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GROWTH IS A MANY SPLENDID THING: ANALYSES IN WITCH FLOUNDER (*GLYPTOCEPHALUS CYNOGLOSSUS*), PATTERNS AND IMPLICATIONS.

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Abstract

Although growth is commonly and conveniently examined in fish as changes in length per unit time, the growth phenomenon represents a numerous array of processes and parameters which a priori have their origin in a bioenergetic model. Conscious of the composite nature of growth, the present study quantifies and conceptualises the multiplicity of growth in the witch flounder (*Glyptocephalus cynoglossus*) and its relationship to the information content resident in the otolith, including the question of age validation. Examination of several otolith parameters (length and wet-, dry- and ash weights of left and right otoliths) indicated that sexual dimorphism occurred after about six years in the right otolith but was about a year older in the left otolith. Sexual dimorphism in total length and standard length was apparent from about seven years of age whereas head length dimorphism was manifest from about four years. Thus, the information resident in the right otolith is greater than that in the left otolith, and the information resident in the head length is greater than that in either the total length or standard length. When sexual dimorphism occurred, it was always the female which was the larger.

Discriminant function analysis (DFA) provides a novel and objective tool in age validation. In the otolith-based DFA it was the weight measures rather than length, in both left and right otoliths, which provided the greatest contributions to age discrimination. The body-based DFA indicated that the greatest discrimination was provided (in descending order of importance) by the "skeleton", head length, and the ventral and dorsal fillets; the gonad and liver, although also providing significant contributions, were much less important. Both the DFA approaches provided conspicuous segregation in the age-groups from two to five years while overlap was greater thereafter. Presenting the results using "predicted" age (i.e. provided on the basis of re-classification of age from DFA) rather than otolith "read" age substantially reduced data-scatter. In both the otolith-based and the body-based DFA's the first discriminant axis primarily explained age related variability. In the body-based DFA, in contrast to the otolith based DFA, the second discriminant axis clearly explained sex related variability. Thus, although both DFA's distinguished age equally well, the body-based DFA was superior in distinguishing both age and sex. Although otolith length and weights are evidently good age discriminators, their use in sex discrimination is equivocal. The apparent overall misclassification of age was about 20% in both DFA approaches. The otolith-based DFA indicated a peak misclassification at about 6 to 8 years; thus occurring just after a recurrent "inflection point" at 4-5 years, noted in the plot of the first discriminant axis against age in both the DFA approaches. The DFA "inflection" age concurs with that at which sexual "size" dimorphism clearly manifests itself in head length, and slightly precedes that at which divergence becomes apparent in otolith length and weight. Although sexual dimorphism in total- or standard lengths was imperceptible, signs of growth inflections were seen at about four years old; these coincide with a reduction in specific growth rate and a marked rise in the gonadosomatic index. This probably reflects the advent of the age at maturity (AFM), in the present study, at 4-6 years in both sexes; changes in the appearance and consistency of otolith zones in witch >5 years old are common and probably indicative of AFM having been reached. As AFM integrates both growth and mortality effects, understanding its variation in the context of bioenergetic and ecological coercion is of particular importance for prudent fisheries management.

INTRODUCTION

Characteristic marks appearing at intervals during the growth of fish otoliths are frequently used as indicators of age (Blacker, 1974; Williams & Bedford, 1974; Jearld, 1983; Casselman, 1987). The accurate determination of age from fish otoliths is essential as subsequent age-related errors, particularly when the degree of error is not constant throughout the life span, may impair the reliability of the estimates for a multitude of population dynamics' parameters (Gulland, 1969; Beverton & Holt, 1957; Ricker, 1975).

Although growth is commonly and conveniently expressed in fisheries biology as changes in length per unit time (Ricker, 1975; Weatherley & Gill, 1987), the growth phenomenon represents an array of processes and parameters which have their origin in a bioenergetic model (Brody, 1945; Brafield & Llewellyn, 1982). Growth is thus a complex concept, encompassing not only energy supplied (e.g. food consumption) but also energy required for different, and at times competing, processes and purposes (Calow, 1985; Hopkins et al., 1986; Reiss, 1989). "Trade-offs" frequently occur when energy is limited; one of the most notable being that the advent of first maturity, with increased energetic investment in gonads, often occurs at the expense of somatic growth or body reserves (Gadgil & Bossert, 1970; Calow, 1985; Clarke, 1987; Wootton, 1990). Unfortunately increased errors in age determination commonly arise after the age at first maturity (AFM) owing to the tendency for otolith zone increments and their clarity to decrease with repeated, often annual, reproductive investment (Blacker, 1974; Rollefsen, 1933). Furthermore, as AFM is probably the single most influential life history characteristic (Cole, 1954; Peters, 1983; Reiss, 1989; Krebs, 1985), with increased mortality frequently being associated with a reduction in AFM, better empirical determination of AFM from improved comprehension of body and otolith growth should offer benefits for prudent fisheries management.

Conscious of the composite nature of growth, regrettably few studies have applied multivariate statistical analyses in examining either otolith growth or the contributions and demands of different body components and processes to growth of the fish and that of the otolith (see though Boehlert, 1985; Hopkins et al., 1986; Rijnsdorp et al., 1990). With reference to witch flounder (*Glyptocephalus cynoglossus*), the present study quantifies and conceptualises the multiplicity of growth (as registered in various key body components) and its relationship to the information content resident in the otolith, including the question of age validation. Discriminant function analysis (DFA) is applied to determine the varying ability of a number of parameters for otoliths (length and wet-, dry- and ash weights of left and right otoliths), body length (total length, standard length, head length) and body weights (weights of: dorsal and ventral fillets, "skeleton", liver, gonad, and stomach with contents) to discriminate fish age and sex. The outcome of the DFA is used to provide empirical criteria for distinguishing AFM in males as well as females. The findings are discussed in the context of current and future perspectives in fisheries research and management, where increasing emphasis is placed upon deciphering bioenergetic and ecological interplay.

MATERIALS & METHODS

Trawling and sampling

Witch flounder were sampled from 220-290 m in November 1986, with a demersal prawn trawl towed by RV "Ottar", at Aglapsvik (69° 30'N 18°13'E) in Malangen, a north Norwegian fjord. Details of the trawl and its deployment are given in Nilssen et al. (1986), Nilsen et al. (1991) and Gutvik (1991).

On deck the witch flounder were sorted from the rest of the catch, and groups of five to 10 fish were packed carefully in sealed polythene bags before being frozen onboard and stored (-20°C) until further treatment in the laboratory ashore.

Weight and length determinations

In the laboratory ashore the frozen witch flounder were thawed overnight at 5°C. Individual fish were placed on a Sauter SM 1600 topweight, and the "round" total weight (TW) determined to an accuracy of 0.01 g. Total length (TL, measured to the nearest mm as the distance from the tip of the lower jaw to the tip of the longest median caudal fin-ray), standard length (SL, measured to the nearest mm as the distance from the tip of the lower jaw to the posterior end of the ultimate caudal vertebra), and head length (HL, measured by vernier callipers to the nearest 0.01 mm as the distance from the tip of the lower jaw to the hindmost point where the operculum meets the body) of individual fish were then determined. General details regarding fish length measurements and associated terminology are given in Lagler (1978), Ricker (1979) and Anderson & Gutreuter (1983).

After thawing, the abdominal cavity was cut open, and the stomach and intestine removed (cut anteriorly at the oesophagus and posteriorly in front of the anus) before the stomach itself was separated (cut posteriorly in front of the pyloric caeca). The total weight of the stomach (SW) was determined before the contents were removed and the stomach itself weighed alone. The liver and gonad (the latter having first been used to determine the sex of the fish) were also removed and weighed separately (liver weight = LW, gonad weight = GW; Mettler HK160 electrobalance, accuracy ± 0.001 g).

After this the fish were filleted by carefully dissecting the right and left (as witch flounder eyes are placed on the right, uppermost side of the body, the two fillets are henceforth referred to as "dorsal" and "ventral" fillets, DF and VF, respectively) swimming muscles away from the skeleton. The swimming muscles with attached skin were individually weighed. Finally the remainder of the fish (comprising the head, skeleton and caudal fin) was weighed and termed the "skeleton" (SkW). All weights were determined with an accuracy of ± 0.01 g by a Sauter SM 1600 balance.

