor reproductive success, manifested by low fecundity or unhealthy progeny, or both, occurring at times of unfavorable environmental conditions, may lead to particularly weak year classes. There is evidence that factors operating at or near the time of spawning affect year-class strength in rockfishes (genus *Sebastes*) along the west coast of North America. Year-class failures of two species of rockfish were found at the extremes of the physical environmental spectrum off the central coast of California during years of very low or very high upwelling (Ralston and Howard, 1995). The data from that investigation suggested that year-class strength of yellowtail rockfish (*Sebastes flavidus)* and blue rockfish (*Sebastes mystinus*) was related to environmental conditions and was established before the pelagic juvenile stage. Further, annual variation in fecundity does not appear to be great enough to account for the variation seen in fishery recruitment of yellowtail rockfish (Eldridge and Jarvis, 1995) or other species (Shepherd and Cushing, 1980). Thus, maternal processes contributing to the health or fitness of embryos or early larvae, in addition to the more often assessed environmental factors, may significantly influence survival and year-class strength.

The assessment of reproductive success includes the determination of both the quantity and quality of progeny because year-class strength may be influenced by the health of newborns as well as by the number produced. Although fecundity is often used as a measure of reproductive success and has been related to biological and environmental factors (Blaxter, 1969), less attention has been given to the assessment of the qualitative aspects of reproductive success. This is due, in part, to the difficulty of determining which variables or processes are valid measures of egg, embryo, or larval health. Various measures have been proposed, such as egg size (Blaxter and Hempel, 1963), histological criteria (Theilacker, 1978), and biochemical analyses, including nucleic acids (Buckley, 1984), enzyme activity (Clarke et al., 1992), and biochemical composition (reviewed by Ferron and Leggett, 1994). All have merits; however, factors such as the degree of relation-

ship to growth or survival potential, ease or cost of analysis (or both), operational feasibility, or the ability to assess adequate numbers of replicates for statistical validity often diminish their utility in routine assessments of reproductive success. Consideration of when, during egg and embryonic development, valid estimates can be made is also critical to accurate assessment of success. Ideally, evaluation at hatching or birth would provide the most accurate determination of health and survival potential, but this event is of very short duration, and obtaining enough individuals to characterize a population or species is difficult.

The nutritional status, or energy content, of embryos and larvae has a clear relationship to growth and survival potential because the amount of metabolically available energy establishes the duration of survival in the environment until adequate food becomes available. Starvation during the early stages of development has been considered a major source of mortality or reduced fitness and may contribute to fluctuations in year-class strength (May, 1974; Shepherd and Cushing, 1980; Rissik and Suthers, 1996).

Low and unstable abundance of prey typifies the environment off central California during winter and early spring (Ainley et al., 1993), the period when many species of viviparous rockfish give birth (Wyllie Echeverria, 1987). Pelagic larvae rely on endogenous nutritional reserves to supplement sparse forage until the biologically productive annual upwelling season begins, usually in late March or April (Bakun, 1975).

This study describes protein and lipid metabolism during embryonic development in two species of the viviparous genus *Sebastes*. A procedure is presented to estimate the lipid and protein composition at parturition, or birth, which provides a measure of nutritional status and thus may be related to the probability for survival at the earliest free-living stage. Nutritional status at birth is presented for yellowtail rockfish and three populations of shortbelly rockfish (*Sebastes jordani*), thereby providing comparisons between congeners occupying different ecological niches and among populations separated spatially. These data are the first documentation of lipid class composition in eggs, embryos, and larvae of a viviparous marine teleost.

