Trout Foraging Failures and the Evolution of Body Size in Stickleback
Author(s): T. E. Reimchen
Source: *Copeia*, Vol. 1991, No. 4 (Dec. 13, 1991), pp. 1098-1104
Published by: American Society of Ichthyologists and Herpetologists
Stable URL: http://www.jstor.org/stable/1446106
Accessed: 18/01/2009 09:22

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/action/showPublisher?publisherCode=asih.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.

American Society of Ichthyologists and Herpetologists is collaborating with JSTOR to digitize, preserve and extend access to *Copeia*.

http://www.jstor.org

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 and predator defense, I recorded incidence of predator-induced injuries of wild stickleback and observed a major increase in injuries among the largest fish. This could indicate that larger stickleback were more likely to escape during trout manipulation than smaller individuals; yet even with the same injury rate among size classes, injury rate would increase with size because larger individuals are older and would have greater opportunities to accumulate injuries (Reimchen, 1988). Consequently, we have no direct evidence that large body size provides a size-refuge from predators or that size-related selection has occurred.

I consider here experimental foraging efficiencies of cutthroat trout during pursuit and manipulation for different body sizes of threespine stickleback. Does large adult body size of stickleback provide a refuge for the size range of trout predators observed in the locality, and what is the association between evasion rate and relative body size of prey and predator?

Methods.—The research was carried out at Drizzle Lake, Queen Charlotte Islands, British Columbia, site of ongoing investigations on sources of mortality and selective forces in the life history of giant stickleback (Reimchen, 1983, 1990; Reimchen and Nelson, 1987). I used six trout (SL #1 = 190 mm, #2 = 195 mm, #3 = 210 mm, #4 = 255 mm, #5 = 315 mm, #6 = 340 mm) for the experiments which bracket the average trout size in the lake (240 mm) and which include representatives of the most abundant size classes which forage on stickleback. Small trout (<140 mm) were rare in the lake and did not regularly forage on stickleback (Reimchen, 1990).

Experiments were carried out in circular net enclosures (2 m diameter) anchored in the littoral zone (approx. 0.2 m water depth). Trout would rarely initiate a pursuit if the stickleback were adjacent to the edge of the enclosure, the preferred position of both trout and stickleback, but would occasionally give pursuit if the stickleback swam across the central area. Releasing the stickleback from a net in the middle of the enclosure produced an increased attack rate, but the trout were disturbed by movement of the net. After experimenting with several release methods, I found that the most consistent method of eliciting an attack was to release stickleback into the center of the enclosure from above the surface (approx. 0.5 m). Immediately upon entry into the water, stickleback accelerated quickly toward the edge of the enclosure during which period the trout gave pursuit. If the stickleback reached the edge, the trout usually terminated pursuit. The two largest trout (#5, #6) did not regularly forage in captivity and provided only limited data on attack success. Because both specimens exhibited similar association between prey size and capture success (chi-square = 4.1, df = 3, $P = 0.25$), I have pooled their data.

A second series of experiments were carried out in a glass aquarium (1.2 m length, 0.6 m width, 0.46 m depth) to allow close-range videotaping of attack and manipulation behavior. I used an intermediate-sized trout (210 mm) for this series. Stickleback were placed in a small net which was held at the surface and then inverted. The stickleback accelerated quickly toward the bottom, and the trout gave pursuit.

In all foraging events, I recorded the outcome of two separate phases: pursuit and, if capture occurred, manipulation.

A. Pursuit phase:

1. Prey rejection—trout approaches stickleback but veers away prior to contact or pursues stickleback briefly before veering away.
2. Prey escape—trout pursues stickleback but stickleback reaches safety at edge of enclosure.
3. Capture—trout seizes stickleback in jaws.

