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ANAL FINLET ABNORMALITIES IN A LITTLE TUNNY, *EUTHYNNUS ALLETTERATUS,* FROM NORTH CAROLINA

Frank J. Schwartz

Reported abnormalities of mackerels (family Scombridae) are rare. A pugheaded bluefin tuna, *Thunnus thynnus,* was cited by Nakamura (1977). Spinal curvatures were noted in a chub mackerel, *Scomber japonicus,* (Kubota, 1982); Graham et al. (1986) found a yellowfin tuna, *Thunnus albacares,* lacking a pectoral fin; while Schwartz (1989) reported pugheadedness, internally fused pelvic fins, and missing dorsal finlets in the little tunny, *Euthynnus alletteratus.* This paper describes the enlargement and growth elongations of anal finlets in a little tunny captured in North Carolina.

A 575 mm standard length (SL), 645 mm total length (TL), 3.3 kg little tunny, UNC 17357, Figure 1, was captured 26 October 1991 on rod and reel just west of the Beaufort Inlet sea buoy situated 7.5 km south of Morehead City, Carteret County, North Carolina. The specimen lacked the typical 4–5 black spots just posterior and below the pectoral fin, instead possessed one pale spot on the left side and three on the right side. All other color features were typical of a little tunny. Other characteristics were: vertebra 39, first dorsal spines 13, second dorsal rays 12, dorsal finlets 8, pectoral fin rays I, 26, pelvic fin rays I, 5, anal rays 12, 8 anal finlets, and a bifid pelvic process. However, anal finlets two and three were atypical by being elongated, branched, and frayed into several elongate appendages other than the typical small flag-like appearance (Fig. 1).

Anal finlet two was 124 mm long overall and extended from the body surface rather than as an elongation of the flag portion of the finlet and encompassed the entire finlet. Black coloration extended from the body for 56 mm and 75 mm along each elongated segment. The outermost aspects of each segment were frayed and cream-white in coloration. Anal finlet three also had two extensions that were each bifurcated and 116 and 112 mm long respectively. The right side elongation was black for 70 mm, the left 75 mm from the body; the remainder was frayed and cream-white. An extra bifurcated "finlet" was part of finlet three and originally was part of the rear finlet flag extension, before it came loose. The bifurcation was 96 mm long, black for 60 mm and frayed and cream-white to its outer extremities.

A roentgenogram of the affected finlets revealed that the supporting finlet pterygiophores were present and "normal" in appearance. Finlet two did not possess the characteristic flag appearance, and all of its elements were part of the growth elongations, while in finlet three part of the flag element was evident which supported the extra bifurcated elements. No bones were evident in any of the growth elongations.

How the elongated finlets functioned while the tunny was swimming and/or how much drag or aid they may have caused the fish remains unknown. The bicoloration and extended finlet growths should have made them and the fish more conspicuous to other fishes, for the creamy-white distal aspects of the finlets

Figure 1. Little tunny caught off North Carolina illustrating elongated finlet growths.

could have perhaps acted as flashing flags, as the fish swam. Finlets are often considered aids in determining the direction a fish will turn or in the case of tunas or tarpon determine which direction the fish will turn or jump.

Acknowledgments

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Evidence of a Genetic Basis for Absence of the Pelvic Skeleton in Brook Stickleback, *Culaea inconstans*, and Notes on the Geographical Distribution and Origin of the Loss

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Evidence of a Genetic Basis for Absence of the Pelvic Skeleton in Brook Stickleback, *Culaea inconstans*, and Notes on the Geographical Distribution and Origin of the Loss

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NELSON, J. S. 1977. Evidence of a genetic basis for absence of the pelvic skeleton in brook stickleback, *Culaea inconstans*, and notes on the geographical distribution and origin of the loss. J. Fish. Res. Board Can. 34: 1314–1320.

Laboratory and field crosses show that the absence of the pelvic skeleton in a brook stickleback population is under partial genetic control. Some offspring of parents lacking the pelvis possess a complete pelvic skeleton, while some offspring of parents with a complete pelvic skeleton lack the pelvis. Although a wide range of morphologically intermediate states exists, intermediates do not predominate in the crosses.

Loss of the pelvic skeleton occurs in Ontario, Saskatchewan, and Alberta. Within Alberta, 23 localities are known where 20% or more of the sticklebacks lack a complete pelvic skeleton. In some localities 95% or more of the individuals lack all trace of the pelvis. Variation in predation is inferred to be the environmental variable causally associated with the presence or absence of the pelvic skeleton. The absence is postulated to have arisen independently in the various localities.

Key words: *Culaea inconstans*, brook stickleback, pelvic skeleton absence, genetic control.

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Des croisements en laboratoire et sur le terrain démontrent que l'absence de squelette pelvien chez l'épinoche à cinq épines est partiellement sous le contrôle génétique. Quelques-uns des descendants de parents dépourvus de pelvis possèdent un squellette pelvien complet, alors que certains descendants de parents à squelette pelvien complet sont dépourvus de pelvis. Bien qu'il y ait une gamme étendue de conditions morphologiques intermédiaires, les intermédiaires ne sont pas dominants dans les croisements.

La perte du squelette pelvien se rencontre en Ontario, en Saskatchewan et en Alberta. En Alberta, on connaît 23 endroits où 20% ou plus des épinoches ne possèdent pas de squelette pelvien complet. A certains endroits, 95% ou plus des individus sont dépourvus de toute trace de pelvis. La variation dans la prédation serait la variable écologique responsable de la présence ou de l'absence du squelette pelvien. Nous sommes d'avis que l'absence de pelvis a pris naissance indépendamment dans les diverses localités.

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MANY groups of fishes lack the pelvic skeleton (fins and underlying pelvis). Within Osteichthyes, the absence represents a loss which has occurred in many phyletic lines. All members of many families may lack the pelvic fins, whereas only one species in a large family may lack them. In only relatively few species, including three of sticklebacks (Gasterosteidae), does the presence and absence of the pelvic skeleton (= pelvics) occur commonly at specific localities in individuals of the same age belonging to what appears to be an interbreeding population or, at least, belonging to what is conventionally regarded as the same species. No other major anatomical structure in fishes is known to vary in this manner. The phenomenon holds the promise of exciting research in evolutionary biology.

The brook stickleback, *Culaea inconstans*, ranges across much of northern North America. In an earlier study of geographic variation (Nelson 1969) five localities in Alberta (near the "short" end of a cline in dorsal and pelvic spine length) were noted to contain sticklebacks in which many individuals lack the pelvics. Additional localities of this species, as well as several for the ninespine stickleback, *Pungitius pungitius*, were found with individuals in which the pelvics

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failed to develop (Nelson 1971; Nelson and Atton 1971; Nelson and Paetz 1972, 1974). The pelvics are rarely absent in the latter species in eastern Canada (Coad 1973). Work has been done in western North America on *Gasterosteus* lacking all or most of their pelvics, both in extant (Larsen 1976; Moodie and Reimchen 1973, 1976) and fossil material (Bell 1974).

This paper presents studies to determine if there is a genetic basis for the loss in brook sticklebacks (as is implicit in any discussion on the selective value or evolutionary significance of the loss), and additional descriptive information on the phenomenon.

Materials and Methods

Four pelvic skeleton states can be recognized in the continuous variation from complete absence to complete expression (illustrated in Nelson and Atton 1971:347): (i) pelvis absent — no trace of any part of the pelvic skeleton, (ii) spineless intermediates — part of the pelvis but no trace of spines, (iii) spined intermediates — right or left spine present, (iv) complete — full development (the small soft ray may occasionally be absent). Pelvic fins, of which the spines are the dominant element, are never present unless the supporting pelvis is well developed. The middle two intermediate states can be variously combined to give three categories, either as spineless, one-spined, and complete, or as pelvisless, intermediate, and complete. The former categorization is useful in dealing with live fish which are not examined carefully; the latter has been adopted for most of the present work. The first two of the four states can only be differentiated by careful analysis with a sharp probe or by staining and clearing the specimen.

Crosses were made in the laboratory and in the field to determine if a genetic component is involved in the presence or absence of the pelvics. It is not possible to determine the extent of nongenetic (environmental) influence on the characters, since each clutch was maintained at the same conditions. No information was obtained on possible differential mortality from abiotic or biotic factors. All parents for the successful crosses were collected from the 5.6 km^2 Astotin Lake, Elk Island National Park, where sticklebacks of various pelvic states can be obtained in large numbers. Collections were made several weeks prior to the spawning season for the field crosses and during the spawning season for laboratory crosses. Fully ripe females, with and without the pelvics, could usually be found from June 11 to July 20. Robinson (1972) and Smiley (1972) give information on the general biology of Astotin Lake sticklebacks.

When studies were initiated on Astotin Lake sticklebacks in 1968 no other fish species were encountered. In 1971 a few fathead minnows (*Pimephales promelas*) were taken and in 1976 they outnumbered sticklebacks in most seine hauls. Historically, Astotin Lake has contained other species of fishes, some of them potential predators of sticklebacks. Northern pike (*Esox lucius*) and suckers (probably *Catostomus commersoni*) occurred until early 1933, but upstream movement from the North Saskatchewan River was blocked thereafter by a dam built in 1932 (Lin 1968). Yellow perch (*Perca flavescens*) were last introduced in 1935, while rainbow trout (*Salmo gairdneri*), brook trout (*Salvelinus fontinalis*), and splake (*S. fontinalis* × *S. namaycush*), were variously stocked between 1962 and 1965 (V. R. Jones and J. C. Ward personal communication). Low oxygen levels in winter and summer usually result in large die-offs of sticklebacks and would prevent the establishment of most fish species.

Brook sticklebacks were collected throughout much of Alberta to gain more information on the distribution of the pelvic absence. Sampling in lakes was usually close to shore in water less than 1.1 m depth.

Laboratory Crosses

Artificial crosses were made in the laboratory, usually within a few hours of the individual's collection. Eggs were extruded with light pressure into a moistened finger bowl (eggs that came out under pressure and appeared unripe were discarded). The testes of a male were immediately removed and chopped with a glass probe and mixed with the eggs. After a few minutes the mixture was rinsed, cleaned of extraneous material, and placed in a container with light aeration (glass containers in a room subject to considerable daily and seasonal temperature change in 1969 and nylon baskets suspended in aquaria in controlled facilities (18–20°C) in subsequent years). Parental material was fixed and later reexamined to verify the state of the pelvic skeleton.

Sixteen crosses were made successfully from June 12 to July 3 in 1969: absent (A) × A (number of crosses, $n = 4$); A × intermediate (left spine and part of left lateral shield missing) ($n = 1$); A × complete (C) ($n = 7$); $C \times C$ ($n = 4$). During this time the temperature varied between 20 and 30 °C (usually within 22–25°C). The rearing temperature was generally 17–27°C (with the cooler temperatures occurring in the autumn). Young were reared to at least 20 mm standard length, when complete development of the pelvic skeleton, if any, would be assured. In 1973 only three crosses ($A \times A$, $n = 1$; $C \times C$, $n = 2$) made on June 11 produced usable offspring. Malachite green was most commonly used to treat for fungus and dead eggs were removed daily.

Field Crosses

In 1973 and 1976 Astotin Lake stock was introduced into small artificial ponds (elongate, deepened ditches of varying lengths) in The University of Alberta Devonian Botanic Garden (approximately 53°24.5′ N, 113°45.5′ W). About 30–60 fish were placed in separate areas, allowed to reproduce naturally, with surviving adults and young collected at the end of the season. Complete recovery was not attempted but different parts of the ponds were sampled.

In 1973 three pure stockings of pelvisless, intermediates, (bony strut to one pelvic spine) and completes were made. An attempt was made to segregate and replicate crosses, but flooding may have mixed stocks.

In 1976 only one of two attempts, involving 62 complete parents, stocked May 20, was successful in a previously unused small pond. This pond, at the time of recovery (August 20), contained several potential predators of sticklebacks (arthropods; vertebrate predators, excluding fish, were also probably present).

Results

Genetic Basis of Pelvic Expression

Results of both the laboratory and 1973 field crosses indicate that there is a genetic component involved in determining whether or not brook stickleback offspring will lack or possess the pelvic skeleton (Fig. 1). The percentage of specific pelvic types arising from particular crosses differs considerably between the laboratory and the field crosses, perhaps because of the greater range in environmental conditions in the ponds or the greater potential in mating combinations (phenotypically identical individuals need not be genotypically identical). In all crosses involving parents lacking the pelvics, the majority of offspring also lack the pelvics. The majority of offspring have a complete skeleton when the parents are also complete. Parents that are intermediate or of extreme states (i.e. $A \times C$) tend to produce offspring of approximately 50% absent and 50% with at least part of the pelvis present. Offspring lacking the pelvis dominate when one parent is lacking the pelvis and the other is intermediate.

The 1976 field matings ($C \times C$) produced quite different results from a similar cross in 1973 in a different pond. Of 4914 individuals recovered, the pelvic skeleton was absent in 5, intermediate without spines in 2, intermediate with one spine in 14, and complete in 4893.

Collections from the ponds in September and October of 1973 produced similar ratios of pelvic states. Variation between replications within intermediates and completes was also low, but some mixing between the replicates of a particular state may have occurred. There was no evidence from limited field observations or analysis of variation between replicates or time of collection to suggest that exchange occurred between ponds (on the assumption that those sections closest to ponds of differing states should be most contaminated). This, however, cannot be completely discounted. The 398 intermediates in the absent and complete crosses were almost equally divided between the

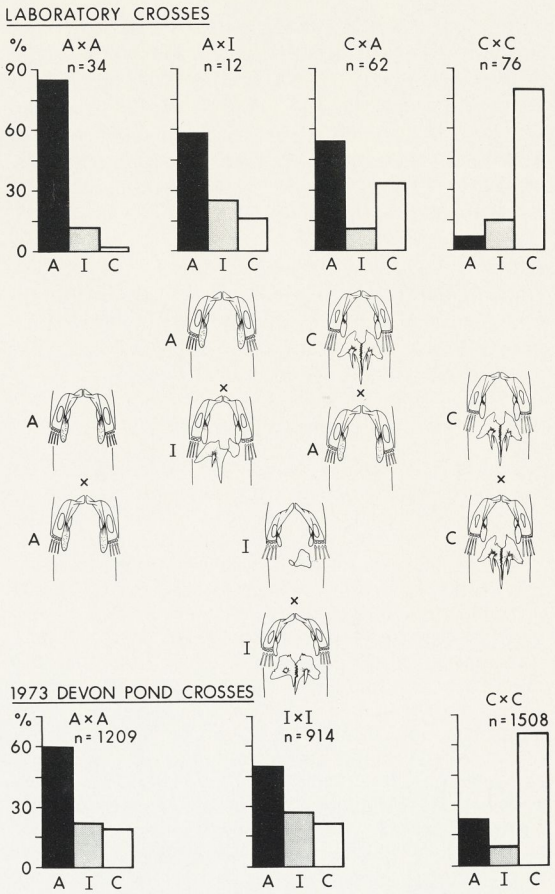

Fig. 1. Inheritance of various pelvic skeleton types in laboratory and field crosses. A = pelvic skeleton absent; I = pelvic skeleton intermediate (partially developed); C = pelvic skeleton complete. Many individuals classed as complete in the laboratory crosses lacked one or both of the soft rays.

unspined (217) and one-spined (181), while of the 250 intermediates of the intermediate pond, 168 were unspined and 82 one spined. In all three ponds, among the one-spined fish there were more left-spined (150) than right-spined (113) individuals ($\chi^2 = 5.2$, significant at the 95% level). In all ponds more fish had five dorsal spines than six as is also true for the lake of parental origin, Astotin. However, the percentage of five to six dorsal spines varied in the 1973 Devon crosses with the state of the pelvic skeleton, with higher percentages of six spines being progressively associated with the more complete pelvics. For example, only 19% of the offspring lacking pelvics from parents lacking pelvics had six dorsal spines; comparable figures for deficient offspring from complete parents and complete

offspring from complete parents were 35 and 42%, respectively. Only a small percentage had fewer than five spines or greater than six.

In the ponds in 1973 there were some differences in sizes of the fish recovered. The offspring of complete parents were larger (25–55 mm) than offspring (15–45 mm) of pelvisless parents. This could be a result of differences in food availability; however, the smaller modal size of various samples of pelvisless offspring (35–44 mm) than completes (45–54 mm) in the complete cross is suggestive of differential growth or mortality within at least the one pond.

The heritability and the mode of inheritance of the various pelvic states cannot be determined from the limited and variable data. There was an exceptionally high mortality in the laboratory crosses which conceivably could have had a differential effect on future pelvic skeleton states. Furthermore, although reproduction and survival seemed surprisingly high in the field ponds, various potential arthropod and tetrapod predators (primarily avian) were present and some differential mortality could have occurred, thereby influencing phenotype ratios.