Materials and methods

Female *S. flavidus* and *S. jordani* were obtained from January to March, the period of reproductive development spanning late vitellogenesis to parturition, at locations off the central California coast. Yellowtail rockfish were captured by hook-and-line at Cordell Bank (38°01'N 123°25'W), a marine bank 37 km west of Pt. Reyes, at depths ranging from 50 to 150 m. Shortbelly rockfish were collected by trawl at 150 to 200 m depth in the proximity of three submarine canyons: Bodega Canyon (ca. 38°13'N 123°22'W), Pioneer Canyon (ca. 37°24'N 122°52'W), and Ascension Canyon (ca. 37°01'N 122°25'W). Fish were held on ice for up to 12 h until examination. Morphometrics (e.g. standard length; body and liver weight) were recorded and ovaries excised, weighed, and stored at –70°C. The stage of oocyte or embryonic development was identified by microscopy according to the classification scheme of Yamada and Kusakari (1991) for *Sebastes schlegeli* (Table 1).

Table 1

Embryo maturation stages (EMS) in *Sebastes flavidus* and *Sebastes jordani*.

EMS	Description
1	Late vitellogenic or migratory nucleus oocyte
2	Formation of germ disc
3	2-celled
4	4-celled
5	8-celled
6	16-celled
7	32-celled
8	64-celled
9	Morula
10	Early blastula
11	Late blastula
12	Beginning of epiboly
13	Early gastrula
14	Late gastrula
15	Embryonic shield
16	Head fold
17	Optic vesicles
18	Somite formation begins
19	Finfold
20	Optic cups
21	Auditory placodes
22	Lens forms
23	Otoliths
24	Pectoral fins
25	Retinal pigmentation
26	Heart pumping
27	Lens transparent
28	Mouth and anus open
29	Peritoneum pigmented
30	Yolk reduction
31	Prehatching
32	Hatching
33	Hatched, preborn larva

Lipids were extracted from oocytes and embryos by the method of Bligh and Dyer (1959). Total lipids were quantified by using thin layer chromatography with flame ionization detection (TLC-FID) by an Iatroscan TH-10 Mark III (MacFarlane et al., 1990; MacFarlane et al., 1993). Lipids were separated into steryl or wax ester, triacylglycerol, nonesterified fatty acid, cholesterol, and polar lipid classes on Chromarods S-III in a solvent bath of hexane:ethyl ether:formic acid at a ratio of 246:54:0.09. Quantification of separated peaks by TLC-FID was accomplished by comparing peak areas to external standard curves for each lipid class. Cholesterol oleate, triolein, oleic acid, cholesterol, and phosphatidylcholine, purchased from Sigma Chemical Co. (St. Louis, MO), were used as standards. Total protein was estimated with the Lowry method by using a bovine serum albumin standard (Lowry et al., 1951).

Analysis of variance (ANOVA) was employed to assess variation in lipids and protein by embryo maturation stage (EMS), rockfish species, or population of shortbelly rockfish. Estimated concentrations of nutrients at parturition were obtained by linear regression. All analyses were performed with SAS statistical software (SAS Institute, Inc., 1989).

Lipids and protein data are presented as concentrations, mg/g wet weight. Changes in concentration during embryonic development represent absolute changes in the quantities of lipids and protein because ovarian mass remained statistically constant through gestation for both species. ANOVA results of the relationship between GSI [gonadosomatic index = (ovary weight/body weight) × 100] and EMS were $P = 0.242$ (F=1.396, df=59) for yellowtail rockfish and $P = 0.622$ (F=0.243, df=202) for shortbelly rockfish. During gestation, changes in organic mass of ovaries were compensated by changes in water concentration. Regression equations for ovarian water concentration by EMS were

Yellowtail rockfish ovarian water (mg/g)
= 608.5 + 8.292(*EMS*),
[df=59, F=203.7, P<0.0001, r^2=0.778]

Shortbelly rockfish ovarian water (mg/g)
= 655.2 + 6.860(*EMS*).
[df=172, F=782.6, P<0.0001, r^2=0.821]

