(in press) located two radio-tagged fish there in 1988. One of the two, an 82.4 cm TL adult, was caught and released approx. 10 km upstream from the Yampa River. Our collection site near Baggs is 125 air km from the Yampa River (perhaps 250 river km because the Little Snake meanders extensively), a distance often traveled by squawfish in the Green River system (Tyus, 1985, 1986). It is, thus, uncertain whether the Baggs specimen was a permanent or temporary Little Snake resident.

More rigorous, long-term sampling of the Little Snake River may lead to a reassessment of the status of other "extinct" native fishes in Wyoming. Humpback chubs were recently discovered in the lower Little Snake River in Colorado (Wick et al., in press). Razorback sucker and possibly bonytail occur in the Yampa River, and these species may also be upstream as well. Regardless, suitable habitat at least for adult big-river fishes remains available in the Little Snake River of Wyoming, and our capture of Colorado squawfish there is positive evidence for that species. The Little Snake River, thus, may be amenable to habitat improvement (for example, by augmentation of depleted flows) in behalf of endangered fishes, and should be considered among potential recovery sites for these "extinct" native fishes.

Acknowledgments.—Collections were under Wyoming Game and Fish Department permit number 125; assistance of M. Stone and J. Longobardi of that agency is appreciated.

Literature Cited

BAXTER, G. T., AND J. R. SIMON. 1970. Wyoming fishes. Wyoming Game Fish Dept., Cheyenne.

HOLDEN, P. B. 1991. Ghosts of the Green River: impacts of Green River poisoning on management of native fishes, p. 43–54, + lit. cited. *In:* Battle against extinction: native fish management in the American West. W. L. Minckley and J. E. Deacon (eds.). Univ. of Arizona Press, Tucson.

JOHNSON, J. E. 1987. Protected fishes of the United States and Canada. Amer. Fish. Soc., Bethesda, Maryland.

MILLER, R. R. 1961. Man and the changing fish fauna of the American Southwest. Pap. Mich. Acad. Sci., Arts, Lett. 46:365–404.

SEETHALER, K. 1978. Life history and ecology of the Colorado squawfish (*Ptychocheilus lucius*) in the upper Colorado River basin. Unpubl. Master's thesis, Utah State Univ., Logan.

TYUS, H. M. 1985. Homing behavior noted for Colorado squawfish. Copeia 1985:213–215.

———. 1986. Life strategies in the evolution of the Colorado squawfish (*Ptychocheilus lucius*). Great Bas. Nat. 46:656–661.

———. 1991. Ecology and management of Colorado squawfish, p. 379–402 + lit. cited. *In:* Battle against extinction: native fish management in the American West. W. L. Minckley and J. E. Deacon (eds.). Univ. of Arizona Press, Tucson.

U.S. FISH AND WILDLIFE SERVICE. 1989. Endangered and threatened wildlife and plants. Code Fed. Regs. 50 Title 17:1–69.

———. 1990. Endangered and threatened wildlife and plants; proposal to determine the razorback sucker (*Xyrauchen texanus*) to be an endangered species. Fed. Regist. 55:21154--21161.

U.S. GEOLOGICAL SURVEY. 1985. Water resources data for Wyoming, water year 1985. U.S. Geol. Surv., Denver, Colorado.

WICK, E. J., J. A. HAWKINS, AND T. P. NESLER. In press. Occurrence of two endangered fishes in the Little Snake River, Colorado. Southwest. Nat.

WILLIAMS, J. E., D. B. BOWMAN, J. E. BROOKS, A. A. ECHELLE, R. J. EDWARDS, D. A. HENDRICKSON, AND J. J. LANDYE. 1985. Endangered aquatic ecosystems in North American deserts with a list of vanishing fishes of the region. J. Arizona-Nevada Acad. Sci. 20:1–62.