B. Manipulation phase:

1. Prey rejection—stickleback escapes or is released from mouth and trout does not pursue or exhibit further interest.
2. Prey escape—stickleback escapes or is temporarily released from mouth, is pursued by trout, but reaches safety of enclosure's edge.
3. Eaten—stickleback consumed. Total manipulation time recorded, number of recaptures recorded.

For clarity, I use the term "escape" in its narrow connotation, as defined above, to separate it from "rejection." Also, I use "evasion" as a collective term to describe response of the stickleback (escape or rejection) and "failure" to describe response of the trout (escape or rejection).

Over a 10-week period, 1705 stickleback were presented individually to trout of which 124 yielded no detectable responses whereas 1581 produced feeding responses. Trout were not fed to satiation on any day, and consequently, feeding motivation was high throughout the experimental period. Stickleback that had been captured by trout but escaped during manipu-

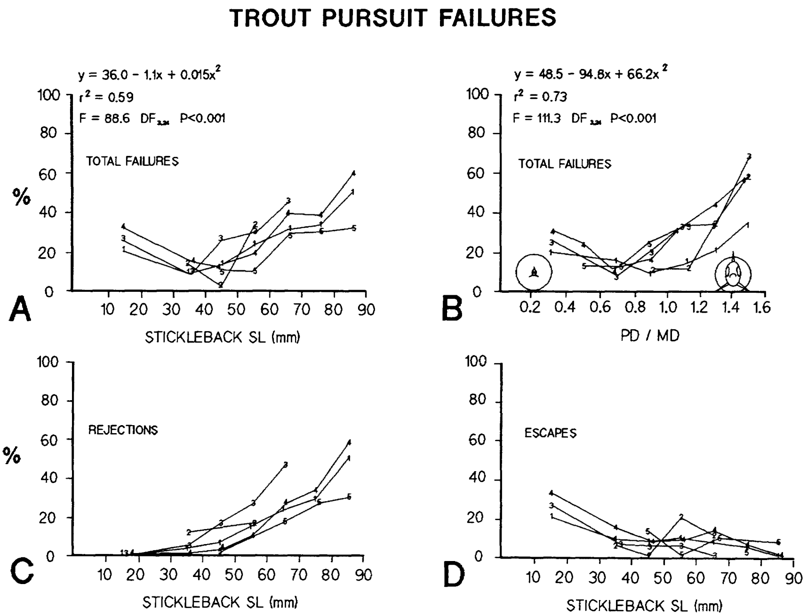

Fig. 1. Incidence of pursuit foraging failures for cutthroat trout. A—Failures in relation to SL of stickleback. B—Failures in relation to PD/MD (prey diameter/mouth diameter of trout). C—Trout rejections in relation to stickleback SL. D—Escapes from trout in relation to stickleback SL. Each line represents results from a different trout (#1—190 mm SL, #2—195 mm, #3—210 mm, #4—255 mm, #5—315 and 340 mm). Inset shows schematic view of stickleback in esophagus of trout for PD/MD ratios of 0.2 and 1.4. Regression lines analyzed with ANOVA.

lation were removed and preserved for analyses of injuries. Those that had evaded capture during pursuit and those to which trout failed to respond were returned to the lake.