Geographical and Morphological Variation in the Presence and Absence of the Pelvic Skeleton

The pelvic skeleton fails to develop in a large proportion of individuals from localities in three Canadian provinces. Two localities are known in Ontario from specimens deposited in the Royal Ontario Museum (ROM). The 12 specimens from Gagnon Lake (49°37′40″ N, 84°34′45″ W; ROM 32064, 32065) and 26 specimens from "Lake no. 30" of the Ontario Ministry of Natural Resources (49°46′ N, 82°19′ W; ROM 32066, 32067) are as follows:

	Gagnon	Lake no. 30
Pelvis absent	4	8
Part of pelvis	2	16
One spine	1	—
Complete	5	2

The Ontario spineless intermediates differ from most Alberta intermediates in the shape of the bone fragments. All have slender bodies and the spines (dorsal and pelvic), when present, are very short. Four localities are known with pelvisless sticklebacks in Saskatchewan (Nelson and Atton 1971), and many more in Alberta (Fig. 2) between latitudes 54.5° and 52.5° N and in Wood Buffalo National Park. These sites are often in close proximity to populations in which all or almost all individuals possess a complete skeleton

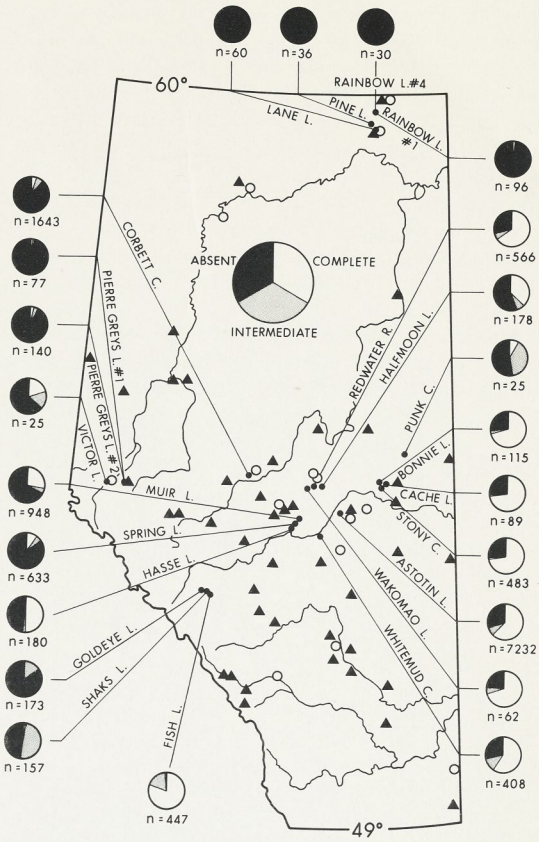

FIG. 2. Proportions of brook sticklebacks in Alberta with varying degrees of pelvic skeleton development (localities shown by small solid circles). Black area = pelvic skeleton absent; shaded area = intermediates; open area = pelvic skeleton complete; 360° = 100% with sample size shown beneath circle. Small open circles denote localities with samples of 10 or more specimens, a low proportion of which lacks all or part of the pelvic skeleton, and localities with nine or fewer specimens, a high proportion of which lacks the skeleton. Solid triangles denote localities with samples of 10 or more specimens all having a fully developed pelvic skeleton (in large samples a very low percentage may lack one or both pelvic spines).

(Fig. 2). The localities range from those having no known individuals with a complete skeleton to those with no known individuals lacking a complete pelvis. Virtually all localities collected over several years show very little difference between years in the ratios of the pelvic state. Outside the above area it is rare to find specimens lacking the pelvic spines in any one collection (Nelson 1969). Moodie (1977) found that the number of brook sticklebacks without the pelvic spines did not exceed 2.7% in any of 45 localities sampled in southern Manitoba.

Of those 23 localities in Alberta with a high proportion (20% or more) of sticklebacks lacking the pelvics, those in the north (Wood Buffalo National Park) and west (Pierre Greys lakes and Corbett Creek) show the highest percentage of such individuals (87.7–100%). Despite this trend, individuals from farther west in British Columbia (Nelson 1969) and to the north in the Northwest Territories (Falk 1972; Nelson and Paetz 1972) possess complete pelvic skeletons or only very rarely lack it (the latter are near Alberta in Wood Buffalo National Park).

Studies of possible differences in vertical distribution within a lake of the pelvic types were not conducted. An analysis of collections made in 6 yr from the 7 m deep Astotin Lake under a variety of shallow-water conditions suggests no marked differences in vertical or horizontal distribution within the areas sampled in that lake.

The frequency of various phenotypes can vary greatly between localities in close proximity. For example, the connected Pierre Greys lakes 1 and 2 have only 1.3 and 2.8% completes, respectively, while of 144 specimens from the landlocked Pierre Greys Lake 3, only about 100 m away, 143 are completes with 1 lacking the right spine. Pelvisless individuals in Goldeye Lake account for 85% of the sticklebacks, while in the nearby tributary, Shaks Lake, they account for only 48% and only 1.5% in nearby Fish (Shunda) Lake. Collections from parts of the higher reaches of Whitemud Creek have about equal proportions of pelvisless (30) to completes (30) in contrast to 28.7% absent for the whole river.

It might be expected that pelvic spines, when present, would be exceptionally short in those localities showing pelvic skeleton deficiency. Plots of pelvic spine length against standard length for individuals from 26 localities, 6 of which contain spineless individuals (Astotin, Corbett, Fish, Muir, Redwater, and Stony) do not suggest any such trend. The range in average spine length (at 32.5 mm standard length) in individuals from the latter six localities is wide (longest in Astotin Lake and shortest in the nearby Redwater drainage and in Fish Lake) and mean spine lengths for all six localities are within the range of localities with individuals always possessing pelvic spines (Lac Ste. Anne sticklebacks had the longest spines; the third Vermillion Lake in Banff National Park had the shortest). Similarly, the slopes of the computed regression lines measuring rate of growth of pelvic spine length vary considerably in the six localities with sticklebacks lacking the pelvics and values are within those calculated for the other localities.

Sticklebacks lacking the pelvic skeleton appear similar to individuals with the skeleton in all other respects. There is no significant sex difference in the four pelvic states in Astotin Lake. Similarly, the overall average (for 1973 and 1975 Astotin fish) of 29% with six dorsal spines, 69.5% with five spines, and 1.5% with three or four is similar in all four pelvic states (unlike the Devon Pond fishes). Of the 269 one-spined intermediates examined from the large 1970 Astotin Lake collection more had the spine on the left side (157) than on the right side (112) ($\chi^2 = 7.5$, significant at the 99% level) (similar to the Devon Pond fishes).

Differences in asymmetry in pectoral ray number with pelvic state are also similar in the two localities examined. Fluctuating asymmetry, as a possible measure of developmental disturbance or "noise", was estimated by summing the absolute differences of pectoral rays on each side and dividing by the sample size (Van Valen 1962). Differences in fluctuating asymmetry were greater between localities than between the pelvic states within the localities as noted below (sample size in parentheses):

	Pelvis absent	Pelvics complete
Redwater River	0.30 (27)	0.32 (100)
Astotin Lake	0.08 (100)	0.10 (100)

The fluctuating asymmetry for 87 pelvisless specimens from Hasse was 0.11 and for 226 from Spring Lake 0.09. These values fall within the 0.02–0.45 range found by Moodie (1977) for southern Manitoba stickleback populations.

Discussion

The similarity of offspring to their parental phenotypes in laboratory and field crosses demonstrates that a genetic component is involved in determining whether or not the pelvic skeleton will be absent or complete. However, differences in rearing water (e.g. in temperature or in ions such as calcium or fluorine) could have some effect. In addition, heritabilities could vary under differing environmental conditions as has been found for other characters by Hagen (1973) and McIntyre and Blanc (1973).

Information from this and other studies can be used to speculate upon the origin and significance of the loss. It is assumed that the pelvic absence (and variations in spine length) is not the result of adaptation to some physicochemical variable or the result of a pleiotropic effect but that it is the result of selective pressure based on some biological variable, namely, from circumstantial evidence, on variations in predation.

There is a strong tendency for long pelvic

spines to be associated with long dorsal spines between populations across North America and a weaker tendency for both to be associated with deep bodies. The resulting difference in cross-sectional area could result from differing predation pressures. The clinal variation in spine length in brook sticklebacks is hypothesized to result from a shift in predator–prey ratios across the range of the species (Nelson 1969:2444) (extrapolating from the experiments of Hoogland et al. 1957). Furthermore, Hagen and Gilbertson (1972) note that dorsal and pelvic spines are significantly longer in western North American threespine stickleback, *Gasterosteus aculeatus* where predators are common. The common absence of piscivorous fish in the "landlocked" lakes with sticklebacks lacking the pelvis (Nelson and Atton 1971; Nelson and Paetz 1974) is thought to be causally involved (e.g. native fish predators are absent from the four lakes in Wood Buffalo National Park where more than 99% of the brook sticklebacks lack the pelvis). The behavioral implications of the loss with respect to fish predation are currently being investigated by Mr J. D. Reist (University of Alberta). The effects of differences in predation on the phenotype of *Gasterosteus* are summarized by Bell (1976).

However, information is lacking on geographical differences in predation on brook sticklebacks (or the possible extent to which predators select various pelvic states). They presumably fall prey to aquatic arthropods and fish-eating birds and are frequently reported from the stomachs of various predaceous fish. Dekker (1976) noted several species of birds feeding on brook sticklebacks and observed a muskrat catching and eating 20 in about 45 min in Beaverhill Lake, situated near Astotin Lake and in the same drainage.

It is not possible to know if in historical terms, selective pressure has favored an increase in spine length in the Mississippi drainage (where they are now relatively long spined) following Wisconsin glaciation, or whether selection has favored short spines as the species dispersed outward from their refugia. Also, considering the parallel absence of the pelvics in *Pungitius* and *Gasterosteus*, the loss could have been present as populations were spreading across North America with various adaptations to the local environment resulting in the present pattern. Two morphs of brook sticklebacks may have invaded after glaciation, one with the pelvic skeleton from a Mississippi refugium and one without the pelvis from a Missouri refugium, with subsequent interbreeding and varying elimination of the girdleless form from most areas. However, I favor the view that pelvic loss occurred independently in most or all of the localities across Canada only after dispersal of a spined form following deglaciation. The loss could be due to the relaxation of selective pressures favoring its full development or to selective pressures favoring loss of the pelvics. The former seems probable in localities exhibiting considerable variation in expression of the character, while the latter seems reasonable in areas with a very low proportion of individuals possessing the pelvics. The condition of wide variation in lakes such as Astotin could be stable under existing selective pressures or be transitory with pelvic expression proceeding toward a monomorphic or dimorphic state.

In Astotin Lake the number of completes seems relatively high compared to the expected frequency of phenotypes in the first generation (35.5% absent, 14.5% intermediate, and 50% complete) if the parental individuals (30% absent, 8% intermediate, and 62% complete) mated at random; this assumes that the various crosses produced the same ratio of phenotypes as observed in the laboratory crosses (with conservative estimates for the intermediates of the two crosses not made which account for 10.6% of the expected crosses). The deviation from the expected could, in part at least, be the result of nonrandom successful mating or differential mortality of the phenotypes either in the lake or in the laboratory crosses.

Before the evolutionary significance of the present phenomenon can be understood it will be necessary to determine (i) if the two extreme types have different adaptive peaks, (ii) if the presence or absence of the pelvic skeleton can serve as an isolating mechanism with assortative mating (pelvic spines in males may serve some function during mating behavior [Hall 1956; Reisman and Cade 1967]), and (iii) if there is selective pressure against the intermediates. These conditions, if present, could result in increased divergence of the two types. The present phenomenon in brook sticklebacks could be the precursor to the situation described by Larson (1976) for the Paxton Lake threespine stickleback, first studied by Dr J. D. McPhail, where the pelvisless benthics have differences in behavior and feeding habits from the girdled limnetics.

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BIOCHEMICAL GENETICS OF PACIFIC BLUE MARLIN, *MAKAIRA NIGRICANS*, FROM HAWAIIAN WATERS[1]

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ABSTRACT

An electrophoretic survey of 35 enzyme-coding gene loci in Pacific blue marlin was accomplished to determine levels of genetic variation and the feasibility of using electrophoresis to study stock structure in this species. Polymorphism ($P_{.99}$) in the marlin was 0.26 and the average heterozygosity (H) was 0.06. Allele frequencies at 11 variable loci were determined for a sample of 95 fish from Kona, Hawaii. The observed levels of polymorphism and heterozygosity suggest that a biochemical genetic analysis of blue marlin stock structure is possible and may reveal stock heterogeneity.

The Pacific blue marlin, *Makaira nigricans*, is the predominant billfish species in the central tropical Pacific. As such, it is an important commercial species and the object of a considerable sport fishery. The average annual catch of this species in the Pacific exceeds 14,000 t (metric tons) (Shomura 1980). The Pacific blue marlin is primarily distributed in equatorial areas, although Japanese longliner catch records indicate that its range extends from lat. 48°N to 48°S. During the Southern Hemisphere summer (December through March) a center of concentration occurs in the western and central South Pacific (between lat. 8°S and 26°S). In the Northern Hemisphere summer (May through October) a center of concentration occurs in the central North Pacific (between lat. 2°N and 24°N). During April and November the fish appear to be concentrated equatorially between lat. 10°N and 10°S (Rivas 1975). There is currently no direct evidence of migration of blue marlin within the Pacific. However, a general movement to the northwestern Pacific during the Northern Hemisphere summer and to the southeastern Pacific during the Southern Hemisphere summer has been postulated by Howard and Ueyanagi (1965) on the basis of the shifting abundance patterns of the fish.

Little is known about spawning, other than that Pacific blue marlin appear to spawn throughout the year in an area 10°-20° on either side of the Equator, and up to 30° on either side of the Equator during the Northern and Southern Hemispheres' respective summer months. In general, the highest spawning densities occur in the western Pacific, with the density decreasing eastward (Strasburg 1970; Matsumoto and Kazama 1974; Rivas 1975). Because of the apparently single equatorial Pacific spawning area, it has been assumed that the species consists of a single unit stock (Yuen and Miyake 1980; Yoshida 1981), yet there has been no direct test of this assumed stock structure. The most recent report available on the condition of the Pacific blue marlin stock considers it to be badly overfished. Yuen and Miyake (1980) calculated that the present fishing effort (commercial longliner effort only, since no data are available on recreational fishing effort) is about twice that suitable for maximum sustainable yield. Because the catch per unit effort of Pacific blue marlin has steadily declined over the past 10 yr, in spite of a fairly constant level of effort, Yuen and Miyake (1980:19) concluded "...that continued fishing at high levels will continue to reduce the abundance of the stock and a recruitment failure will become a distinct possibility."

The importance of being able to define subpopulations or stocks of fishes with respect to the formulation of appropriate fishery management schemes has long been recognized (Marr 1957). This problem is especially acute for species (such as Pacific blue marlin) which are highly migra-

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tory, subjected to an oceanwide multinational fishery, and which, because of relatively low catches, are not well suited to tag-recapture studies. In fact, the pressing need to understand blue marlin stock structure has been recognized for some time (Shomura 1980; Yoshida 1981).

The electrophoretic analysis of protein polymorphisms in natural populations can be a powerful approach for analyzing genetic aspects of population structure in sexually reproducing organisms. For this reason, the technique has been applied to the study of racial or subpopulation differentiation in numerous invertebrates and vertebrates (Ayala 1976). Because of the basic importance of information on subpopulation or stock structure to fisheries management (Berst and Simon 1981), population genetic studies have been conducted for many species of fishes [reviewed by de Ligny (1969) and Allendorf and Utter (1979)]. Most of the fishes investigated to date have been freshwater species or marine forms which are either inshore shallow-water species or demersal species.

Stock heterogeneity for oceanic species has not generally been reported (but see Fujino 1976; Fujino et al. 1981). Although open water, pelagic species *may* be characterized by large panmictic cosmopolitan populations, this pattern has not yet been clearly established. One problem in testing this hypothesis has been the unusually low levels of genetic variability observed to date in several large marine vertebrates such as skipjack tuna (Fujino 1970) and seals (McDermid et al. 1972; Bonnell and Selander 1974). Indeed, Selander and Kaufman (1973) have even suggested that large, mobile vertebrates may generally have low levels of heterozygosity—a characteristic which, if true, would preclude definitive stock analysis using electrophoretic techniques (but see Ryman et al. 1980). The general lack of progress in defining stock structure in oceanic fishes, such as scombroids, using electrophoretic methods, is attributable to several factors. Many of the reports in the literature have been preliminary in nature dealing with small samples of fish and few variable loci. Although such small sample sizes are not unexpected given the remote, far-seas nature of many of the commercial fisheries, they severely limit the subsequent statistical treatment of the data. Similarly, the analysis of only one or two polymorphisms reduces the likelihood of demonstrating any population subdivision which may exist. Finally, the schooling and/or highly migratory nature of many of these fishes makes it difficult to plan and execute adequate sampling programs.

The study described in the present report was designed to determine the suitability of utilizing electrophoretic techniques to study stock structure in the Pacific blue marlin. Three specific questions were addressed:

1) How much and what kind of electrophoretically detectable genetic variation is there in the Pacific blue marlin? Specifically, is there enough genetic variation to allow an electrophoretic analysis of stock structure in this species?
2) What combinations of enzymes, tissues, and buffer systems can be utilized in a study of genetic variation in this species?
3) What allele frequency distributions characterize the population of Pacific blue marlin in Hawaii?

MATERIALS AND METHODS

Muscle, liver, heart, eye, and brain samples were dissected from Pacific blue marlin landed at the Hawaiian International Billfish Tournament held at Kailua-Kona, Hawaii, in August 1980. All tissue samples were taken immediately after each fish had been weighed, and all fish had been dead for at least 1 h but <8 h. The dissected tissues were initially placed on ice and subsequently transferred to a freezer within 12 h. The time delay between fish capture and the freezing of dissected tissues did not seem to adversely affect any of the polymorphic enzymes screened with the possible exception of L-iditol dehydrogenase which could only be scored in 84 of the 95 fish analyzed. Tissues were stored frozen at -20°C until extracted.

Tissue extracts were prepared by homogenization using a loose-fitting, motorized stainless steel pestle in polycarbonate centrifuge tubes. The extraction buffer consisted of 0.1M Tris-HCl pH 7.0 containing 1×10^{-3}M EDTA and 5×10^{-5}M $NADP^+$. After homogenization, the extracts were centrifuged at $25{,}000 \times g$ for at least 30 min. Supernatants were transferred to individually labeled glass vials, capped, and stored at -75°C until the electrophoretic analysis was completed.

The supernatants were subjected to horizontal starch gel electrophoresis (modified from Selander et al. 1971), using some 15 different buffers. The gels were made using Lot 60F-0558 starch

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BIOCHEMICAL AND MORPHOLOGICAL EVOLUTION OF HAWAIIAN BONEFISHES (*ALBULA*)

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Abstract

*Shaklee, J. B. and C. S. Tamaru (Hawaii Institute of Marine Biology, P.O. Box 1346, Kaneohe, Hawaii 96744 and Department of Zoology, University of Hawaii, Honolulu, Hawaii 96822) 1981. Biochemical and morphological evolution of Hawaiian bonefishes (*Albula*). Syst. Zool., 30:125–146.*—Electrophoretic analysis of the protein products of 84 presumed gene loci for over 180 specimens reveals that two distinct species of bonefishes occur in Hawaiian waters. Both species are characterized by low levels of within-species variation (H = 0.005 and 0.022). However, the two species are well differentiated from each other; they possess fixed allelic differences at about 70% of the loci screened and have a calculated genetic distance of 1.16. There is no evidence that the two species hybridize although they co-occur on both a macro and a microgeographic scale. The magnitude of genetic differentiation between the two species suggests that they have been separate genetic units for approximately the last 20–30 million years.

