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Oxygen consumption of gestating female *Sebastes schlegeli:* estimating the reproductive costs of livebearing

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Synopsis

During gestation, live-bearing fishes incur physiological energy costs, including provision of energy and respiratory gases to the developing embryos and removal of waste products. Fecundity in the genus *Sebastes* is high, and the ovaries represent a significant portion of the weight of gestating females. In this study, we compare oxygen consumption of gestating females with non-gestating females and males of kurosoi, *Sebastes schlegeli*, to estimate these costs. Oxygen consumption by pregnant females is significantly higher than that of males and immature females at similar sizes and weights. We estimate that a 1.5 kg gestating female consumes 68% more oxygen than a non-gestating fish during the 51.5-day period of gestation. Such an increase in oxygen consumption rates may have important implications to the metabolic scope of gestating females. The additional oxygen consumed by gestating females is greater than that predicted for the embryos alone, suggesting that costs of increased gill ventilation, ionic and osmotic regulation and cardiac output are relatively high. Such energetic costs represent a quantifiable expense of the viviparous mode of reproduction in *Sebastes* as compared with oviparous species.

Introduction

The costs of reproduction in fishes typically involve more than just production of gametes (Wootton 1985). While a variety of adaptations for parental care exist (Balon 1975), live-bearing fishes are faced with the problems of supply of oxygen and nutrients to developing embryos. Hypertrophy of the gas exchange systems of maternal ovaries (Amoroso 1960) and embryos (Webb & Brett 1972, Dobbs 1975) is an example of morphological adaptation, but energetic costs are incurred as well. Several studies have estimated oxygen consumption by embryos in vitro (Moser 1967a, Webb & Brett 1972, Boehlert & Yoklavich 1984, Berglund et al. 1986), but few have considered actual oxygen consumption rates in vivo. These rates may be estimated by considering the relative increase in oxygen consumption by gestating females as compared with spent or immature females or males (Webb & Brett 1972) and may provide insights into the additional costs of reproduction in livebearers.

In the viviparous genus *Sebastes*, oxygen consumption of embryos in vitro increases with devel-

opmental stage either linearly (*S. melanops,* Boehlert & Yoklavich 1984) or exponentially (*S. schlegeli*, Boehlert et al. 1986; *S. caurinus*, Dygert & Gunderson 1991). Catabolism during development consumed from 39% (*S. caurinus*) to 88% (*S. schlegeli*) of the initial yolk energy. Gestation times are quite long given the egg size in *Sebastes*; at 10° C, the 0.8 mm egg and embryo of *S. melanops* takes 37 days from fertilization to parturition, whereas the 1.2 mm egg and embryo of *S. schlegeli* takes 51.5 days. The latter is up to 8 times the incubation time of equivalent-sized pelagic eggs (Ware 1975) and 5–8 times longer than for the related lecithotrophic live-bearing scorpaenid *Sebastiscus marmoratus* (Nakanishi 1991). Boehlert et al. (1986) raised the question as to whether oxygen tension inside the ovarian fluid may be considerably lower than ambient values and that estimates of in vitro oxygen consumption may therefore be higher than in vivo rates. A similar problem exists in the oxygen consumption of embryos in gelatinous masses of frog eggs (Burggren 1985). Although *Sebastes* have a very well-developed arterial blood supply system to each ovary (Moser 1967b), the fecundity in this genus is high (Gunderson et al. 1980, Boehlert et al. 1982), and the oxygen demands of the embryos also must be high. In the present study, we estimate the oxygen consumption of embryos in vivo by measuring oxygen consumption of female *S. schlegeli* with gestating embryos as compared with males and non-gestating females, and estimate the relative costs of livebearing in this species.

Materials and methods

Experiments were conducted at the Hokkaido Institute of Mariculture at Shikabe, 4–12 June 1985. Two sources of fish were used. The first was captive stock reared from embryos for periods up to 8 years (Kusakari 1978); the second was fish collected at Otobe in the Sea of Japan on 22 May and 1 June 1985. During the experiments, fish were held in tanks (1.8 × 1.8 × 1.1 m) in running ambient seawater (temperature, 10.6–14.4° C) and starved at least 2 days before use.