Investigations of accuracy and precision during length and weight determinations were conducted as described in Gutvik (1991).

Ovaries, testes and sex determination

The sex and degree of gonad maturity of individual fish were determined as described by Gutvik (1991) incorporating information in Fulton (1891), Otterstrøm (1914), Powles (1965), Pitt (1966), and Jákupsstovu & Haug (1988).

Immature ovaries are seen as right, thin-walled, transparent and sac-like and lie posterior to the vent in an extended body cavity, one on each side of the ventral caudal-vertebrae (Otterstrøm 1914). The ovaries are shiny and vary from a pale colour in juveniles to more white or creamy-yellow in colour in older females. Mature ovaries are reddish, the eggs are visible, and they fill the extended body cavity as far back as the caudal fin. The ovaries on the right side are larger than those on the left side. The sex of witch flounder with mature ovaries may also be discerned by holding the fish against a strong light (Bowers 1960).

The testes do not have the same elongated shape nor do they fill the extended body cavity to the same extent as the ovaries. The testes are flatter and more lobed than the ovaries. In juveniles the testes are relatively transparent while in older fish they are more white or opaque. In older, mature males the testes are full or distended and the right one is larger than the left one. In the case of right males (TL<20 cm), the testes were tiny and particularly hard to discern with the naked eye, although females of similar size could also be problematical. In the case of difficult specimens sex determination required the morphological inspection of gonads under a Wild M3 stereomicroscope at 6.4 x magnification.

<u>Otoliths and age determination.</u>

One of the commonest methods of determining age in fish is by counting growth zones in hard body parts, especially those in the otoliths (Bagenal & Tesch 1978; Blacker 1974, Härkönen 1986). In the present study the sagittae were extracted from the sacculi of witch flounder using scalpel and tweezers (Williams & Bedford 1974, Jearld 1983), and then stored in numbered vials containing 30% ethanol in filtered seawater (Härkönen 1986). Prior to age reading the otoliths were removed from their vials and rubbed between the thumb and index finger to remove mucus and debris (Bowers 1960; Bagenal & Tesch 1978). Age was read with the sagittae immersed in glycerol, using reflected light on a dark background such that opaque zones appear white and hyaline zones appear dark (Jearld 1983). Ethanol preserves the otoliths during storage, while it and the glycerol enhance the visibility and counting of the ring-structures which form the basis for age interpretation (Williams & Bedford 1974).

The use of reflected light against a dark background has previously been used for witch flounder by Bowers (1960) and Powles & Kennedy (1967). Although Molander (1925) and Bowering (1976) also used the same manner of illumination, they applied it to ground and not whole otoliths. Grinding of the otoliths was not used in the present study as ring-structures were generally considered to be easily discernible. In the case of "young" fish (< 5-7 years old) age was primarily read from the inner side of the right otolith, while in older fish (> 5-7 years old) the inner side of the left otolith was mostly used (Molander 1925). In older fish, the ring-structures in the left otolith were generally spaced more evenly and were more distinct (Molander 1925, Bowering 1976), but the right otolith was easier to read in some cases.

In this paper *rings* and *zones* are used synonymously and describe bands of concentric *hyaline* or *opaque* material (the former being a zone composed primarily of translucent material that passes light, the latter being a zone composed primarily of white, optically dense material) seen in the otolith and counted for age determination. An *annulus* refers to a ring or zone (hyaline or opaque) deposited with annual periodicity. Reviews of terminology and definitions used in fish ageing are provided by Jensen (1965), Casselman (1983) and Jearld (1983).

A Wild-Heerbrugg M3 stereomicroscope (6.4 - 40 x magnification) was used for viewing and counting the number of hyaline zones (annuli) present. The outermost, edge-zone of the otolith was also noted as either opaque or hyaline. The otoliths in witch flounder can vary from a more circular shape in juveniles to the assumption of a more rounded-square shape in older fish (Molander 1925, Härkönen 1986). Innermost, the otoliths have a darker nucleus followed by a broader white zone. Outside these followed the first opaque zone, followed by the first hyaline zone, and alternate zones thereafter depending on the age of the fish. It was generally relatively simple to distinguish between opaque and hyaline zones in fish up to five to seven years of age. In younger fish (< 5-7 years old) the opaque zones were wider than the hyaline ones, while in older fish the opaque zones became narrower and age determination was more laborious. Otoliths which were especially demanding regarding reading and interpretation were examined several times over longer intervals.

Witch flounder are noted for having a relatively lengthy spawning period spanning from March to September, with a presumed peak from May to July (Bigelow & Schroeder 1953). Egg development (spawning to hatching) takes 7-8 days at 7.8 to 9.4 ^{o}C (Ehrenbaum 1905, Bigelow & Schroeder 1953, Russell 1976). The yolk sac of the larva is absorbed after about 10 days (Ehrenbaum 1905, Nybelin 1935). On the basis of this and our own observations, the hatching time (birth date) of Malangen witch flounder was set as 01 June, and the age of fish from otolith readings estimated to the nearest month. Thus fish (both males and females) caught in November with a single hyaline and two opaque zones were considered to be 17 months old. Some of these fish exhibited the initiation of an outermost hyaline zone.

The lengths of the left and right sagittae were measured to the nearest 0.06 mm, and their wet weights and dry weights (after drying for 48 hr in a desiccator with self-indicating silica gel) were determined to the nearest 0.001 mg. Both sagittae were analyzed for ash (weighed to the nearest 0.001 mg, after incineration at 540^{o}C in a muffle-furnace).

The age-group system (Cushing 1981) is used to describe the year of life of the fish; 0-group refers to those in their first year (< 12 months old), I-group are those in their second year (13-24 months old) and so forth.

Data-base and statistical and empirical treatment

Data for 20 variables [sex, age, total length, caudal length, head length; total body weight, and weights of "skeleton", dorsal and ventral fillets, gonad, liver, stomach with contents; lengths and wet-, dry-, and ash-weights of left and right sagittal-otoliths] for individual witch flounder were registered in the SYSTAT data editor (Wilkinson, 1988a).

Descriptive statistics for the examined age-groups were calculated using the STATS module of SYSTAT (Wilkinson, 1988a).

Discriminant Function Analysis (DFA) in the SYSTAT MGLH module (Wilkinson, 1988a) was employed to analyse and test for differences in otolith size (length and various weight parameters) and body components among the examined age-groups, and to identify the contribution of these features in discriminating among the a priori categorized age-groups (i.e. observed ages, read from otolith annuli). DFA generates a set of orthogonal discriminant functions, or canonical variates, that maximize the ratio of among-groups residual variance to the within-groups residual variance (Fisher, 1936; Cooley and Lohnes, 1971; Atchley and Bryant, 1975). The Wilk's lambda statistic and its approximate transformation to the F-statistic were used to test for differences between population (age-group) centroids (see Porebski, 1966). The success of the discriminant functions can be assessed by constructing a contingency table of "correct" and "incorrect" with respect to *a priori* allocations of individuals to age-groups and sexes, and testing with the likelihood ratio chi-square test in the TABLES module of SYSTAT (Wilkinson, 1988a). Two DFA's were performed on the witch flounder data: the first using otolith length and weights (wet, dry, and ash), the second using body lengths (total length, standard length, head length) and body component (dorsal and ventral fillets, "skeleton", gonad, liver, stomach with contents) weights. Logarithmic (ln_e) transformations were applied to all otolith, body length and body component data.

Trend fitting

Where it has been desirable to fit a curve illustrating a basic trend in the data, this has been achieved by avoiding semi-subjective regression techniques and rather using "locally weighted scatterplot smooth" ("Lowess") methods (Cleveland 1979) implemented in the SERIES module in SYSTAT and in SYGRAPH (Wilkinson 1988a, b).