Although the two species of bonefishes in Hawaii are superficially very similar morphologically, there are a number of significant differences. The distributions of vertebral counts for the two species are completely non-overlapping, and the mean values for several meristic variables (including numbers of lateral-line scales, branchiostegal rays, and gill rakers) are significantly different in the two species. The single best field character for diagnosis is the shape of the lower jaw which is broadly rounded in one species and more angular and pointed in the other species. A number of traits associated with the head and feeding (lower jaw shape, number of gill rakers, shapes of tooth patches, and number of teeth) differ in the two species.

Stepwise discriminant function analysis using 31 morphological characters demonstrates that the two species have distinctively different overall morphologies and that they can be distinguished with over 99% accuracy. [Speciation; electrophoresis; discriminant function analysis; *Albula*.]

Virtually all species which occur over a large geographic range exhibit measurable variation in various characteristics. In many cases, this geographic variation is associated with particular localities or regions within the species' range. Such localized differentiation frequently has a genetic component and is often attributed to adaptation to particular sets of environmental and biological variables characterizing each locality. Differences such as these may take the form of smoothly changing clines through space, or may appear discontinuous. The heterogeneity and isolating effects of the physical environment as well as the vagility and dispersal abilities of the species involved are major determinants of the actual pattern which occurs in any given case. To the extent that such geographic variation has a genetic component, it is a measure of the racial or population differentiation within a species and may be attributed to restricted gene flow between the populations over long periods of time. This geographic variation can contribute to, or be an expression of, the eventual reproductive isolation of groups which is the central element of the process of speciation.

Studies of evolution and speciation have long focused on intraspecific and interspecific variation of morphological characters. The results of many of these investigations have contributed directly to our understanding of anatomical variation in species but are difficult to interpret on genetic grounds, because of the major effect certain environmental variables have on the expression of various morphological traits. In many fish species, both meristic and morphometric charac-

ters are dramatically affected by environmental conditions such as temperature, salinity, food availability, etc. (Hubbs, 1926; Barlow, 1961; Garside, 1966; Fowler, 1970; Johnson and Barnett, 1975).

It is now possible, due largely to technological advances of the past twenty years, to look more directly at genetic variation within and among species using techniques such as protein electrophoresis, microcomplement fixation, and DNA restriction endonuclease mapping and sequencing. Numerous investigations utilizing these techniques have generally confirmed previously reported differences within or among species (Ayala, 1975a; Markert, 1975) and have often provided a much more precise and detailed description and understanding of genetic differentiation. One of the most remarkable results of these studies is the demonstration of high levels of genetic variation within and among populations of many organisms, including both invertebrates and vertebrates (reviewed by Lewontin, 1974; Ayala, 1975b; Nevo, 1978). Data generated by these studies have made it possible, for the first time, to compare and contrast morphological and biochemical evolution. In most cases, a direct correspondence between the two has been found such that species or populations which are most distinct on morphological grounds are also most distinct genetically. However, two noticeable exceptions to this have been noted. One is the case of marked morphological differentiation with little measurable genetic (biochemical) change. This is best illustrated by organisms such as the Hawaiian *Drosophila* where many morphologically distinct species pairs exhibit little or no detectable electrophoretic differentiation (Carson et al., 1975; Johnson et al., 1975). The opposite case has been well documented for certain marine invertebrates such as six sibling species of polychaetes (*Capitella*) which are morphologically nearly identical yet show major genetic differentiation (Grassle and Grassle, 1976). The relationship between anatomical and biochemical evolution has been actively studied by A. C. Wilson and colleagues (Wilson et al., 1974; King and Wilson, 1975; Prager and Wilson, 1975) using various groups of vertebrates. The fundamental independence of the rates of morphological and biochemical evolution has been well documented by these studies.

Relatively little information on the relationship of anatomical and biochemical evolution in marine fishes is available. The single exception is the four *Menidia* spp. studied by Johnson and collaborators (Johnson, 1975a and b; Mickevich and Johnson, 1976). The results of these investigations can be summarized as follows: a) each of the four species of *Menidia* is readily distinguishable by electrophoretic analysis, although clinal variations in gene frequencies complicate the distinctions, b) consistent morphological differences occur among the species, and c) there is a general congruence in the patterns of phylogenetic relationships among species derived from biochemical and from morphological data sets.

In an effort to understand better the evolution and speciation of marine fishes, we initiated a study of biochemical and morphological variation in the bonefish, *Albula vulpes* (Linnaeus). *Albula vulpes*, one of two currently recognized species in the genus, occurs as a common component of the inshore, shallow-water fish fauna in tropical and subtropical marine environments world-wide (Wheeler, 1975; Nelson, 1976). The other recognized species in the subfamily is *Albula nemoptera* (Fowler) (=*Dixonina nemoptera*), known only from the Atlantic and Pacific coasts of the Americas. The bonefish is a primitive teleost related to the eels, and to the tarpon and ox-eye (*Megalops*), and ladyfishes (*Elops*) (Greenwood et al., 1966; Greenwood, 1977). Like these other fishes, the bonefish has a distinctive, long-lived, pelagic leptocephalus larval stage (Hollister, 1936).

Several aspects of the bonefish make it an ideal subject for the present study. The bonefish has an extensive range,

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Deformed Vertebral Column and Caudal Region in a Beluga, *Huso huso**

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Key words: Beluga, *Huso huso*, deformed vertebral column, caudal region

Sturgeons, especially in Russia, support major commercial fisheries despite great loss of habitat (Rochard et al., 1990). Sturgeons are valued not only for their meat and eggs, but also for products derived from the swim-bladder membrane—gelatin and glue, and for the dried spinal cord. Sturgeon heads are rich in gelatin-containing substances and are an important food product ("golovizna"). Oil can be extracted from the liver (Vladykov and Greeley, 1963).

The beluga, *Huso huso*, is one of the most important species of sturgeons caught and raised in Russia, particularly for hybridizing with other sturgeon species (Barannikova, 1987). No data have appeared in the literature on the beluga or its hybrids in regard to deformities (Schwartz, 1972, 1981).

In 1985, during a study of sturgeons and their hybrids at the Zoological Institute of the Academy of Sciences of the former USSR (ZIN), Saint Petersburg, a beluga (ZIN No. 1267, Fig.) was found that had a deformed vertebral column and trunk. The principal characters of this deformed fish (in mm) are: total length 287.0; head length 96.5; head width at the gill cover 52.5; width of the interorbital distance 23.3; snout length 37.0; curvature of the snout above horizontal 10.6; length of the pectoral fin 46.5; length of the ventral fin 18.7; eye diameter 7.0; width of mouth 29.6; length of barbels (from left to right) 18.7, 16.9, 16.1, 19.5; predorsal length 226; prepectoral length 93.0; preventral length 205; preanal length 245; gap between the dorsal and caudal fins 7.1; dorsal scutes 11; central lateral scutes 28 below the dorsal fin; in all 39; lower lateral scutes 12; scutes between the anus and anal fin, 2. Barbels with membranes on their posterior edges are 5 mm in width. Twisting of the body and vertebral column began at the origin of the dorsal fin base and took the form of sharp arch. The anal fin and lower lobe of the caudal fin were bent into an S curve. The posterior end of the vertebral column is pointed; the dorsal fin had no lobes. Black areas border the upward twisted part of the snout from each side. A black patch is seen along the lower surface of the snout. Coloring on the body and scutes is normal. The pectoral and ventral fins were squared and not pointed as in *Acipenser*.

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SPINAL AND BODY DEFORMITY IN BELUGA STURGEON, *Huso huso*, FROM RUSSIA

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Key Words: sturgeon; *Huso huso*; body deformities; Russia.

Sturgeon fisheries of the world, particularly in Russia, are extensive yet declining because of overfishing and continued habitat destruction and alteration (Rochard et al., 1990). Sturgeons are valued not only for their flesh and eggs, but gelatin and glue are products made from the lining of the swim bladder and the spinal cord "yaziga." Heads of sturgeons are rich in gelatinous substances and are a valuable food product "golovizna" while oil is made from sturgeon livers (Vladykov and Greeley, 1963).

The beluga sturgeon, *Huso huso,* is one of the most important sturgeons captured and cultivated in Russia, especially when hybridized with other sturgeons (Barannikova, 1987; Nikoljukin, 1970). However, considering the many sturgeons captured or hybridized each year, no mention of any deformity has been reported either for *Huso huso* or its hybrids (Dawson, 1964, 1966, 1971; Dawson and Head, 1976; Schwartz, 1972, 1981, and an ongoing world literature compilation of hybrids).

In 1985 while examining sturgeons and their hybrids at the Zoological Institute, Akademia Nauka, then USSR, at St. Petersburg, a specimen of *Huso huso* (Specimen No. ZIL N1267; Fig. 1) was found that possessed a spinal and body deformity.

Salient features of the deformed sturgeon were (all lengths in millimeters): total deformed length 287.0, head length 96.5, head width at opercle 52.5, interorbital width 23.3, snout length 37.0, snout curvature dorsally from the horizontal 10.6, pectoral fin length 46.5, pelvic fin length 18.7, eye length 7.0, mouth width 29.6, barbel lengths (from left to right) 18.7, 16.9, 16.1, 19.5, predorsal distance 226, distance to pectoral fin 93.0, distance to pelvic fin 205, distance to anal fin 245, dorsal–caudal fin interspace 7.1, dorsal scutes 11, mid lateral line scutes 28 to dorsal fin 39 total, and ventral lateral scutes 12, anus to anal fin scutes 2. The barbels were lobed posteriorally for a width of 5 mm. Body and spinal curvatures began at the level of the dorsal fin anterior base as a sharp arc dorsally. An "S" shape curvature included the anal and lower caudal fin lobes. The end of the spinal column terminated in a point; there was no dorsal fin lobe. Black streaks outlined the curved upward portion along each side of the snout. A black streak occurred along the ventral surface of the snout. The body coloration and scutes

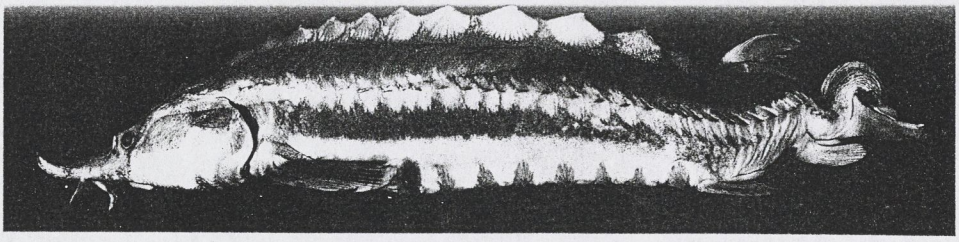

FIG. 1. Deformed beluga sturgeon from Astrakhan.

were normal. The pectoral and pelvic fins were square rather than pointed as in *Acipenser.*

Little is known about the specimen, ZIL N1267, other than it was obtained from the Department of Fishery Industry, Astrakhan, in 1902.

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Genetic Variation and Population Subdivision in Australian Barramundi, *Lates calcarifer* (Bloch)

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Abstract

Starch gel electrophoresis of enzymes and polyacrylamide gel electrophoresis of muscle proteins were used to study genetic variation in 589 barramundi from three widely separated regions in northern Australia. Presumed genetic variation was observed at 16 loci (out of 46 screened). However, only 11 of these were polymorphic at the $p_{0.99}$ level. The average heterozygosity in this species was 0·032. In nearly all cases, genotypic proportions agreed closely with Hardy–Weinberg expectations. Repeated sampling in each region revealed little or no change in allele frequencies over a period of several months. Similarly, comparisons of allele frequencies for fish from marine and from freshwater localities in the south-eastern Gulf of Carpentaria failed to reveal significant genetic differences between habitats. Between-region heterogeneity χ^2 tests indicated substantial genetic differentiation at 10 of the 11 polymorphic loci. These data indicate the existence of at least three distinct stocks or subpopulations of barramundi in Australia.

Introduction

The barramundi, *Lates calcarifer* (Bloch) (Centropomidae), is a tropical, Indo-west Pacific species ranging from the Persian Gulf to Australia and Papua New Guinea (Greenwood 1976). In Australia, the species ranges from the Ashburton River (east of Exmouth Gulf) in Western Australia, across the north of the continent, and southward along the east coast of Queensland to the Mary River at Maryborough (Fig. 1). It is euryhaline and is known to inhabit freshwater ponds and rivers, tidal swamps, estuaries, and coastal reefs. Adults are long-lived (>10 years) and grow to a large size (>100 cm total length, >20 kg weight) (Reynolds and Moore 1982). There is evidence that barramundi in both Papua New Guinea and Australia are protandrous hermaphrodites—individuals first becoming sexually mature as males and subsequently becoming functional females (Moore 1979; Davis 1982, 1984). Although adults are known to prosper in entirely freshwater habitats, rearing studies in Thailand have indicated that successful embryonic development and hatching in this species require brackish waters (salinity >10) and that optimal salinity for larvae is 20–25 (Wongsomnuk and Manevonk 1973). These characteristics of barramundi mean that adults living in freshwater habitats must move downstream to brackish waters to reproduce successfully. It is generally thought that barramundi spawn in coastal waters. In Papua New Guinea, such coastal spawning often occurs after extensive downstream or alongshore migrations (Moore 1982; Moore and Reynolds 1982).

Throughout much of its range, *L. calcarifer* supports substantial fisheries. In Australia, it supports a major commercial gillnet fishery. Total commercial barramundi landings in Australia have varied from 181 t liveweight in 1969–1970 to 1686 t in 1977–1978 (Cameron 1982). In addition, the species supports a considerable angling sport fishery.

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Accurate catch statistics for this amateur fishery are not available, but estimates indicate that its total yield is high (Bandaranaike and Hampton 1979; Griffin 1979, 1982). Indeed, it seems likely that the overall harvest of the recreational fishery may equal or exceed that reported for the commercial fishery.

The decline in total commercial landings of barramundi since 1978, the recognition of the monetary and recreational values of the barramundi fisheries, and a desire to ensure the long-term viability of these fisheries have focused considerable attention on management programs for this species in Australia (Grey and Griffin 1979; Rohan 1981). Both Queensland and the Northern Territory have recently instituted numerous specific management initiatives.

Effective, long-term management of Australia's barramundi resource will also be dependent upon an understanding of the genetic basis of population structure in the species. That is, it is necessary to know whether or not multiple breeding groups or stocks contribute to the total resource and what the qualitative and quantitative contributions of each stock are. Furthermore, since management plans are usually administered on a geographic basis, information regarding the actual boundaries separating such barramundi stocks is essential to the formulation of an optimal management scheme.

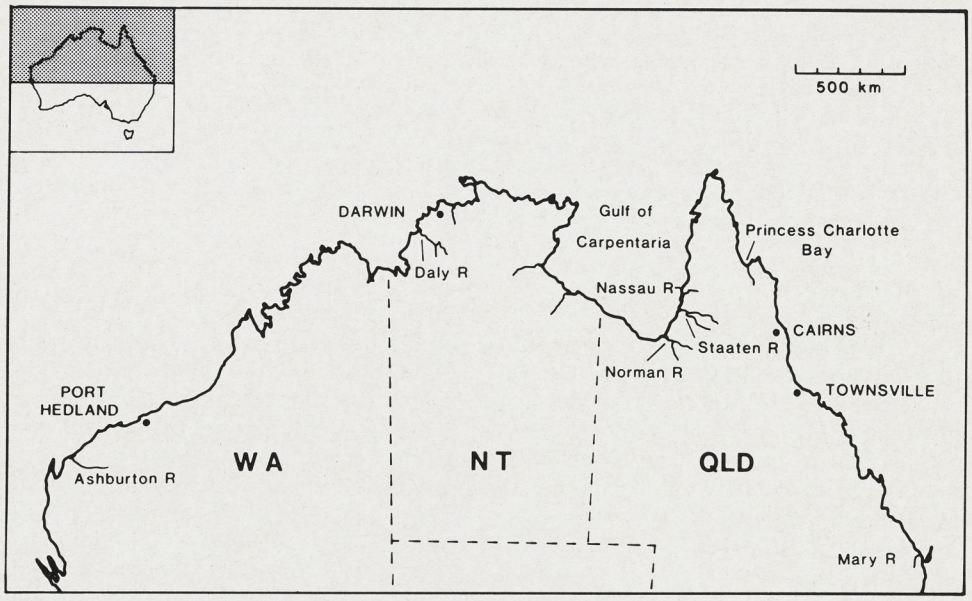

Fig. 1. Map showing the three localities in northern Australia sampled for barramundi in the present study.

The present investigation was undertaken to determine the nature and level of electrophoretically detectable genetic variation in *L. calcarifer* and to assess whether or not there was evidence for the existence of multiple barramundi stocks in Australian waters. The ultimate goal of this research program is to provide a stock basis for management of the fisheries.

Materials and Methods

Field Collection and Sample Preparation

Adult barramundi were collected from three widely separated geographic regions: the Princess Charlotte Bay area in north-eastern Queensland (from Cape Melville north-west to Lloyd Bay), the south-eastern Gulf of Carpentaria in northern Queensland (from the Norman River north to the Nassau River), and the Daly River in the north-western Northern Territory (adjacent to Anson Bay). They

GENETIC VARIATION AND POPULATION STRUCTURE IN A DEEPWATER SNAPPER, *PRISTIPOMOIDES FILAMENTOSUS*, IN THE HAWAIIAN ARCHIPELAGO

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ABSTRACT

Pink snapper were collected from six different locations in the Hawaiian Archipelago and subjected to starch gel electrophoretic analysis. Of a total of 44 enzyme-coding loci screened for genetic variation, 5 polymorphic loci were detected (Adh, Gpi-A, Iddh, Ldh-C, and Umb). Each polymorphic locus exhibited two common alleles (range of individual locus heterozygosity = 0.293-0.495). The heterozygosity averaged over all 44 loci was 0.047. Observed genotype distributions at the five polymorphic loci were in general agreement with Hardy-Weinberg equilibrium expectations. However, when the collections were subdivided into two major age groups (fish about 2-5 years old vs. fish 5-14 years old), significant differences in allele frequency between groups were detected for both alcohol dehydrogenase and lactate dehydrogenase-C.