Two days prior to the beginning of experiments, fish were weighed and measured, and sex was determined after fish were anesthetized in tricaine methanesulfonate (MS–222, 60 mg · l^{-1}). (Reference to trade names does not imply endorsement by the National Marine Fisheries Service). Females were catheterized, and developing embryos removed following techniques of Boehlert & Yoklavich (1984). Embryos were staged using scheme described by Yamada & Kusakari (1991). Estimates of time since fertilization (as a function of development stage) were calculated from the equation in Boehlert et al. (1986).

The respirometer consisted of a cylindrical fish chamber constructed of acrylic tubing (20 cm in diameter). One end was sealed with 1.3 cm thick acrylic sheet, except for a small water intake hole. The opposite end had a similar acrylic sheet with a 0.95 cm thick circular piece cut to fit the inner diameter of the cylindrical fish chamber. Silicone sealer and Teflon tape made an effective seal when the chamber was closed and held in place with an elastic band. The respirometer volume was 13.2 l. Incoming water was saturated with air and entered the chamber at one end. At the opposite end, water was collected through tubing and connected to a housing for the oxygen electrode (Takara Thermistor Instrument Co. recording dissolved oxygen meter, Model No. R-F), which was immersed in the water bath. The oxygen electrode was calibrated each morning in air-saturated seawater at the experimental temperature and zeroed in seawater containing potassium metabisulfite.

Prior to an experiment, fish were anesthetized in MS-222 to minimize handling stress and transferred to the respiration chambers, which were then sealed. Fish in the respirometers typically recovered from the anesthesia within 3–5 min and assumed normal orientation; experiments were started at this point. The respirometers were held in a tank (1.8 × 1.1 × 0.65 m), which was filled to maintain a constant flow of air-saturated seawater. The tank was partially covered with black plastic during experiments. Fish activity was visually monitored, and oxygen content of the outflowing water was recorded at 5–10 min intervals. Flow rates (33.84–92.64 l · h^{-1}) were adjusted to fish size so that oxygen content in the respirometer typically

decreased to equilibrium values after 10–20 min. The experiment was terminated after the oxygen level had not changed over a 10-min period, then ambient oxygen content was determined. Oxygen consumption rates (ml $0_2 \cdot h^{-1}$) were determined by multiplying the change in oxygen concentration of inflowing and outflowing water by the flow rate. For each animal, a mean value of oxygen consumption was computed from two replicates. Experimental periods for each replicate averaged 43 min. Our estimates may be considered routine metabolic rates (Fry 1971). Control experiments were run with empty respirometers, and the drop in oxygen content was negligible.

Although ambient temperatures varied (10.6–14.4° C) during experiments because no temperature control was available, the temperature change during each experiment did not exceed 0.4° C. To compensate for the temperature differences among experiments and to facilitate comparison with estimates of respiration rates of embryos reported in Boehlert et al. (1986), we adjusted the measured rates of oxygen consumption to values at 12.5° C by using a Q_{10} of 1.6. This latter value was chosen because it represents the acclimated Q_{10} value in *S. diploproa* (Boehlert 1978) and such temperature fluctuations are normally experienced by *S. schlegeli* in this season.

Specimens were divided to two groups based upon reproductive status. The first group comprised males, immature females and spent females; the second, females with gestating embryos at different stages of development. The respiration rates as a function of weight for the first group were fitted to a curve, which could then be used to predict normal respiration rates (i.e., for non-gestating fish). Estimates from this curve could then be applied to the second group; the difference between observed and predicted respiration rates was attributed to oxygen consumption by embryos within the ovaries plus associated costs of livebearing.

Results

Gestating fish with embryos at various stages of development were typically much heavier at a given length than were males (n = 32) and immature or spent females (n = 11). The length-weight curves (Fig. 1) for these groups are as follows:

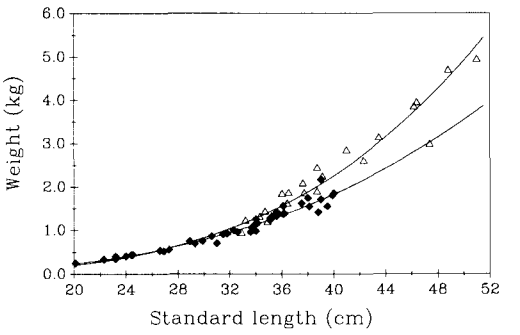

Fig. 1. Length-weight relationships of *Sebastes schlegeli*. The triangles and upper curve represent data from gestating females. Diamonds and the lower curve represent males and immature spent females. The fitted curves (equations 1, 2) are listed in the text.

