Abstract.—Nutritional dynamics of yellowtail rockfish, *Sebastes flavidus*, were analyzed from the perspective of temporal changes in tissue composition of liver, muscle, mesentery, and gonad to determine aspects specific to female reproduction. Monthly tissue composition data over an annual reproductive cycle indicated that females accumulated greater somatic tissue energy reserves than did males during the summer and fall months. Maternal lipid and protein reserves were depleted in a reciprocal relation with ovarian growth during the winter. The greatest declines of lipid and protein occurred in mesenteries and muscle, respectively. Females lost approximately 40% more somatic tissue than males during the time interval from ovarian development to parturition. Lipid was the primary energy source, contributing 74% of the energy lost from somatic tissues for female-specific reproductive purposes. Two-thirds of lipid depleted from maternal soma was for adult metabolic maintenance. Of the other one-third, 43% was gained in ovary tissue during development, leaving 57% for reproductive metabolic costs. Protein increased 220% in ovaries relative to female-specific somatic protein loss, indicating de novo ovarian synthesis. This study is the first report of comprehensive tissue composition dynamics and allocation to reproduction in a viviparous marine teleost. The analytical design used demonstrated the significance of each tissue component and the temporal pattern of allocation to reproductive development.

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Nutritional dynamics of reproduction in viviparous yellowtail rockfish, *Sebastes flavidus*

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Maternal nutritional status and the allocation of nutrients into developing young are important factors contributing to reproductive success in fish. Previous investigations have shown that nutritional status can influence fecundity and the vitality of offspring (Anokhina, 1959; Rijnsdorp, 1990; DeMartini, 1991; Kjesbu et al., 1991). By determining the temporal patterns of somatic and gonadal tissue components involved in fish nutritional dynamics, we can improve our understanding of energy and nutritional needs for successful reproduction.

Several studies of nutrient dynamics in fish have used chemical composition analyses of primary body constituents, including lipid, protein, glycogen, water, and ash components, to assess physiological status and the level of available nutritional reserves (Love, 1970; Caulton and Bursell, 1977; Cui and Wootton, 1988). These reserves have been shown to vary by species and interannually in location, quantity, and the sequence of allocation into reproductive development (Sargent, 1976; Medford and Mackay, 1978; Henderson et al., 1984; MacFarlane et al., 1993). Generally, the principal source of nutritional energy reserve in fish is lipid (Sargent, 1976; Sargent et al., 1989). Protein, primarily used in structural development and enzyme synthesis, may also be an additional source of energy when lipid reserves are depleted (Mommsen et al., 1980; Walton and Cowey, 1982).

Many temperate fish species follow a similar seasonal pattern of nutrient dynamics, where energy reserves are accumulated in the summer and depleted during the winter reproductive period (Shul'man, 1974). The transfer of nutrients from somatic reserves into ovarian growth has been indicated by the reciprocal relationship between the depletion of somatic stores and ovarian development (MacKinnon, 1972; Dawson and Grimm, 1980; Dygert, 1990). While this general pattern has been documented in oviparous species, little data on nutritional dynamics are available for viviparous teleosts (Wourms et al., 1988). For the marine viviparous genus *Sebastes*, only changes in tissue lipids have been measured in relation to reproduction (Guillemot et al., 1985; Larson, 1991; MacFarlane et al., 1993).

The yellowtail rockfish, *Sebastes flavidus*, range from San Diego, California, to Kodiak Island, Alaska (Eschmeyer et al., 1983), and are important both commercially and recreationally (Reilly et al.[1]; Pacific

[1] Reilly, P. N., D. Wilson-Vandenberg, D. Watters, J. E. Hardwick, and D. Short. 1993. On board sampling of the rockfish and lingcod commercial passenger fishing vessel industry in northern and central California, May 1987–December 1991. Calif. Dept. Fish Game Admin. Report. 93-4, 242 p.

Fisheries Management Council[2]). Distinctive characteristics of the reproductive strategy of yellowtail rockfish (e.g. small testes, copulation months before fertilization, quiescent testes during period of ovarian development [Eldridge et al., 1991], and nonmigratory behavior [Pearcy, 1992]) allow male nutrient dynamics to serve as adult metabolic controls. Consequently, nutritional energy expenditures specific to female reproduction can be estimated by the difference between female and male dynamics.