Repetitive samples in 1979 and 1980 from two localities suggested that the allele-frequency distributions were stable during the period of the study. Contingency χ^2 tests of the entire data set failed to reveal significant genetic differences among the five primary localities (Maro Reef, French Frigate Shoals, Necker, Molokai, and Hawaii) or between the two major areas (Northwestern Hawaiian Islands and main Hawaiian Islands) represented by the collections. The mean value of Wright's F_{ST} for the five polymorphic loci was 0.005 indicating little subpopulation differentiation.

The data fail to reveal significant genetic differentiation among localities. Indeed, the results are entirely consistent with the existence of a single, panmictic stock of pink snapper throughout the Hawaiian Archipelago.

The pink snapper, or opakapaka, *Pristipomoides filamentosus,* is a deepwater species found throughout the Indo-West Pacific, including South Africa, Japan, Australia, the Philippines, Samoa, and the Hawaiian Islands (Kami 1973). In the Hawaiian Islands it occurs in significant numbers from Hawaii in the southeast through Maro Reef in the northwest and is found in greatest abundance at depths of 80-150 m (Ralston 1980). For the past 15 or more years, this snapper has been the dominant species in the deep-sea handline fishery in Hawaii (Hawaii Division of Fish and Game 1960-80[3]; Ralston and Polovina 1982). Due largely to the developing fishery in the Northwestern Hawaiian Islands (NWHI) the annual commercial harvest of *P. filamentosus* has increased from about 33 t in 1970 to 105 t in 1980 (Hawaiian Division of Fish and Game footnote 3).

Spawning of pink snapper in Hawaii appears to be concentrated in the fall of the year, and presumed annual fecundity may be as high as 1×10^6 eggs per female (B. S. Kikkawa[4]). Fertilization in opakapaka is external and the eggs are planktonic. After hatching, the larvae remain pelagic for about 1-2 mo during which time they attain a size of 20-25 mm (J. Leis[5]). Adults are essentially demersal but virtually nothing is known about the magnitude of adult movements, either daily or seasonally.

The present genetic investigation of stock structure in *P. filamentosus* was initiated to address two questions relevant to the future management of this fishery. First, was there any detectable stock heterogeneity within the entire Hawaiian Archipelago? Second, and specifically relating to the potential impact of the emerging fishery in the NWHI on the existing fishery in the main Hawaiian Islands, was there evidence that popu-

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[3]Hawaii Division of Fish and Game. 1960-80. Commercial fish landings. Mimeogr., var. pag.

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lations in the NWHI were differentiated, and thus independent, from populations in the main islands?

MATERIALS AND METHODS

All specimens were obtained using commercial handline gear and were either frozen or iced at sea. Details of the collections are presented in Table 1. One series of samples (from French Frigate Shoals and Maro Reef) was filleted at sea, and the remaining carcasses (containing the tissues of interest) were preserved in an ice cold brine solution. This means of sample handling had the unfortunate effect of inactivating some of the enzymes (especially glucosephosphate isomerase and lactate dehydrogenase) so that these two enzymes could not be reliably scored in these samples. Initial screening for polymorphic loci in the pink snapper was conducted on extracts of white skeletal muscle, red skeletal muscle, heart, eye, brain, and liver. Each of these tissue samples was dissected from fresh or frozen specimens and homogenized in an equal volume of 0.1 M Tris-HCl pH 7.0 buffer (containing 1×10^{-3} M EDTA and 5×10^{-5} M $NADP^+$) using a loose fitting, motorized pestle. Homogenates were centrifuged for at least 20 min at a minimum of $20{,}000 \times g$ (liver supernatants were routinely centrifuged a second time to minimize lipid content). The resulting supernatants were transferred to individually labeled glass vials which were capped and stored at −75°C until the electrophoretic analysis was completed.

TABLE 1.—Collection details for total samples and individual collections of *Pristipomoides filamentosus* used in the electrophoretic analysis.

Collection[1]	Number	Dates	Average size[2]
Maro Reef	129	Oct. 1978-Nov. 1980	584 (±130)
a	12	Oct. 1978	
b	59	Oct. 1979	
c	9	Oct. 1979-Nov. 1980	
d	49	Nov. 1980	
French Frigate Shoals	254	Mar. 1979-May 1980	372 (±125)*
a	27	Mar. 1979	
b	67	Oct.-Nov. 1979	
c	46	May 1980	
d	114	Nov. 1980	
Necker	127	Mar. 1979-Nov. 1980	519 (±104)**
a	107	Mar.-May 1979	
b	20	Nov. 1979-Nov. 1980	
Kauai	25	Feb.-Apr. 1981	441 (±90)
a	20	Feb. 1981	
b	5	Apr. 1981	
Molokai	118	Mar. 1979-Apr. 1981	333 (±47)
a	9	Mar. 1979	
b	20	Sept. 1979	
c	5	July 1980	
d	84	Mar.-Apr. 1981	
Hawaii	63	June 1979-Apr. 1981	393 (±55)
a	17	June-July 1979	
b	46	Mar.-Apr. 1981	

[1] See figure 1 of Shaklee and Samollow (1984) for locality information.
[2] Fork length, FL (±1 standard deviation) in mm.
*FL of 38 fish from collections a and b unknown.
**FL of 79 fish from collection a unknown.

Electrophoresis

The supernatants were analyzed by horizontal starch gel electrophoresis (Selander et al. 1971). Each enzyme system surveyed in the initial screening for genetic variation was electrophoresed on from two to eight different buffer systems using extracts of several different tissues. Following electrophoresis, isozyme patterns were visualized using standard recipes (modified from Shaw and Prasad 1970; Selander et al. 1971; Siciliano and Shaw 1976). The umbelliferyl esterase (often called EST-D in the literature) was visualized using 4-methylumbelliferyl acetate as substrate.

Gel Scoring and Data Analysis

Patterns of enzyme variation which were consistent with the subunit structure of the homologous protein in other fishes (when known) and simple genetic models were scored and recorded as genotypes. Names of enzymes and Enzyme Commission numbers follow the recommendations of the Commission on Biochemical Nomenclature (1973). For multilocus enzyme systems, loci were given alphabetic designations to indicate homology with known forms (e.g., Gpi-B and Ldh-C). With the exception of one very rare allele (observed once) for both ADH and UMB, each of the polymorphic enzymes screened exhibited only two detectable alleles. These two alleles are referred to hereafter by their relative electrophoretic mobility from the origin as f (= fast) and s (= slow).

Tests of Hardy-Weinberg equilibrium and calculations of average heterozygosity (H) were accomplished as described in Shaklee and Samollow (1984). A locus was considered polymorphic if the frequency of the most common allele was ≤ 0.95.

Two types of χ^2 tests were used to test for genetic differentiation and, therefore, stock heterogeneity. First, for all polymorphic loci, contingency tests of all possible pairwise combinations of localities were conducted. Second, contingency tests comparing pooled samples representing the main Hawaiian Islands and the NWHI were conducted for all loci. Wright's F_{ST} statistic (Wright 1965, 1978) was calculated using the BIOSYS-1 computer program (Swofford and Selander 1981).

New Records, Distribution and Diagnostic Characters of Virginia Ictalurid Catfishes With An Adnexed Adipose Fin

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ABSTRACT.—Recent introductions of *Ictalurus melas* and *Pylodictis olivaris* and the discovery (possible introduction) of *I. brunneus* has raised the number of ictalurids with an adnexed adipose fin to eight species in the Roanoke River drainage. Introduction of *I. furcatus* to other drainages raised the Virginia total to nine. Although most of these species are widely distributed in North America, none is native in all Virginia drainages. Most species have been variously introduced, and *I. brunneus* and *I. platycephalus* exhibit an atypical distributional interrelationship. Key characters for separating these two flathead bullheads from typical bullheads (*I. melas, I. natalis, I. nebulosus*) are described, and some diagnostic characters different from those generally used are emphasized for distinguishing *I. brunneus* from *I. platycephalus,* and *I. melas* from *I. nebulosus.* These and characters of other ictalurids with an adnexed adipose fin are discussed; a key is provided for the species of Virginia drainages.

INTRODUCTION

Exceptional or significant new records, occasional recent misidentifications, vexatious old records, and an atypical distributional interrelationship between two Virginia ictalurids led to this report. Although most species have been long known, the ictalurids with an adnexed (free) adipose fin still present at least local problems in identification, and consequently may subvert zoogeographic studies in North America. Problems have extended elsewhere. For example, Banarescu (1968) found that the bullhead widely introduced in Europe was actually *Ictalurus melas* (Rafinesque) instead of *I. nebulosus* (Lesueur). Important external characters are few, and most are variable and widely shared among similar appearing, often sympatric species; no consistently present external character state of juvenile and adult *Ictalurus* appears unique to a single species.

The Roanoke River drainage is now known to harbor eight species of ictalurids with an adnexed adipose fin, a larger complement than occurs in the Mississippi River basin. A total of nine species is now known from Virginia: *I. brunneus* (Jordan), snail bullhead; *I. catus* (Linneaus), white catfish; *I. furcatus* (Lesueur), blue catfish; *I. melas,* black bullhead;

I. natalis (Lesueur), yellow bullhead; *I. nebulosus,* brown bullhead; *I. platycephalus* (Girard), flat bullhead; *I. punctatus* (Rafinesque), channel catfish; *Pylodictis olivaris* (Rafinesque), flathead catfish. Of this assemblage, *I. melas* and *Pylodictis* are considered to be introduced, and *I. brunneus* probably so, to the Roanoke drainage; the same is true for the status of *I. furcatus* and *I. brunneus* in Virginia.

This report discusses the distribution of each species in Virginia and extralimitally where pertinent. Diagnostic characters with the greatest utility and ease in identifying these species within the study area are discussed and employed in a key. Osteological and other differences among *Ictalurus* species are found in Paloumpis (1964), Yerger and Relyea (1968), Smith and Lundberg (1972), and Lundberg (1975).

Concepts of genera, subgenera, and species groups follow Lundberg (1975). However, regarding our discussion of species identification, for practical purposes we artificially group *I. catus* with the "forktail catfishes," *I. furcatus* and *I. punctatus* of the subgenus *Ictalurus. Ictalurus catus* actually is placed, in the subgenus *Amiurus,* in the *catus* group with the species we collectively refer to as "flathead bullheads," i.e., *I. brunneus, I. platycephalus* and *I. serracanthus* Yerger and Relyea. The other three species, our "typical bullheads," *I. melas, I. natalis* and *I. nebulosus,* are referred by Lundberg to the *natalis* group of the subgenus *Amiurus.*

METHODS AND MATERIALS

Methods of counting and mensuration follow those outlined by Hubbs and Lagler (1958) and Yerger and Relyea (1968), with one difference from the latter study. Removal of the gill arch for gill raker counts was necessary only in the smallest specimens; otherwise a slit at the dorsal and ventral junctions of the operculum, and adduction of the latter, were sufficient to expose gill rakers. All rakers on the right arch including rudiments on lower limb, were counted; fused rakers were counted as one. To count anal rays it was necessary to expose them by slitting the anal fin base and peeling the skin back. All anterior rudimentary rays were counted; the last two rays with a basal conjuncture were counted as one.

Measurements were made using Helios dial calipers for all proportionally expressed characters (as % SL) and for standard length (SL) of smaller specimens; they were recorded to the nearest 0.1 mm. The SLs of large specimens were obtained with a beam compass and a steel rule, and recorded to the nearest 0.5 mm. Counting was aided by the use of a variable magnification stereo dissecting microscope. The counts from one *I. melas,* 33.6 mm SL, were omitted from tabulation due to extreme low counts (rakers incompletely developed).

Complete locality data on specimens examined are on file at Roanoke College. Flathead bullhead localities are depicted in Figure 1 and are listed in sequence from downstream to upstream. Typical bullhead localities are presented by basin or drainage and therein

alphabetically by state and tributary. All specimens were from Virginia drainages, except for *I. melas,* which was supplemented by material from other states. Localities for both sections are followed by institutional abbreviation and catalog number. Roanoke College and Virginia Commonwealth University are followed by collector's initials and field number.

Institution and agency abbreviations used are:

ACE, U.S. Army Corps of Engineers
CU, Cornell University
DPC, Duke Power Company
FWS, U.S. Fish and Wildlife Service
LC, Lynchburg College
RC, Roanoke College
SCS, Soil Conservation Service
UMMZ, University of Michigan Museum of Zoology
UNC, University of North Carolina at Charlotte
USNM, National Museum of Natural History, Smithsonian
UT, University of Tennessee at Knoxville
VCGIF, Virginia Commission of Game and Inland Fisheries
VCU, Virginia Commonwealth University
VFU, Virginia Cooperative Fisheries Unit
VIMS, Virginia Institute of Marine Science
VPI, Virginia Polytechnic Institute and State University

Collections from the following sources are housed at Roanoke College: ACE, FWS, LC, SCS, VCGIF; some of the collections originally at VCU are also at Roanoke College. Numbers that follow these series refer to collection reference numbers used for a data bank concerning the freshwater fishes of Virginia.

Ictalurus brunneus

Dan River system. — VA: Dan R. RC VCGIF 230; RC FWS 8; NC: Country Line Creek RC ACE 15; Rattlesnake Creek RC ACE 18; VA: RC VCGIF 229; NC: Pumpkin Creek RC ACE 16; VA: Dan R. RC EGM Va-23; Fall Creek RC ACE 2; Dan R. RC FWS 6; Dan R. RC FWS 1; NC: Dan R. DPC 50101-09 and -11; DPC 50101-10, 50107-06; DPC 50101-18; DPC 50101-12 and -19; UNC 76-95.

Ictalurus platycephalus

Chowan River system. — VA: Great Creek RC SCS 8; N. Meherrin R. RC HJP 44, VCU HJP 100.

Lower Roanoke River system (below Dan River mouth). — VA: Flat Creek VPI 1029; Miles Creek VPI 1037; NC: Grassy Creek RC REJ 865; VA: Beaver Pond Creek RC REJ 863.

Lower Dan River system (below Smith River mouth). — VA: Banister R. VCU HJP 84; NC: Cascade Creek ACE 89; Dan R. DPC 50107-07.

Smith River and tributaries (Dan River system). — VA: Leatherwood

Creek RC ACE 80; Beaver Creek CU 13921; Town Creek VPI 984; Green Brook RC ACE 134; Smith R. RC HJP 60.

Upper Dan River system (above Smith River mouth). — NC: Buffalo Creek RC ACE 108; Jacob Creek RC ACE 115; Belews Lake DPC 50107-12 and -18.

Upper Roanoke River system (above Dan River mouth). — VA: Difficult Creek RC REJ 856; Twittys Creek VFU 109; Wards Fork USNM 101324; Turnip Creek RC REJ 873; Falling R. RC HJP 59; Little Falling R. RC HJP 75; Seneca Creek VCU HJP 82; trib. Little Otter R. LC 30; Leesville Reservoir RC REJ 333; Pigg R. RC REJ 402; Blackwater R. VPI 989; Maggodee Creek VPI 990, 974 and CU 43587 (split collection); Ellie Creek VPI 975; Blackwater R. VPI 690; 2187; South Fork Blackwater R. VPI 2188; North Fork Blackwater R. VPI 1755.

Ictalurus natalis

York River drainage. — VA: Pond Creek RC JRR 124; Smoots Pond RC JRS 23; Ta River RC JRR 134.

James River drainage. — VA: Barrows Creek RC TZ 156; Maury R. RC NMB 73; Tuckahoe Creek RC JRR 131.

Roanoke River drainage. — VA: Beaver Pond Creek RC REJ 863; Great Creek RC SCS 8; Lake Jordan RC JRS 22; Little Buffalo Creek RC REJ 869; Roanoke R. RC REJ 781.

Tennessee River drainage. — VA: Clinch R. RC REJ 503; Clinch R. RC REJ 611; North Fork Holston R. RC NMB 153; RC NMB 157.

Ictalurus nebulosus

York River drainage. — VA: Bunch Creek RC SCS 24; Smoots Pond RC JRS 23.

James River drainage. — VA: Herring Creek RC TZ 157; Jordans Branch Creek RC VCU-B-JB-1.

Roanoke River drainage. — NC: Anderson Swamp Creek RC REJ 867; Belews Lake DPC 50106-15; Flat Creek RC REJ 866; VA: Back Creek RC WJM; Ballows Creek RC ACE 34; Banister R. RC HJP 80; Beaver Pond Creek RC REJ 863; Dan R. RC FWS 6; Falling R. RC REJ 815; Grassy Creek RC REJ 860; Green Branch RC ACE 134; Lawsons Creek RC ACE 26; Mason Creek RC REJ 524; Old Woman Creek RC REJ 401; Pigg R. RC REJ 402; RC DLJ 26; RC DLJ 6; Lake Drummond VPI 1218; Lake Jordan RC JRS 22.

New River drainage. — VA: Meadow Creek RC JRR 207.

Ictalurus melas

Roanoke River drainage. — NC: Belews Lake DPC 50105-07; VA: Grassy Creek RC REJ 860; Little Buffalo Creek RC REJ 869.

Peedee River drainage. — NC: trib. Yadkin R. UMMZ 138401.

Tennessee River drainage. — TN: Big Sandy R. UT 48.114; Dry Creek UT 48.202; Duck R. UT 48.294; Sims Spring Branch UT 48.284; VA: Copper Creek RC REJ 348.

Cumberland River drainage. — TN: East Fork Stones R. UT 48.7.

Green River drainage. — TN: Hurricane Creek RC REJ 560.

Coosa River drainage. — TN: Coahulla Creek UT 48.57; Mill Creek UT 48.56; UT 48.285.

Mississippi River basin. — TN: backwater Mississippi R. UT 48.26.

Hatchie River drainage. — TN: ditch UT 48.109.

Forked Deer River drainage. — TN: Nixon Creek UT 48.249; slough UT 48.250.

Red River drainage. — LA: ditch VPI 2758; Shepherd Bayou VPI 2342.

Sabine River drainage. — LA: Sabine R. VPI 2652.

DISTRIBUTION

The ictalurids with an adnexed adipose fin generally occur in moderate to large streams and main river channels of all physiographic provinces in Virginia except the Blue Ridge, from which they are essentially absent except for upper New River. Most species readily adapt to reservoir and farm pond habitats, and a few, notably *I. catus, I. furcatus* and *I. punctatus,* tolerate estuarine conditions. One species, *I. brunneus,* commonly occurs in moderate currents (Yerger and Relyea 1968; Bryant et al. 1979; D. Cloutman, pers. comm.) as well as sluggish currents and backwaters with soft bottoms (M. Corcoran, pers. comm.), which are typically inhabited by the remaining species. When collected during daylight most of these species are associated with cover such as undercut banks, logs and boulders. The following discussion includes consideration of native or introduced status in the drainages.