Gestating females: $W = (5.7524 \times 10^{-6}) L^{3.4910}$, $n = 25$, $r^2 = 0.937$, (1)

and

Non-gestating fish: $W = (3.3677 \times 10^{-5}) L^{2.9554}$, $n = 43$, $r^2 = 0.976$. (2)

The weight increase of gestating females compared with non-gestating fish was most evident after about 32 cm standard length (SL), and the divergence between the two curves increased with increasing length. This is related to rapidly increasing fecundity with length (Kusakari 1991).

Fish were generally inactive in the respirometers after the first few minutes. In one case, however, considerable activity was observed, and bouts of activity could be seen on the strip chart recording of oxygen consumption. Oxygen consumption rates of this fish were nearly twice that of inactive fish of similar weight and were not used in our analysis.

Oxygen consumption rates were determined for 23 non-gestating fish, including 19 males, 2 immature females and 2 spent females, and also for 17 gestating females with embryos at stages 1 to 30. Respiration rates typically increased with increasing body weight for non-gestating and gestating fish

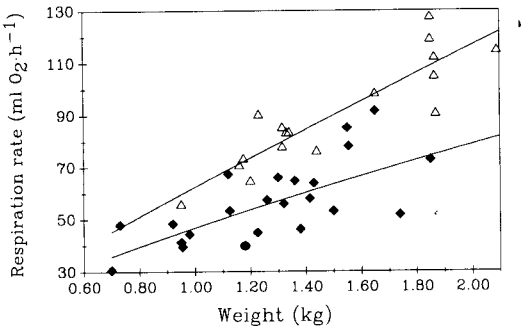

Fig. 2. Oxygen consumption rates as a function of weight for *Sebastes schlegeli*. Triangles represent values from gestating females, and diamonds for males, immature females and spent females. All values are scaled to 12.5° C using a Q_{10} value of 1.6. The corresponding lines representing the fitted curves (equations 3, 4) are in the text.

(Fig. 2). Data from non-gestating fish were fitted to the curve

$$Q = 46.734\ W^{0.7515},\ n = 23,\ r^2 = 0.524, \qquad (3)$$

where Q = oxygen consumption rate (ml $0_2 \cdot h^{-1}$) and W = body weight (kg). At a given body weight, respiration rates were much higher for females with developing embryos. Data from these females were fitted to the curve

$$Q = 62.383\ W^{0.9014},\ n = 17,\ r^2 = 0.81. \qquad (4)$$

These two curves (Fig. 2) are significantly different (analysis of covariance, $p < 0.01$).

Developmental stage of embryos corresponded to estimates of time since fertilization from 0.01 to 45.3 days (Table 1; birth is estimated to occur at 51.5 days after fertilization). Since respiration rates of embryos increase exponentially with time in *S. schlegeli*, the variability in the respiration rates for gestating females may be partially a result of the variation in the stage of development of embryos in the ovary. Post-fertilization fecundity was estimated and then multiplied by the oxygen consumption rate of embryos at the appropriate stage of development from the equations given in Boehlert et al. (1986). The resulting estimate of the total oxygen consumption rate of embryos in each gestating female was also adjusted to a temperature of 12.5° C

Table 1. Data on respiration rates and embryos of gestating female *Sebastes schlegeli* used in the experiments. All respiration rates are adjusted to a temperature of 12.5° C by using a Q_{10} value of 1.6.

Fish weight (g)	Respiration rate (ml $O_2 \cdot h^{-1}$)	Adjusted respiration rate 1.5 kg fish (ml $O_2 \cdot h^{-1}$)	Excess respiration (ml $O_2 \cdot h^{-1}$)	Time since fertilization (days)	Total embryo respiration rate (ml $O_2 \cdot h^{-1}$)	Live-bearing cost (ml $O_2 \cdot h^{-1}$)
1315	85.56	96.51	39.59	35.50	37.65	1.94
1870	90.87	75.08	18.16	29.80	25.25	− 7.08
1200	64.91	78.91	21.99	35.50	37.65	− 15.67
1865	105.08	86.50	29.58	32.60	30.73	− 1.15
1440	76.39	79.17	22.25	35.50	37.65	− 15.40
1650	98.54	90.42	33.50	35.50	37.65	− 4.16
1850	119.21	98.31	41.39	38.60	46.80	− 5.41
950	55.90	83.84	26.92	26.20	19.62	7.30
2090	114.88	85.47	28.55	28.20	22.57	5.99
1175	73.48	91.65	34.73	12.60	7.56	27.18
1160	70.93	89.40	32.48	14.40	8.58	23.90
1230	90.47	109.02	52.10	29.80	25.25	26.85
1330	83.55	93.20	36.28	0.01	3.13	33.15
1340	83.68	92.70	35.78	23.70	16.46	19.31
1850	127.80	105.10	48.18	44.60	71.27	− 23.10
1315	78.10	87.89	30.97	42.50	61.52	− 30.55
1865	112.25	92.15	35.23	45.30	74.86	− 39.63