RESULTS

Otolith length and weight characteristics and age determinations

Plots of wet weight, dry weight, and ash weight of right and left otoliths as a function of otolith length all show a weak positive exponential relationship, with the otoliths of female fish being slightly heavier than males for otoliths larger than about 5.5 mm (Fig. Fig. 1 A-F). Plots of otolith length and weights (wet, dry, and ash) as a function of fish age (read from the otoliths) shows an approximately linear relationship, with the otoliths of females becoming larger than those of males from 6 years of age in the right otolith while the bifurcation point for the left otolith was about a year older (Fig. 2 A-H).

Age related body length measures

In total length and standard length a clear sexually related divergence, with females becoming larger than males, is only apparent from about 7 years of age, while in the case of head length divergence is notable from about four years of age (Fig. 3 A-C).

Age related variation in total body weight and body components

In November, the dorsal fillet is heavier than the ventral one in both males and females, and the weight of the two fillets combined is approximately equivalent to that of the "skeleton". At this time of the year, the gonads are small in both sexes and they together with the liver and stomach with its contents account for < 2% of the total body weight (Fig. 4 A-D.).

The weights of dorsal and ventral fillets, and that of the skeleton, show a weak exponential increase with age but no clear sexual differences are apparent (Figs. 5 A, B & F). The weight of the stomach with its contents exhibits a large degree of scatter with relation to both age and sex (Fig. 5 E). Liver weights of both males and females increase relatively slowly up to an inflection point at six years of age after which a steeper rate of increase is notable (Fig. 5 C). The ovaries increase in weight relatively slowly up to about five years of age after which an acceleration is clearly seen, whereas the testes exhibit a weak rate of increase over the whole age range (Fig. 5D).

Analysis of age and sex discrimination

Discriminant function analysis using otolith length and otolith weight parameters

The discriminant function analysis using otolith length and weights (wet, dry, ash) indicates that although all the variables provide highly significant ($P < 0.001$) contributions to age discrimination, dry weight and wet weight provide the greatest contributions (Table 1). Nearly all the variance in the age data is explained along the first discriminant axis (DF1) and a large degree of segregation in the age-groups is seen from two to five years while there is a larger degree of overlap thereafter (Figs. 6 A & B). Comparisons of the centroids with 95% confidence limits for "read" age and "predicted" age clearly show that less overlap of age groups is seen after five years of age in the latter case (Figs. 6 A & B). A plot of DF1 against "read" and "predicted" age indicates an inflection point in both cases, with regard to the inclination in the relationship, at about 4 years (Figs. 6 C & D); a greater degree of separation is attained between the sexes from five years onwards using "predicted" age rather than "read" age.

Discriminant function analysis using body length and body weight parameters

The discriminant function analysis using body length (total length, standard length, head length) and body weight (weights of: dorsal and ventral fillets, "skeleton", liver, gonad, and stomach with contents) parameters indicates that although all the variables provide highly significant ($P < 0.001$) contributions to age discrimination, the greatest contributions are provided (in descending order of importance) by the "skeleton", head length, and the ventral and dorsal fillets (Table 2). As opposed to the DFA using the otolith parameters, a significant proportion of the variance in the data is also accounted for by the second discriminant axis (DF2) (Table 2). The first discriminant axis (DF1), as in the case of the otolith based DFA, primarily explains the age related variability (Figs. 7 A-D). However, in contrast to the otolith based DFA, the second discriminant axis (DF2) clearly explains the sex related variability (Figs. 7 E & F). A plot of DF1 against "read" and "predicted" age reiterates the distinct inflection point in the inclination of the relationship, at about 4-5 years (Figs. 7 C & D). Although a large degree of segregation is seen in the data from 3-6 years-old, intermingling with regard to sex is more evident for the 2 year-olds (they are though distinct from the other groups with regard to age). In fish > 6 years old distinction with regard to age/sex is less apparent, reflecting a combination of reduced age-related increments as well as fewer data (Figs. 7 A & B).

Classification of age and sex using the two discriminant approaches

A tabulation of "correct" and "incorrect" age and sex classification (a priori "correct" age and sex denoted by the age read from the otolith and the sex determined from anatomical examination of the gonads respectively) as indicated by discriminant function analysis highlights a number of interesting features in the otolith and body based approaches (Table 4, Fig. 8 A-D). In the case of sex, the otolith based DFA suggests an overall incorrect determination of about 20% with misclassifications being apparent throughout most (2 to 8 year-olds) of the ages examined (Fig. 8 A), while the body based DFA suggests an overall incorrect determination of about 7% with misclassifications only being apparent from 3 to 6 years old (Fig. 8 B). In the case of age, both the otolith and body based DFA's indicated an overall incorrect determination of about 20%, with the most widespread misclassification occurring about 6 to 8 years in the case of the otolith based DFA (Fig. 8 C) while the body based DFA misclassification was relatively widespread from about 4 years and older (Fig. 8 D).

Plots and linear regressions of the relationship between DFA predicted age (involving otolith parameters, and body parameters) and read age (Fig. 9 A & B) show highly significant relationships ($P<0.001$) with the regression constants (α) not being significantly different from 0 and the regression coefficient (β) not being significantly different from 1 in both cases. It is evident that discrepancies between predicted and read age become more common from 6 years of age in the otolith based DFA (Fig. 9 A), while discrepancies are become apparent from about 4 years of age in the body based DFA (Fig. 9 B).

DISCUSSION

The length and weights (expressed as wet-, dry-, and ash weights) of the right and left otoliths of the witch flounder exhibited clear-cut, positive relationships with the "read" age of the fish. This was also true for the relationship between the various body length (total length, standard length, and head length) measures and "read" age. Sexual dimorphism first became apparent at different ages depending on the particular "size" standard applied: divergence occurred after about six years of age in the right otolith while it was about a year older in the left otolith, in the case of total length and standard length sexual divergence was apparent from about seven years of age but in head length divergence was notable from about four years of age. When sexual dimorphism occurred, it was always the female which was the larger. These findings are in general accordance with widespread knowledge of witch flounder which indicate that, where size-at-age differences have been apparent, it is the female as a rule which is the larger sex (Beacham, 1982, 1983; Bowering, 1987, 1989; Molander, 1935; Bowers, 1960; Nilsen et al., 1991), although as a species the size at age differences have rarely been shown to be substantial. However, the present study clearly illustrates that the particular measures used to express growth are of considerable importance: the information resident in the right otolith is greater than that in the left otolith, and the information resident in the head length is greater than that in either the total length or standard length. This is clearly seen with regard to the ability to discern dimorphism ("divergence") at an earlier age as well as the degree of divergence.

Discriminant function analysis (DFA) is used relatively frequently in stock classification and biometrics (Pimentel, 1979; Misra & Ni, 1983; Taylor & McPhail, 1985) but appears to have been well-nigh neglected for the purpose of age discrimination (see though Hopkins et al., 1989). The present study indicates that DFA offers a novel and objective investigative-tool in fish age validation. Being a multivariate technique it allows the various measures involved to be ranked with regard to their ability to discriminate, and furthermore applies the measures *jointly* in the task of discrimination (Pimentel, 1979; Legendre & Legendre, 1983). In the case of the otolith-based DFA, it was apparent that although all the employed variables provide highly significant contributions to age discrimination, it was the weight measures (wet-, dry-, and ash weights) in both the otoliths which provided the greatest contributions. The superiority of weight, being a mass measure, over length in otolith based age determinations is to be anticipated. Recent studies (Pawson, 1990; Fletcher, 1991) have emphasised the applicability of otolith weight in ageing fish. The body-based DFA indicated that the greatest contributions were provided (in descending order of importance) by the "skeleton", head length, and the ventral and dorsal fillets; the gonad and liver, although also providing significant contributions, were much less important - these characteristically exhibit substantial short-scale temporal variability (e.g., gonads in near-adult and adult fish exhibit seasonal maturation cycles superimposed on age, and livers undergo transient changes in size according to digestive or feeding conditions and in females commonly exhibit seasonal size-variability associated with ovarian maturation cycles; Krivobok, 1964; Love, 1970; Hopkins et al., 1986).