Ictalurus brunneus. — The snail bullhead is known in the Roanoke drainage only from the Dan River system above Kerr Reservoir, North Carolina and Virginia (Fig. 1). It was first collected from the lower Dan in 1976 just above this reservoir, and was subsequently taken in low numbers from the main channel and a few tributaries. Prior to the Dan records, Yerger and Relyea (1968) reported its northern limits as the upper Cape Fear and Peedee River drainages, North Carolina, both adjacent on the south to the Dan.

The distributional relationship in the Roanoke drainage of *I. brunneus* and *I. platycephalus,* the closest relative of *I. brunneus* (Lundberg 1975), appears unique. Yerger and Relyea (1968) found that, although the species are broadly sympatric and occasionally syntopic in several drainages, *I. brunneus* tends to be more frequently found in, and perhaps differentially favors, higher gradient areas in the upper parts of those drainages. In the Mobile drainage, where only *I. brunneus* occurs, this species was found only in the upper section, in Georgia, over hard bottom in riffles and moderate currents (Bryant et al. 1979). Although both species occupy upper and lower reaches of many streams, this distribution pattern was not regarded as atypical since higher and lower gradient

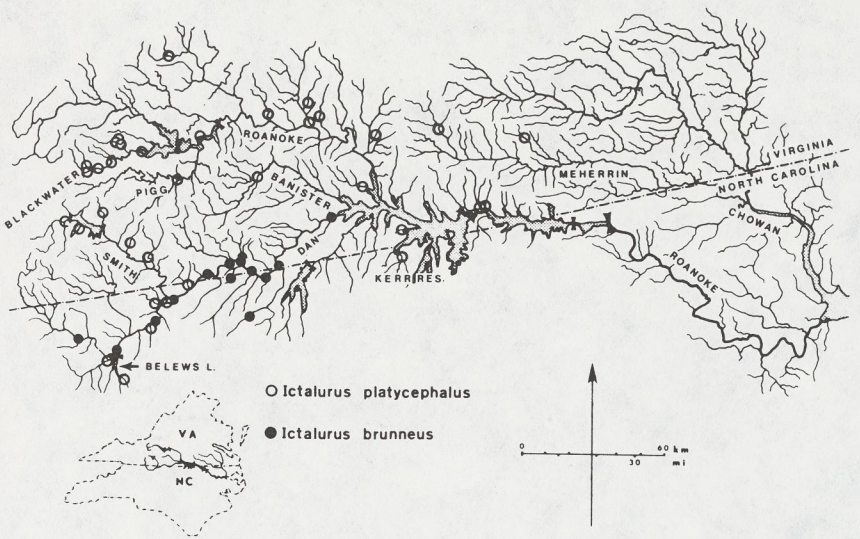

Fig. 1. Distribution of *Ictalurus brunneus* and *I. platycephalus* in the Roanoke River drainage, North Carolina and Virginia.

regimes occur in many parts of these streams (Yerger and Relyea 1968). Extensive surveys of the Neuse drainage for *Ictalurus*, and less extensive surveys of other Carolinean Atlantic Slope drainages, revealed that *I. brunneus* is more abundant, sometimes greatly so, than *I. platycephalus* (M. Corcoran, pers. comm.). Corcoran also determined that, at least in the Neuse, both species are generally absent from the Coastal Plain. Thus, previous concepts of a preference by *I. brunneus* for upper stream sections may partly relate to its numerical abundance over *I. platycephalus*. However, in the Roanoke drainage, only *I. platycephalus* appears to currently occur in the main trunk Roanoke system and the Smith River tributary of the Dan River. In both these systems it extends upstream well through moderate gradients into Blue Ridge foothills.

The apparent absence of *I. brunneus* from most of the Roanoke drainage, including the Chowan system of the lower Roanoke, and the wide geographic and ecological range of *I. platycephalus* therein, suggest that *I. brunneus* was recently introduced to the Dan. Prior absence of *I. brunneus* would have allowed *I. platycephalus* to become widely established. The apparent current exclusion of *I. brunneus* from montane sections of the Dan system thus may relate to former establishment of *I. platycephalus*.

Belews Lake, an upper Dan system impoundment (Fig. 1), was reportedly stocked with *I. melas* by a "concerned citizen" to improve fishing (W. Smith, pers. comm.). These introduced *I. melas* may have

been transferred from the Yadkin system of the Peedee, where both *I. brunneus* and *I. melas* occur. Although *I. brunneus* is not known from the lake (D. Cloutman, pers comm.) it occurs in the immediate area, and the *I. melas* stocking may have included the superficially similar *I. brunneus*. Belews Creek was impounded in 1970 and the lake reached full pool in 1973 (Harrell et al. 1973). If *I. brunneus* dispersed from the Belews Lake area, its mobility would have been similar to that of introduced *Pylodictis olivaris* now spreading in the Cape Fear drainage (M. Corcoran, pers. comm.). However, the Belews Lake area may not have been the point of origin; possibly more than one stocking occurred.

Ictalurus catus. — White catfish are native to the major Atlantic slope drainages of Virginia, occurring widely in Piedmont and Coastal Plain parts of large streams and reservoirs. Jordan (1889) reported it from Maury (North) River and elsewhere in the upper James drainage in the Ridge and Valley. It also has been taken in South Fork Shenandoah River (Potomac drainage) in the Ridge and Valley. Clay (1975) noted that *I. catus* introduced to Kentucky were from the James River.

Ictalurus furcatus. — The presence in Virginia of the blue catfish, a primarily Mississippi basin and Gulf slope species, has been widely reported, but the species has only recently been verifed as introduced. It was stocked in lower Rappahannock (1975 and 1977) and James (1977) rivers by the Virginia Commission of Game and Inland Fisheries (L. Hart, pers. comm.). Juvenile specimens from these stockings have since been collected by Virginia Institute of Marine Science personnel (J. Gourley, pers. comm.; VIMS specimens examined by us). It is not known whether the species is reproducing. *Ictalurus furcatus* is unknown from the Potomac, York, New, Roanoke and Tennessee (in Virginia) River drainages. Records from the Potomac and New River drainages are discussed in detail.

Ictalurus furcatus may have been introduced into the Potomac River near Washington, D.C., between 1898 and 1905. The old U.S. Fish Commission rearing and holding ponds in that area were an early active center of fish dispersal. It was not recorded by Smith and Bean (1898), but was reported as introduced (probably with *I. punctatus*) based on 1905 records by Bean and Weed (1911), and by McAtee and Weed (1915) based on two specimens collected in 1912. We located an adult *I. punctatus* (USNM 70281) previously misidentified as *I. furcatus*, apparently one of the specimens on which McAtee and Weed (1915) based their record. Radcliffe and Welsh (1916) reported *I. furcatus* from the Chesapeake and Ohio canal, along the Potomac River, Maryland. The single specimen was reportedly sent to Washington, but it was not found by us at the USNM. It is unknown whether *I. furcatus* was introduced and failed to establish, or if all records are actually of *I. punctatus*. Elser (1950) and Manville (1968) based their records of *I. furcatus* on these early reports. A second body of literature (Wiley 1970;

Jenkins et al. 1972; Lee et al. 1976; Stauffer et al. 1978) reported *I. furcatus* from the Potomac based on records of Schwartz (1961). Frank J. Schwartz (pers. comm.) later felt that these specimens were "odd *I. punctatus*"; no Potomac *I. furcatus* were found in collections of Chesapeake Biological Laboratory, University of North Carolina Institute of Marine Sciences, and Virginia Institute of Marine Science, which house Schwartz's collection (F. Schwartz, J. Stauffer, J. Gourley, pers. comm.). *Ictalurus furcatus* has not been collected in recent extensive surveys of the Potomac River from Maryland—West Virginia (Energy Impact Associates), along Virginia above Great Falls (E. Enamait, pers. comm.), or from Washington, D.C., downstream (J. Gourley, pers. comm.). If ever introduced into the Potomac River near Washington, D.C., it probably shares extirpated status with *Percopsis omiscomaycus* (Walbaum) and *Percina caprodes* (Rafinesque).

In the New drainage, *I. furcatus* was reported introduced into the West Virginia section (Schwartz *in* Jenkins et al. 1972), but no specimens were seen. Cope's (1868) record of *I. "caerulescens"* in the Virginia section was based on *I. punctatus* (Fowler 1945:81). Addair's (1944) records from West Virginia of *I. "anguilla"* probably are of only *I. punctatus*. His New River, West Virginia, specimens at the UMMZ are *I. punctatus*. Hocutt et al. (1978) listed *I. furcatus* as a hypothetical inclusion to the Greenbrier River fauna based on Addair (1944). Ross (1959) repeated reports by game wardens of "blue catfish" from the New River in three Virginia counties. Also, a single record was reported (specimen discarded) by personnel of the VCGIF from Claytor Lake, New River impoundment. The above two reports of *I. furcatus* are considered to be of *I. punctatus*, based on the absence of *I. furcatus* from extensive New River surveys by Hocutt et al. (1973), Stauffer et al. (1975, 1976) and others, and because nonspotted channel catfish have often been misidentified as blue catfish.

Ictalurus melas. — The black bullhead probably is native to Virginia in only the Tennessee and Big Sandy drainages. Until recent collections in the Roanoke drainage, it was thought to be absent from Atlantic slope drainages. Hence, we considered records of collections and literature compilations (Abbott et al. 1977) for *I. melas* to be *I. nebulosus*, a species with which it is sometimes confused. However, recent records from Belews Lake (see *I. brunneus*), from Dan River above Belews Lake, North Carolina (UNC 76-93), from two Virginia tributaries of Kerr Reservoir, and two specimens (UMMZ 138480) taken in 1940 from the North Carolina section of the upper Peedee drainage, prompted us to reconsider records from the Atlantic slope. Collections of *I. nebulosus* from the Roanoke drainage (including Kerr Reservoir preimpoundment collections and the Chowan system) in Virginia were examined, and no *I. melas* were discovered. Also, none were reported from extensive surveys of the North Carolina parts of the Roanoke and Chowan systems (Smith 1963; Carnes 1965). The absence of *I. melas* from earlier collections strongly

suggests that its presence in the Roanoke is the result of single or multiple introductions. Because of difficulties of identification, until specimens are examined we still consider *I. melas* to be absent elsewhere on the Atlantic slope in Virginia. Other species recently introduced into the Roanoke drainage in the North Carolina part of the Dan at Belews Lake are *Notropis lutrensis* (Baird and Girard) and *Pimephales promelas* (Rafinesque) (DPC 30407-04 and 31201-02, respectively).

The occurrence of *I. melas* in the New River drainage is also problematic. It appears to have been introduced but now possibly extirpated. The only extant specimens known are four juveniles from Fries, a town on New River, taken in 1939 by B. Smith (USNM 109467). The only other record of *I. melas* is from Reed Creek at Wytheville based on unretained specimens (Wollitz 1968). Wollitz (pers. comm.) thought the Reed Creek specimens resulted from introduction. *Ictalurus melas* has not been taken in recent extensive New River and tributary surveys in Virginia, or from New River tributaries in West Virginia (Hocutt et al. 1978, 1979). Hocutt et al. (1978) reported *I. melas* as stocked in Sherwood Lake, Greenbrier River system, West Virginia. Like other bullheads, it may be widely introduced in farm ponds.

Ictalurus natalis. — The yellow bullhead is native to Virginia, occurring in all drainages except the New. The only record for the latter, from the Gauley River system of the lower New, West Virginia, may represent an introduction (Hocutt et al. 1979).

Ictalurus nebulosus. — The brown bullhead is native to the Atlantic slope of Virginia; it occurs in all Atlantic slope drainages as well as being the only ictalurid known from the diminutive freshwater ichthyofauna of the southern part of the Delmarva Peninsula. *Ictalurus nebulosus* is probably introduced to the New drainage. In Virginia it is known from only two collections, both from tributaries entering New River below Claytor Lake: a juvenile (VPI 2039) was rotenoned in1971 from East River just above its mouth and immediately upstream from the Virginia — West Virginia state line; and two juveniles were collected in 1972 from Meadow Creek, Montgomery County. Hocutt et al. (1979) reported another specimen taken in 1976 from a lower New River tributary system, West Virginia. It may have been stocked in farm ponds in much of the state, but is unknown from the Tennessee River drainage in Virginia.

Ictalurus platycephalus. — The flat bullhead occurs only in the Roanoke drainage, including the Meherrin River branch of the Chowan system, in Virginia; this is the northern limit of its distribution (Yerger and Relyea 1968; Fig. 1). The species generally occurs in small to moderate-size streams draining the Piedmont, where it inhabits sluggish waters and is known from reservoirs. In the Roanoke drainage it extends into smaller streams than it is "typically" associated with elsewhere on the Atlantic Slope. The possible historical absence of *I. brunneus* in the

Roanoke drainage may have allowed it to invade smaller stream habitats thought to be typically occupied by only *I. brunneus* when the two species are sympatric. The first life history study of *I. platycephalus* was conducted by Olmstead and Cloutman (1979).

Ictalurus punctatus. — The channel catfish is native in the Tennessee and Big Sandy drainages in Virginia and, based on Cope's 1867 record (see *I. furcatus*), probably native in the New River above Kanawha Falls. It has been introduced in all Atlantic slope drainages in the state (Jenkins et al. 1972).

Pylodictis olivaris. — The flathead catfish is native to the Tennessee, Big Sandy, and New drainages in Virginia. It has recently been introduced into the James and Roanoke drainages. Introduction into lower James River near Surry accidentally occurred in 1965 when a temporary holding pond at Hog Island Game Refuge washed out during a storm and released about 50 *P. olivaris*. A 20 to 30 pound *P. olivaris* was seen by Dean Estes (Virginia Electric Power Co. biologist) in 1977; it was taken on a trotline near Surry (J. Gourley, pers. comm.). Hart (1978) reported the introduction into Smith Mountain Reservoir (the most upstream reservoir on the Roanoke River, Fig. 1) of one specimen in 1976 and five in 1977. Specimens from 10 inches long to 10 pounds weight, taken from the Roanoke River near Brookneal below Smith Mountain Lake, were observed in 1978-79 by L. Hart (pers. comm.).

DIAGNOSTIC CHARACTERS

The following account and critique of distinguishing characters includes summaries of our data as well as characters abstracted from the literature. Discussion of diagnostic features is supplemented by frequency distributions of counts for Virginia *Ictalurus (Amiurus)* in Tables 1-3, comparison of eye sizes (Fig. 2), and fins (shape and pigmentation), as well as premaxillary teeth configurations (Fig. 3). We emphasize that the following discussion pertains to Virginia *Ictalurus* (except where supplemented; see Methods and Materials), and is limited to characters with known or reputed utility in identifying species. Mention of somatic and fin pigmentation is generally avoided, as many aspects of coloration are variable in all species of *Ictalurus*. Although the Virginia *Ictalurus* fauna is artificially enriched in species, the species are easily distinguished. To reduce redundancy, diagnostic features are discussed by the following groups: the flathead bullheads, the typical bullheads, and the *Ictalurus* with forked tails. Characters of the monotypic genus *Pylodictis* are listed only in the key at the end of this section.

Flathead bullheads. — This group is represented in Virginia by *I. brunneus* and *I. platycephalus*. The species were clearly distinguished first by Yerger and Relyea (1968), who recognized the flathead bullheads as a group but did not provide a key character for its separation from the

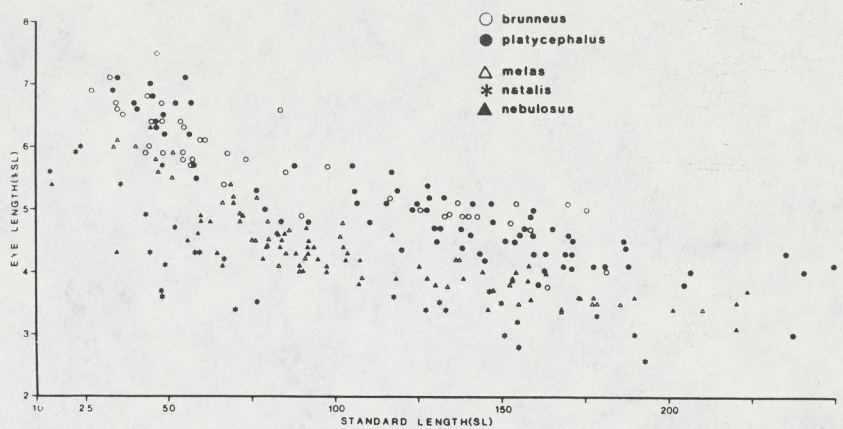

Fig. 2. Relationship of eye length (as % SL) to SL in Virginia *Ictalurus (Amiurus)* with emarginate caudal fins.

typical bullheads group. The flathead bullheads are best distinguished from other bullheads by the presence of a large dark basal blotch, its upper edge straight or convexly rounded, in the dorsal fin (Fig. 3D). The blotch was also recognized as a key character and figured for *I. platycephalus* by Eddy (1969), and depicted for *I. brunneus* by Smith-Vaniz (1968). Eye size is secondarily useful in separating the groups, the size being moderate in flatheads and small in typical bullheads. Although size varies allometrically relative to SL, more pronouncedly in small juveniles (Fig. 2), the differences between the groups are generally obvious, with little overlap when comparing specimens of similar lengths. The third member of the flathead bullhead group, *I. serracanthus,* a primarily Floridean species, also has the dorsal blotch and moderate eye size character states (figure and description in Yerger and Relyea 1968). Head shape of flathead and typical bullheads is variable, from essentially flat to slightly convex dorsally in flatheads, versus usually more elevated or markedly convex in typical bullheads. Overlap in head shape and eye size is such that sole reliance on either character for group separation will result in some misidentifications.