Number of foraging events recorded for each trout were #1—464, #2—97, #3—357, #4—514, #5—149. Failure frequencies for each trout were analyzed for absolute size of stickleback. Numbers of stickleback used in each size class were 10–20 mm = 213; 20–30 mm = 11; 30–40 mm = 215; 40–50 mm = 501; 50–60 mm = 278; 60–70 mm = 221; 70–80 mm = 95; 80–90 mm = 47. Because maximum swallowing ability of a gape-limited predator is a function of its jaw width (Werner, 1974), I also used the ratio of prey diameter (PD) to mouth diameter (MD) as a measure of relative size. Mouth diameter of trout was measured as the distance between the posterior tips of the opposing maxillae with the mouth closed. On 12 preserved specimens (range in SL, 120–380 mm), the regression of MD on SL was $MD = -1.347 + 0.111*SL$ ($r^2 = 96\%, P < 0.001$). Potential width of the stickleback approximates the diameter of a circle in contact with the erect dorsal and pelvic spines (Fig. 1B). To determine diameter, I measured body depth, length of second dorsal spine, length of left pelvic spine, and maximum width of ventral plate on 568 individuals collected from the lake (for description of measurements, see Reimchen et al., 1985). On 60 of these fish, I measured angular deflection of the pelvic spine below the horizontal. Average deflection was 20.9 degrees (range 10–30), and there was no significant difference over the size range examined (35 mm–85 mm, r = 0.00). From these values, maximum diameter could then be determined geometrically. Prey diameter was regressed against SL to yield the equation $PD = -8.74 + 0.492*SL$ ($r^2 = 97.4\%$, $P < 0.001$). Potential body diameter is increased 230% by elevation of the dorsal and pelvic spines. Number of stickleback used in each PD/MD grouping were: 0.2–0.4 = 212; 0.4–0.6 = 55; 0.6–0.8 = 288; 0.8–1.0 = 362; 1.0–1.2 = 308; 1.2–1.4 = 165; 1.4–1.8 = 191.

Results.—Pursuit phase: Among all stickleback presented (range in SL, 12–90 mm), 24.5% evaded capture during pursuit by trout. Aver-

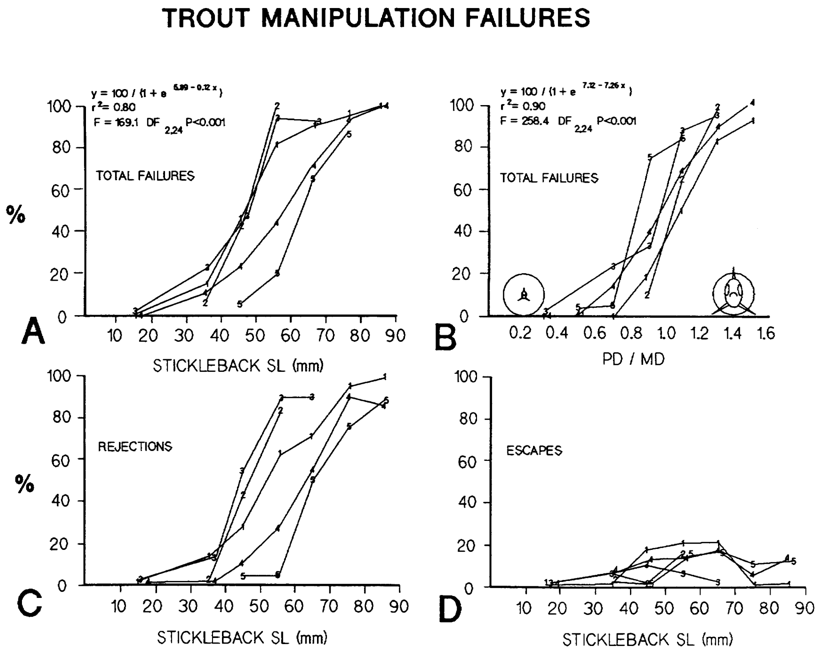

Fig. 2. Incidence of manipulation foraging failures for cutthroat trout. A—Failures in relation to stickleback SL. B—Failures in relation to PD/MD (prey diameter/mouth diameter of predator). C—Trout rejections in relation to stickleback SL. D—Prey escapes in relation to stickleback SL. Each line represents data from a different trout (#1—190 mm SL; #2—195 mm, #3—210 mm, #4—255 mm, #5—315 and 340 mm). Inset shows schematic view of stickleback in esophagus of trout for PD/MD ratios of 0.2 and 1.4. Regression lines analyzed with ANOVA.

age frequency in the enclosure (23.7%, n = 1224) was similar to that in the aquarium (25.2%, n = 357). Failures exhibited a bimodal curve when plotted against stickleback SL with intermediate-sized stickleback (30–50 mm SL) having the lowest incidence of evasions (Fig. 1A). A second order polynomial provided a reasonable statistical fit to the data ($r^2 = 59\%, P < 0.001$). Comparable trends occurred with relative body size (Fig. 1B), also described by a second order equation ($r^2 = 73\%, P < 0.001$). Failure frequencies did not differ substantially between trout (range 22–32%, F-ratio = 0.25 $df_{4,22}$, $P > 0.9$), but as expected, the largest trout were marginally more successful than smaller trout at capturing larger stickleback.