Both the otolith- and body-based DFA approaches exhibited conspicuous segregation in the age-groups from two to five years while there was a greater degree of overlap thereafter. However, presenting the results using "predicted" age (that provided on the basis of re-classification of age on the basis of the DFA) rather than "read" age improved coherence by reducing the scatter in the data. In both the otolith-based and the body-based DFA's the first discriminant axis primarily explains the age related variability. In the body-based DFA, in contrast to the otolith based DFA, the second discriminant axis clearly explained the sex related variability. Thus, although both DFA-approaches distinguish well with regard to age, the body-based DFA provides superior distinction for <u>both</u> age and sex. Rather unexpectedly, the body-based DFA was equally proficient at age discrimination as the otolith-based DFA: both indicated that there had been an overall misclassification of about 20%. The degree of misclassification in the case of the otolith-based DFA peaked about 6 to 8 years; thus occurring just after the "inflection point" at 4-5 years, noted in the plot of the first discriminant axis against age in both otolith-based as well as the body-based DFA's. The DFA "inflection" age concurs with that at which sexual "size" dimorphism clearly manifests itself in head length, and slightly precedes that at which divergence becomes apparent in otolith length and weight. Although no sexual dimorphism in total- or standard lengths is perceptible, they both exhibit indications of an inflection at about four years of age; these coincide with a levelling off in the specific growth rate (Gutvik, 1991) and rises in the gonadosomatic index (Gutvik unpubl.). These points are all indicative of age at maturity (AFM) being reached at similar ages (4-6) years in males and females. Changes in the appearance and consistency of otolith zones in witch >5 years old are common (Gutvik & Hermannsen, unpubl.); similar sudden changes have been noted in the otoliths of plaice and indicative of AFM having been reached (e.g. Rijnsdorp et al., 1990; Rijnsdorp & Storbeck, 1991).

Although the use of otolith length and weights are of great potential in age discrimination, their use in sex discrimination appears to be poor. Examination of "incorrect" sex via otolith-based DFA suggested an overall misclassification of 21.2 %. This value, however, has to be treated with some scepticism as sex determination was carried out very carefully in the present study, with recourse to microscopic analysis when standard visual observations of the gonads were of little benefit. It is practically impossible, for example, to misidentify the sex of a large witch- such that suggestions of mistaken sex determinations in about 50% of 8 year olds is unreasonable. The body-based DFA suggests a sexual misclassification of about 7% overall; as the majority of confusion is due to younger (3-6 years) males mistaken sex is a contingency, albeit small.

The advent of maturation in fish is dependent on reaching a definite size or age (Alm, 1959; Weatherley & Gill, 1987). Age appears to be the most important in species which mature early, while size is the more important factor in those which mature late (Roff, 1982). The inherent plasticity of fish in responding to environmental perturbations can result in changes in the age and/or size of first maturation (AFM) as growth rate changes (Stearns & Crandall, 1984). The AFM has a great influence on population growth rates (Cole, 1954; Stearns, 1976; Roff, 1984, 1991). In witch flounder, studies from the Canadian northwestern Atlantic indicate that AFM and/or size at first maturity (SFM) can vary from area to area (Bowering, 1976). Beacham (1983) related this to differences in ambient temperature affecting growth rates. In the majority of fish species males often exhibit a lower AFM and SFM than females (Nikolskii, 1969), and this often applies to witch flounder (Bowering, 1976). In witch flounder, AFM has become lowered in areas where stocks have been relatively heavily fished and older age-groups have disappeared (Beacham, 1983; Bowering, 1976); SFM (expressed as length) was roughly similar in males and females, probably reflecting dissimilar growth rates in the two sexes. As AFM integrates both growth and mortality effects, which are classically highly correlated (Beverton & Holt, 1959; Alm, 1959; Adams, 1980; Hoenig, 1983; Roff, 1991), monitoring AFM and its variation has an excellent potential for examining environmental change, particularly in the context of fisheries management. Data on witch flounder indicates that the lower limit of AFM is about 4 years (Molander, 1935; Bagenal, 1963): fishing intensity that has forced the population AFM close to this level has generally been followed by stock collapses and overfishing characteristics (Bowering, 1987, 1989; Gutvik, 1991; Nilsen, Gutvik & Hopkins, in prep.).

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Table 1. Discriminant function analysis involving 8 age-groups (2-9 years old) of witch flounder from Malangen, northern Norway, involving length, wet weight, dry weight, and ash weight of the right and left otoliths (sagittae). F= Fisher-value; d.f. = degrees of freedom; significance level P<0.001 (***).

SINGLE DEGREE OF FREEDOM POLYNOMIAL CONTRASTS ($d.f._1$=15, $d.f._2$=50)

Right otolith	**F**	**P**
Dry weight	72.5	***
Wet weight	72.4	***
Ash weight	70.0	***
Length	51.0	***

Left otolith	**F**	**P**
Dry weight	54.7	***
Wet weight	53.8	***
Ash weight	49.2	***
Length	46.3	***

MULTIVARIATE TEST STATISTICS

Wilks' lambda	= 0.008		
F-statistic	= 2.540	DF = 120, 318	P = ***
Pillai trace	= 2.307		
F-statistic	= 1.351	DF = 120, 400	P = *
Hotelling-Lawley trace	=24.508		
F-statistic	= 8.425	DF = 120, 330	P = ***

Theta = 0.957, S = 8, M = 3.0, N = 20.5, P = ***

TESTS OF RESIDUAL ROOTS

Roots 1-8
Chi-square statistic = 253.4, DF = 120, P = 0.00
Roots 2-8
Chi-square statistic = 86.1, DF = 98, P = 0.79
Roots 3-8
Chi-square statistic = 53.8, DF = 78, P = 0.98

Table 2. Discriminant function analysis of age (involving 8 a priori age-groups, 2-9 years old) of male and female witch flounder from Malangen, northern Norway, involving body lengths (total length, standard length, head length) and weights (weights of: dorsal and ventral fillets, "skeleton", liver, and gonad). F= Fisher-value; d.f. = degrees of freedom; significance level P<0.001 (***).

SINGLE DEGREE OF FREEDOM POLYNOMIAL CONTRASTS ($d.f._1=15$, $d.f._2=88$)

	F	P
"Skeleton"	63.7	***
Head length	63.4	***
Ventral fillet	58.7	***
Dorsal fillet	57.4	***
Total length	55.1	***
Standard length	50.0	***
Liver weight	35.8	***
Gonad weight	29.4	***

MULTIVARIATE TEST STATISTICS

Wilks' lambda	= 0.008		
F-statistic	= 5.668	DF = 120, 588	P = ***
Pillai trace	= 2.460		
F-statistic	= 2.605	DF = 120, 704	P = *
Hotelling-Lawley trace	=16.496		
F-statistic	=10.894	DF = 120, 634	P = ***

Theta = 0.929, S = 8, M = 3.0, N = 39.5, P = ***

TESTS OF RESIDUAL ROOTS

Roots 1-8
Chi-square statistic = 434.5, DF = 120, P = 0.00
Roots 2-8
Chi-square statistic = 193.2, DF = 98, P = 0.00
Roots 3-8
Chi-square statistic = 85.9, DF = 78, P = 0.25
Roots 4-8
Chi-square statistic = 53.6, DF = 60, P = 0.70

Table 3. "Correct" and "incorrect" age and sex classification (a priori "correct" age and sex denoted by age read from the otolith and sex determined from anatomical examination of the gonads respectively) involving otolith (lengths, and wet, dry, and ash weights of right and left otoliths) and body (total length, standard length, and head length, and weights of dorsal and ventral fillets, "skeleton", gonad, and liver) based discriminant function analysis, in witch flounder from Malangen, northern Norway. CS and CA = no.'s of fish classified as having "correct" sex and "correct" age respectively; %IS and %IA = percentage of fish classified as having "correct" sex and "correct" age respectively. Age/sex 2 -9 years of age, where m = males and f = females, sum = m+f for given age, SUM = sum of all ages (2-9).