using a Q_{10} of 1.6. The 'non-gestating' weight of the gestating female (estimated from standard length and equation 2) was used to estimate respiration rate from equation 3. Excess respiration rate was determined by subtracting the resulting values from the observed respiration rates. Excess respiration rates were positively correlated with the total oxygen consumption rate for embryos ($r^2 = 0.637$, $p = 0.006$) and can be attributed to the sum of respiration by embryos and live-bearing costs.

To this point, our analysis was confounded by variations in the stage of development and in female size; these variations made it difficult to compare the contribution of the two components of excess respiration (Table 1). For this reason, we adjusted the measured oxygen consumption rates of gestating females, using the weight exponent in equation (4), to a uniform weight of 1.5 kg. This value corresponds to a 35.6 cm SL fish with an estimated post-fertilization fecundity of 126 923 embryos. The associated oxygen requirement of the ovaries varied with the age of the embryos from 3.13 to 74.86 ml $0_2 \cdot h^{-1}$ (Table 1). The same fish in non-gestating condition would have a corresponding weight of 1.3 kg (equation 2) and an estimated respiration rate of 56.92 ml $0_2 \cdot h^{-1}$ (equation 3). The mean excess respiration of these adjusted data is 33.39 ml $0_2 \cdot h^{-1}$. Estimates of live-bearing costs (excess respiration minus respiration rate of embryos) have a negative relationship with the time since fertilization (TSF, in days), as follows:

$$Q_e = 46.533 - 1.5434\ (TSF),$$
$$n = 17,\ r^2 = 0.762, \qquad (5)$$

where Q_e is excess respiration less embryo respiration rate. This relationship suggests that live-bearing costs to gestating females are high early in gestation and decrease to negative values with further development of the embryos (Table 1, Fig. 3). The value approaches zero at about 30 days, which corresponds to a developmental stage of 26.5, near the time when the embryo begins consuming ovarian fluid (Boehlert et al. 1986). This stage is characterized by pigmented eyes with nearly complete lens and fully formed otoliths, rectum and urinary bladder (Yamada & Kusakari 1991).

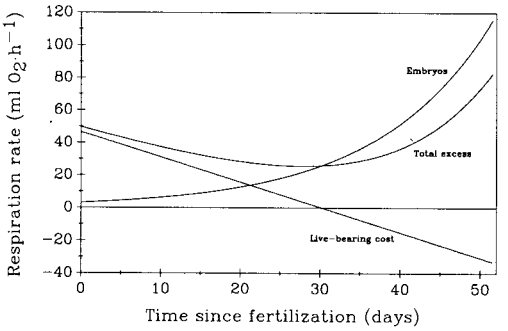

Fig. 3. Dynamics of excess oxygen consumption during gestation for a 1.5 kg gestating female. The respiration of embryos is taken from fecundity multiplied by respiration rate of individual embryos (from Boehlert et al. 1986) and adjusted to a temperature of 12.5° C. The straight line is the estimate of live-bearing cost from equation 5 and Figure 4. The final line represents the sum of these two.

A summary of the proportions of oxygen consumption of a 1.5 kg gestating female *S. schlegeli*, when partitioned to total oxygen consumption of embryos and the live-bearing costs from equation (5), shows a slight dip followed by a rapid rise in total excess respiration rate (Fig. 3). Integrating these functions over the 51.5 days of gestation, one can estimate the total additional oxygen consumed by a 1.5 kg gestating female. Embryo oxygen consumption would require 39 575 ml 0_2, and the live-bearing cost would amount to 8393 ml 0_2. The oxygen consumed by a non-gestating fish over 51.5 days (from integration of equation 3) would be 70 352 ml 0_2. Thus, the total excess respiration represents an increase of 68% of the oxygen necessary for routine respiration over the period of gestation.