Knowledge of the nutritional dynamics specific to female reproduction may contribute understanding to the causes of interannual variability of larval production and health (Moser and Boehlert, 1991). The typical nutrient dynamic pattern may be altered by episodic environmental perturbations that impact reproductive output. Phenomena such as El Niños modulate the duration and intensity of upwelling, thus lowering oceanic productivity and subsequent energy flow (Boje and Tomczak, 1978; Ainley, 1990). In fact, Lenarz and Wyllie Echeverria (1986) suggested that the 1983 El Niño adversely influenced fat accumulation and reproduction in yellowtail rockfish.

The purpose of the present study was to determine the temporal dynamics of tissue components in somatic and ovarian tissues in relation to the annual reproductive cycle for yellowtail rockfish. Our objective was to determine the allocation of tissue components for nutrition and energy committed to female reproductive development. This report presents the first comprehensive nutritional dynamics study on a marine viviparous species.

Materials and methods

Adult yellowtail rockfish were collected by hook-and-line at depths of 50 to 150 m from Cordell Bank, a marine bank located approximately 20 nautical miles west of Point Reyes, California (38°01'N, 123°25'W). Specimens were obtained monthly during one reproductive cycle from May 1987 to April 1988. Fish were immediately placed on ice and returned to the laboratory for analyses.

Within 24 hours of capture, ovarian or testicular stage and morphometrics were recorded and tissues were excised for proximate and chemical analysis. Tissues removed included liver, gonad, and a section of muscle from the epaxial portion of the fish just below the spinous dorsal fin. In addition, mesenteric fat deposits attached to the viscera were dissected and weighed.

Muscle mass for individual fish was estimated by a regression equation. We regressed muscle weight on body weight minus gonad weight from representative fish spanning the typical total body weight range (800 to 1600 g) for yellowtail rockfish from Cordell Bank. Muscle mass was determined by

$$\text{muscle (g)} = 24.51 + 0.433\,[\text{body weight (g)} - \text{gonad weight (g)}]. \quad (r=0.994, P<0.0005)$$

Determinations of water, ash, and protein content were performed on fresh tissues. Samples analyzed for water content were dried at 80°C to a constant weight and cooled in a desiccator prior to weighing. Dried tissues were incinerated for 4 hours at 550°C to measure ash content. Protein concentration was assayed by the Lowrey method (Lowrey et al., 1951) with bovine serum albumin (Sigma Chemical Co., St. Louis, MO) as a standard.

Tissue samples for lipid and glycogen determinations were stored at –70°C and analyzed within one month of collection. Lipid was extracted in duplicate from 1 to 2 g of liver, gonad, and muscle by the biphasic method of Bligh and Dyer (1959) following homogenization with a Polytron homogenizer (Brinkman Inc., Westbury, NY). Total lipid was quantified by automated thin layer chromatography/flame ionization detection (TLC/FID), by using an Iatroscan TH–10 Mark III (Iatron Laboratories Inc., Tokyo, Japan) with T Datascan software (RSS Inc., Bemis, TN). Triplicates of 1 µl were spotted on Chromarods S-III, dried, and scanned by the FID at 3.1 mm/sec, 0.95 kg/cm^2 hydrogen pressure and air flow of 2000 mL/min. Peak areas were converted to total lipid weight by using external standards prepared gravimetrically from lipid extracts of *S. flavidus* livers. Standard concentrations were attained by evaporating the organic layer to dryness and reconstituting with chloroform to known concentrations ranging from 2 to 70 µg lipid/µL. Chromarods were cleaned with 9N sulfuric acid, rinsed in Milli-Q water and stored in a desiccator between analytical runs.

Glycogen content was measured by the anthrone method (Carroll et al., 1956). Values were standardized with glycogen from rabbit liver (Sigma Chemical Co., St. Louis, MO).