PAUL C. MARSH, *Center for Environmental Studies, Arizona State University, Tempe, Arizona 85287-3211,* AND MICHAEL E. DOUGLAS, W. L. MINCKLEY, AND ROSS J. TIMMONS, *Department of Zoology and Museum, Arizona State University, Tempe, Arizona 85287-1501.*

Copeia, 1991(4), pp. 1092–1098

MEASURING PARENTAL INVESTMENT IN NONSPHERICAL EGGS.—The growing body of life-history information on fishes has prompted an increase in the number of comparative studies attempting to find patterns in this data (Moser et al., 1984; Gross, 1987; Mitton and Lewis, 1989). Egg size is a commonly reported and examined life-history parameter because it provides an estimate of parental investment in offspring. The ideal measure of this investment is egg mass or egg volume; however, it is frequently impractical (or impossible) to directly measure these values because of the small size of many fish eggs or the lack of suitable instruments. Therefore, the most commonly reported measure of egg size is egg diameter (Breder and Rosen, 1966; Moser et al.,

1984) because this can often be measured using calipers or by a microscope fitted with an ocular micrometer. Unfortunately, egg diameter only properly applies to spherical eggs, and many fishes lay eggs that are nonspherical (Breder, 1943). For example, ellipsoidal eggs are found in at least two dozen families of fishes (Table 1). Several other egg shapes are also found, though much less commonly. Eggs of some species of Gobiesocidae, Blenniidae, and Tripterygiidae are hemispherical (pers. obs.; Breder and Rosen, 1966; Thresher, 1984) whereas other gobiesocid eggs are generalized ellipsoids. There are also some irregularly shaped fish eggs: some Syngnathidae have pear-shaped eggs (Fritzsche, 1984); the darters of the percid genus *Microperca* produce eggs with a distinct indentation on one side (Burr and Ellinger, 1980); and the eggs of many gobies cannot be described by any regular geometric shape (Breder, 1943). In some cases, the departure from a spherical shape is not significant, but for others the shapes of nonspherical eggs present problems for studies of egg size because measurements of these eggs cannot be directly compared with those of spherical eggs. Previous researchers have dealt with this problem by using the length of the longest axis of the egg, or by averaging the lengths of the long and short axes to obtain a linear measure of egg size. Both of these methods will overestimate the size of nonspherical eggs. Herein, I propose an alternate measure for nonspherical egg shapes that can be used to compare these eggs with spherical eggs.

Nonspherical eggs can be compared with spherical eggs by calculating the "effective diameter" of nonspherical eggs. The effective diameter is the diameter the egg would be if it were reshaped into a sphere of the same volume as the nonspherical egg. Most nonspherical eggs are referred to as ellipsoidal. Such an egg has a long major axis and two minor axes of equivalent length and resembles a sphere stretched along one axis. This shape is technically called a prolate spheroid, but I will refer to it as an ellipsoid in keeping with common practice. The volume of an ellipsoidal egg, assuming a major axis of length a and minor axes of length b, is given by

$$V = \tfrac{4}{3}\pi(\tfrac{1}{2}a)(\tfrac{1}{2}b)^2 = \tfrac{1}{6}\pi ab^2. \qquad [1]$$

The volume of a spherical egg of diameter d is

$$V = \tfrac{1}{6}\pi d^3. \qquad [2]$$

Setting [1] and [2] equal to each other, we derive a formula for the effective diameter (d_e) of an ellipsoidal egg:

$$d_e = [ab^2]^{1/3}. \qquad [3]$$

Using formula [3], it is possible to calculate the effective diameter of ellipsoidal eggs given the lengths of the major and minor axes. Because in many cases these axis lengths have been reported in the literature, new data need not be collected to calculate the effective diameter. The effective diameters of these eggs can then be compared directly with the diameters of spherical eggs. If desired, effective diameter can easily be converted to volume using equation [2]. Table 1 provides the axes lengths and effective diameters for some ellipsoidal eggs. Note that, as the ratio of major to minor axis length increases, so too does the error from using their average as the measure of diameter.

It is possible to derive similar formulae for other nonspherical egg shapes (Table 2). Oblate spheroids have two major axes of equal length and one minor axis (disc shaped). It is not known whether any fish eggs truly are of this shape, though some gobiesocid eggs might be (Breder, 1943). A few eggs are generalized ellipsoids, meaning that they have three axes, each of different length. The clingfish, *Gobiesox strumosus*, has axes of 0.94, 0.79, and 0.67 mm (Runyan, 1961) for an effective diameter of 0.79 mm. *Blennius galerita* has hemispherical eggs with a basal diameter of 2.0 mm (Breder and Rosen, 1966). The effective diameter of these eggs is 1.6 mm.