Results and discussion

There was a progressive decline in total lipid and protein during embryogenesis in yellowtail rockfish, *Sebastes flavidus* (Fig. 1). The concentration of total lipid decreased from a mean of 149.8 mg/g in unfertilized, late vitellogenic oocytes (EMS 1) to an estimated concentration of 48.4 mg/g for fully formed, hatched larvae (EMS 33) at parturition. Although no pregnant females were caught with embryos at EMS 33, the goodness-of-fit (r^2 value) of the linear regression of lipid concentration on embryo maturation stage (Table 2) suggested that calculation of total lipid at parturition was valid (Table 3). Similarly, protein declined from 225.9 mg/g during EMS 1 to 52.1 mg/g at EMS 33 (Fig. 1; Table 3). These data indicate that yellowtail rockfish embryogenesis consumed more protein than lipid for nutritional requirements because protein concentration declined 77% during development whereas total lipids decreased 68%. From an energetic perspective, however, lipid was predominantly utilized. Using values for physiologically available energy density of 39.6 kJ/g of lipid and 20.1 kJ/g of protein (Brett and Groves, 1979), we found that the 101.4 mg lipid/g embryo depleted during embryogenesis yielded 4.02 kJ of energy, whereas the 173.8 mg protein/g embryo yielded 3.49 kJ. The predominance of lipid as an energy source for viviparous reproductive development in yellowtail rockfish has been demonstrated previously (MacFarlane et al., 1993; Norton and MacFarlane, 1995). The consumption of yolk proteins, particularly those with high molecular weights > 70 kDa, during embryonic maturation of yellowtail rock-

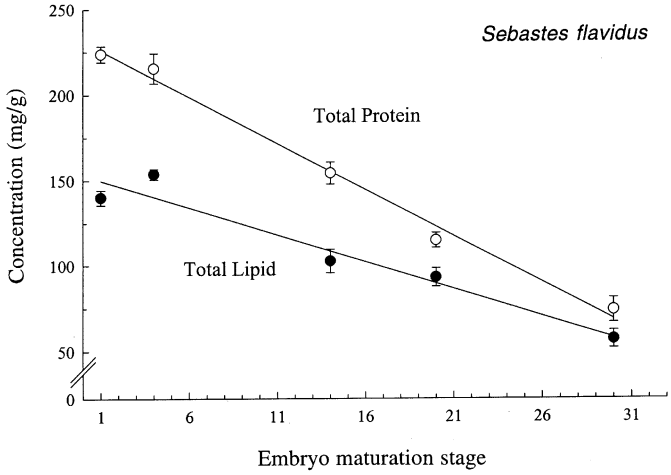

Figure 1

Total lipid and protein concentrations in oocytes and embryos by embryo maturation stage (EMS) in female yellowtail rockfish, *Sebastes flavidus*, from prefertilized oocytes (EMS 1) through the yolk-reduction stage (EMS 30). Data presented as means ± SE. Mean number (range) of females assayed at each EMS was 12 (9–17). See Table 1 for descriptions of EMS.

Table 2

Linear regression parameter estimates for mean protein and lipid concentrations in rockfish embryos in relation to embryo maturation stage (EMS). Data are for yellowtail rockfish (*Sebastes flavidus*) and three populations of shortbelly rockfish (*Sebastes jordani*) from Ascension, Pioneer, and Bodega Canyons. ND = below detection (<0.3 µg); NS = $P > 0.05$. TAG = triacylglycerols; NEFA = nonesterified fatty acids; CH = cholesterol; PL = polar lipids.