To evaluate variation in tissues and their components over the reproductive cycle, tissue component concentrations were converted to component masses by determining the product of tissue mass and component concentration. Since tissue and component masses are a function of fish size, we adjusted the

[2] Pacific Fishery Management Council. 1992. Status of the Pacific coast groundfish fishery through 1990 and recommended acceptable biological catches for 1993: stock assessment and fishery evaluation. Document prepared for the council and its advisory entities. Pacific Fishery Management Council, Portland, OR.

data to compensate for size variation. Tissue and component masses were converted to natural logarithms [ln(X + 0.01)] and subjected to the general linear model analysis of covariance (ANCOVA) by using the natural log of standard length (ln SL) to adjust for individual size differences among monthly samples. The adjusted means and standard errors of tissue and component masses were backtransformed by taking their antilogs. ANCOVA also determined the statistical significance of tissue and component variation across the reproductive cycle within each sex. We determined differences among specific monthly means by Duncan's multiple contrast test with $\alpha = 0.05$. Differences in monthly means between sexes were assessed by t-tests. All analyses were performed within the Number Cruncher Statistical Software package (NCSS, Provo, UT).

We estimated the contribution of somatic nutritional components to female reproduction by determining changes in tissue component masses between the onset of rapid ovarian growth and parturition. The decrease in somatic component quantities from maximal values before December to minimal levels in March was calculated for each tissue for each sex. Likewise, ovarian accumulation of nutritional components was calculated as the gain in mass from November to maximal values in December or January. Since male yellowtail rockfish are sexually quiescent during this interval (Eldridge et al., 1991), declines in their somatic nutritional components reflect utilization for adult metabolic maintenance. Differences in net losses of somatic components between males and females were considered estimates of allocations specific to female reproduction.

Results

Size variation

Monthly mean standard lengths (±SE) for females and males were 36.5 ±0.7 cm and 35.3 ±0.4 cm, respectively (Table 1). Differences in length between sexes and among males over the entire study interval were not significant (P>0.05). Because there were differences among monthly mean lengths of females (P<0.01), analysis of covariance eliminated tissue or component mass variation due to size.

Temporal dynamics

Ovarian development was largely synchronous within the yellowtail rockfish population from the onset of recrudescence in May through late vitellogenesis in November, as documented histologically by Bowers (1992) and MacFarlane et al. (1993) (Fig. 1). During December, females were in late vitellogenesis and migratory nucleus stages. Since fertilization occurred in January, both late oocyte and early embryonic stages were represented. In February, all females were in mid to late gestation. Parturition, or larval release, was completed in March when ovaries returned to a small, spent condition.

In males, testicular development was evident in August and September; in all other months testes were regressed and quiescent (Fig. 1). Copulation appeared to have occurred in September and October; sperm were stored in ovaries prior to fertilization.

During the annual reproductive cycle, ovarian mass increased 11-fold from September through December (Fig. 1). The most significant increase occurred during late vitellogenesis between November and December. Ovaries reached maximum size by January and retained mass through February. In comparison, testes reached maximum size in September and were less than 5% of ovarian mass between December and February.

The masses of liver, muscle, and mesenteric fat varied significantly (P<0.01) across the annual repro-

Table 1

Monthly mean standard length (SL) ± standard error (SE) for female and male yellowtail rockfish, *Sebastes flavidus*. Female mean lengths with same superscript were not significantly different (P > 0.05). Mean SL for males did not vary significantly among months, and did not differ significantly from females (P>0.05). n = sample size.

	Females			Males		
Month	n	SL	SE	n	SL	SE
May	6	33.0^{a}	0.9	4	37.2	0.6
June	5	37.0^{abc}	2.2	5	35.9	0.7
July	6	40.5^{c}	1.2	4	37.4	1.7
Aug	5	40.3^{c}	0.8	5	35.0	0.8
Sept	9	35.7^{abc}	1.3	1	32.0	—
Oct	5	36.7^{abc}	1.5	5	34.6	0.8
Nov	6	37.4^{abc}	1.7	4	37.1	0.9
Dec	5	35.1^{ab}	1.6	5	34.7	1.0
Jan	6	37.0^{abc}	2.3	5	35.6	0.8
Feb	5	32.7^{a}	1.7	5	34.0	0.4
Mar	5	38.2^{bc}	1.1	5	34.5	1.5
Apr	5	34.8^{ab}	1.5	5	36.0	0.8
Monthly mean		36.5	0.7		35.3	0.4