Partitioning pursuit failures showed that, of the 380 failures, 53.7% resulted from trout rejection of the stickleback and 46.3% resulted from active escape of the stickleback. Rejections (Fig. 1C), which were rare for small stickleback (<30 mm), were positively correlated with SL ($r = 0.86, P < 0.001$). The majority of adult stickleback were rejected, even among the largest trout. In contrast, prey escapes (Fig. 1D) were largely independent of length, apart from an increased escape frequency in stickleback fry ($r = -0.59, P = < 0.002$).

Manipulation phase: In total, 1201 stickleback were captured by the trout of which 40.4% were not swallowed (enclosure, 42.5%, n = 934; aquarium, 32.9%, n = 267). Failures by each trout were closely correlated with SL (Fig. 2A) increasing from 0% for the smallest stickleback to 90% for the largest stickleback (>80 mm, $r^2 = 80\%$, $P < 0.001$). The greatest rate of increase in failures occurred for 40–50 mm stickleback in the small trout and for 60–70 mm stickleback in the largest trout.

Total failures plotted against PD/MD ratios (Fig. 2B) yielded similar trends to that observed for SL. I observed no failures where PD/MD was less than 0.4. However, as PD/MD increased, failures increased rapidly to about 90% at PD/MD = 1.4. Each trout exhibited a similar trend.

Partitioning the 491 manipulation failures demonstrated that 75.1% of these were a result of rejection of the prey and 24.9% were active prey escape. Rejections (Fig. 2C) were strongly positively correlated with SL ($r = 0.85$, $P < 0.001$) whereas escapes (Fig. 2D) showed no consistent association ($r = 0.33$, $P = 0.11$).

Discussion.—These experiments demonstrate that body size of stickleback is a major predictor of predator foraging failures. One of the distinctive attributes of *Gasterosteus* is the large dorsal and pelvic spines which function not only to increase body size but also to puncture mouth parts of predators (Hoogland et al., 1957). The spines on the Drizzle Lake stickleback are disproportionately larger than in most other populations (Reimchen et al., 1985) and, when fully erect, produce a cross-sectional profile and diameter (PD) that is 230% greater than original body diameter. Yet, this may not be effective diameter if trout readily fracture the spines and swallow the stickleback. Because manipulation failures of the trout increased sharply when PD approached MD, which is the theoretical maximum swallowing size for a gape-limited predator (Werner, 1974), it is evident that this measure of diameter provides an accurate description of effective body size. Relative protection afforded to adult stickleback, as a consequence of their large size, also was a function of predator size. However, even for the largest trout used in the experiments (315 and 340 mm), adult stickleback still had an 80% chance of evasion during manipulation. Because trout larger than 300 mm are rare in the lake and average size is only 240 mm (Reimchen, 1990), it is clear that the population of adult stickleback would be largely immune from successful trout predation. Analyses of trout stomachs from this locality confirms the low predation levels on adults (Reimchen, 1990). Furthermore, the increased manipulation failures among larger stickleback observed in the experiments predicts a size-dependent increase of injuries (i.e., manipulation failures) in the natural population, which has been observed (Reimchen, 1988). These results support the conclusions of Moodie (1972b) that trout predators will contribute to the maintenance of gigantism in these populations.