	OTOLITH						BODY					
AGE/SEX	CS	IS	%IS	CA	IA	%IA	CS	IS	%IS	CA	IA	%IA
2m	5	0	0	5	0	0	3	0	0	3	0	0
2f	4	1	20	5	0	0	3	0	0	3	0	0
Sum 2	9	1	10	10	0	0	6	0	0	6	0	0
3m	5	0	0	5	0	0	8	1	11,1	9	0	0
3f	2	3	60	4	1	20	11	0	0	10	1	9,1
Sum 3	7	3	30	9	1	10	19	1	5	19	1	5
4m	4	0	0	4	0	0	11	3	21,4	8	6	42,9
4f	3	2	40	5	0	0	8	0	0	8	0	0
Sum 4	7	2	22,2	9	0	0	19	3	13,6	16	6	27,3
5m	5	0	0	4	1	20	10	1	9,1	7	4	36,4
5f	4	1	20	4	1	20	9	0	0	7	2	22,2
Sum 5	9	1	10	8	2	20	19	1	5	14	6	30
6m	4	1	20	4	1	20	8	1	11,1	7	2	22,2
6f	3	2	40	2	3	60	10	1	9,1	8	3	27,3
Sum 6	7	3	30	6	4	40	18	2	10	15	5	25
7m	2	0	0	1	1	50	2	0	0	2	0	0
7f	2	2	50	1	3	75	4	0	0	2	2	50
Sum 7	4	2	33,3	2	4	66,7	6	0	0	4	2	33,3
8m	1	1	50	2	0	0	2	0	0	2	0	0
8f	2	1	33,3	2	1	33,3	3	0	0	2	1	33,3
Sum 8	3	2	40	4	1	20	5	0	0	4	1	20
9m	3	0	0	3	0	0	2	0	0	1	1	50
9f	3	0	0	3	0	0	3	0	0	3	0	0
Sum 9	6	0	0	6	0	0	5	0	0	4	1	20
SUM	52	14	21,2	54	12	18,2	97	7	6,7	82	22	21,2

FIGURE LEGENDS

Figure 1. Weight as a function of length in otoliths of male and female witch flounder from Malangen, northern Norway. A and B, wet weights of right and left otoliths respectively; C and D, dry weights of right and left otoliths respectively; E and F, ash weights of right and left otoliths respectively.

Figure 2. Lengths and weights of otoliths as a function of fish age read from otoliths in male and female witch flounder from Malangen, northern Norway. A and B, lengths of right and left otoliths respectively; C and D, wet weights of right and left otoliths respectively; E and F, dry weights of right and left otoliths respectively; G and H, ash weights of right and left otoliths respectively.

Figure 3. A) Total length, B) caudal length, and C) head length as a function of fish age read from otoliths in male and female witch flounder from Malangen, northern Norway.

Figure 4. Variation in the contribution of body components (dorsal and ventral fillets, "skeleton", gonad, liver, stomach with contents) to total body weight (sum of all components = total body) as a function of age read from otoliths in witch flounder from Malangen, northern Norway. A and B, weights for males and females respectively; C and D, percentages for males and females respectively.

Figure 5. Variation in the weight of body components (dorsal and ventral fillets, "skeleton", gonad, liver, stomach with contents) as a function of age in male and female witch flounder from Malangen, northern Norway. A, dorsal fillet; B, ventral fillet; C, liver; D, gonad; E, stomach weight with contents; F, "skeleton".

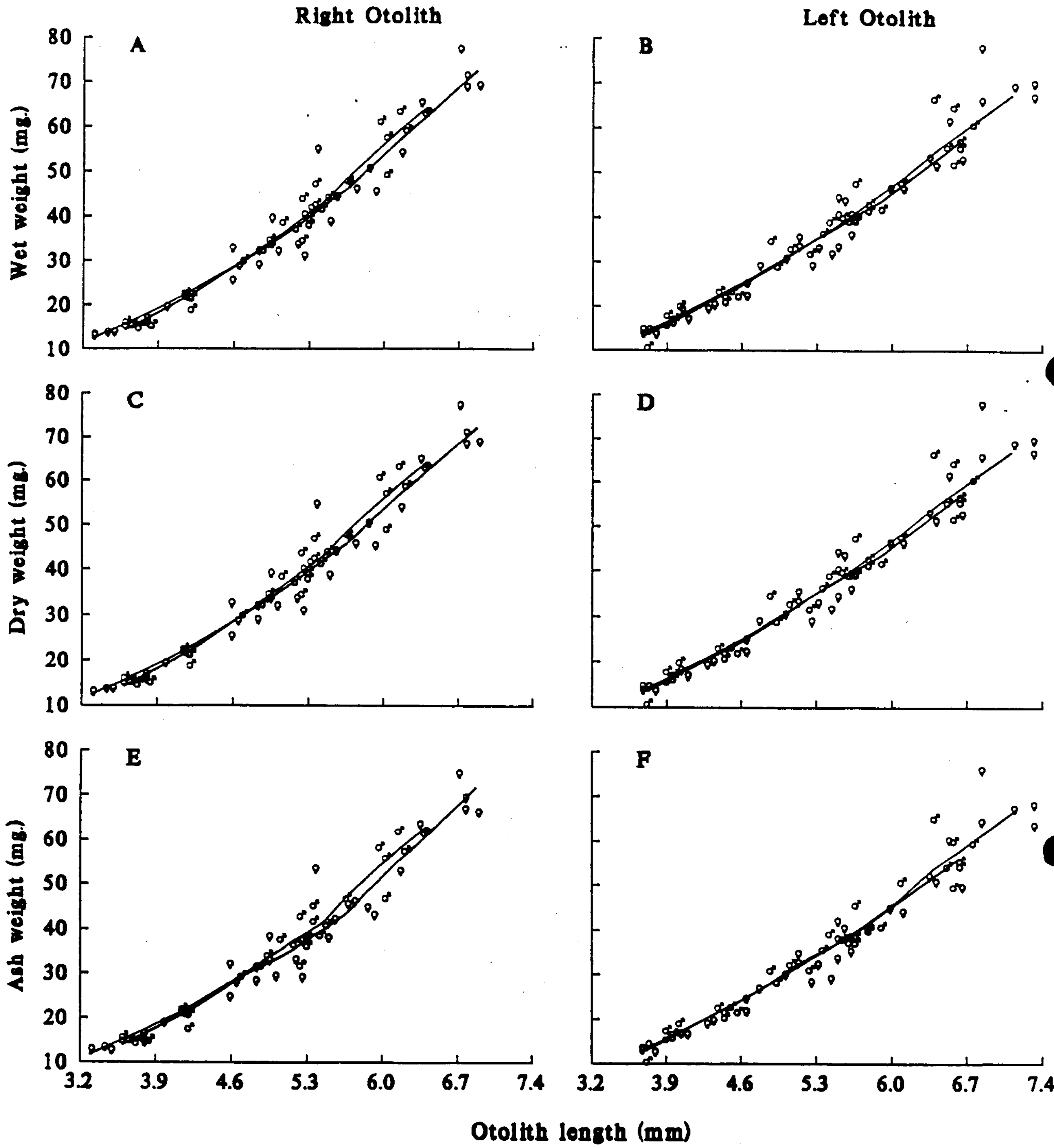
Figure 6. Discriminant function analysis involving otolith characteristics (lengths, and wet, dry, and ash weights of right and left otoliths) in witch flounder from Malangen, northern Norway. A and B, plot of the first two discriminant axes (DF1 and DF2) showing 95% confidence ellipses for centroids (males and females combined) based on "read" age (age read from otoliths) and "predicted" age (age designated from discriminant function analysis) respectively; C and D, plot of the first discriminant axis (DF1) against "read" and "predicted" age respectively (sexes separated)

Figure 7. Discriminant function analysis of age (2-9 years-old) and sex involving body length (total length, standard length, and head length) and body components (dorsal and ventral fillets, "skeleton", gonad, liver, stomach with contents) in witch flounder from Malangen, northern Norway. A and B, plot of the first two discriminant axes (DF1 and DF2) showing individual 95% confidence ellipses for centroids of males (lower) and females (upper) from 3 to 6 years-old (ellipses for other ages omitted due to excessive intermixing) based on "read" age (age read from otoliths) and "predicted" age (age designated from discriminant function analysis) respectively; C and D, plot of the first discriminant axis (DF1) against "read" and "predicted" age respectively (sexes distinct). E and F, plot of the second discriminant axis (DF2) against "read" and "predicted" age respectively, with Cleveland smoother trend inserted separately the two sexes.