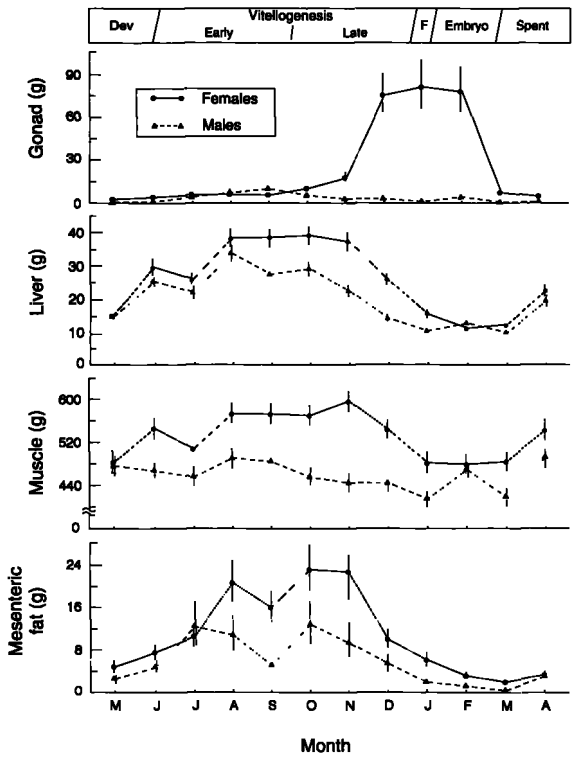

Figure 1

Annual ovarian reproductive cycle and monthly tissue wet weights for gonad, liver, muscle, and mesenteric fat of yellowtail rockfish, *Sebastes flavidus*. Values are means ±SE in grams adjusted by ANCOVA for variations in fish size. Temporal sequence of ovarian maturation stages are shown in bar across the top; recrudescence or early development (Dev), early and late vitellogenesis, fertilization (F), embryogenesis (Embryo), and spent.

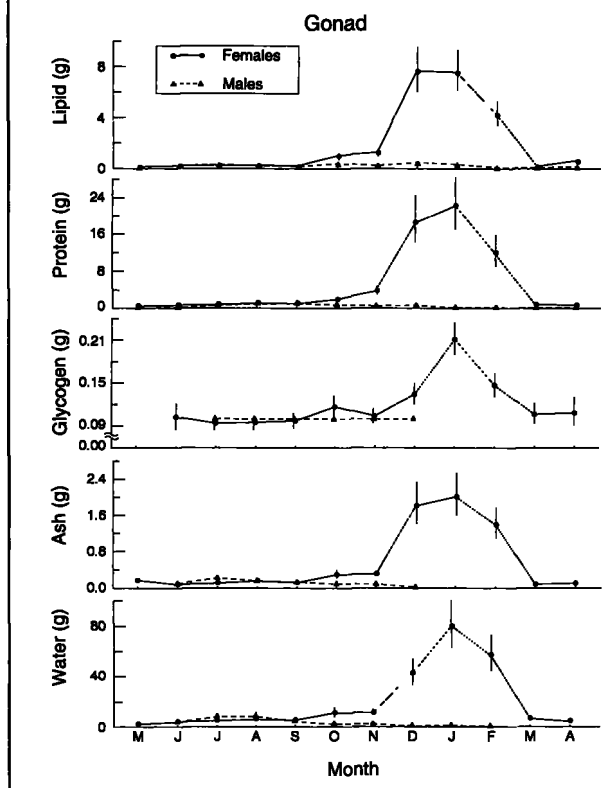

Figure 2

Monthly lipid, protein, glycogen, ash, and water content in gonad tissues of yellowtail rockfish, *Sebastes flavidus*, during one reproductive cycle. Values are means ±SE in grams on a wet weight basis. Missing male values are due to small testes size.

ductive cycle in both sexes (Fig. 1). These somatic tissues increased in mass during the summer and remained elevated into fall. Females accumulated significantly more mesenteric fat, liver, and muscle than did males ($P<0.001$). Declines in female somatic tissues in the fall and winter, during late vitellogenesis and embryogenesis, were inversely related to the accretion of ovarian tissue.

Temporal changes of ovarian tissue components followed a pattern similar to ovarian mass (Fig. 2). Protein and lipid increased 22-fold and 7-fold, respectively, from vitellogenesis in October to early gestation in January. Although glycogen showed a significant increase ($P<0.001$), quantities were always small, representing less than 1% of ovarian mass. Ash and water profiles reflected increased ovarian mass. At maximal size, water accounted for about 70% of ovary mass. Fluctuation in the masses of testicular components were insignificant compared with ovarian changes. In many cases, testicular quantities were insufficient to perform analyses of all constituents.