Ictalurus brunneus and *I. platycephalus* are best distinguished from each other by barbel pigmentation and premaxillary teeth configuration, and secondarily by meristics. Most juveniles and adults of *I. brunneus* examined had profusely dark pigmented mental (chin) barbels, whereas most specimens of *I. platycephalus* had unpigmented or slightly pigmented, pale mental barbels. The absence of profusely developed mental barbel pigment in *I. brunneus* usually occurs in specimens smaller than 100 mm SL. In *I. platycephalus* the presence of slightly pigmented mental barbels occurs mostly in adults, particularly in the lateral pair of barbels; the

medial mental barbels rarely possess melanophores, and then only basally. Additionally, the maxillary barbels of *I. platycephalus* usually appear bicolored (leading edge pale, posterior edge dark), whereas in *I. brunneus* these barbels are uniformly dark.

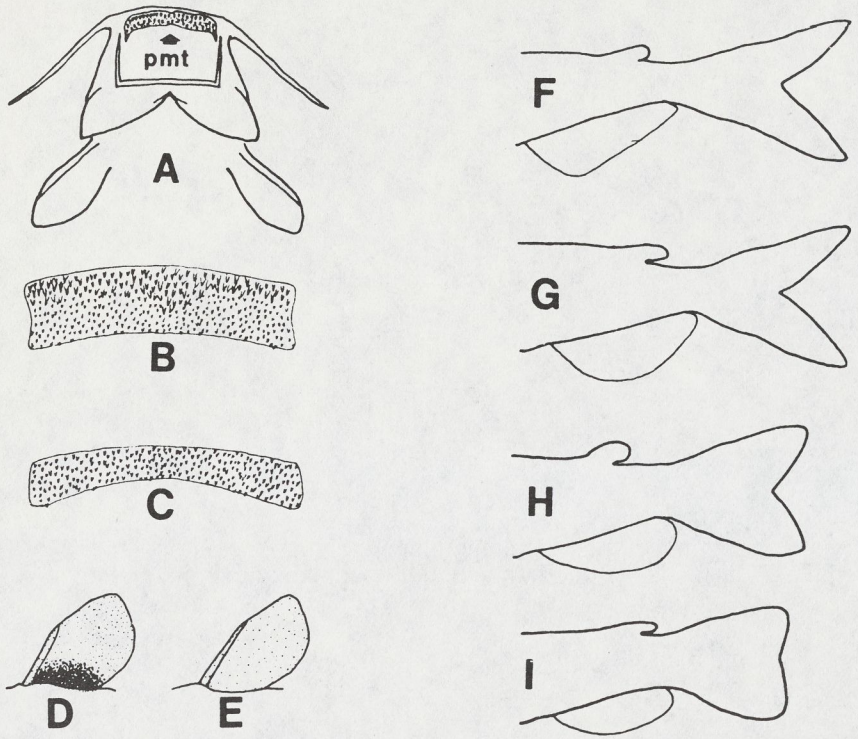

Fig. 3. Diagnostic features of some Virginia ictalurids: A, ventral aspect showing premaxillary tooth patch of *Pylodictis;* B, premaxillary tooth patch of *I. brunneus;* C, premaxillary tooth patch of *I. platycephalus;* D, flathead bullhead dorsal fin with dark basal blotch; E, dorsal fin of typical bullhead; F, fin profiles of *I. furcatus;* G, fin profiles of *I. punctatus;* H, fin profiles of *I. catus;* I, profile of an emarginate caudal fin.

The premaxillary tooth patch of *I. brunneus* differs from *I. platycephalus* in being wider, fairly uniform in width, and usually possessing lateral edentations in the patch (Fig. 3B). The cardiform teeth of *I. brunneus* are more numerous along an anterior-posterior axis (teeth not forming rows) than in *I. platycephalus,* and occur in two distinct sizes. Large cardiform teeth are positioned along the anterior margin of the tooth patch, and are often additionally arranged in a medial, triangular configuration. The tooth patch of *I. platycephalus* usually lacks lateral edentations and is occasionally slightly constricted medially (Fig. 3C).

The cardiform teeth of *I. platycephalus* are small and fairly uniform in size. The premaxillary tooth patch and cardiform teeth size differences are not evident in small specimens. These characters were first recognized by Lundberg (1970).

The greatest meristic differences between *I. brunneus* and *I. platycephalus* are in anal rays and a character index (Tables 2 and 3). Frequency ranges of all counts differed slightly from data of Yerger and Relyea (1968), indicating possible geographic variation. A slightly higher range of character index values exists in Roanoke drainage *I. brunneus* when compared to data of Yerger and Relyea (1968) from some more southerly drainages, and results in greater meristic overlap between the two species in the Roanoke.

The difference in mouth position between the species conformed to Yerger and Relyea's (1968) description; however, we do not advocate general use of the character, as the difference seems to be only an average one and is not as obvious as barbel pigmentation.

Typical bullheads. — Three species of typical bullheads (or the *natalis* group of Lundberg 1975) inhabit Virginia waters: *I. natalis, I. nebulosus* and *I. melas.* These are best separated from the flathead bullhead group by the absence of a discrete dark blotch at the base of the dorsal fin (Fig. 3E) and by small eye size (Fig. 2).

Ictalurus natalis is easily distinguished from the others by its unpigmented mental barbels. The dark blood pigments in vessels of these barbels should not be confused with the presence of melanophores. Preserved blood in mental barbels appears as a dark line. The remaining species, *I. nebulosus* and *I. melas,* have often been reported to be separable by the character of the serrae on the posterior edge of the pectoral spine: moderate serrae in *I. nebulosus,* weak serrae in *I. melas* (Trautman 1957; Blair et al. 1957; Hubbs and Lagler 1958; Pflieger 1975; and others). The posterior pectoral spine serrae in *I. melas* are variable, being absent to moderately developed. Although most often weakly developed in adult *I. melas,* the pectoral serrae are unreliable for consistently distinguishing *I. melas* from *I. nebulosus. Ictalurus melas* is best distinguished from *I. nebulosus* by higher (rarely overlapping) gill raker counts (Table 1). The single *I. melas* possessing 15 gill rakers on the right arch had 17 on the left arch.

Fin pigmentation differences have also been reported. Of these characters, only the depigmented "bar" at the caudal base of *I. melas* is consistently present, and then only in larger juveniles and adults. However, it is often evident only when directly compared to specimens of *I. nebulosus.*

Forked-tail Ictalurus. — Of the three species in this group, *I. catus* is readily separated by a moderately forked tail (Fig. 3H) and low anal ray counts, usually 22-24, (22-25, $\bar{x}$ = 23.1). Variation exists in the anal ray count ranges reported for *I. catus:* 19-22 (Jordan and Evermann 1896);

Table 1. Frequency distribution of gill raker counts (total) for subgenus *Amiurus* of Virginia.

Species	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	N	$\bar{x}$	S.D.
I. melas						1	3	6	18	15	3	1			1	48	18.3	1.42
I. nebulosus				8	28	11	1									48	14.1	0.69
I. natalis			3	6	7	6	1		2							26	14.3	1.64
I. platycephalus	4	10	28	29	4	1	2	1								78	12.4	1.14
I. brunneus		1	3	8	12	5	12	1	1							43	14.4	1.53

Table 2. Frequency distribution of anal ray counts for subgenus *Amiurus* of Virginia.

Species	17	18	19	20	21	22	23	24	25	26	27	28	N	$\bar{x}$	S.D.
I. melas			2	5	15	7	10	5	3				47	21.7	2.41
I. nebulosus		2		2	8	20	8	8					48	22.1	1.37
I. natalis								7	6	6	4	2	25	25.4	1.20
I. platycephalus					4	32	27	14		1			78	22.7	0.91
I. brunneus		8	22	9	3	1							43	19.2	0.92

Table 3. Frequency distribution of character index (anal rays minus gill rakers) for subgenus *Amiurus* of Virginia.

Species	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	N	$\bar{x}$	S.D.
I. melas	5	2	5	10	9	8	7		1								47	3.6	1.93
I. nebulosus					2		3	11	15	10	7						48	8.0	1.41
I. natalis							1	1		2	5	3	8	3	2	1	26	11.2	2.07
I. platycephalus							2	1	2	11	29	21	9	3			78	10.3	1.34
I. brunneus		1	4	7	5	12	5	7	1	1							43	4.8	1.83

18-21 (Blair et al. 1957); 18-24 (Trautman 1957); 19-23 (Eddy 1969); 18-22 in key, 19-23 in text (Clay 1975). The larger ranges and lower extremes of these counts may have resulted from failure to count all anterior rudimentary rays in at least some of the material examined by these authors. Smith-Vaniz (1968) reported a count range similar to ours (21-26, $\bar{x}$ = 23). The gap in the "bony ridge" between the head and dorsal fin (a disjuncture between the supraoccipital and the anterior process of the first pterygiophore), reported in keys by Hubbs and Lagler (1958) and Clay (1975), was consistently present in *I. catus*. However, a disjuncture also occurs in juveniles of *I. punctatus* and *I. furcatus*.

Until recently, anal ray counts were reported to have little overlap between *I. furcatus* and *I. punctatus* (Trautman 1957; Blair et al. 1957; Pflieger 1975; and others). However, Clay (1975) reported anal ray count ranges to be 27-34 for *I. furcatus* and 23-29 for *I. punctatus* and emphasized the need to consider anal fin shapes (Fig. 3F, G). An obvious character when present are the spots on young to adult *I. punctatus,* but adults often lack them. W. Ralph Taylor (pers. comm.) informed us of a difference in the gas bladders of *I. furcatus* and *I. punctatus;* that of *I. furcatus* has an elongate posterior extension and that of *I. punctatus* does not. The gas bladder difference is illustrated by Pflieger (1975).

KEY TO VIRGINIA ICTALURIDS WITH AN ADNEXED ADIPOSE FIN

1. Premaxillary tooth patch with posterolateral extensions (Fig. 3A); upper lobe caudal fin partially depigmented (varies in adults) ..... *Pylodictis olivaris.*
   Premaxillary tooth patch without posterolateral extensions; upper lobe caudal fin not partly depigmented ..... 2.
2. Caudal fin deeply forked (Fig. 3F, G) ..... 3.
   Caudal fin moderately forked to emarginate (Fig. 3H, I) ..... 4.
3. Anal fin margin usually rounded (Fig. 3G); anal rays 23-29; young to small adults often with spots ..... *Ictalurus punctatus.*
   Anal fin margin straight (Fig. 3F); anal rays 27-34; never spotted ..... *I. furcatus.*
4. Caudal fin moderately forked (Fig. 3H); anal rays usually 22-24 (22-25) ..... *I. catus.*
   Caudal fin emarginate (Fig. 3I) ..... 5.
5. Dorsal fin with dark basal blotch (Fig. 3D); eye size moderate (flathead bullheads) ..... 6.
   Dorsal fin without dark basal blotch (Fig. 3E); eye size small (typical bullheads) ..... 7.
6. Mental barbels usually without pigment (pigment may be present in large specimens on lateral barbels, rarely on medial); leading edge of maxillary barbels pale

(appearing bicolored); premaxillary tooth patch of large juveniles and adults as in Figure 3C; gill rakers usually 10-14 (10-17); anal rays usually 22-24 (21-26) ..... *I. platycephalus.*
Mental barbels usually profusely pigmented (occasionally pigment only developed basally in small specimens); maxillary barbels uniformly dark; premaxillary tooth patch in large juveniles and adults as in Figure 3B; gill rakers usually 12-16 (11-18); anal rays usually 18-20 (18-22) ..... *I. brunneus.*

7. Mental barbels usually pale; anal rays usually 24-27 (24-28); gill rakers usually 12-15 (12-18) ..... *I. natalis*
Mental barbels usually profusely pigmented ..... 8.

8. Gill rakers usually 17-20 (15-24); a rectangular depigmented area often present at base of caudal fin in adults ..... *I. melas.*
Gill rakers usually 13-15 (13-16); caudel base with uniform pigmentation ..... *I. nebulosus.*

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The Spawning Activities of Fresh Water Smelt, with Special Reference to the Sex Ratio

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OBSERVATIONS ON *Mola* BASKING BEHAVIOR, PARASITES, ECHENEIDID ASSOCIATIONS, AND BODY-ORGAN WEIGHT RELATIONSHIPS

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Abstract: Observations are presented on three ocean sunfish, *Mola mola,* and one sharptail mola, *Mola lanceolata,* that stranded in North Carolina coastal waters. Morphometric and scientific data are presented along with body-organ weight observations. Each species was heavily parasitized by cestodes suggesting that the basking behavior of molas results from a sick parasitized dying condition rather than an urge to bask. A live remora was found lodged in the gular region. It survived even though the mola had been out of water for 17 h.

Key Words: *Mola*; ocean sunfish; basking; body-organ weight relationships.

INTRODUCTION

Molas, ocean sunfishes, reported since Greek and Roman times, are cosmopolitan in the warm marine waters of the world (Gudger, 1936, 1937). An occasional stray specimen enters or is carried into cooler, fresher temperate waters (Van Bruggen, 1983). Molas swim in an upright position by sculling with their dorsal and anal fins, but are usually encountered lying on their sides basking in surface waters (Norman and Fraser, 1938). When captured or stranded their ungainly size and shape (*Mola mola* attains a length of 3.0 m and weight of 1,000 kg; *M. lanceolata* 3.0 m and +600 kg) make them difficult to handle. Few molids have been examined in detail. Their external parasites have been noted (Threlfall, 1967; Hewitt, 1968, 1971; Anderson and Cupka, 1973; Thulin, 1973; Lozera and Odense, 1974; Margolis and Arthur, 1979) and although the skull, external morphology, and internal anatomy of the tail have been described (Cleland, 1862; Vignal, 1881; Gregory, 1933; Gregory and Raven, 1934), few investigators have dissected or examined them internally. We, therefore, present data and comments on two molids from North Carolina waters, the ocean sunfish, *Mola mola,* and the sharptail mola, *Mola lanceolata.* Included are body-organ weight relationships, morphometric data, internal parasites, an interesting echeneidid relationship, and an explanation for the basking behavior characteristic of molids.

Smith (1907), Brimley (1939), Funderburg and Eaton (1952), Anderson and Cupka (1973), and Lee (1986) documented the presence of *M. mola* or *M. lanceolata* in North Carolina or South Carolina waters. Many of those records were based on basking sightings. While most investigators recognized that molas fre-

Table 1

Morphometric relationships (mm), in percent of total length, for *M. mola* and *M. lanceolata* from North Carolina.

	M. mola			*M. lanceolata*
	20 June 1986 UNC 16961	16 May 1980	24 Oct. 1976	5 Jan. 1986 UNC 16934
Total length	952	1,126	1,764	1,740
Postdorsal length	24.9	25.0	25.0	26.4
Depth body	64.1	62.0	55.3	52.2
Pectoral fin length	14.0	13.7	14.5	9.8
Gill slit length	5.8	6.0	5.0	5.2
Orbit	4.8	4.4	4.3	3.6
Interorbital distance	17.8	17.9	—	12.6
Anal fin base/height	17.3/35.5	17.4/40.1	19.0/34.5	19.5/32.7
Dorsal fin base/height	22.9/41.3	22.3/42.8	26.5/34.7	21.6/38.7
Tail length/height	12.1/54.0	21.9/50.9	15.1/43.2	27.7/45.4
Snout length	11.4	12.9	9.1	8.6
Mouth width	6.8	—	damaged	4.3
Lower jaw length	6.2	—	damaged	—
Distance to dorsal fin	48.3	61.3	53.2	50.0
Distance to dorsal hump	17.3	30.6	25.7	13.2

quent inshore marine waters, Lee (1986) contended that ". ... *M. mola* . . . is an epipelagic migrant in North Carolina's waters." Of the numerous inshore occurrences of molas noted by one of us (F.J.S.), three *M. mola* and one *M. lanceolata* have been examined in detail (Tables 1, 2). Additional specimens are preserved whole in the University of North Carolina (UNC), Institute of Marine Sciences (IMS) fish collection.

METHODS

The largest *M. mola* studied, 281.2 kg, was snagged 24 October 1976 in the Atlantic Ocean 9.6 km south of the Knuckle Buoy southeast of Morehead City, North Carolina. The 74.8-kg specimen was entangled in a gill net set 16 May 1980 in Long Creek, a tributary to Neuse River and Pamlico Sound located 9.0 km northeast of Harlow, North Carolina. The smallest *M. mola* stranded at Drum Inlet opposite Atlantic, North Carolina, 20 June 1986. The only specimen of *M. lanceolata* examined stranded 5 January 1986 at Atlantic Beach, North Carolina. Each *Mola* was transported to IMS for measurement and dissection. Measurements (in millimeters) were taken using a 4.5-m metal tape. Gross body weights were obtained to nearest 0.45 kg with a platform balance while organ weights were determined on a Mettler 3000 balance to the nearest 0.1 g. Selected organ or body parts were subsequently preserved in 10% formalin, transferred into 70% isopropyl alcohol, and curated in the UNC fish collection.

OBSERVATIONS

Morphometric data for our North Carolina molids fit those listed by Gudger (1937), Brimley (1939), Funderburg and Eaton (1952), and Anderson and Cupka (1973) (Table 1). The caudal fin of *M. mola* seems to change the most in terms

Table 2

Body-organ weight, in percent of total body weight, relationships for *M. mola* and *M. lanceolata* from North Carolina.

	M. mola			*M. lanceolata*
	20 June 1986 UNC 16961	16 May 1980	24 Oct. 1976	5 Jan. 1986 UNC 16934
Dorsal fin	2.6	1.1	1.8	2.5
Anal fin	1.6	1.2	1.9	1.9
Pectoral fin	0.6	0.1	0.23	0.12
Caudal fin	7.7	3.6	2.6	5.6
Eye	1.0	0.2	0.06	0.15
Liver	1.9	1.6	1.6	1.90
Kidney	1.3	—	—	0.46
Heart	1.0	0.15	0.12	0.12
Intestines	5.5	9.8	3.8	7.5
Gonads	0.04	0.05	0.16	0.2
Brain	0.01	0.01	—	0.06
Blood	0.05	0.60	0.03	0.60
Skeleton, skin, and soft structures	75.10	88.66	87.41	79.0
Body weight kg	35.3	74.8	281.2	145.1
Sex	♀	♂	♂	♂

of body-organ weight relationship, decreasing as a percentage of total body weight with growth (Table 2). The skeleton and soft structures in the specimens we examined comprise 75–88 percent of the total weight. All other organs except the intestines contribute little to the overall weight of a *Mola.* The intestines vary from 3.8 to 9.8 percent of the total body weight (Table 2). Because the gonads were undeveloped they too make up a minor portion of the overall body weight. Most literature body weight reports (Gudger and MacDonald, 1935; Brimley, 1939) are based on often exaggerated visual estimates; hence, no comparisons are possible to body-organ percentages noted herein.