Discussion

Within the framework of reproductive effort in fishes, a variety of expenses are incurred. While the major energetic expense of most oviparous fishes is the elaboration of the gonads, selected species develop secondary sexual characters, undergo reproductive migrations and incur various costs associated with some form of parental care (Calow 1985). In livebearers, the costs of protecting the embryos

can include additional work for the cardiac system in supplying blood to the ovaries, greater work for the branchial pump, increased costs of osmotic and ionic regulation as more blood passes through the gills and, in some cases, provision of additional nutrition to the embryos (Webb & Brett 1972, Boehlert & Yoklavich 1984). In *S. schlegeli*, significantly greater respiration rates in gestating females suggest a much higher level of energy consumption than in non-gestating fish of equal weight (Fig. 2). These differences are even greater for fish of equal length since gestating fish are heavier at a given length (Fig. 1). Much of this excess oxygen consumption may be consumed by developing embryos, but additional oxygen consumption by the maternal system is also necessary during gestation (Fig. 3).

The reduction of live-bearing costs to values below the estimated respiration rate of the embryos (Fig. 3) occurs about 30 days after fertilization and coincides with developmental stages 26–27. Boehlert et al. (1986) have suggested that respiration rates measured in vitro for embryos may have been slightly inflated for two reasons. First, the rates have been measured in air-saturated saline, whereas the ovarian fluid may have values below saturation. Second, activity by later stage embryos in the respiration flasks may inflate the measured values. The respiration rates may be indirectly estimated if it is assumed that the only source of additional nutrition for embryos comes from resorption of embryos dying early in gestation; that is, from an energy standpoint (but not from exchange of respiratory gases and metabolic waste products), the ovaries are a closed system. This has been hypothesized by Boehlert et al. (1986) and is supported by ingestion of yolk proteins by late stage embryos (K. Takano personal communication). The energy decrease in the ovary during gestation for the 1.5 kg female is about 95.2 kcal. This is based both upon the reduction in fecundity due to unfertilized eggs and death of embryos, and the decreased energy content per embryo (1.48 cal) as compared with a newly fertilized egg (1.59 cal). Partitioned over the surviving embryos, this amounts to about 0.75 cal each, compared with the estimated catabolic utilization of 1.386 cal from Boehlert et al. (1986). If this assumption is correct, the values of in vivo respiration of embryos may be inflated by as much as 85%, and a greater proportion of the excess respiration may be attributed to that needed by the female for the other costs associated with livebearing. A recalculation of the data for the respiration of *S. schlegeli* embryos by using only values for embryos younger than 30 days after fertilization (prior to activity exhibited in the Gilson respirometer flasks) results in an estimated catabolic utilization of about 0.70 cal, which is nearly in agreement with that calculated above.

These data can be used to estimate the costs incurred in reproduction by our hypothetical, 1.5 kg (35.6 cm SL) gestating female. First, the excess oxygen consumption during gestation is represented by the sum of the integrals of the two curves in Figure 3; a total of 47 968 ml 0_2 is consumed above that estimated for normal respiration. This is equivalent to 222.0 kcal based on the oxycalorific conversion of Elliot & Davison (1975). This figure should be reduced by the difference between initial and final energy content of the ovary; the difference is used here as an estimate of the catabolic energy usage and amounts to 95.2 kcal. Thus, the additional cost to the female would be 126.8 kcal. Partitioned among the embryos at parturition, this results in an additional energy commitment by the female of 1.00 cal per embryo. Given that the initial energy content of the egg is 1.59 cal at fertilization (Boehlert et al. 1986), this figure suggests that the energetic cost of livebearing in this species is 62.9% higher than that of oogenesis alone.