Variable	r^2	Intercept ±SE	P	Slope ±SE	P
S. flavidus (*n*=60)					
Total lipid	0.946	153.0 ± 7.6	<0.001	–3.17 ± 0.44	<0.005
Total protein	0.993	231.3 ± 4.6	<0.0001	–5.43 ± 0.27	<0.001
S. jordani					
All canyons (*n*=212)					
Total lipid	0.884	89.4 ± 3.8	<0.0001	–1.86 ± 0.17	<0.0001
Total protein	0.895	167.8 ± 6.0	<0.0001	–2.85 ± 0.27	<0.0001
Esters	0.695	7.4 ± 0.5	<0.0001	–0.17 ± 0.02	<0.0001
TAG	0.917	43.0 ± 1.7	<0.0001	–0.98 ± 0.08	<0.0001
NEFA	0.141	–0.1± 0.1	NS	0.01 ± 0.00	NS
CH	0.639	3.8 ± 0.2	<0.0001	–0.05 ± 0.01	<0.0001
PL	0.889	35.4 ± 1.4	<0.0001	–0.66 ± 0.06	<0.0001
Bodega Canyon (*n*=49)					
Total lipid	0.699	81.0 ± 6.9	<0.0001	–1.54 ± 0.32	<0.001
Total protein	0.676	174.1 ± 14.9	<0.0001	–3.17 ± 0.69	<0.001
Esters	0.750	7.3 ± 0.6	<0.0001	–0.16 ± 0.03	<0.0001
TAG	0.704	37.4 ± 3.5	<0.0001	–0.80 ± 0.16	<0.0001
NEFA	ND	ND	ND	ND	ND
CH	0.503	3.4 ± 0.3	<0.0001	–0.04 ± 0.01	<0.01
PL	0.665	32.8 ± 2.6	<0.0001	–0.54 ± 0.12	<0.001
Pioneer Canyon (*n*=102)					
Total lipid	0.844	88.3 ± 4.2	<0.0001	–1.97 ± 0.18	<0.0001
Total protein	0.714	177.0 ±10.8	<0.0001	–3.29 ± 0.46	<0.0001
Esters	0.766	7.4 ± 0.5	<0.0001	–0.18 ± 0.02	<0.0001
TAG	0.835	44.6 ± 2.5	<0.0001	–1.12 ± 0.11	<0.0001
NEFA	0.284	–0.2 ± 0.1	NS	0.01 ± 0.00	<0.01
CH	0.719	3.9 ± 0.2	<0.0001	–0.06 ± 0.01	<0.001
PL	0.838	32.7 ± 1.4	<0.0001	–0.62 ± 0.06	<0.0001
Ascension Canyon (*n*=61)					
Total lipid	0.419	90.4 ± 8.0	<0.0001	–1.36 ± 0.41	<0.005
Total protein	0.451	165.1 ±11.8	<0.0001	–1.93 ± 0.59	<0.005
Esters	0.227	7.2 ± 1.0	<0.0001	–0.11 ± 0.05	<0.05
TAG	0.348	42.4 ± 4.6	<0.0001	–0.68 ± 0.24	<0.01
NEFA	0.072	0.1 ± 0.1	NS	0.00 ± 0.00	NS
CH	0.257	3.8 ± 0.3	<0.0001	–0.03 ± 0.01	<0.05
PL	0.520	36.9 ± 2.6	<0.0001	–0.55 ± 0.14	<0.001

fish has also been reported (MacFarlane and Bowers, 1995). Calculations of lipid and protein utilization for embryogenesis in yellowtail rockfish represent net consumption and conservative estimates because at least some maternal contributions to embryo development occur during gestation (MacFarlane and Bowers, 1995). Radio-labelled phosphatidylcholine injected into the circulatory system of pregnant females resulted in radioactivity in embryos, indicating matrotrophy for this phospholipid. The extent to which matrotrophy exists for other lipids and protein is unknown.

As in yellowtail rockfish, total lipid and protein concentrations declined linearly according to stage of development in embryos of shortbelly rockfish, *Sebastes jordani* (Fig. 2).