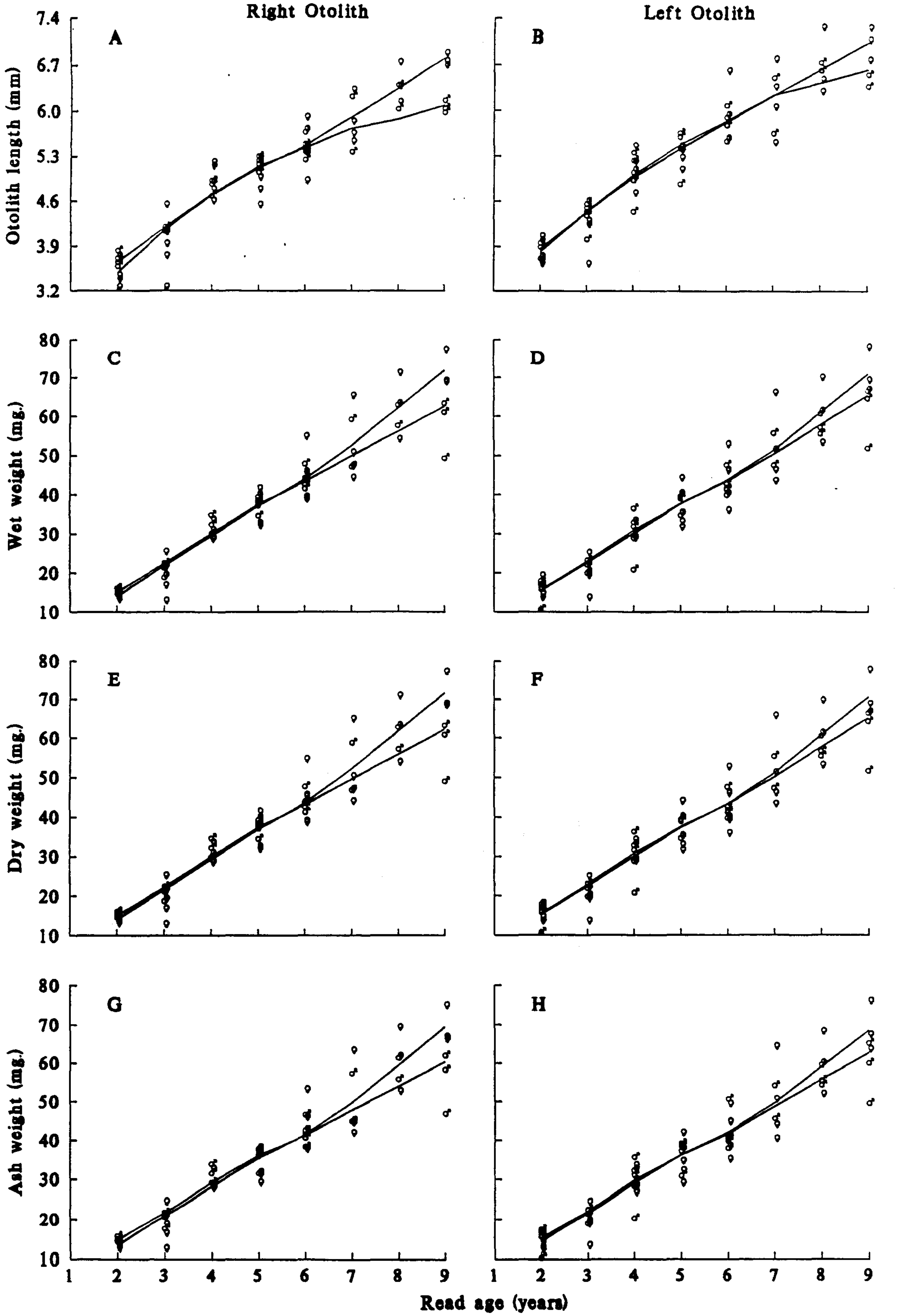
Figure 8. The percentage "incorrect" classification of sex and age in witch flounder, from Malangen (northern Norway) using otolith- and body-based discriminant function analysis (DFA). A) % "incorrect" sex using otolith-based DFA, B) % "incorrect" sex using body-based DFA, C) % "incorrect" age using otolith-based DFA, D) % "incorrect" age using body-based DFA. A priori "correct" age and sex denoted by age read from the otolith and sex determined from anatomical examination of the gonads respectively. Otolith-based DFA involves: the lengths, and wet-, dry-, and ash weights of right and left otoliths; body-based DFA involves: total length, standard length, and head length, and weights of dorsal and ventral fillets, "skeleton", gonad, and liver. Age/sex 2 -9 years of age, where m = males and f = females, s = m+f for given age, S = sum of all ages (2-9).

Figure 9. Plots of "predicted" age (age designated from discriminant function analysis) against "read" age (age read from otoliths) in the case of A) otolith (lengths, and wet, dry, and ash weights of right and left otoliths) based discriminant function analysis, and B) body length (total length, standard length, and head length) and body component (dorsal and ventral fillets, "skeleton", gonad, liver, stomach with contents) based discriminant function analysis, in witch flounder from Malangen, northern Norway. No.'s by the data points denote the number of observations.