That the total 'excess' respiration of females during gestation remains fairly constant (Fig. 3) suggests that some upper limit for oxygen consumption may exist. Metabolic scope may be defined as the difference between the maximum active metabolic rate supportable by aerobic metabolism and standard metabolic rate (Fry 1971); this topic has recently been reviewed by Priede (1985). Activity levels and metabolic scope in fishes are generally related to the gill morphology, particularly some index of gill surface area to body weight (Gray 1954, De Jager & Dekkers 1975); the ability to better extract oxygen from water allows a greater metabolic scope for the more active species (Priede

1985). Benthic species of *Sebastes* such as *S. schlegeli* are not typically highly active fishes and are, in many cases, territorial (Larson 1980). Although the gill surface areas of *Sebastes* species have not been measured, the related scorpaenid *Scorpaena porcus* has a relatively low index for gill area, falling into the same general range of values for other demersal fishes (Pauly 1981). Since gill surface area is typically a function of length, the additional weight added during parturition in female *Sebastes* (Fig. 1) alone will add oxygen demand with the same gill surface area. This will presumably require increased cardiac output under resting conditions. It would be of interest in this context to compare allometric relationships of gill surface area in male and female *Sebastes*, because males might not show such increased respiratory needs.

While the added weight and respiratory demands of developing embryos will contribute to a general decrease in the metabolic scope, other factors must also be considered, including general swimming activity and energy for digestion (specific dynamic action, SDA; Beamish 1974). Vahl & Davenport (1979) have demonstrated an increase of 60% of the metabolic rate in *Blennius pholis* associated with a large ration; they attributed this increase to apparent SDA, suggesting that, in this fish and other species [interpreting data from Muir & Niimi (1972) and Beamish (1974)], a single, large ration may decrease the scope for activity by some 50% for several hours. In *S. schlegeli*, the difference between respiration rates of gestating and non-gestating fish (Fig. 2) increases with increasing length, from 35% for a 30 cm SL fish to 117% for a 50 cm SL fish (Fig. 4). The values for larger fish are significantly in excess of the rates cited for the SDA-mediated increase by Vahl & Davenport (1979). Further, the increases associated with gestation are not transitory, as are those associated with SDA, but last for 51.5 days in *S. schlegeli* (Boehlert et al. 1986). We hypothesize that gestating *Sebastes* may thus attempt to minimize other sources of oxygen uptake.

Priede (1985) suggested that many fish species must time their feeding activities to keep metabolic rate within the limits of metabolic scope. Over the extended period of gestation, *Sebastes* may need to

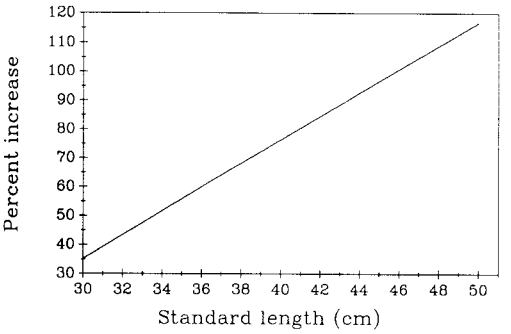

Fig. 4. Increase in oxygen consumption for gestating female *Sebastes schlegeli* as a function of standard length. Values were calculated by first estimating weights from equations (1) and (2) and then determining the respective respiration rates from equations (3) and (4).

make accommodations for the reduced metabolic scope associated with the increased respiratory load. Two mechanisms may serve this purpose. First, *Sebastes* females may either feed at lower rations or, later in gestation, cease feeding to minimize the costs of SDA and the swimming activity necessary for feeding. Such cessation of feeding late in gestation has been noted for *S. flavidus* (Eldridge et al. 1991). The energy necessary for maintenance during this period could come from the fat stores accumulated earlier in the season. Guillemot et al. (1985) have noted in five species of *Sebastes* that the accumulation of fat in females is concurrent with gametogenesis and the depletion of fat precedes parturition. Fat is deposited for a longer period and in greater amounts in females than in males. Thus, energy stores may allow a reduced feeding rate and, thereby, a lower SDA component to the reduction of metabolic scope.

A second mechanism to increase overall metabolic scope may be to seek lower temperatures, where tissue metabolism is depressed and oxygen content of the water is greater (Priede 1985). *Sebastes* could conceivably do this in two ways. First, the reproductive season could be timed such that gestation occurs during colder months. Spawning seasonality in some *Sebastes* species occurs throughout the year off the west coast of North America, but the majority of the species spawn in winter and spring months (Parrish et al. 1981). Second, gestating fe-

males could migrate to deeper, colder waters. Sexually segregated schools of *S. marinus* and *S. mentella,* for example, exhibit different migration patterns (Sorokin 1961), which may be related to spawning. Gunderson (1971) has noted a similar phenomenon in *S. alutus* and suggested that this species releases larvae in the deepest (and therefore coldest) part of the depth range. Thus, within a season, behavioral thermoregulation may also play a role in the female reproductive process.