Dynamics of liver components were dissimilar across the reproductive cycle and between sexes (Fig. 3). Lipid and protein increased from late spring into summer in both sexes; the greatest net gain in female lipid was between July and August. In August, lipid was about 40% of liver mass, whereas protein contributed 10–15%. After August, female liver lipid decreased, but protein remained elevated during vitellogenesis until January. Significantly more liver protein was retained in females than in males from October to January ($P<0.001$). Both female and male liver glycogen followed a temporal pattern of a bimodal increase in the spring and summer with a decrease in the winter. The quantity of glycogen was only a small portion of total liver weight. Water in female liver accounted for a large portion of retained liver mass relative to males during late summer and fall (September through December).

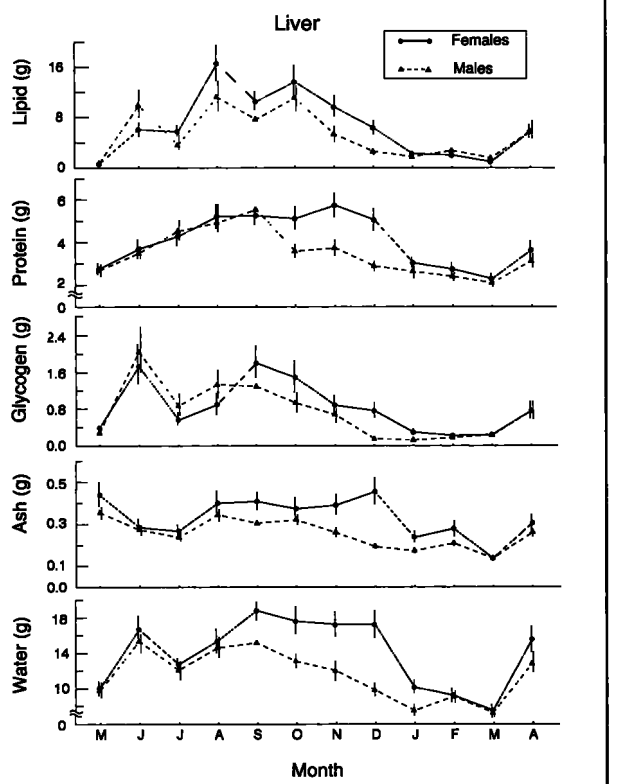

Figure 3

Monthly lipid, protein, glycogen, ash, and water content in liver tissues of yellowtail rockfish, *Sebastes flavidus*, during one reproductive cycle. Values are means ±SE in grams on a wet weight basis.

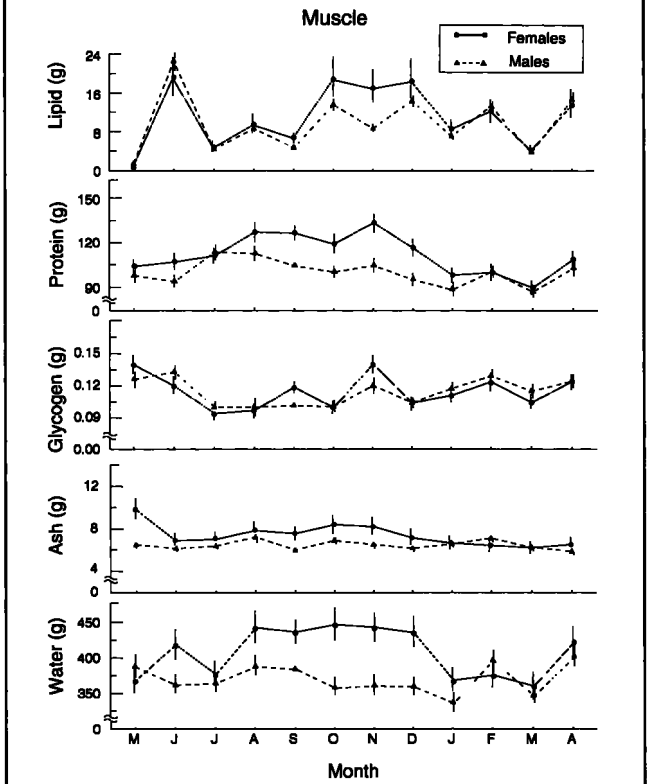

Figure 4

Monthly lipid, protein, glycogen, ash, and water content changes in muscle tissues of yellowtail rockfish, *Sebastes flavidus*, during one reproductive cycle. Values are means ±SE in grams on a wet weight basis.