Embryonic development consumed 55% of the protein and 68% of the total lipid present at fertilization. Thus, both species of rockfish metabolized the same proportion of total lipids, whereas protein was conserved in shortbelly rockfish in relation to yellowtail rockfish embryogenesis. It should be noted, however, that yellowtail rockfish had significantly greater protein resources for embryogenesis at fer-

Table 3

Estimated concentrations of lipids and protein in *Sebastes flavidus* and *Sebastes jordani* larvae at birth. *S. jordani* data are for all populations combined and for each of three populations at Bodega, Pioneer, and Ascension submarine canyons. Values presented as mean ± SD in mg/g wet weight. TAG = triacylglycerols; NEFA = nonesterified fatty acids; CH = cholesterol; PL = polar lipids.

		Sebastes jordani			
Variable	*Sebastes flavidus*	All	Bodega	Pioneer	Ascension
Protein	52.1 ± 5.2	73.6 ± 6.4[1]	69.3 ±10.2	68.5 ± 6.3	101.3 ± 9.1[4]
Total lipid	48.4 ± 8.5	28.1 ± 3.7[2]	29.4 ± 4.7[3]	23.3 ± 2.7	45.7 ± 6.4[4]
Esters	—	1.9 ± 0.4	1.9 ± 0.4[3]	1.4 ± 0.3	3.8 ± 0.7[4]
TAG	—	10.5 ± 2.0	11.0 ± 2.4[3]	7.6 ± 1.6	20.1 ± 3.7[4]
NEFA	—	0.1 ± 0.1	—	0.2 ± 0.0	0.0 ± 0.1
CH	—	2.1 ± 0.1	2.0 ± 0.2	2.0 ± 0.1	2.9 ± 0.2[4]
PL	—	13.6 ± 1.4	14.5 ± 1.8[3]	12.1 ± 0.9	18.9 ± 2.1[4]

[1] Significantly greater than that for *S. flavidus* (P<0.0001).
[2] Significantly less than that for *S. flavidus* (P<0.01).
[3] Greater than that for *S. jordani* at Pioneer Canyon (P<0.001).
[4] Greater than that for *S. jordani* at Bodega and Pioneer Canyons (P<0.0001).

tilization than did shortbelly rockfish, 225.9 mg/g compared with 165.0 mg/g (Table 2). At birth, the estimated concentration of protein in shortbellly rockfish larvae was significantly greater than that in newborn yellowtail rockfish (P<0.0001); however, the total lipid concentration was less (P<0.01) (Table 3). That shortbelly rockfish have less lipid at parturition suggests they have a greater urgency for feeding than yellowtail rockfish soon after birth, or else catabolism of tissue protein would be required for maintenance, reducing the probability of survival.

Energetically, lipid was the predominant fuel for embryo development for shortbelly rockfish, as for yellowtail rockfish. The 59.4 mg lipid/g embryo metabolized between fertilization and parturition represented 2.35 kJ/g, and the 91.3 mg protein/g embryo represented 1.84 kJ/g.

Total energy consumed for embryogenesis was significantly greater in yellowtail rockfish than in shortbelly rockfish (P<0.0001). The production of a gram of fully formed, hatched, preborn larval yellowtail rockfish required the expenditure of 7.51 kJ of energy. For shortbelly rockfish, the equivalent energetic cost was 4.19 kJ/g of EMS-33 larvae. Because the average weight of ovaries at late stages of gestation was 204.9 ± 16.9 g (n=17) in yellowtail rockfish but only 43.4 ± 2.8 g (n=21) in shortbelly rockfish, requirements for maternally supplied nutrients were much greater for yellowtail rockfish. For comparison, the mean standard length and total weight for female yellowtail rockfish was 36 ± 0.5 cm and 1304 ± 55 g versus 21 ± 0.2 cm and 150 ± 4 g for the shortbelly rockfish assessed in this study.