Future comparative studies of fish egg size should use the effective diameter of nonspherical eggs in their analyses, rather than averaging the axes, or using only the longest axis. Similarly, researchers examining nonspherical eggs should endeavor to report the lengths of the major and minor axes, not just the longest axis as is commonly done, to aid future comparative studies. Furthermore, it is also necessary to report whether the eggs were taken from the ovary, were found after laying, and whether they were water hardened or preserved. Frequently this information is not provided, and it can make a substantial difference to egg size (Fleming and Ng, 1987).

For comparative studies involving egg size and linear values such as fish length, effective diameter provides a convenient linear measure of egg size. However, for comparisons involving three-dimensional values such as fish weight,

TABLE 1. MEASUREMENTS OF SOME ELLIPSOIDAL EGGS. Ratio is the ratio of the major axis to the minor axis. d_e (effective diameter) is explained in the text. The d_e for some Gobiidae is only approximate because some of these eggs depart from an ellipsoidal shape. Ellipsoidal eggs are also found in the Salmonidae (Fleming and Ng, 1987), Aplocheilidae (Able, 1984), Aulorhyncidae (Breder and Rosen, 1966), Ostraciidae (Aboussouan and Leis, 1984), Scaridae (Winn and Bardach, 1960), Bothidae and Soleidae (Ahlstrom et al., 1984), but quantitative data were not available.

Species	Major axis (mm)	Minor axis (mm)	Ratio	d_e (mm)	Reference[a]
Petromyzontidae					
Entosphenus tridentatus	1.18	1.07	1.1	1.11	16
Lampetra richardsoni	1.09	1.03	1.1	1.05	16
Amiidae					
Amia calva	2.8	2.2	1.3	2.38	4
Engraulididae					
Anchoa hepsetus	1.5	0.69	2.2	0.89	3
Anchoa mitchilli	0.84	0.65	1.3	0.71	11
Anchoviella argyrophana	1.2	0.68	1.8	0.82	3
Anchoviella tri	1.73	0.58	3.0	0.83	4
Cetengraulis mysticetus	1.2	0.6	2.0	0.76	4
Engraulis austalis	1.13	0.55	2.1	0.70	3
Engraulis capensis	1.55	1.02	1.5	1.17	3
Engraulis encrasicholus	1.37	0.81	1.7	0.97	3
Engraulis japonicus	1.4	0.62	2.3	0.81	3
Engraulis mordax	1.34	0.66	2.0	0.84	10
Stolephorus baganensis	1.24	0.72	1.7	0.86	3
Stolephorus heterolobus	1.23	0.60	2.1	0.76	3
Stolephorus indicus	1.15	0.81	1.4	0.91	11
Stolephorus insularis	1.92	0.69	2.8	0.97	11
Stolephorus zollingeri	1.13	0.55	2.1	0.70	3
Stolephorus tri	1.25	0.68	1.8	0.83	3
Cyprinidae					
Acheilognathus cyanostigma	3.69	1.07	3.4	1.62	4
Acheilognathus tabira	2.01	1.31	1.5	1.51	4
Pseudorasbora parva	1.7	1.1	1.5	1.27	4
Rhodeus armarus	2.5	1.27	2.0	1.59	4
Clariidae					
Clarias mossambicus	2.0	1.5	1.3	1.7	4
Ophidiidae					
Ophidion scrippsae	1.06	1.00	1.1	1.02	10
Carapidae					
Carapus acus	0.9	0.75	1.2	0.80	3
Carapus dentatus	1.32	1.05	1.3	1.13	3
Antennariidae					
Histrio histrio	0.7	0.6	1.2	0.63	19
Scomberesocidae					
Cololabis saira	1.83	1.56	1.2	1.65	4
Scomberesox saurus	2.52	2.32	1.1	2.38	5
Syngnathidae					
Hippocampus abdominalis	2.3	1.4	1.6	1.7	4
Syngnathus schlegeli	1.24	1.0	1.2	1.1	4
Dactylopteridae					
Dactylopterus volitans	0.80	0.72	1.1	0.75	3

TABLE 1. CONTINUED.