In terms of quantity, protein content and water content were largely responsible for variation in muscle mass (Fig. 4). Protein content in female muscle increased 30% from July through November and was significantly greater than that in males ($P<0.005$). Muscle protein declined significantly in vitellogenic females after November ($P<0.01$). Males experienced a gradual decline in muscle protein from July to January. Lipid accounted for less than 5% of muscle mass in both sexes. In the fall, females had greater muscle lipid than males ($P\leq0.05$); lipid levels were similar during the other periods.

Muscle glycogen and ash content in females and males changed little across the reproductive cycle and did not appear to coincide with other component dynamics. Also, muscle glycogen content was an order of magnitude lower than liver glycogen.

Nutritional energy dynamics

By calculating changes in quantities of somatic and gonadal components from the onset of ovarian development to parturition, a mass balance of nutritional energy dynamics relative to the female annual reproductive cycle was constructed (Table 2).

Females lost 94 g of somatic tissue from the start of ovarian development through parturition. Virtually all of this loss was lipid (51 g) and protein (41 g). Females lost 27 g, or about 40% more somatic reserves than did males.

Lipid was mobilized from all somatic tissues. From the total lipid loss of 51 g in females, mesenteric fat contributed the most, 21 g, followed by liver and muscle. Mesenteric fat was also the greatest source of lipid loss in males; however, females used approximately 8 g more lipid from mesenteries than did males during the annual cycle. Overall, females lost 17 g more lipid from soma than did males, suggesting that about two-thirds of lipid depleted from somatic stores was used for adult maintenance.

Both females and males lost protein, primarily from muscle, during the time interval of ovarian maturation. Females mobilized 37 g of protein from muscle tissue, which was about 10 grams more than

Table 2

Mean net change in tissue components during annual reproductive cycle of yellowtail rockfish, *Sebastes flavidus*. All values in grams or kilocalories adjusted by ANCOVA for fish size variation. Differences (diff) are changes from start of ovarian development to parturition with male data as baseline. Net gain(+) and loss(–) indicated.

Tissue	Sex	Lipid	Protein	Glycogen	Total
Liver	♀	–15.5	–3.4	–1.6	–20.5
	♂	–10.1	–3.6	–1.2	–14.9
	diff	–5.4	+0.2	–0.4	–5.6
Muscle	♀	–14.6	–37.4	–0.04	–52.0
	♂	–11.1	–27.6	+0.01	–38.7
	diff	–3.5	–9.8	–0.05	–13.3
Mesentery	♀	–21.3			–21.3
	♂	–13.1			–13.1
	diff	–8.2			–8.2
Σ soma	♀	–51.4	–40.8	–1.6	–93.8
	♂	–34.3	–31.2	–1.2	–66.7
	diff (g)	–17.1	–9.6	–0.4	–27.1
	(kcal)	–161.6	–54.2	–1.6	–217.4
Ovary	(g)	+7.4	+21.2	+0.1	+28.7
	(kcal)	+69.9	+119.8	+0.4	+190.1
Ovary	(g)	0.43	2.2	0.25	1.06
Σ soma (diff)	(kcal)				0.87

that mobilized by males. Depletion of liver protein was similar in both sexes and accounted for only about 10% of the total protein loss. Mesenteric fat deposits are almost exclusively lipid.

Glycogen dynamics in both female and male somatic tissues were insignificant to the mass balance. Data are included here to complete the nutritional energy budget for reproduction.

Somatic component losses in females in excess of those in males showed 63% was lipid and 35% protein. By converting to energy equivalents (lipid, 9.45 kcal/g; protein, 5.65 kcal/g; carbohydrate, 4.10 kcal/g), we determined that 74% of female-specific energy depletion was lipid, whereas only 25% was from protein.