The significant difference in energy required to produce a gram of larvae in the hatched, preborn stage in the two rockfish species may relate to differences

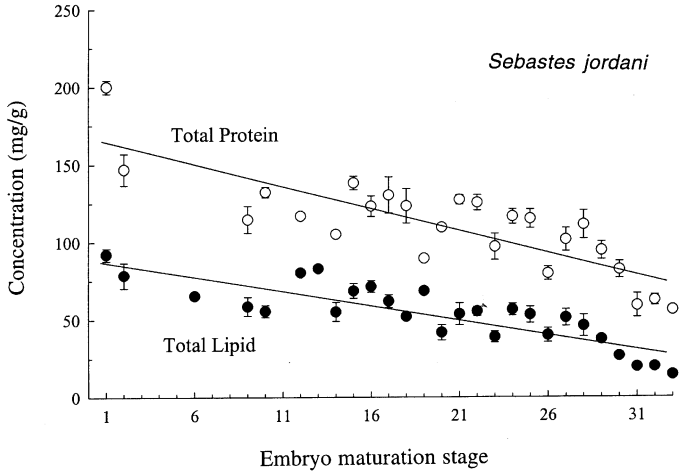

Figure 2

Total lipid and protein concentrations in oocytes and embryos in female shortbelly rockfish, *Sebastes jordani*, from prefertilized oocytes (EMS 1) through the hatched preborn larval stage (EMS 33). Data (means ± SE) from shortbelly rockfish from populations at all three submarine canyons are shown. Mean number (range) of females assayed at each EMS was 8 (1–21). See Table 1 for description of EMS.

in reproductive strategy. Yellowtail rockfish produce about 700,000 eggs/female (Eldridge and Jarvis, 1995) whereas shortbelly rockfish fecundity is about 16,500 eggs/female (Eldridge[1]). Also, yellowtail rockfish eggs and hatched larvae are considerably smaller than those of shortbelly rockfish (Matarese et al., 1989; Eldridge[1]). Greater energy consumption for production of yellowtail rockfish larvae may be a consequence of greater energy required for the synthesis of more larvae, their organelles, and subsequent cellular differentiation.

The relative importance of lipids and protein as sources of nutrition during embryonic and larval development in oviparous fishes has been presented in other reports. In the marine teleost, *Sparus aurata*, free amino acids were the main source of energy during the relatively short embryonic period (ca. 51–58 h postfertilization) whereas lipids and protein did not supply substantial energy until after hatching (Rønnestad et al., 1994). Winter flounder (*Pseudopleuronectes americanus*), by contrast, used small amounts of carbohydrate first, then protein until hatching (Cetta and Capuzzo, 1982). Lipid depletion did not occur until after hatching. Protein concentrations were stable, whereas lipids were catabolized in eggs and newly hatched larvae of Senegal sole (*Solea senegalensis*) (Mourente and Vasquez, 1996). According to these researchers, this pattern of lipid metabolism is characteristic of temperate marine fishes with eggs containing oil globules, high lipid content, and short developmental periods. The rockfish species in the present study are temperate marine teleosts that contain oil globules and high lipid levels. However, they are viviparous and have relatively lengthy development, yet catabolize both protein and lipids for energy-consuming processes, thus emphasizing the great variability and lack of generality in the sources and patterns of nutrient use for embryonic and larval development in fishes.

Total lipid concentrations can be considered a measure of physiological condition of larvae (Ferron and Leggett, 1994), and thus an indicator of potential reproductive success, but not all types, or classes, of lipids are equivalent with respect to metabolic availability or *in vivo* energy yield. Therefore, fractionation of total lipids into classes representative of energy-yielding and structural functions provides greater knowledge of the amount of energy available to sustain growth and survival once the larvae are released into the environment.