Species	Major axis (mm)	Minor axis (mm)	Ratio	d_e (mm)	Reference[a]
Scorpaenidae					
Scorpaena guttata	1.26	1.18	1.1	1.21	20
Scorpaena notata	0.88	0.76	1.2	0.80	20
Scorpaena porcus	0.92	0.84	1.1	0.87	20
Scorpaena scrofa	0.88	0.68	1.3	0.74	20
Plesiopidae					
Plesiops semeion	0.9	0.6	1.5	0.69	4
Cichlidae					
Cichlasoma cyanoguttatum	2.2	1.7	1.3	1.85	1
Cichlasoma nigrofasciatum	2.5	1.9	1.3	2.08	1
Tilapia esculenta	4.5	4.0	1.1	4.16	6
Tilapia galilaea	3.0	2.2	1.4	2.44	6
Tilapia karamo	5.2	4.5	1.2	4.72	6
Tilapia macrocephala	2.9	2.3	1.3	2.48	3
Pomacentridae					
Abudefduf saxatalis	0.95	0.55	1.7	0.66	17
Amphiprion chrysopterus	2.4	0.9	2.7	1.25	2
Amphiprion percula	2.2	0.91	2.4	1.22	3
Amphiprion bicinctus	3.3	1.2	2.8	1.68	4
Chromis caerulus	0.63	0.46	1.4	0.51	18
Chromis dispilus	1.0	0.61	1.6	0.72	8
Chromis multilineata	0.6	0.5	1.2	0.53	12
Chromis notatus	0.76	0.58	1.3	0.63	4
Dascyllus trimaculatus	0.70	0.49	1.4	0.55	7
Heliastes chromis	0.72	0.50	1.4	0.56	3
Pomacentrus leucorus	0.85	0.45	1.9	0.56	3
Pomacentrus leucostictus	0.8	0.40	2.0	0.50	3
Blenniidae					
Blennius inaequallis	0.78	0.62	1.3	0.67	3
Blennius palmicornis	1.25	1.08	1.2	1.13	3
Blennius pavo	1.2	1.04	1.2	1.09	3
Ecsenius bicolor	0.75	0.5	1.5	0.57	19
Petroscirtes bhattacharyae	0.80	0.53	1.5	0.61	4
Schindleriidae					
Schindleria pietschmanni	1.30	0.50	2.6	0.69	21
Ammodytidae					
Ammodytes laneolatus	0.8	0.3	2.7	0.42	3
Ammodytes tobianus	0.8	0.3	2.7	0.42	3
Eleotrididae					
Eleotris oxycephala	0.40	0.32	1.3	0.34	15
Mogurnda mogurnda	2.6	0.9	2.9	1.28	4
Parioglossus taeniatus	1.3	0.6	2.2	0.78	4
Gobiidae					
Acanthogobius flavimanus	5.5	0.9	6.1	1.65	15
Acentrogobius neilli	0.4	0.14	2.9	0.20	3
Acentrogobius masago	1.2	0.4	3.0	0.58	4
Aphia minuta	1.0	0.8	1.3	0.86	3
Bathygobius soporator	2.39	0.41	5.8	0.74	3
Chaenogobius urotaenia	3.0	1.0	3.0	1.44	4
Chaeturichthys hexanema	2.9	0.8	3.6	1.23	4

TABLE 1. CONTINUED.