The interplay of temperature and oxygen content of water may have impacts on both growth and distribution of *Sebastes*. Boehlert & Kappenman (1980) noted latitudinal trends in growth in two species, with faster growth in the northern parts of the range, where water temperatures are lower and oxygen content higher. Because members of this genus are typically restricted to subarctic and temperate waters (Barsukov 1981), the interplay between temperature and dissolved oxygen may restrict not only the scope for activity and growth of *Sebastes*, but may also make viviparity impractical in lower latitudes from an energetic standpoint. It would thus be interesting to compare the relative temperature-oxygen tolerances of male, non-gestating female and gestating female *Sebastes*. Interannual variability in either food supply or temperature conditions may similarly have large effects on reproduction. Lower food availability in El Niño years, for example, may result in lower fat deposition in *Sebastes* (Lenarz & Echeverria 1986). This may result in either lower somatic growth or reduced fecundity (Wootton 1973). Further, interannual variability in physical conditions may result in variability in the level of nutrition provided to embryos in viviparous fishes (Trexler 1985). The effects of fish size, food availability and physical factors thus have important implications to reproduction in the genus *Sebastes*.

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References cited

Amoroso, E.C. 1960. Viviparity in fishes. Symp. Zool. Soc. Lond. 1: 153–181.

Balon, E.K. 1975. Reproductive guilds of fishes: a proposal and definition. J. Fish. Res. Board Can. 32: 821–864.

Barsukov, V.V. 1981. A brief review of the subfamily Sebastinae. J. Ichthyol. 21: 1–26.

Beamish, F.W.H. 1974. Apparent specific dynamic action of largemouth bass, *Micropterus salmoides*. J. Fish. Res. Board Can. 31: 1763–1769.

Berglund, A., G. Rosenqvist & I. Svensson. 1986. Reversed sex roles and parental energy investment in zygotes of two pipefish (Syngnathidae) species. Mar. Ecol. Prog. Ser. 29: 209–215.

Boehlert, G.W. 1978. Changes in the oxygen consumption of prejuvenile rockfish, *Sebastes diploproa*, prior to migration from the surface to deep water. Physiol. Zool. 51: 56–67.

Boehlert, G.W., W.H. Barss & P. Lamberson. 1982. Fecundity of the widow rockfish, *Sebastes entomelas,* off the coast of Oregon. U.S. Fish. Bull. 80: 881–884.

Boehlert, G.W. & R.F. Kappenman. 1980. Variation of growth with latitude in two species of rockfish (*Sebastes pinniger* and *S. diploroa*) from the northeast Pacific Ocean. Mar. Ecol. Prog. Ser. 3: 1–10.

Boehlert, G.W., M. Kusakari, M. Shimizu & J. Yamada. 1986. Energetics during embryonic development in the kurosoi, *Sebastes schlegeli* Hilgendorf. J. Exp. Mar. Biol. Ecol. 101: 239–256.

Boehlert, G.W. & M.M. Yoklavich. 1984. Reproduction, embryonic energetics, and the maternal-fetal relationship in the viviparous genus *Sebastes* (Pisces: Scorpaenidae). Biol. Bull. (Woods Hole) 167: 354–370.

Burggren, W. 1985. Gas exchange, metabolism, and 'ventilation' in gelatinous frog egg masses. Physiol. Zool. 58: 503–514.

Calow, P. 1985. Adaptive aspects of energy allocation. pp. 13–31. *In*: P. Tytler & P. Calow (ed.) Fish Energetics: New Perspectives, Johns Hopkins University Press, Baltimore.

De Jager, S. & W.J. Dekkers. 1975. Relations between gill structure and activity in fish. Neth. J. Zool. 25: 276–308.

Dobbs, G.H. 1975. Scanning electron microscopy of intraovarian embryos of the viviparous teleost *Micrometrus minimus* (Gibbons), (Perciformes: Embiotocidae). J. Fish Biol. 7: 209–214.

Dygert, P.H. & D.R. Gunderson. 1991. Energy utilization by embryos during gestation in viviparous copper rockfish, *Sebastes caurinus*. Env. Biol. Fish. 30: 165–171.

Eldridge, M.B., J.A. Whipple, M.J. Bowers, B.M. Jarvis & J.

Gold. 1991. Reproductive performance of yellowtail rockfish, *Sebastes flavidus*. Env. Biol. Fish. 30: 91–102.