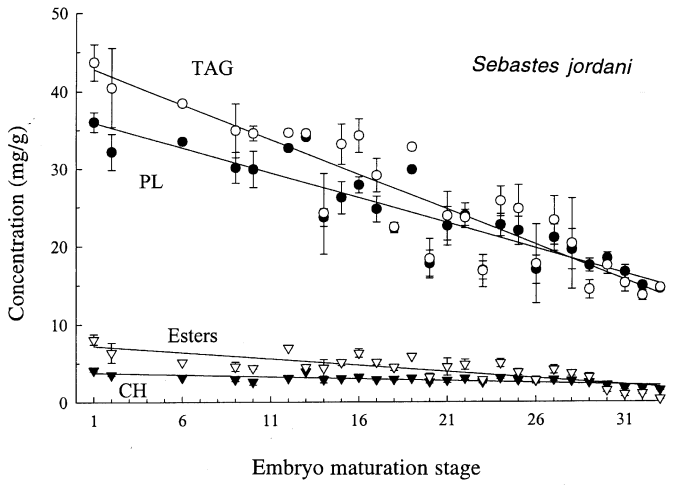

Figure 3

Changes in lipid classes during embryonic maturation in shortbelly rockfish, *Sebastes jordani*. Data (means ± SE) are from populations at all three submarine canyons. Number of females assayed for each EMS is same as in Figure 2. See Table 1 for description of EMS.

Total lipid from shortbelly rockfish embryos was fractionated into five lipid classes: steryl/wax esters (esters), triacylglycerols (TAGs), nonesterified fatty acids (NEFAs), cholesterol (CH), and polar lipids (PLs). The separations were not performed on yellowtail rockfish embryos owing to loss of samples before chromatographic analysis.

Triacylglycerols (TAGs) and PLs were the predominant lipids in all stages of embryonic maturation and showed the greatest declines during development (Fig. 3). Cholesterol (CH) and esters were found in much lower concentrations and declined slightly, but significantly, during embryogenesis (Fig. 3; Table 2). Nonesterified fatty acids (NEFAs) were found in very low concentrations and did not vary significantly by stage of maturation (Table 2).

The depletion of TAG and PL from fertilization to birth indicates the oxidation of these lipid classes for energy-requiring embryogenic processes. The use of TAG for energy storage and fuel during embryonic and larval development is well known in fishes (Boulekbache, 1981; Vetter et al., 1983; Tocher and Sargent, 1984; Fraser, 1989). Polar lipids, consisting mainly of phospholipids, such as phosphatidylcholine and phosphatidylethanolamine, although used as fundamental structural units of all biological membranes, have been shown to be a significant source of energy also for embryonic development in

[1] Eldrige. M. B. 1997. Tiburon Laboratory, Southwest Fisheries Science Center, 3150 Paradise Drive, Tiburon, CA 94720. Unpubl. data.

other fishes (Sargent, 1995). The relative contribution of TAG and PL to the energy demands of embryonic development varies by species. Whereas in cod (*Gadus morhua*) (Fraser et al., 1988; Finn et al., 1995) and Atlantic herring (*Clupea harengus*) (Tocher et al., 1985) PL was the major source of energy, in Senegal sole (Mourente and Vasquez, 1996) and gilthead sea bream (Rønnestad et al., 1994), TAG was primarily catabolized. In Atlantic salmon (*Salmo salar*), the PL phosphatidylcholine and TAG were used equally to meet energy requirements (Cowey et al., 1985).

The changes in lipid composition during embryogenesis in yellowtail and shortbelly rockfishes described here represent the first data of this kind for rockfishes or any viviparous marine teleost. The use of PL as a primary source of energy may be consistent with results from previous research revealing that phosphatidylcholine was supplied to developing embryos of yellowtail rockfish from maternal sources both before and during development (MacFarlane and Bowers, 1995). Perhaps the facility to supply phospholipids matrotrophically enhances their use as energy-yielding substrates. High concentrations of TAG in prefertilized eggs (EMS 1) and its importance as an energy source are not unexpected because both species feed heavily on euphausiids (Brodeur and Pearcy, 1984), which contain large amounts of TAG (Fricke and Oehlenschläger, 1982).