Species	Major axis (mm)	Minor axis (mm)	Ratio	d_c (mm)	Reference[a]
Chasmichthys dolichognathus	4.15	1.35	3.1	1.96	3
Chasmichthys gulosus	4.65	1.22	3.8	1.91	3
Clevelandia ios	0.74	0.57	1.3	0.62	4
Crystallogobius nilssoni	1.78	0.57	3.1	0.83	3
Ctenogobius bergi	4.0	1.1	3.6	1.69	4
Ctenogobius dotui	2.0	0.4	5.0	0.68	4
Eutaenichthys gilli	2.7	0.8	3.4	1.20	4
Evorthodus lyricus	0.45	0.20	2.3	0.26	15
Glossogobius brunneus	3.5	1.05	3.3	1.57	3
Gobiosoma bosci	1.26	0.44	2.9	0.62	3
Gobiosoma robustum	1.5	0.53	2.8	0.75	3
Gobius ferrugineus	1.0	0.72	1.4	0.80	3
Gobius flavescens	0.7	0.57	1.2	0.61	3
Gobius jozo	2.8	0.62	4.5	1.02	3
Gobius lidwilli	1.2	0.7	1.7	0.84	4
Gobius microps	0.9	0.68	1.3	0.75	3
Gobius niger	1.17	0.28	4.2	0.45	3
Gobius minutus	1.0	0.55	1.8	0.67	3
Gobius nudiceps	1.8	0.97	1.9	1.19	3
Gobius ostreicala	1.8	0.45	4.0	0.71	4
Gobius paganellus	2.24	0.80	2.8	1.13	3
Gobius pictus	0.8	0.62	1.3	0.67	3
Luciogobius guttatus	2.5	0.7	3.6	1.07	4
Luciogobius saikaiensis	3.0	1.3	2.3	1.72	4
Mistichthys luzonensis	0.5	0.09	5.6	0.16	3
Percottus glehni	3.8	1.3	2.9	1.86	15
Periophthalmus barbarus	0.76	0.61	1.2	0.66	4
Pterogobius elapoides	2.3	0.8	2.9	1.14	4
Pterogobius zonoleucus	2.1	0.6	3.5	0.91	4
Rhinogobius similis	2.5	0.63	4.0	1.00	4
Stigmatogobius hoevenii	2.83	1.25	2.3	1.64	3
Triaenopogon barbatus	1.5	0.5	3.0	0.72	4
Tridentiger undicerneus	1.15	0.45	2.6	0.62	4
Tridentiger trigonacephalus	1.4	0.6	2.3	0.80	4
Typhlogobius californiensis	0.83	0.75	1.1	0.78	9
Gobioididae					
Taenioides rubicundus	1.3	0.7	1.9	0.86	15
Gobiesocidae					
Chorisochismus dentex	1.47	0.92	1.6	1.08	3
Lepadogaster bimaculatus	1.37	1.08	1.3	1.17	3
Lepadogaster candollii	1.24	1.07	1.2	1.12	3
Lepadogaster gouani	1.8	1.50	1.2	1.59	3
Lepadogaster lepadogaster	1.8	1.5	1.2	1.60	4
Trachelochismus melobesia	1.65	1.35	1.2	1.44	13
Trachelochismus pinnulatus	1.81	1.48	1.2	1.58	13
Alabetidae					
Alabes rufus	1.2	1.0	1.2	1.06	4

[a] 1—pers. obs.; 2—Allen, 1975; 3—Breder, 1943; 4—Breder and Rosen, 1966; 5—Collette et al., 1984; 6—Fryer and Iles, 1972; 7—Garnaud, 1957; 8—Kingsford, 1985; 9—MacGinitie, 1939; 10—Matarese and Sandknop, 1984; 11—McGowan and Berry, 1984; 12—Myrberg et al., 1967; 13—Ruck, 1971; 14—Ruck, 1973; 15—Ruple, 1984; 16—Scott and Crossman, 1979; 17—Shaw, 1955; 18—Swerdloff, 1970; 19—Thresher, 1984; 20—Washington et al., 1984; 21—Watson et al., 1984.

TABLE 2. FORMULAE FOR CALCULATING THE VOLUME AND EFFECTIVE DIAMETER (d_e) OF SEVERAL NONSPHERICAL EGG SHAPES.

Egg shape	Description	Volume	d_e
Ellipsoid (prolate spheroid)	1 major axis (a) 2 minor axes (b) of equal length	$\frac{4}{3}\pi(\frac{1}{2}a)(\frac{1}{2}b)^2$	$[ab^2]^{1/3}$
Oblate spheroid	2 major axes (a) of equal length 1 minor axis (b)	$\frac{4}{3}\pi(\frac{1}{2}a)^2(\frac{1}{2}b)$	$[a^2b]^{1/3}$
Generalized ellipsoid	3 unequal axes (a,b,c)	$\frac{4}{3}\pi abc$	$[abc]^{1/3}$
Hemispheroid	1 major axis (a)	$\frac{1}{12}\pi a^3$	$0.79a$

egg volume is a more appropriate measure of egg size. Effective diameter can easily be converted to volume, and vice versa (using equation [2]).