Lipid, protein, and glycogen accumulated in the ovaries during vitellogenesis and gestation with a net gain of 29 g (Table 2). Protein accounted for 21 g and lipid 7 g of the net accumulation. The lipid gained in ovaries represented 43% of the lipid depleted from female soma in excess of male losses. The 21-g gain in ovary protein during ovarian development was a 220% net increase relative to female-specific somatic protein loss. Unlike somatic tissue depletion where lipid accounted for the greatest energy loss, protein accretion contributed the greatest amount of energy to the fully developed ovaries (63%). Summing all components, the ratio of ovarian tissue generated to somatic organic matter depleted was balanced (i.e. 1.06).

Discussion

Yellowtail rockfish follow a viviparous mode of reproductive development with significant maternal investment (MacFarlane et al., 1993). Their reproductive strategy provided a model to determine nutritional energy dynamics of female viviparous reproduction. Males could be used to estimate adult metabolic maintenance because testicular development and other reproductive functions are quiescent during the period of ovarian growth and somatic reserve depletion. Moreover, the depletion of somatic reserves was directly reciprocal to ovarian growth, allowing a more accurate estimation of nutrient mobilization for ovarian development. Consequently, differences between female and male somatic losses reflect costs for female reproduction. Since this species does not migrate (Carlson and Haight, 1972; Carlson and Barr, 1977; Pearcy, 1992), there is no energy utilization for increased locomotion, as found with anadromous or catadromous fishes.

In yellowtail rockfish, somatic energy reserves were accumulated in both sexes during the summer and fall and depleted over winter when food availability decreased greatly (Hobson and Chess, 1988; Ainley, 1990). Although female soma gained greater mass than males during the summer, tissue masses were about the same in both sexes at the end of winter. Approximately 40% more somatic reserves were depleted from females than from males between October or November (maximal somatic mass) and March, or during the period spanning vitellogenesis to parturition. This difference was attributed to utilization of these reserves for ovarian development and related reproductive costs.

The location and quantitative importance of somatic reserves varies interspecifically in teleosts (Love, 1970; Weatherley and Gill, 1987). Interestingly, in yellowtail rockfish, a largely inactive fish,

somatic depletions were greatest in muscle. Muscle loss occurs in other fish (e.g. capelin and sockeye salmon) as well, but unlike yellowtail rockfish, these species often have high metabolic demands for migration in addition to reproduction (Idler and Bitners, 1960; Henderson et al., 1984).

Although muscle was the site of greatest net depletion of somatic tissue, mesenteric fat contributed more energy than muscle for female-specific costs of reproduction. Previous studies have demonstrated the importance of mesenteric fat as an energy source in yellowtail rockfish (Guillemot et al., 1985; MacFarlane et al., 1993). Lipid stored in mesenteries seems to be readily mobilized for reproduction in this live-bearing species as well as other oviparous fishes (Idler and Bitners, 1960; Ince and Thorpe, 1976; Jezierska et al., 1982).

In yellowtail rockfish, lipid was the main source of energy for female reproduction. About one-third of total lipid depleted from female soma was available for reproduction. Lipid lost from all the major reserve tissues equalled 74% of the total somatic energy mobilized for female-specific reproductive development. Lipid is typically the primary source of energy for reproduction in oviparous teleosts (Sargent, 1976; Sargent et al., 1989). Data from yellowtail rockfish suggest the importance of lipid for reproduction extends to marine viviparous fishes.

Female-specific protein loss from yellowtail rockfish somatic tissues was approximately half that of lipid. The utilization of protein from muscle as a supplemental source of energy for reproduction has been reported in some oviparous fishes (Niimi, 1972; Medford and Mackay, 1978; Jobling, 1980). But this contrasts with herring, where Iles (1984) and Bradford (1993) suggested that somatic protein was the primary fuel for gonad development whereas storage lipid supported nonreproductive metabolic processes.

Determining the partitioning of somatic reserves between reproduction and adult metabolism is very difficult in most teleosts. Reproductive strategies involving factors such as sex differences in activity, simultaneous development of testes and ovaries, migration, and somatic energy accumulation concurrent with gonadal development obscure fractional distribution. Because the yellowtail rockfish reproductive strategy, including physiological processes and behavior, does not include these factors (Carlson and Barr, 1977; Eldridge et al., 1991; Pearcy, 1992), we were able to estimate the nutritional energetic costs directed toward oocyte and embryo development. Forty-three percent (43%) of female-specific somatic lipid depletion was incorporated into ovaries, leaving 57% for reproductive metabolism.