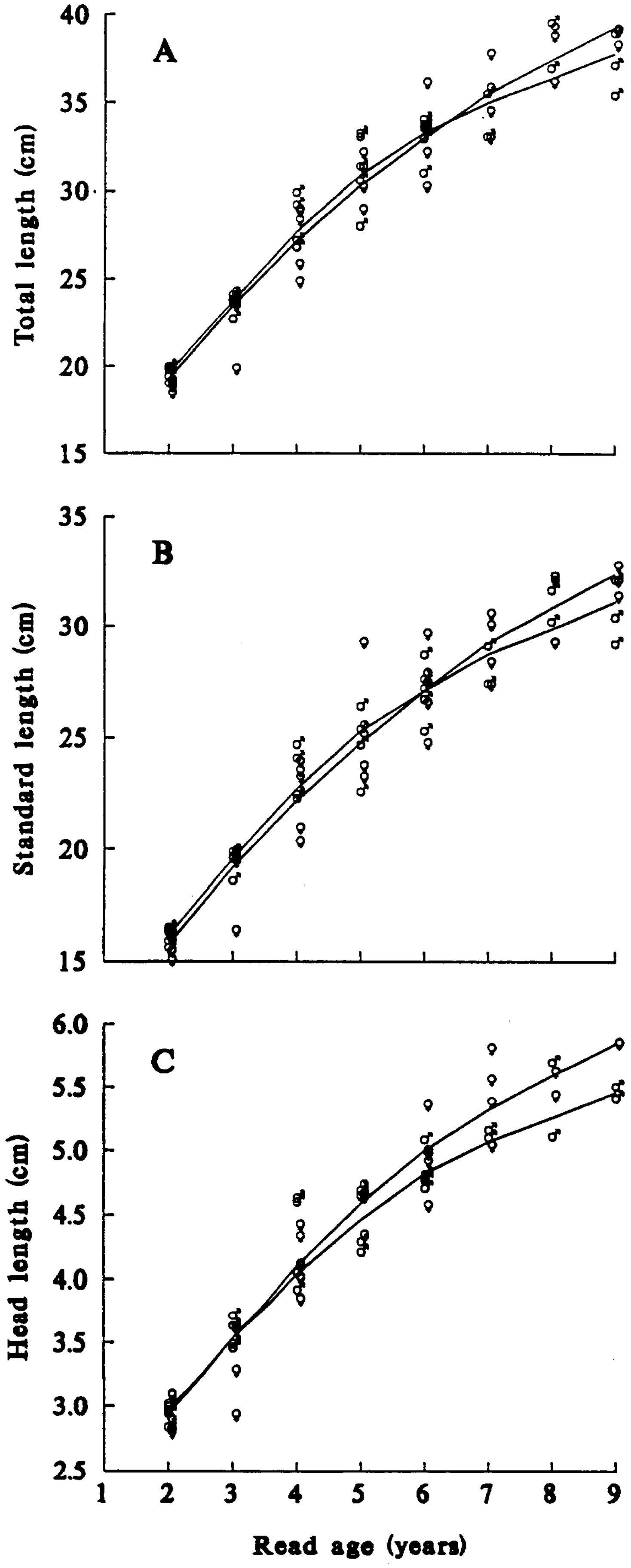
Gutvik et al. FIG. 1 A-F



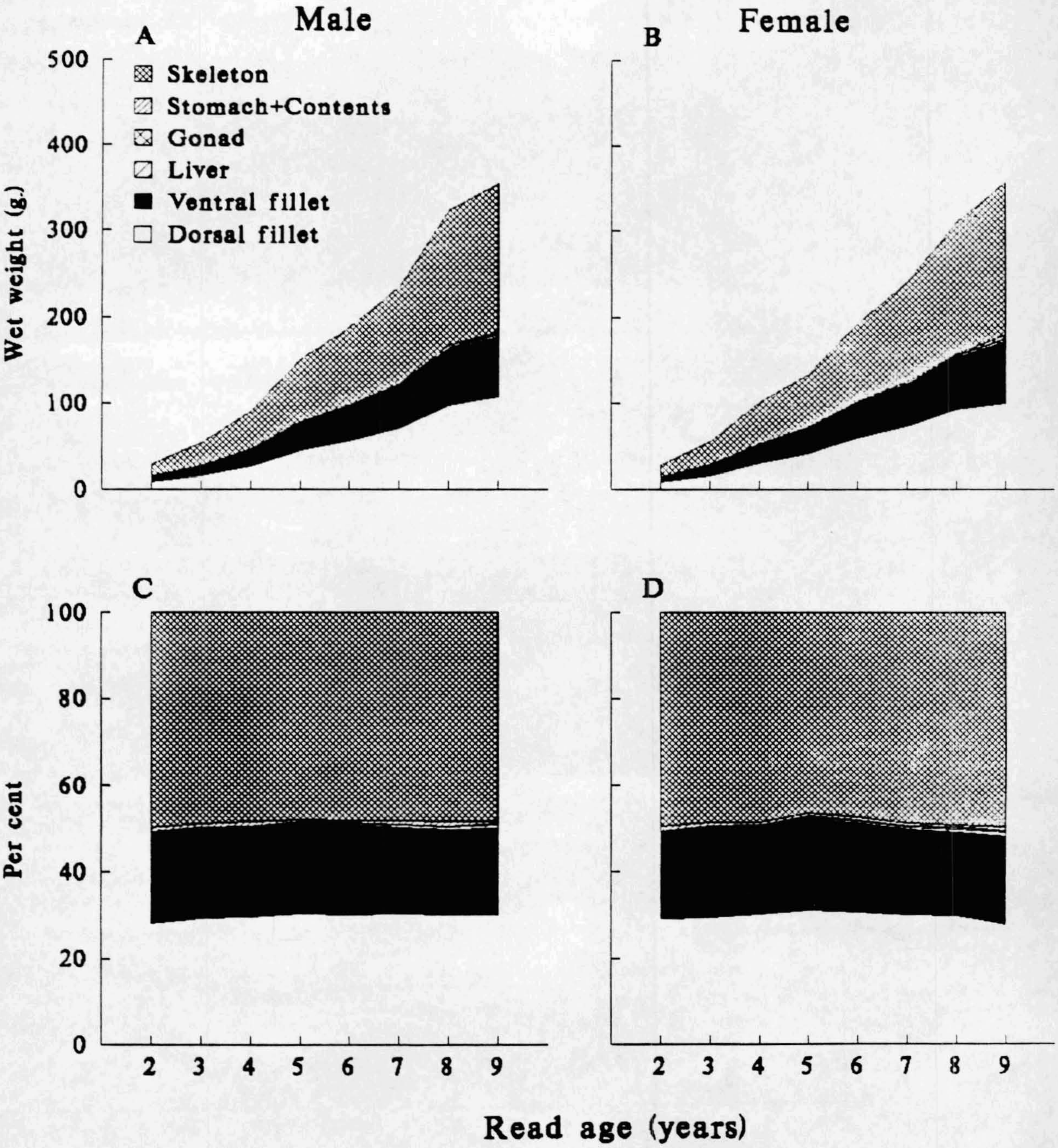
Gulvik et al. FIG. 2 A-H



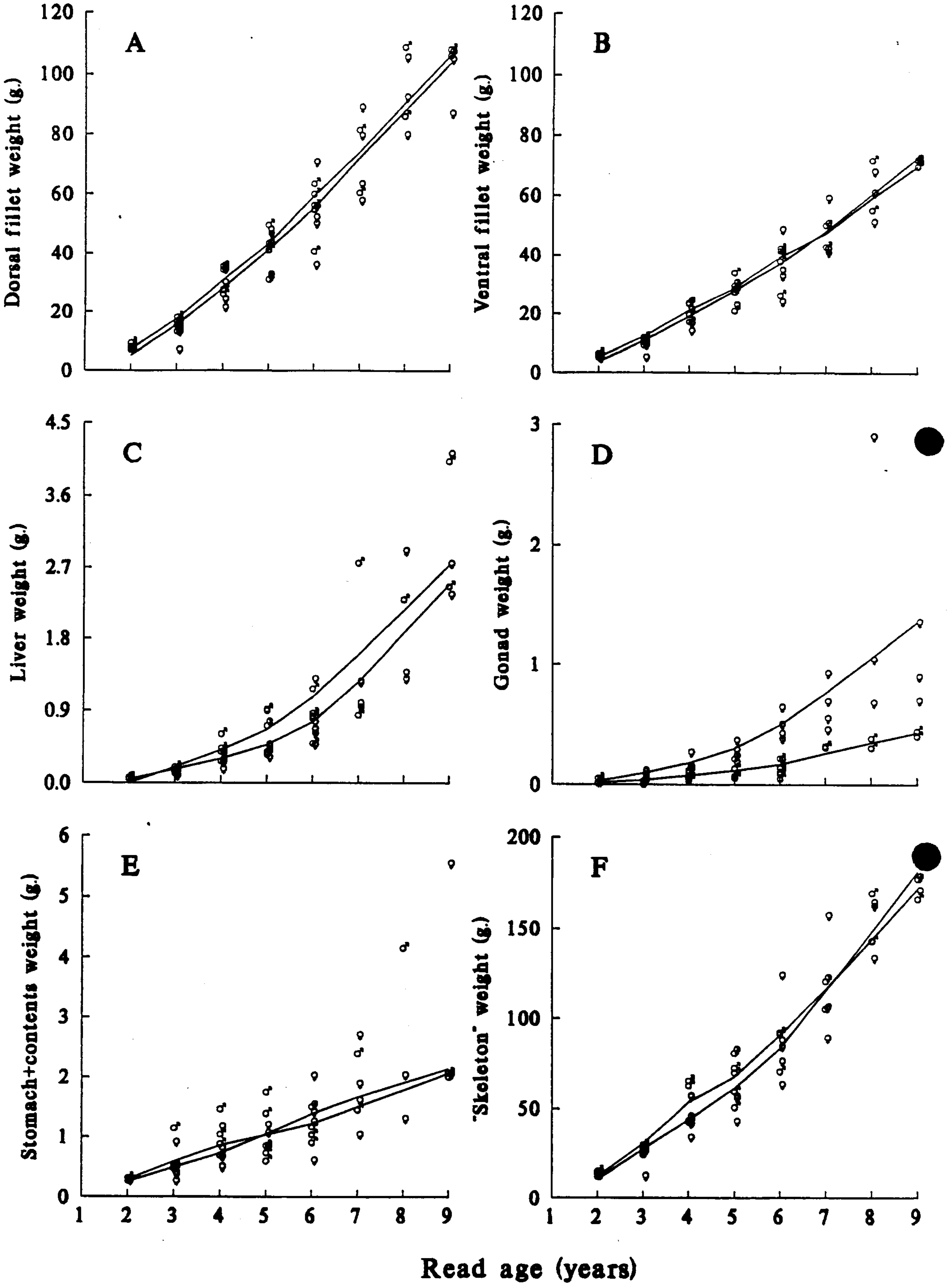