Egg size is only a first step toward understanding parental investment in fish eggs. It is important that parental investment research questions be explicit about exactly what is being compared. For example, if the question concerns the quantity of material from which the offspring forms its body, then egg size is a reasonable starting value for comparisons. On the other hand, if the question concerns the quantity of investment that the parent puts into each egg, then the analysis should properly include not only the investment in the egg contents but also any attachment devices (e.g., hooks, filaments) or external casings (e.g., the raft structure of anglerfishes, the egg cases of many sharks) surrounding the egg. These extras can be much larger than the actual eggs (Thresher, 1984), and few if any data exist to quantify investment in these structures.

Acknowledgments.—I was supported by a University of Toronto Doctoral Fellowship, and the research was supported in part by an NSERC of Canada Operating Grant to M. R. Gross.

LITERATURE CITED

ABLE, K. W. 1984. Cyprinodontiformes: development, p. 362–368. *In:* Ontogeny and systematics of fishes. H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson (eds.). Am. Soc. Ich. Herp. Spec. Publ. 1.

ABOUSSOUAN, A., AND J. M. LEIS. 1984. Balistoidei: development, p. 450–459. *In:* Ontogeny and systematics of fishes. H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson (eds.). *Ibid.* 1.

AHLSTROM, E. H., K. AMAOKA, D. A. HENSLEY, H. G. MOSER, AND B. Y. SUMIDA. 1984. Pleuronectiformes: development, 640–670. *In:* Ontogeny and systematics of fishes. H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson (eds.). *Ibid.* 1.

ALLEN, G. R. 1975. Anemonefishes (2d ed.). T.F.H. Publications, Neptune, New Jersey.

BREDER, C. M., JR. 1943. The eggs of *Bathygobius soporator* (Cuvier and Valenciennes) with a discussion of other non-spherical teleost eggs. Bull. Bingham Oceanogr. Coll. 8:1–49.

———, AND D. E. ROSEN. 1966. Modes of reproduction in fishes. Natural History Press, Garden City, New York.

BURR, B. M., AND M. S. ELLINGER. 1980. Distinctive egg morphology and its relationship to development in the percid fish *Etheostoma proeliare.* Copeia 1980:556–559.

COLLETTE, B. B., G. E. MCGOWEN, N. V. PARIN, AND S. MITO. 1984. Beloniformes: development and relationships, p. 335–354. *In:* Ontogeny and systematics of fishes. H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson (eds.). Am. Soc. Ich. Herp. Spec. Publ. 1.

FLEMING, I. A., AND S. NG. 1987. Evaluation of techniques for fixing, preserving, and measuring salmon eggs. Can. J. Fish. Aquat. Sci. 44:1957–1962.

FRITZSCHE, R. A. 1984. Gasterosteiformes: development and relationships, p. 398–405. *In:* Ontogeny and systematics of fishes. H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson (eds.). Am. Soc. Ich. Herp. Spec. Publ. 1.

FRYER, G., AND T. D. ILES. 1972. The Cichlid fishes of the Great Lakes of Africa. T.F.H. Publications, Neptune, New Jersey.

GARNAUD, J. 1957. Ethologie de *Dascyllus trimaculatus* (Ruppell). Bull. Inst. Oceanogr. Monaco 1096: 1–10.

GROSS, M. R. 1987. Evolution of diadromy in fishes. Am. Fish. Soc. Symp. 1:14–25.

KINGSFORD, M. J. 1985. The demersal eggs and planktonic larvae of *Chromis dispilus* (Teleostei: Pomacentridae) in north-eastern New Zealand coastal waters. N. Z. J. Mar. Freshwater Res. 19:429–438.

MACGINITIE, G. E. 1939. The natural history of the blind goby, *Typhlogobius californiensis* Steindachner. Am. Midl. Nat. 21:489–505.

MATARESE, A. C., AND E. M. SANDKNOP. 1984. Identification of fish eggs, p. 27–31. *In:* Ontogeny and systematics of fishes. H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson (eds.). Am. Soc. Ich. Herp. Spec. Publ. 1.

MCGOWAN, M. F., AND F. H. BERRY. 1984. Clupeiformes: development and relationships, p. 108–126. *In:* Ontogeny and systematics of fishes. H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson (eds.). *Ibid.* 1.

MITTON, J. B., AND W. M. LEWIS, JR. 1989. Relationships between genetic variability and life-history features of bony fishes. Evolution 43:1712–1723.