Whether trout were the primary selective force leading to the evolution of gigantism or possibly secondary to other factors such as sexual selection remains unknown. The rarity of gigantism in the species combined with the broad geographical distribution of trout and other predatory fish weaken any simple association. McPhail (1977) proposed that large adult size of stickleback would be expected to occur if predatory trout were small because there would be increased likelihood of manipulation failures of larger prey. However, the large size would also be expected if trout were very large, equivalent to an "arms race" between the predator and prey (Vermeij, 1982). Neither prediction is supported by this study given that the average and range of trout sizes observed in Drizzle Lake are typical of those reported for other coastal lakes (Nilsson and Northcote, 1981). Rather than differences in predator size, the relative amount of predation on different size-classes may be critical. Adult body sizes in guppies (*Poecilia reticulata*) from the Caribbean were associated with locality differences in age-specific predation (Reznick and Endler, 1982), with larger body size and delayed reproduction occurring where predation was predominantly on juveniles (Reznick and Bryga, 1987). However, apart from the current study location (Reimchen, 1990), there is relatively little known of the age-specific predation regime in different stickleback populations to evaluate this association.

Predators that are highly efficient at foraging can exert only weak selection on their prey because few prey evade consumption after initial detection (Vermeij, 1982). This may apply to squawfish (*Ptychocheilus oregonense*) and garter snakes (*Thamnophis hammondi*) which exhibited no failures after attacking stickleback (Moodie et al., 1973; Bell and Haglund, 1978). This seems also to apply in the case of cutthroat trout manipulating small stickleback (<40 mm SL); following capture, these stickleback rarely escaped and were rarely rejected. Analyses of predator-induced injuries (i.e., manipulation failures) in the population confirms this experimental result because juvenile stickleback, a major component of the trout diet in this population (Reimchen, 1990), have exceptionally low incidence of injuries (Reimchen, 1988). It follows that postcapture selection on spines, and associated traits such as lateral plates which buttress the spines (Reimchen, 1983), would be weak in these size classes.

Most evasions of the stickleback were due to rejections by the trout, and in both pursuit and manipulations phases, rejections were strongly correlated with body size of the stickleback. It is highly probable that this is a causal relationship because the most rapid increase in rejections occurred when PD approached MD. Active escape of the stickleback from trout was largely unrelated to body size of the stickleback both during pursuit and following capture. The only exception to this was the increased escapes of juvenile stickleback in the pursuit phase. This was unexpected because these recently hatched fry appear highly vulnerable with limited swimming speed. Trout, which were collected in spring, prior to the seasonal recruitment of fry, would not have had direct experience with such small stickleback other than during the previous summer and thus were probably less efficient with these prey. I also observed that evasive maneuvers of juveniles differed from those of larger stickleback. Rather than swimming rapidly away from the trout, as do larger stickleback, a juvenile often remained motionless in the water column as the trout approached, but when the trout was within several centimeters, the juvenile accelerated over or beside the head of the trout and down to the substrate where it remained motionless. Trout were unable to turn at sufficiently sharp angles to follow the stickleback and, therefore, did not usually relocate the prey after completing the turn. Such escape behavior was highly effective and is predicted when predators have a much lower turning radius compared to their prey (Howland, 1974).

Differential predation has been reported on meristic phenotypes in threespine stickleback. Stickleback with seven lateral plates were less frequent than expected in stomachs of field-captured trout (Hagen and Gilbertson, 1973), those with eight lateral plates were more frequent than expected (Moodie, 1972b), and those with five lateral plates had higher survivorship than non-fives when exposed to garter snakes (Bell and Haglund, 1978). Juvenile stickleback with 31 vertebrae were consumed less frequently than those with other vertebral counts (Swain and Lindsey, 1984). Although size was excluded as a source of variation in each of these studies, the striking association between body size and predator failures in the current experiments justifies additional caution. Even a small amount of covariation between body size and meristic traits, as recently shown with vertebral number (Swain and Lindsey, 1984; Reimchen and Nelson, 1987), could confound any interpretations if size was ignored.