Henderson et al. (1984) employed an analytical design well-suited to determining somatic lipid partitioning among adult maintenance, reproductive metabolism, and ovarian accretion in capelin, *Mallotus villosus*. Although ovaries accumulated 38% of mobilized somatic lipid and testes gained none, both sexes mobilized essentially the same quantity of somatic lipids. The absence of a difference between sexes in lipid mobilization precluded estimation of allocations between gonadal metabolism and adult maintenance.

Significant increase in ovarian protein during maturation was expected because de novo synthesis is required for oocyte and embryonic proliferation. However, the net increase in ovarian protein was 220% of female-specific somatic loss and indicated a dietary source during late vitellogenesis and gestation. Although there is a general paucity of prey in the California Current ecosystem during the winter (Hobson and Chess, 1988; Ainley, 1990) and stomach contents of yellowtail rockfish samples were minimal at this time (Whipple[3]), feeding remains the most likely source for the excess protein accumulated in the ovary. Data from yellowtail rockfish off the Washington and Oregon coast showed that they may feed over winter (Brodeur and Pearcy, 1984). Since we observed frequent regurgitation during capture, it is possible that expulsion of stomach contents contributed to imprecise estimation of feeding intensity in the yellowtail rockfish of the present study.

There are limited data on female-specific nutritional dynamics in other species. Thus, it may be beneficial to compare allocations from soma to gonadal tissue, uncorrected for sex differences, for yellowtail rockfish to those of other fishes. Such comparisons do not provide information on the partitioning of nutrients for various female metabolic and reproductive processes, only the net transfer to ovaries. For yellowtail rockfish, the gain of lipid and protein in ovaries during reproductive development was 14% and 52% of somatic depletions, respectively. This net transfer of lipids into ovaries was mid-range in comparison with values in oviparous species. Net lipid transfers of 38% in capelin (Henderson et al., 1984), 22% in plaice, *Pleuronectes platessa* (Dawson and Grimm, 1980), 8% in sockeye salmon, *Oncorhynchus nerka* (Idler and Bitners, 1960), and 5% in English sole, *Pleuronectes vetulus* (Dygert, 1990) have been reported. Protein transfers in yellowtail rockfish are comparable to English sole, 55% (Dygert, 1990). In plaice 48% more protein accumulated in ovaries than was lost from soma during oocyte

[3] Whipple, J. A. 1988. National Marine Fisheries Service, Southwest Fisheries Science Center, Tiburon Laboratory, 3150 Paradise Drive, Tiburon, CA 94920. Unpubl. data.

development, but plaice are known to feed during this time (Dawson and Grimm, 1980).

The efficiency of net transfer between somatic tissues and ovaries, or the ratio of ovary tissue gained during development to the total somatic tissue lost, was about 30% in yellowtail rockfish. This compares with 33% in English sole (Dygert, 1990), 43% in plaice (Dawson and Grimm, 1980), and 23% in American plaice, *Hippoglossoides platessoides* (MacKinnon, 1972), suggesting that although the temporal sequence of nutritional dynamics may differ between oviparous and viviparous teleosts, the quantitative budgets are similar.

The present study documents the first comprehensive analysis of the nutritional energetics of reproduction in a viviparous marine teleost. Although there are many similarities to oviparous species, the reproductive nutritional energetics of this viviparous species are likely adaptive to environmental constraints of the upwelling-dominated productivity pattern of the California Current ecosystem. Energy reserves, mainly lipid, were accumulated in intestinal mesenteries and other somatic tissues in both sexes through the summer upwelling (feeding) season. Females acquired greater amounts of lipid and protein than did males. These reserves were depleted to a greater extent in females for ovarian development, as well as in adult metabolism and survival over winter when ecosystem productivity is low. This strategy results in the release of larvae at the onset of improved feeding conditions when upwelling renews. Because lipid is the most important energy source allocated to ovarian development, inadequate accumulation of lipid reserves in females during the typically productive period of the year may alter the maternal energy balance. Thus, periodic perturbations, such as El Niños, may result in reduced nutritional input to developing larvae and consequently lower reproductive success or pelagic larvae survival.

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