MOSER, H. G., W. J. RICHARDS, D. M. COHEN, M. P. FAHAY, A. W. KENDALL, JR., AND S. L. RICHARDSON (eds.). 1984. Ontogeny and systematics of fishes. Am. Soc. Ich. Herp. Spec. Publ. 1.

MYRBERG, A. A., JR., B. D. BRAHY, AND A. R. EMERY. 1967. Field observations on reproduction of the damselfish, *Chromis multilineata* (Pomacentridae), with additional notes on general behavior. Copeia 1967:819–827.

RUCK, J. G. 1971. Development of the lumpfish, *Trachelochismus melobesia* (Pisces: Gobiesocidae). Zool. Publ. Vict. Univ. Wellington 57:1–9.

———. 1973. Development of the clingfishes, *Diplocrepis puniceus* and *Trachelochismus pinnulatus* (Pisces: Gobiesocidae). *Ibid.* 64:1–12.

RUNYAN, S. 1961. Early development of the clingfish, *Gobiesox strumosus* Cope. Chesapeake Sci. 2:113–141.

RUPLE, D. 1984. Gobioidei: development, p. 582–591. *In:* Ontogeny and systematics of fishes. H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson (eds.). Am. Soc. Ich. Herp. Spec. Publ. 1.

SCOTT, W. B., AND E. J. CROSSMAN. 1979. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 1–966.

SHAW, E. S. 1955. The embryology of the sergeant major, *Abudefduf saxatalis.* Copeia 1955:85–89.

SWERDLOFF, S. N. 1970. Behavioral observations on Eniwetok damselfishes (Pomacentridae: *Chromis*) with special reference to the spawning of *Chromis caeruleus.* Copeia 1970:371–374.

THRESHER, R. E. 1984. Reproduction in reef fishes. T.F.H. Publications, Neptune, New Jersey.

WASHINGTON, B. B., H. G. MOSER, W. A. LAROCHE, AND W. J. RICHARDS. 1984. Scorpaeniformes: development, p. 405–428. *In:* Ontogeny and systematics of fishes. H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson (eds.). Am. Soc. Ich. Herp. Spec. Publ. 1.

WATSON, W., E. G. STEVENS, AND A. C. MATARESE. 1984. Schindlerioidei: development and relationships, p. 552–554. *In:* Ontogeny and systematics of fishes. H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson (eds.). *Ibid.* 1.

WINN, H. E., AND J. E. BARDACH. 1960. Some aspects of the comparative biology of parrot fishes at Bermuda. Zoologica (New York) 45:29–34.

R. M. COLEMAN, *Department of Zoology, University of Toronto, Toronto, Ontario M5S 1A1, Canada.*
Accepted 11 Oct. 1990.

Copeia, 1991(4), pp. 1098–1104

TROUT FORAGING FAILURES AND THE EVOLUTION OF BODY SIZE IN STICKLEBACK.—One advantage to increased adult size in fishes is defense against gape-limited piscivores (Popova, 1967; Zaret, 1980). Handling time increases sharply as size of prey approaches maximum swallowing ability of a predator (Werner, 1974; Hoyle and Keast, 1987, 1988), and the implicit advantage to prey in these conditions is that their escape probabilities are improved. However reasonable this assumed advantage, there remains little experimental data that have addressed the relationships between predator foraging failures and increased body size of the prey during pursuit and manipulation. Such failures are fundamental to the evolution of defenses against predators (Vermeij, 1982).

Threespine stickleback (*Gasterosteus aculeatus* vary from 30–60 mm SL over their European and North American distribution (Wootton, 1984 for review), but in several disjunct lake populations in western North America, gigantism occurs, with adults ranging from 80–115 mm (Moodie, 1972a; Moodie and Reimchen, 1976; Bell, 1984). Attributes of morphology and life history, including strong predation pressure, of the giant form in Mayer Lake led Moodie (1972b) to suggest that large body size was an adaptation against trout predators. At a different lake population where gigantism also occurs, predation by cutthroat trout (*Oncorhynchus clarki*) was prevalent (Reimchen, 1990). Adult stickleback appeared to be a less preferred prey than subadults and juveniles, suggesting an advantage to large size. Yet these predators could simply be consuming each size class of stickleback in proportion to the abundance in the population, and as such no size-refuge may be involved. As a separate method to evaluate size