In conclusion, these results demonstrate that pursuit and manipulation failures of trout are significantly associated with PD/MD, and these failures are a plausible mechanism for the evolution of gigantism in stickleback. When empirically derived from analyses of predator stomachs, PD/MD ratios may provide a direct estimate of the potential for selection among different populations or size classes.

Acknowledgments.—My appreciation goes to S. D. Douglas and M. A. Bell for comments on the manuscript and to C. Davies, J. B. Foster, N. MacKay, and J. Miller for technical assistance. This work was supported by an operating grant (NRC 2354) from the Natural Sciences and Engineering Research Council of Canada.

LITERATURE CITED

BELL, M. A. 1984. Gigantism in threespine stickleback: implications for causation of body size evolution. Copeia 1984:530–534.

———, AND T. R. HAGLUND. 1978. Selective predation of three-spined sticklebacks *Gasterosteus aculeatus* by garter snakes. Evolution 32:304–319.

HAGEN, D. W., AND L. G. GILBERTSON. 1973. Selective predation and the intensity of selection acting upon the lateral plates of threespine sticklebacks. Heredity 30:273–287.

HOOGLAND, R. D., D. MORRIS, AND N. TINBERGEN. 1957. The spines of sticklebacks (*Gasterosteus* and *Pygosteus*) as a means of defence against predators (*Perca* and *Esox*). Behaviour 10:205–237.

HOWLAND, H. C. 1974. Optimal strategies for predator avoidance: the relative importance of speed and maneuvrability. J. Theor. Biol. 47:333–350.

HOYLE, J. A., AND A. KEAST. 1987. The effect of prey morphology and size on handling time in a piscivore, the largemouth bass (*Micropterus salmoides*). Can. J. Zool. 65:1972–1977.

———, AND ———. 1988. Prey handling time in two piscivores, *Esox lucius* and *Micropterus salmoides*, with contrasting mouth morphologies. *Ibid.* 66:540–542.

MCPHAIL, J. D. 1977. Inherited interpopulation differences in size at first reproduction in threespine stickleback, *Gasterosteus aculeatus* L. Heredity 38: 53–60.

MOODIE, G. E. E. 1972a. Morphology, life history and ecology of an unusual stickleback (*Gasterosteus aculeatus*) in the Queen Charlotte Islands, Canada. Can. J. Zool. 50:721–732.

———. 1972b. Predation, natural selection and adaptation in an unusual stickleback. Heredity 28: 155–167.

———, AND T. E. REIMCHEN. 1976. Phenetic variation and habitat differences in *Gasterosteus* populations of the Queen Charlotte Islands. Syst. Zool. 25:49–61.

———, J. D. MCPHAIL, AND D. W. HAGEN. 1973. Experimental demonstration of selective predation on *Gasterosteus aculeatus*. Behaviour 47:95–105.

NILSSON, N. A., AND T. G. NORTHCOTE. 1981. Rainbow trout (*Salmo gairdneri*) and cutthroat trout *S. clarki*) interactions in coastal British Columbia Lakes. Can. J. Fish. Aquat. Sci. 38:1228–1246.

Popova, O. A. 1967. The "predator-prey" relationship among fishes, p. 359–376. *In:* The biological basis of freshwater fish production. S. D. Gerking (ed.). Blackwell Scientific Publications, Oxford, England, and Edinburgh, Scotland.

Reimchen, T. E. 1983. Structural relationships between spines and lateral plates in threespine stickleback *Gasterosteus aculeatus.* Evolution 37:931–946.

———. 1988. Inefficient predators and prey injuries in a population of giant stickleback. Can. J. Zool. 66:2036–2044.

———. 1990. Size-structured mortality in a stickleback–trout community. Can. J. Fish. Aquat. Sci. 47: 1194–1205.