Elliot, J.M. & W. Davison. 1975. Energy equivalents of oxygen consumption in animal energetics. Oecologia 19: 195–202.

Fry, F.E.J. 1971. The effect of environmental factors on the physiology of fish. pp. 1–99. *In*: W.S. Hoar & D.J. Randall (ed.) Fish Physiology, vol. 6, Academic Press, New York.

Gray, I.E. 1954. Comparative study of the gill area of marine fishes. Biol. Bull. (Woods Hole) 107: 219–225.

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

Gunderson, D. 1971. Reproductive patterns of Pacific ocean perch (*Sebastodes alutus*) off Washington and British Columbia and their relation to bathymetric distribution and seasonal abundance. J. Fish. Res. Board Can. 28: 417–425.

Gunderson, D.R., P. Callahan & B. Goiney. 1980. Maturation and fecundity of four species of *Sebastes*. Mar. Fish. Rev. 42: 74–79.

Kusakari, M. 1978. Mariculture experiments for mass production of juvenile *Sebastes schlegeli*. pp. 117–139. *In*: Annu. Rep. Hokkaido Inst. Mariculture.

Kusakari, M. 1991. Mariculture of kurosoi, *Sebastes schlegeli*. Env. Biol. Fish. 30: 245–251.

Larson, R.J. 1980. Influence of territoriality on adult density in two rockfishes of the genus *Sebastes*. Mar. Biol. (Berl.) 58: 123–132.

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

Moser, H.G. 1967a. Reproduction and development of *Sebastodes paucispinis* and comparison with other rockfishes off southern California. Copeia 1967: 773–797.

Moser, H.G. 1967b. Seasonal histological changes in the gonads of *Sebastodes paucispinis* Ayres, an ovoviviparous teleost (Family Scorpaenidae). J. Morph. 123: 329–353.

Muir, B.S. & A.J. Niimi. 1972. Oxygen consumption of the euryhaline fish aholehole (*Kuhlia sandvicensis*) with reference to salinity, swimming, and food consumption. J. Fish. Res. Board Can. 29: 67–77.

Nakanishi, T. 1991. Ontogeny of the immune system in *Sebastiscus marmoratus*: histogenesis of the lymphoid organs and effects of thymectomy. Env. Biol. Fish. 30: 135–145.

Parrish, R.H., C.S. Nelson & A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California current. Biol. Oceanogr. 1: 175–203.

Pauly, D. 1981. The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. Meeresforsch. Rep. Mar. Res. 28: 251–282.

Priede, I.G. 1985. Metabolic scope in fishes. pp. 33–64. *In*: P. Tytler & P. Calow (ed.) Fish Energetics: New Perspectives, Johns Hopkins University Press, Baltimore.

Sorokin, V.P. 1961. The redfish: gametogenesis and migrations of the *Sebastes marinus* (L.) and *Sebastes mentella* Travin. Rapp. P. -V. Reun. Cons. Int. Explor. Mer 150: 245–250.

Trexler, J.C. 1985. Variation in the degree of viviparity in the sailfin molly, *Poecilia latipinna*. Copeia 1985: 999–1004.

Vahl, O. & J. Davenport. 1979. Apparent specific dynamic action of food in the fish *Blennius pholis*. Mar. Ecol. Prog. Ser. 1: 109–113.

Ware, D.M. 1975. Relation between egg size, growth, and natural mortality of larval fish. J. Fish. Res. Board Can. 32: 2503–2512.

Webb, P.W. & J.R. Brett. 1972. Oxygen consumption of embryos and parents, and oxygen transfer characteristics within the ovary of two species of viviparous seaperch, *Rhacochilus vacca* and *Embiotoca lateralis*. J. Fish. Res. Board Can. 29: 1543–1553.

Wootton, R.J. 1973. The effect of size of food ration on egg production in the female three-spined stickleback, *Gasterosteus aculeatus*. J. Fish Biol. 5: 89–96.

Wootton, R.J. 1985. Energetics of reproduction. pp. 231–254. *In*: P. Tytler & P. Calow (ed.) Fish Energetics: New Perspectives, Johns Hopkins University Press, Baltimore.

Yamada, J. & M. Kusakari. 1991. Staging and the time course of embryonic development in kurosoi, *Sebastes schlegeli*. Env. Biol. Fish. 30: 103–110.