The liver of each *M. mola* and *M. lanceolata* examined was heavily infected and riddled with the trypanorhynch cestode, *Molicola horrida,* and the pseudophyllidea cestode, *Anchistrocephalus microcephalus* (Fig. 1). The latter also occupied the intestines of both species, by the thousands.

Dissection of the gill and oral cavity of the male *M. lanceolata* revealed a live 170 mm standard length (SL) (203 mm total length), 71.2 g *Remora remora* (UNC 16935). It was lodged in the gular region with its head pointing toward the mouth and the tail resting near bases of the gills (Fig. 1). This condition persisted even though the host *M. lanceolata,* which beached at 1700 h, had been removed from the water and immediately transported to IMS where it remained out of water for 17 h prior to dissection the next morning, 6 January 1986. No residual water was found in the gular or gill chamber area. The 5 January 1986 night air temperatures on the IMS dock ranged from 0–7°C yet the *Remora* was alive and active when removed from the host. Reduced internal body temperatures of the *Mola* and *Remora* could have decreased the *Remora*'s respiration rate thereby prolonging its survival. Another *M. lanceolata* (1,780 mm TL) stranded at Banks Channel, Wrightsville Beach, North Carolina, 14 November 1984 (air temperature

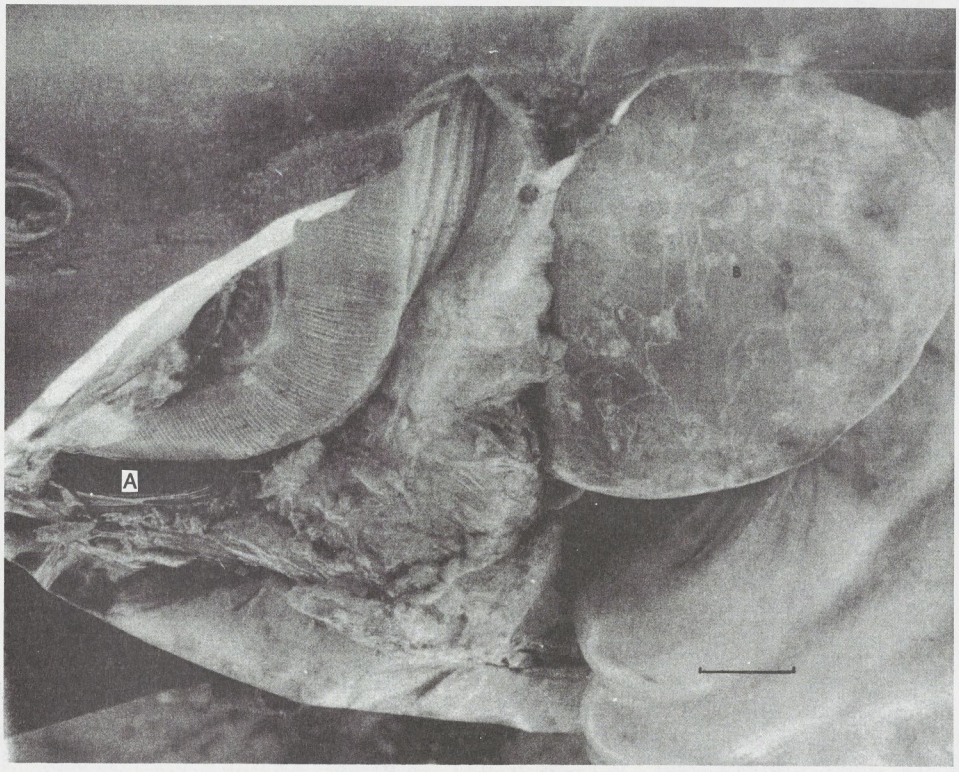

FIG. 1. Left lateral view of *M. lanceolata* indicating position of *R. remora* (A) and of heavily infested liver (B). Bar on figure = 47 mm.

10°C, water 11.5°C) harbored a 183 mm SL (218 mm TL), 90.9 g *R. brachyptera* (UNC-W 84-1). While one of us (D.G.L.) pushed the mola back into deeper waters, the echeneidid apparently disengaged and was readily captured. It could not be determined if the echeneidid had been in the gill chamber even though we had carefully inspected the exterior of the mola prior to pushing it off the beach. It is unlikely that the *Remora* had been associated with another species as all but resident fish vacate North Carolina inshore sound and beach waters by October.

DISCUSSION

Gregory and Raven (1934) presented the most detailed study of the anatomy of *M. mola.* Cleland (1862), Vignal (1881), and Gudger (1936) commented on *Mola mola* anatomy but did not determine any body-organ weight relationships. Gregory and Raven (1934) speculated that the powerful muscles of the throat and opercular fold cause a strong flush of water within the gill chamber of a *Mola.* They noted that the inner gill openings of molas are restricted slits; hence, remoras frequenting the gill or oral chambers most likely enter through the mouth rather than through the slit-like opercular opening. Perhaps entrance occurs as remoras are feeding on parasites that associate with molas (Cressey and Lachner, 1970). Although the literature is replete with observations of remoras on molids or in their oral chambers, few remoras were found near the gills. Gudger (1922) reported

that a specimen of *R. osteochir* (as *Rhomochirus*) had been found in the gills of *M. mola,* but failed to note where or how it was situated. Likewise, while *M. lanceolata* is known to serve as a host to *R. remora* and *R. brachyptera* (Schultz et al., 1960; Cressey and Lachner, 1970) only *R. remora* and *R. osteochir* have been found "in" the gills (Funderburg and Eaton, 1952). Although remoras could attach to the denticle-like structures of the skin of a *Mola,* they might enhance their association by entering the gill chamber where the remora would be flushed with water and have immediate access to food ingested by the host. Although Gray (1954) determined the gill area of *E. naucrates* and noted it a "fish of moderate activity," life sustaining limits or exposure time to low oxygen levels are unknown for echeneidids. Strasburg (1957) did however note that one *E. naucrates* died in a tub without circulating water after 21 h. Whether this was caused by a lack of oxygen, temperature, etc., remains uncertain. In our case no water was passed over or into the gill chamber of the *Mola* once it had been removed from the ocean, yet the *R. remora* was alive after being out of water for 17 h. Perhaps the heavy mucous that surrounds a remora (Lachner, pers. commun., 1986) provided the needed moisture for survival. Also, remoras have survived when accidentally introduced into a freshwater lake (Lachner, pers. commun., 1986) further illustrating their wide tolerance to environmental conditions.

Fraser-Brunner (1951) was the first to speculate that basking molas may be sick or dying and supported the idea that they may be heavily infested with parasites. This speculation went unsubstantiated as they performed no internal examination of any basking molid. Fitch and Lavenberg (1971) simply said dead molas may have parasites. Myers and Wales (1930) found a 0.75 to 1 m long *M. mola* dead and "disabled" on the bottom of Monterey Bay, California, while others were floating (basking) nearby, but made no effort to determine the cause of the behavior. Gotshall (1961) noted a mass die-off of molas in Monterey Bay, California, in 1960, again without examination of the specimens. It is unlikely that low or warm water temperatures cause the basking behavior reported for molas as the internal temperature of a mola is near that of the sea waters frequented (Morrow and Mauro, 1950).

Only Threlfall (1967) and Margolis and Arthur (1979) record the cestode, *Tetrarhynchus elongatus,* associated with the livers of molas. Fitch and Lavenberg (1971) noted tapeworms in molas at death; all others simply found argulid, copepod, or caligid parasites on or trematodes and cestodes in molas. Threlfall (1967) did not find *A. microcephalus* in the intestines of *M. mola.* In contrast, Margolis and Arthur (1979) found four species of trematodes (genera *Accacladium, Accacladocoelium, Odhnerium,* and *Dihemistephanus*) in intestines of mola. The discovery of the numerous *Molicola* and *Anchistrocephalus* in every *Mola* examined leads us to suggest that it is a sick and/or dying condition brought on by a heavy parasite load that contributes to the basking behavior of molas rather than the need to sun themselves.

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Mississippi, determined the parasites. E. Lachner, National Museum of Natural History, Washington, D.C., reviewed the manuscript and provided additional ecological insights for echeneidids. G. Safrit of IMS assisted with most of the dissections. B. Bright typed the final version of the paper.

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Robert E. Vincent

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Evolution of the Feeding Mechanism in Primitive Actinopterygian Fishes: A Functional Anatomical Analysis of *Polypterus, Lepisosteus,* and *Amia*

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ABSTRACT The comparative functional anatomy of feeding in *Polypterus senegalus, Lepisosteus oculatus,* and *Amia calva,* three primitive actinopterygian fishes, was studied by high-speed cinematography (200 frames per second) synchronized with electromyographic recordings of cranial muscle activity. Several characters of the feeding mechanism have been identified as primitive for actinopterygian fishes: 1) Mandibular depression is mediated by the sternohyoideus muscle via the hyoid apparatus and mandibulohyoid ligament. 2) The obliquus inferioris and sternohyoideus muscles exhibit synchronous activity at the onset of the expansive phase of jaw movement. 3) Activity in the adductor operculi occurs in a double burst pattern—an initial burst at the onset of the expansive phase, followed by a burst after the jaws have closed. 4) A median septum divides the sternohyoideus muscle into right and left halves which are asymmetrically active during chewing and manipulation of prey. 5) Peak hyoid depression occurs only after peak gape has been reached and the hyoid apparatus remains depressed after the jaws have closed. 6) The neurocranium is elevated by the epaxial muscles during the expansive phase. 7) The adductor mandibulae complex is divided into three major sections—an anterior (suborbital) division, a medial division, and a posterolateral division.

In *Polypterus,* the initial strike lasts from 60 to 125 msec, and no temporal overlap in muscle activity occurs between muscles active at the onset of the expansive phase (sternohyoideus, obliquus superioris, epaxial muscles) and the jaw adductors of the compressive phase. In *Lepisosteus,* the strike is extremely rapid, often occurring in as little as 20 msec. All cranial muscles become active within 10 msec of each other, and there is extensive overlap in muscle activity periods.

Two biomechanically independent mechanisms mediate mandibular depression in *Amia,* and this duality in mouth-opening couplings is a shared feature of the halecostome fishes. Mandibular depression by hyoid retraction, and intermandibular musculature, consisting of an intermandibularis posterior and interhyoideus, are hypothesized to be primitive for the Teleostomi.

The Actinopterygii or ray-finned fishes is by far the most diverse group of vertebrates; it includes more than 23,000 fossil and recent species. This tremendous diversity in number is mirrored by their extensive morphological and behavioral variations in prey-capture mechanisms and strategies. Diversity in jaw morphology is a hallmark of the actinopterygian radiation.

To date the major study of feeding mechanisms in primitive actinopterygian fishes is that of Schaeffer and Rosen ('61). They examined the major adaptive levels in the evolution of the feeding mechanism of ray-finned fishes and proposed hypotheses of jaw function at each level. Their analysis was, of necessity, gradal.

Within the last decade, functional anatomists have begun to analyze experimentally the feeding mechanisms of fishes and to test the hypotheses of earlier investigators who had suggested possible patterns of jaw movement based on post mortem manipulations (e.g.,

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Alexander, '66, '67; van Dobben, '35; Gunther and Deckert, '53; Holmquist, '10; Kampf, '61; Kirchhoff, '58; Tchernavin, '53). Experimental studies have involved high-speed cinematography (e.g., Dutta, '68; Liem, '67b; '70; Lauder, '79; Nyberg, '71), electromyographic analyses of cranial muscle activity (Ballintijn et al., '72; Elshoud-Oldenhave and Osse, '76; Lauder and Liem, '80; Liem, '73, '78; Liem and Osse, '75; Osse, '69), measurement of buccal cavity pressures (Alexander, '69; '70; Liem, '78), and strain gauge analysis (Lauder and Lanyon, in press). Almost all of these studies have focused on feeding in advanced teleost fishes, while primitive members of the Teleostei and other actinopterygian groups have been largely neglected.

An analysis of the functional anatomy of feeding in primitive ray-finned fishes is of particular importance in providing comparative data on fish feeding mechanisms and in aiding in morphological interpretations of fossil fishes. Such observations may support inference of function from structure in extinct taxa, and will allow a reinterpretation of the functional and phylogenetic significance of several features in the earliest ray-finned fishes. Examination of primitive taxa may reveal characters that corroborate (or refute) current hypotheses (Gardiner and Bartram, '77; Greenwood et al., '73; Liem and Lauder, in press; Patterson and Rosen, '77; Wiley, '79) of the systematic relationships of actinopterygians (see Table 1 for example).

This paper focuses on a comparative functional analysis of feeding in *Polypterus senegalus, Lepisosteus oculatus,* and *Amia calva,* three primitive living actinopterygian fishes. "Primitive actinopterygian" as used here refers loosely to all non-teleost actinopterygians. Although there has been some debate during the last century over the phylogenetic position of *Polypterus,* most of the recent evidence indicates that it is an actinopterygian (Gardiner, '73; Liem and Lauder, in press; Wiley, '79).

MATERIALS AND METHODS

All fishes studied experimentally were caught in the wild and obtained through commercial suppliers. Fish were acclimated to laboratory water and temperature (25°C) for several weeks before experimental work was begun; each fish was housed in a separate 80 liter tank.

Fine-wire bipolar electrodes (Evenohm S) were implanted in the cranial muscles using the technique of Basmajian and Stecko ('62). The fishes were anesthetized during implantation with tricaine methane sulfonate, 200–400 mg/liter. Up to twelve pairs of electrodes were implanted at one time, although only five channels could be synchronously recorded during an experiment. This allowed multiple combinations of muscles to be investigated during any given recording session by simply changing leads at the connector. A dental drill was used to drill small (1 mm diameter) holes in the dermal bones overlying many of the cranial muscles (especially in *Lepisosteus* and *Amia*) to allow access to the muscle belly. The electrodes were glued together into a thin cable, color coded, and attached to a small plastic clamp (visible in Figs. 6, 10). The clamp either was anchored to a wire passing just dorsal to the epaxial musculature but ventral to the dorsal scales *(Lepisosteus, Polypterus),* or was screwed directly to the skull *(Amia).* Electrodes were implanted for up to three weeks and, although no deterioration in signal quality was noticed in this period, the electrodes usually worked loose after two weeks.

During recording sessions, the color-coded electrode leads were attached to a slip-ring, rotating connector, that was located just above the water surface and connected to Gould-Brush biomedical amplifiers. Electrical signals were stored on a Honeywell 5600 tape recorder at 37.5 cm/sec and played back for analysis at 4.7 cm/sec through a Gould 260 strip chart recorder.

High-speed films (200 frames per second) were synchronized with the electromyographic recordings by a special synchronization unit that counted pulses from the high-speed camera and placed a series of coded pulses (see Figs. 6, 10, 13: SYN) onto the tape recorder. The films were taken with a Photosonics 16-1PL camera on Kodak 4X Reversal and 4X Negative film. Three 600W Smith-Victor filming lights provided illumination for filming with a shutter speed of 1/1200 second. A short period of training (two weeks) was usually necessary to accustom the fishes to feed with the lights on.

More than 150 feeding sequences were examined for *Lepisosteus* (4 specimens, including MCZ 54289, 54291), 125 for *Amia* (2 specimens, including MCZ 54287), and 100 for *Polypterus* (2 specimens, including MCZ 54290), all taken over a two-year period. *Polypterus* was fed meal worms *(Tenebrio),* whereas *Amia* was fed pieces of smelt *(Osmerus)* and live (occasionally lightly anesthetized) goldfish *(Carassius auratus). Lepisosteus* was fed goldfish exclusively.

Comparative anatomical observations were

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Ontogeny and Phylogeny of Tooth Attachment Modes in Actinopterygian Fishes

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ABSTRACT There are four major tooth attachment modes in actinopterygians. Type 1 mode is characterized by complete ankylosis of the tooth to the attachment bone; it is the primitive attachment mode for actinopterygians. In Type 2 mode there is a ring of collagen between the tooth base and the bone. In Type 3 mode mineralization extends near or to the bone at the anterior tooth border, and there is a relatively large collagen area on the posterior surface of the tooth; Type 3 teeth are hinged with an anterior axis of rotation. Type 4 teeth also have a relatively large posterior collagen area, but there is no collagenous connection between the anterior basal tooth border and the attachment bone; Type 4 teeth are hinged, with a posterior axis of rotation. Types 2, 3, and 4 attachment modes appear to result from retardation of mineralization and resemble, with some modifications, ontogenetic stages in the development of Type 1 mode; they are considered to be paedomorphic features. Attachment modes 2, 3, and 4 are each associated with a major evolutionary lineage within the Teleostei. The degree to which paedomorphosis has been a factor in teleostean evolution is discussed.

The importance of ontogenetic phenomena to evolutionary processes is becoming widely acknowledged. The combination of developmental biology with the study of phylogeny promises to be one of the most important events in evolutionary biology since the development of population biology in the 1920's. Although one of the reasons for this new emphasis has been the inability of population genetics to provide answers to some fundamental questions in evolution (Lewontin, '74), it also has become clear that the evolution of many large and diverse plant and animal groups may be correlated with shifts in ontogenetic development which have resulted in major morphological and ecological changes (Gould, '77; Liem, '73). Alberch et al. ('79) attempted to provide a model in which ontogenetic sequences can be quantified and compared as ontogenetic trajectories. There is also interest in the utility of ontogenetic studies in the construction of cladistic and phylogenetic hypotheses (Nelson, '78).

The evidence presented below suggests that paedomorphic (sensu Gould, '77) tooth development can be associated with major phylogenetic groups of teleost fishes. Retardation of ontogenetic pathways has resulted in two specialized tooth attachment modes, one of which results in a hinged tooth. A third specialized attachment mode includes developmental retardation followed by active destruction of predentine on the anterior tooth border, resulting in a second type of hinge mechanism.

MATERIALS AND METHODS

A large number of actinopterygian fishes were examined for this study; they are listed in Table 1, which is a phylogenetic classification, above the family level. Because tooth replacement occurs continuously in the vast majority of actinopterygians, all ontogenetic stages can be seen in adult specimens.