———, and J. S. Nelson. 1987. Habitat and morphological correlates to vertebral number in a freshwater teleost, *Gasterosteus aculeatus.* Copeia 1987:868–874.

———, E. M. Stinson, and J. S. Nelson. 1985. Multivariate differentiation of parapatric and allopatric populations of threespine stickleback in the Sangan River watershed, Queen Charlotte Islands. Can. J. Zool. 63:2944–2951.

Reznick, D., and J. A. Endler. 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). Evolution 36:160–177.

———, and H. Bryga. 1987. Life-history evolution in guppies: 1. Phenotypic and genotypic changes in an introductory experiment. *Ibid.* 41:1370–1385.

Swain, D. P., and C. C. Lindsey. 1984. Selective predation for vertebral number of young sticklebacks, *Gasterosteus aculeatus.* Can. J. Fish. Aquat. Sci. 41:1231–1233.

Vermeij, G. J. 1982. Unsuccessful predation and evolution. Am. Nat. 120:701–720.

Werner, E. E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. J. Fish. Res. Bd. Canada 31:1531–1536.

Wootton, R. J. 1984. A functional biology of sticklebacks. Univ. of California Press, Berkeley and Los Angeles.

Zaret, T. M. 1980. Predation and freshwater communities. Yale Univ. Press, New Haven, Connecticut and London, England.

T. E. Reimchen, *Department of Biology, University of Victoria, PO Box 1700, Victoria, British Columbia V8W 2Y2, Canada. Field address: Box 970, Queen Charlotte City, British Columbia V0T 1S0, Canada.* Accepted 17 Sept. 1990.

Copeia, 1991(4), pp. 1104–1109

SEASONAL VARIATION IN USAGE OF A COMMON SHELTER RESOURCE BY JUVENILE INQUILINE SNAILFISH (*LIPARIS INQUILINUS*) AND RED HAKE (*UROPHYCIS CHUSS*).—The inquiline snailfish, *Liparis inquilinus,* and the red hake, *Urophycis chuss,* are marine fishes that have overlapping shelter requirements. During the first months after settlement from the plankton, juveniles of each species seek refuge in the mantle cavity of the sea scallop, *Placopecten magellanicus* (Welsh, 1915; Musick, 1969; Able and Musick, 1976). Because both of these fishes are commensals, in the same host species, but not obligate ones, biotic interactions are possible. These interactions would be most apparent during periods of overlap in sea scallop occupancy. Although both fishes have been collected inside as well as outside of sea scallops (Musick, 1969; Able and Musick, 1976), there have been no studies of the seasonal nature of use of the sea scallops by these two fishes, especially during periods of overlap. Here we describe the seasonal pattern of shelter use for these two species associated with a sea scallop population at one location and discuss the implications for the survival of these newly settled fishes.

Liparis inquilinus (Liparidae) ranges from Cape Hatteras, North Carolina, to Nova Scotia, Canada (Able, 1973). Adult *L. inquilinus* spawn in March and April, larvae hatch from demersal eggs in May at 5 mm, and juveniles appear in scallops during July, when the fish are 14–45 mm in total length (Able and Musick, 1976; Able et al., 1986). Snailfish are not found in large numbers in scallops after Nov., and one-year-old fish are thought to migrate inshore to spawn (Able and Musick, 1976).

Urophycis chuss (Gadidae) ranges over the western North Atlantic continental shelf from North Carolina to Nova Scotia (Musick, 1969; Musick, 1974). Adult fish spawn between the months of April and Oct.; and the eggs, larvae, and prejuveniles remain in the plankton for 1–2 mo (Musick, 1969; Markle et al., 1982). From Sept. to Dec., prejuveniles migrate from the plankton to the benthos and become inquiline within the mantle cavity of sea scallops (Musick, 1969; Steiner et al., 1982; Garman, 1983). Recruitment of prejuveniles to the benthos increases markedly through the months of Oct. and Nov., and the timing of this descent is de-