Lipid class composition has been promoted as a measure of nutritional condition for larvae of a variety of oviparous marine fish, including Atlantic cod (Lochmann et al., 1995), Atlantic herring (Fraser et al., 1987), and anchovy *Engraulis mordax* (Håkanson, 1989). Depending upon the species, the quantities of TAG or PL, or both, related to the probability for survival. Lochmann et al. (1995) suggested that survival was related to a condition index based on a discriminant function of TAG, PL, and defatted dry weight in laboratory and field-collected cod larvae. Triacylglycerol (TAG) was regarded as the critical variable in condition for herring (Fraser et al., 1987) and anchovies (Håkanson, 1989).

It is reasonable to apply this concept to the assessment of larvae from viviparous species as well. The nutritional status of larvae just prior to parturition would represent their condition at the start of life in the marine environment and would be related to their ability to survive until adequate feeding occurs. The presence of an oil globule in rockfish larvae during the early days after birth argues for the importance of lipids for energy. For rockfish, the amounts of TAG at birth should be related to survival potential because this lipid class is the predominant component in oil globules of most fishes (Henderson and Tocher, 1987; Heming and Buddington, 1988) and has consistently been shown to correlate with physiological condition (Fraser, 1989).

We analyzed embryos in pregnant female shortbelly rockfish from populations living in the proximity of three submarine canyons off the central California coast. The purpose was to determine the variability in metabolism of lipid classes for specific populations and the estimated concentrations of each lipid class at birth, thus providing a measure of nutritional status and relative probability for survival. When lipid class concentrations were assessed in embryos from the separate populations, there were differences in the amounts and rates of depletion during intraovarian development (Table 2). Two-way ANOVA determined there were significant differences among populations at the three canyons, despite being located within about a one-degree latitude span off the central California coast. All lipid classes, except NEFA, varied significantly by EMS ($P<0.0001$), population ($P<0.0001$), and the interaction of population and EMS ($P\leq0.05$).

The changes in concentrations of lipid classes were linearly related to EMS for embryos from each population (Table 2). Parameter estimates from linear regressions of each lipid class by stage of embryonic maturation revealed that rates of metabolism differed among the populations (Table 2). The greatest catabolic rates of TAG and PL were found in embryos from the Pioneer Canyon population. Rates of protein depletion were also greater in embryos from Pioneer Canyon and lowest in those from Ascension Canyon.

In conjunction with initial concentrations of protein and lipid classes at fertilization, the rates of nutrient metabolism can be used to estimate concentrations at parturition (EMS 33). The greater rates of nutrient utilization for embryos in females from the population at Pioneer Canyon resulted in the lowest levels of nutritional stores at birth of the three populations evaluated (Table 3). Conversely, newborn larvae from females at Ascension Canyon contained the greatest concentrations of lipids and protein, suggesting that they have a greater likelihood of survival until suitable feeding conditions exist.

The differential status of nutrient levels in larvae at birth may contribute to differences in survival rate among the populations and, thus, influence the diversity of the species year class. Parturition occurs during the winter when oceanic conditions prevail along the California coast. This is the period of lowest primary and secondary productivity annually (Ainley, 1990). Until marine conditions become favorable for biological productivity, usually in April

when seasonal upwelling and increasing solar radiation stimulate phytoplankton growth, larvae must subsist on the combined resources of endogenous reserves and limited prey abundance. During the days following birth, the quantity of lipid reserves may influence the length of time larvae can persist until adequate forage is available to sustain survival and growth. Starvation has been considered a factor in recruitment variability in rockfish species (Moser and Boehlert, 1991). Larvae from populations with lesser energy reserves may experience greater mortality, thereby reducing their representation in the year class for the species along the entire coast.

The use of lipid and protein data as an indicator of nutritional condition at birth for rockfish in the genus *Sebastes* marks an extension of such data to viviparous fishes for the first time. Previously, lipid class analyses have been employed for condition assessments only in oviparous fish embryos (Tocher et al., 1985; Fraser et al., 1988) and larvae (Fraser, 1989; Håkanson, 1989; Lochmann et al., 1995).

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