Preparation of material for histological examination involved decalcification of formalin-fixed tissues for 1–5 days in 5% formic acid solution. Tissues were embedded in Paraplast, cut into 7-μm sections, and stained with hematoxylin and eosin. Preparation of material for the scanning electron microscope (SEM) involved cleaning tooth-bearing bones in borax and trypsin (using ingredients in the proportions recommended by Taylor ('67) for clearing and staining), dehydration in an ethanol series, and air drying. Much material was cleared using a modification of Taylor's ('67) technique and stained with alizarin red; this clearly differentiates mineralized dentine

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TABLE 1. Phylogenetic classification of selected actinopterygian fishes with distribution of tooth attachment/depression modes[1]

Taxon		Museum number[2]	Attachment mode type: Jaw teeth	Attachment mode type: Pharyngeal teeth
Brachiopterygii				
	Polypteridae			
	Polypterus senegalensis[3,4,8]	MCZ 48164	1	0
Chondrostei				
	plesion Redfieldiid sp.	MCZ 9271	1	?
	Polyodontidae			
	Polyodon spathula[3]	MCZ 54923	1	0
Ginglymodi				
	Lepisosteidae			
	Lepisosteus oculatus[8]	MCZ 39650	1	1(?)
Halecostomi				
	plesion Semionotidae			
	†*Semionotus* sp.	AMNH 1328	1	?
Halecomorphi				
	plesion Caturidae			
	†*Caturus furcatus*	MCZ 5324	1	?
	Amiidae			
	Amia calva[3]	MCZ 8970	1	1
	†*Amia fragosa*	MCZ 9264	1	?
Teleostei				
Teleostei, incertae sedis				
	†*Pachythrissops propterus*	MCZ 8297	1	?
Osteoglossomorpha				
	Osteoglossidae			
	Osteoglossum bicirrhosum[3]	MCZ 54927	1	1
	Scleropages formosus[3]	MCZ 54924	1	1
	Hiodontidae			
	Hiodon alosoides[3]	MCZ 54926	1	1
	Notopteridae			
	Papyrocranus sp.[3]	MCZ 54925	1	2
Elopocephala				
Elopomorpha				
	Elopidae			
	Elops saurus[3]	USNM 128290	2	2
	Megalopidae			
	Tarpon atlanticus[3]	USNM 199836	2	2
	Anguillidae			
	Anguilla rostrata[8]	MCZ 9307	2	2
	Synaphobranchidae			
	Synaphobranchus kaupi	MCZ 53881	2	2
Clupeocephala				
Clupeomorpha				
	Denticipitidae			
	Denticeps clupeoides[3,6]	MCZ 56428	2	2
	Clupeidae			
	Etrumeus sadina[3]	USNM 188950	1	2
	Harengula pensacolae[3]	USNM 221203	1	1
	Microthrissa royauxi[8]	MCZ 48116	2	2

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FUNCTIONAL ANATOMY OF FEEDING IN THE BLUEGILL SUNFISH, *LEPOMIS MACROCHIRUS*: *IN VIVO* MEASUREMENT OF BONE STRAIN

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SUMMARY

The suction feeding mechanism of the bluegill sunfish, *Lepomis macrochirus*, was studied in unrestrained fishes by the simultaneous recording of cranial muscle electromyograms, opercular cavity pressures, and opercular bone strain patterns. The electromyographic profile was similar to that of other advanced teleosts and consisted of preparatory, expansive, and compressive phases. The pectoral girdle remained nearly stationary during the strike. Opercular cavity pressures showed peak negative values of 145 cm H_2O followed by a positive afterpressure of up to 50 cm H_2O as water flowed out of the opercular chamber. Characteristic 'coughing' patterns showed an initial positive phase, followed by a negative phase, and then a final positive pressure pulse. Bone strain on the operculum was measured with rosette and single element strain gauges. Peak principal compression during the strike was 1800 $\mu\varepsilon$ and the peak strain rate was -615×10^3 $\mu\varepsilon$/s, more than ten times that previously recorded in vertebrate bone during normal activity. Opercular bone strain results from the rapid reduction of pressure in the opercular cavity which causes the operculum to deform medially and does not result from muscle activity. The observed strain pattern is consistent with a stress regime of bending and twisting moments applied to the operculum during feeding. Two prominent orthogonal bony struts on the medial opercular surface are hypothesized to resist these bending and twisting moments.

INTRODUCTION

In the last ten years the mechanics of feeding in fishes has been the subject of a large number of investigations. Beginning with Osse (1969) who first used electromyography as a means of ascertaining cranial muscle activity during feeding, electromyography and high-speed cinematography have been used with increasing frequency to study the mechanics of feeding in primitive teleost fishes (Ballintijn, van den Berg & Egberink, 1972; Lauder, 1979; Lauder & Liem, 1979) and in advanced teleost fishes (Elshoud-Oldenhave & Osse, 1976; Liem, 1973, 1978; Liem & Osse, 1975).

Despite these experimental studies, very few direct measurements exist of the pressures generated in the mouth cavity during feeding. Alexander (1969, 1970) provided the first measurements of pressures in the mouth cavity of fishes by training fish to take food which was slipped over the end of a pressure transducer tube. He found that different species varied widely in the peak negative pressures generated during feeding (from -80 cm H_2O in *Ictalurus* to -400 in *Pterophyllum*) and that the mean duration of the negative pressure pulse could be as short as 30 ms. Only recently, however, have *in vivo* pressures been measured in unrestrained fishes capturing elusive prey (Liem, 1978). No studies have examined pressure changes in the opercular cavity during feeding.

One technique, potentially an extremely useful tool for analysing the mechanics of feeding and the relationship between form and function of the fish musculoskeletal system, has yet to be applied to non-mammalian vertebrates: the use of strain gauges *in vivo* to determine the patterns of bone strain occurring during normal functional activity. Strain gauge analysis has been used most extensively to study mammal locomotion (Cochran, 1972; Lanyon, 1974; Lanyon & Baggott, 1976; Lanyon & Smith, 1970; Turner, Mills & Gabel, 1975) although recently Hylander (1977, 1979) and Weijs & DeJongh (1977) have used strain gauge techniques to analyse mammalian mastication.

The aims of this study are (1) to investigate experimentally the suction feeding mechanisms of an advanced teleost fish *Lepomis macrochirus*, the bluegill sunfish (Family Centrarchidae), with particular reference to the role of the opercular bone in suction feeding, (2) to test the applicability of strain gauge techniques to the analysis of form–function relationships in fishes, and (3) to examine strain-related parameters with regard to the significance of the characteristic acellular bone structure in advanced teleost fishes.

MATERIALS AND METHODS

Fish

Five large specimens of *Lepomis macrochirus* were chosen for experimental study from a sample seined from local streams and ponds around Boston, Massachusetts. The fish were acclimated to laboratory water and temperature (25 °C) and were each confined in separate 80 l tanks. The size of the fish ranged from 15 to 20 cm total length; the larger individuals were used for EMG, opercular cavity pressure, and strain gauge experiments while the smaller ones were used exclusively for electromyographic studies. The fish were fed a mixed diet of commercially prepared 'flake food', live meal worms, pieces of dead smelt (*Osmerus*) and live goldfish (*Carassius auratus*), all of which they ate readily. Fish were deprived of food for up to a week before an experiment.

Electromyography

Bipolar fine-wire electrodes were implanted in the cranial muscles using the method of Basmajian & Stecko (1962). Up to ten pairs of electrodes were implanted simultaneously. The bipolar wires were colour coded, glued together, and attached to a lightweight plastic clamp which was fastened to a wire passing through the

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ASYMMETRICAL MUSCLE ACTIVITY DURING FEEDING IN THE GAR, *LEPISOSTEUS OCULATUS*

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SUMMARY

Prey capture in the spotted gar, *Lepisosteus oculatus*, was studied by high-speed cinematography synchronized with electromyographic recordings of cranial muscle activity. Muscle activity patterns were recorded during each of the three major phases of feeding: the initial strike at the prey, manipulation of the prey following capture, and swallowing. With one exception, the obliquus superioris, all muscles at the strike are active in a bilaterally symmetrical pattern. During the manipulation phase two distinct muscle activity patterns occur: one is characterized by symmetrical activity in the epaxial muscles and obliquus inferioris, the other by complete asymmetry between the right and left sternohyoideus, obliquus superioris, and epaxial muscles. Low-amplitude manipulatory movements are characterized by activity in one side of the sternohyoideus only, all other muscles being generally inactive. The adductor mandibulae and obliquus inferioris are always active symmetrically. Asymmetrical activity in the sternohyoideus, epaxial muscles, and obliquus superioris correlates with lateral head movements during feeding and acts to rotate prey into the preferred orientation for swallowing. The pattern of asymmetrical activity between right and left side muscles is discussed in relation to previous studies of feeding which utilized only unilateral muscle recordings.

INTRODUCTION

The experimental analysis of the feeding mechanism of fishes has focused increasingly in recent years on the definition of bone movements and associated muscle activity occurring during prey capture. While the important early studies of Alexander (1966, 1967*a*, *b*) primarily utilized manipulation of preserved specimens and cinematography to examine the mechanics of prey capture, recent investigators have turned to the use of electromyography to determine the timing of muscle electrical activity and its relationship to jaw bone movement (Ballintijn, van den Burg & Egberink, 1972; Elshoud-Oldenhave & Osse, 1976; Lauder & Liem, 1979; Liem, 1978; Liem & Osse, 1975; Osse, 1969). Without exception these investigators have recorded muscle activity from one side of the head only, and assumed that the rapid (30–300 ms) prey-capture mechanism of fishes would result in bilaterally symmetrical muscle activity. To some extent this assumption is justified by evidence

that the initial strike at a prey is governed by a central nervous system oscillator which elicits a preprogrammed pattern of muscle activity during the strike (Liem, 1978).

The hypothesis that the preprogrammed motor output itself could be asymmetrical has not been considered and only within the last few years have the first bilateral recordings of cranial muscles been obtained (Sibbing, 1976; Liem, 1978; Lauder, 1980).

Liem (1980*a*, *b*) has recently discovered asymmetries between right and left side muscles in bottom-feeding cichlid fishes. Jaw movements during algae scraping are presumably subject to nearly continuous peripheral feedback and asymmetrical movements of the jaws may allow more efficient algae removal from uneven surfaces.

In this study we report asymmetrical patterns of cranial muscle activity during feeding in the primitive actinopterygian fish, *Lepisosteus oculatus*, the spotted gar. The recorded asymmetries involve not only differences between right and left side muscles, but also between the anterior and posterior portions of the sternohyoideus muscle. The observed asymmetrical activity is associated with specific patterns of prey manipulation prior to deglutition and graphically reveals the dangers of using unilateral muscle recordings to analyze the functional anatomy and mechanics of feeding in fishes.

The generally symmetrical muscle activity pattern at the strike will be considered elsewhere (Lauder, 1980), where a complete electromyographic profile of 13 cranial muscles will be compared with the strike in other primitive actinopterygians (*Amia* and *Polypterus*). We will focus here on the pronounced asymmetrical activity in certain muscles and its functional significance during feeding.

MATERIALS AND METHODS

Fish

Four commercially obtained spotted gars ranging in length from 20 to 30 cm in total length were used for electromyographic and cinematographic studies. All individuals showed the same patterns of asymmetrical muscle activity. Representative specimens have been deposited in the Fish Department of the Museum of Comparative Zoology (MCZ 54289; 54291).

Each fish was confined in a separate 80 l tank and acclimated to laboratory water and temperature (25 °C) over a period of several weeks. All gars were fed live goldfish (*Carassius auratus*) exclusively and food was withheld for up to a week before an experiment.

Electromyography

Fine-wire tin–copper bipolar electrodes (Evanohm S, 0·051 mm diameter, W. B. Driver, Newark, N.J., U.S.A.) were implanted in the cranial and anterior body musculature using the technique of Basmajian & Stecko (1962). Due to the large rhomboid scales and thick layers of dermal bone covering many of the muscles, small (1 mm diameter) holes were drilled through the bone with a dental drill to allow easy access to the muscle surface for electrode implantation. The electrode pairs were colour-coded, glued together, and attached to a small plastic clamp

Unusually Large Pinfish, *Lagodon rhomboides* (Pices: Sparidae) Caught in North Carolina Waters

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Pinfish, *Lagodon rhomboides* (Pisces: Sparidae), occur along the North American coast from Cape cod to Yucatan, Mexico, and Bermuda (Boschung 1992; Boschung *et al.* 1983; Robins and Ray 1986). Caldwell's (1957) life history study, especially its age and growth (maximum age 7, 328 mm Total Length (TL)) remains the most comprehensive study of the species (Darcy 1985). Maximum reported sizes ranged between 355 and 437 mm TL (Boschung *et al.* 1983, Robins and Ray 1986; Simmons 1957). Gordon (1957) documents a 362 mm TL pinfish caught 8 June 1955 off Point Judith, RI. This paper examines the length-weight, standard length SL/TL, TL/SL, and age relationships of 12 large pinfish caught between 1973 and 1995 from North Carolina and nearby Atlantic Ocean waters.

Methods: Twelve large pinfish, 230 to 398 mm TL, were captured between August 1973 and October 1995 in 12 m semi-balloon otter trawls or by hook and line (Table 1). Standard length (SL) and TL's were measured in millimeters; body weights were in grams (g) (Table 1). Scales taken from above the lateral line and below a specimen's dorsal fin were aged following Caldwell (1957) and Hansen (1969). Length-weight relationships were expressed using the formula $\log w = a + b \log L$. All but the 1981 caught specimens were preserved and curated in the UNC fish collection, Morehead City, North Carolina (Table 1).

Observations and Discussion: Caldwell (1957) noted Florida pinfish length/weight relationships were $\log w = 2.9126 \log L - 4.3734$ while those from Texas were $\log w = 2.9030 \log L - 4.3530$ (Cameron 1969). Schwartz *et al.* (1979) examined 730 (30-239 mm SL) pinfish from the Cape Fear River, NC, and gave the length-weight regression as $\log w = 3.10 \log L - 4.73$. The SL/weight regression for the recent large North Carolina pinfish was $\log w = 3.05 \log L - 4.59$, $r = 0.9647$ and the data extended size and weight limits to 331 mm SL, 398 mm TL, and 1358.4 g. One large 1020.6 g North Carolina pinfish (length not known), captured off Harkers Island, NC in 1992 was unavailable for analysis. Aging of 11 of the large North Carolina pinfish revealed that the smallest (183 mm SL) was four years old, other ages 5-7, and the largest eight years old (Table 1). Conversion factors of 0.78 for SL/TL and 1.51 for TL/SL relationships (Table 1) agreed with those noted by Cameron (1969) and Jorgenson and Miller (1968) for Texas and Georgia pinfish. Capture dates suggested that summer-fall-winter caught pinfish were near or in the open ocean prior to their winter spawning offshore.

Acknowledgments: William Buck, Wrightsville Beach, NC, provided the large 1995 caught pinfish, F. Rohde, NC Marine Fisheries, Wilmington, NC, transported it to Morehead City for study. J. Guthrie, NC Marine Fisheries, Morehead City, NC, permitted examinations of his Cape Lookout mounted specimen. C. Barans, SC Dept. Natural Resources, Charleston, SC, searched unsuccessfully South Carolina data bases for large pinfish captures. L. White typed the manuscript.

Table 1. Standard (SL) and total (TL) lengths (mm), ages, weights, (g) and SL/TL, TL/SL conversion factors for 12 large pinfish caught in North Carolinian waters between 1973 and 1995. (T = otter trawl, HL = hook and line)

Date	Location	UNC Catalogue Number	N	Capture Method	SL	TL	Weight	Age	SL/TL	TL/SL
26 Aug 1973	Atlantic Ocean 34°31N, 76°14.5W	8121	4	HL	183	234	178.4	4	0.74	1.28
				HL	202	264	222.9	5	0.77	1.31
				HL	228	301	365.8	6	0.76	1.32
				HL	255	335	535.9	7	0.76	1.31
11 June 1981	Atlantic Ocean 24 Km SE of Cape Lookout	- -	1	HL	320	385	1358.4	-	0.83	1.20
26 Dec 1983	Beaufort Bar Cape Lookout	16662	4	T	205	262	303.3	5	0.78	1.27
					206	265	365.9	5	0.78	1.29
					219	280	422.0	5	0.78	1.28
					222	280	391.6	5	0.79	1.26
1 Jan 1985	Atlantic Ocean 1.5 S. of Atlantic Beach	16815	2	T	182	230	181.8	5	0.79	1.26
				T	208	262	290.0	5	0.79	1.26
18 Oct 1995	Wrightsville Beach Bridge at Intracoastal Waterway New Hanover Co.	17494	1	HL	331	398	940.5	8	0.83	1.20
Means					230.1	291.3	463.0		0.78	1.27

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ON THE EVOLUTION OF THE JAW ADDUCTOR MUSCULATURE IN PRIMITIVE GNATHOSTOME FISHES

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ABSTRACT. The primitive condition of the adductor mandibulae musculature in gnathostomes is a large unsubdivided, fan-shaped muscle mass originating from the palatoquadrate and inserting on the lateral aspect of the mandible. Unspecialized suborbital fibers extend posteriorly from the palatoquadrate to insert laterally on the lower jaw, and an intramandibular adductor division is absent. The Actinopterygii, Actinistia, Dipnoi, and Choanata primitively possess three distinct components of the adductor mandibulae: a suborbital division, a medial division, and a posterolateral division, as well as medial intramandibular adductor fibers. The suborbital division of the adductor mandibulae has been lost in teleosts and, independently, in coelacanths and living lungfishes. Devonian lungfishes and early choanates possessed both the suborbital and intramandibular adductor muscle components.

INTRODUCTION

Towards the end of the nineteenth and in the first half of the twentieth century, a large number of investigators were concerned with the homologies of the jaw musculature between the different vertebrate classes (Allis, 1897, 1917, 1923; Edgeworth, 1935; Kesteven, 1942, 1943, 1944; Lightoller, 1939; Luther, 1913; Souché, 1932; Vetter, 1874). The musculature of the mandibular arch was the subject of special attention and several attempts were made to precisely link each branchial arch muscle with its serial homologue on the mandibular arch [see Lightoller (1939) for an example of this procedure carried to an extreme]. In recent years, little work has been done on the evolution of the musculature in primitive gnathostomes, despite the discovery of significant new fossil material that allows more accurate reconstruction of the musculature in extinct taxa.

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