Gutvik et al. FIG. 3 A-C



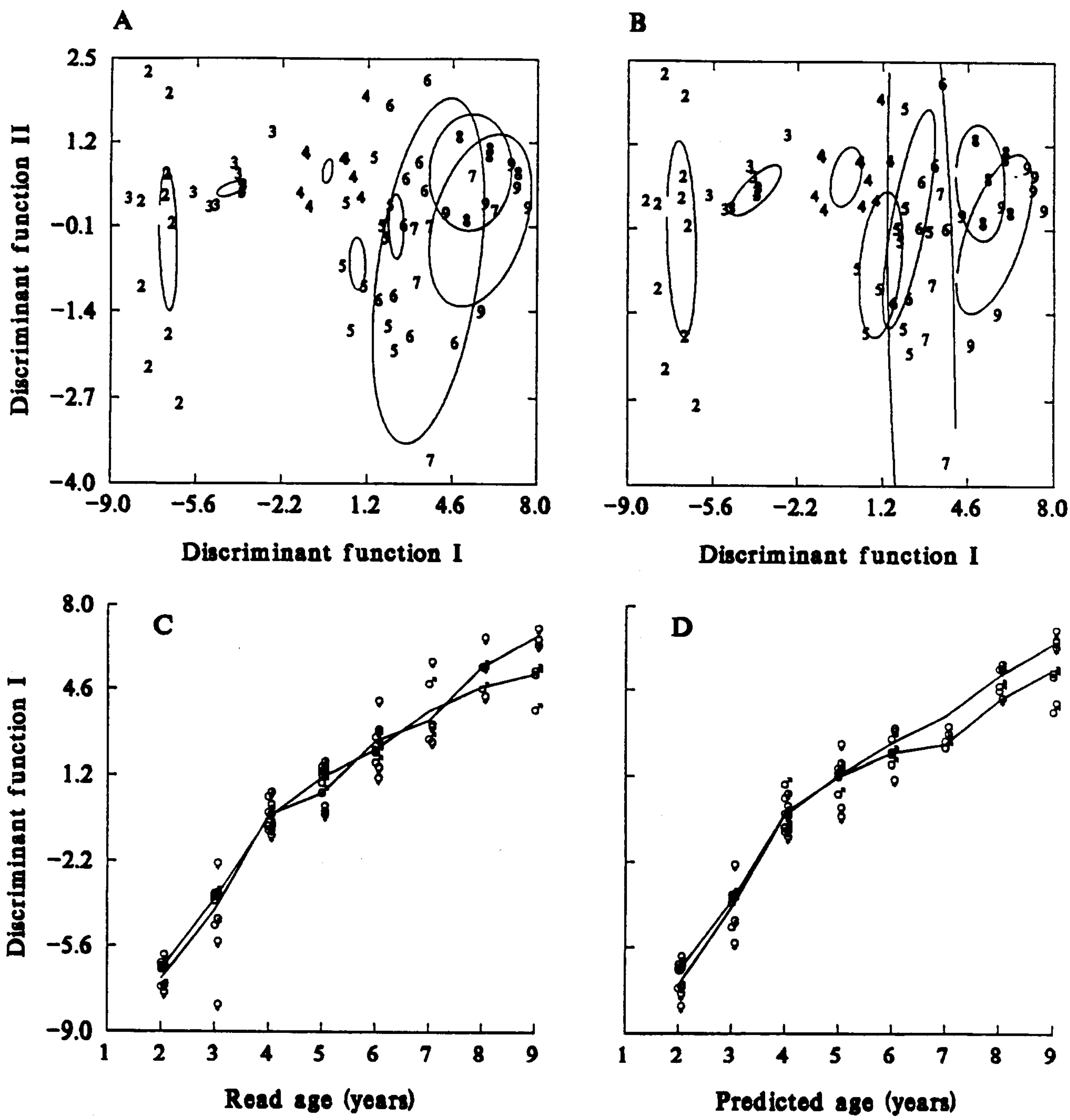
Gubvik et al. FIG 4 A-



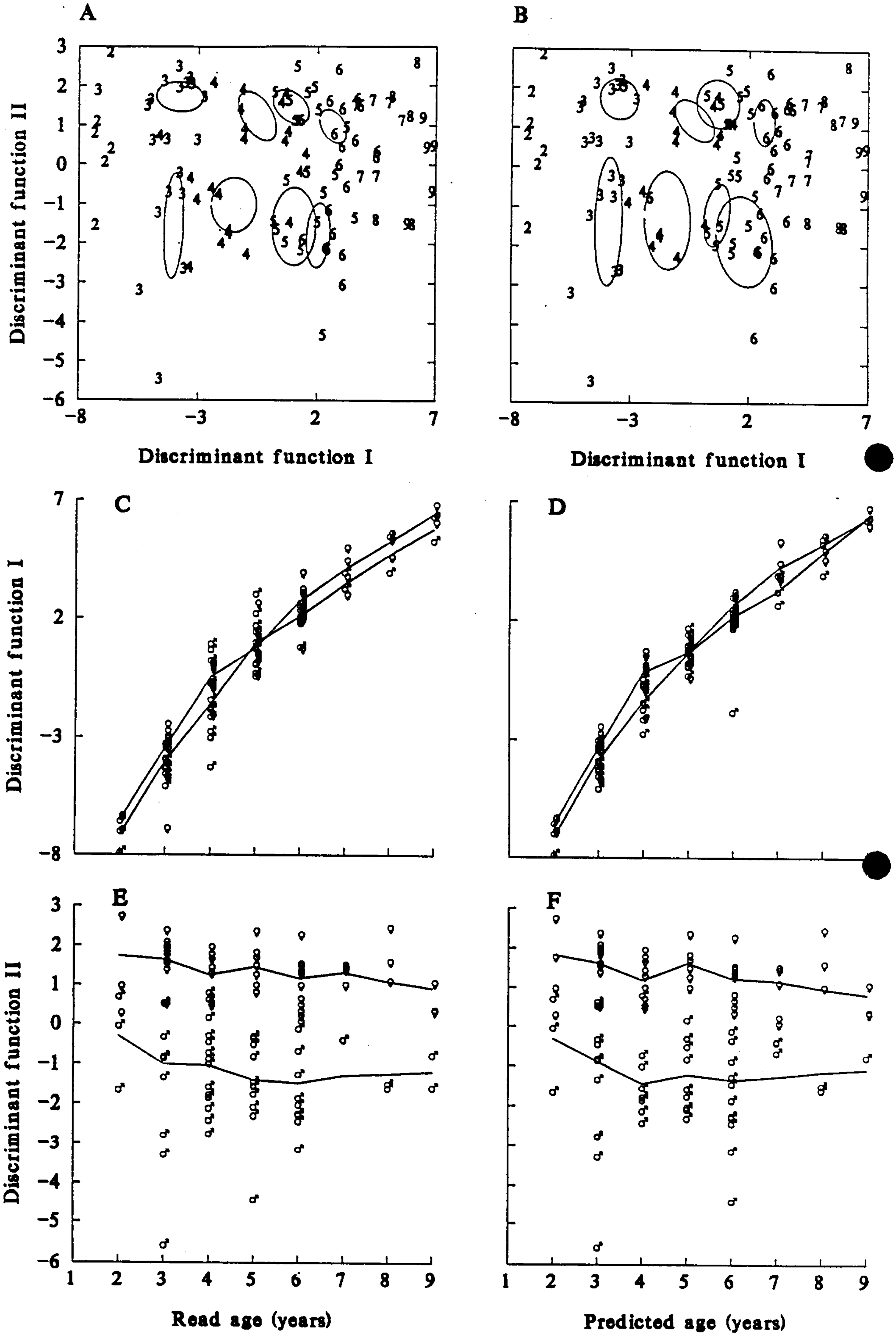
Gulbrk et al. FIG. 5 A-F



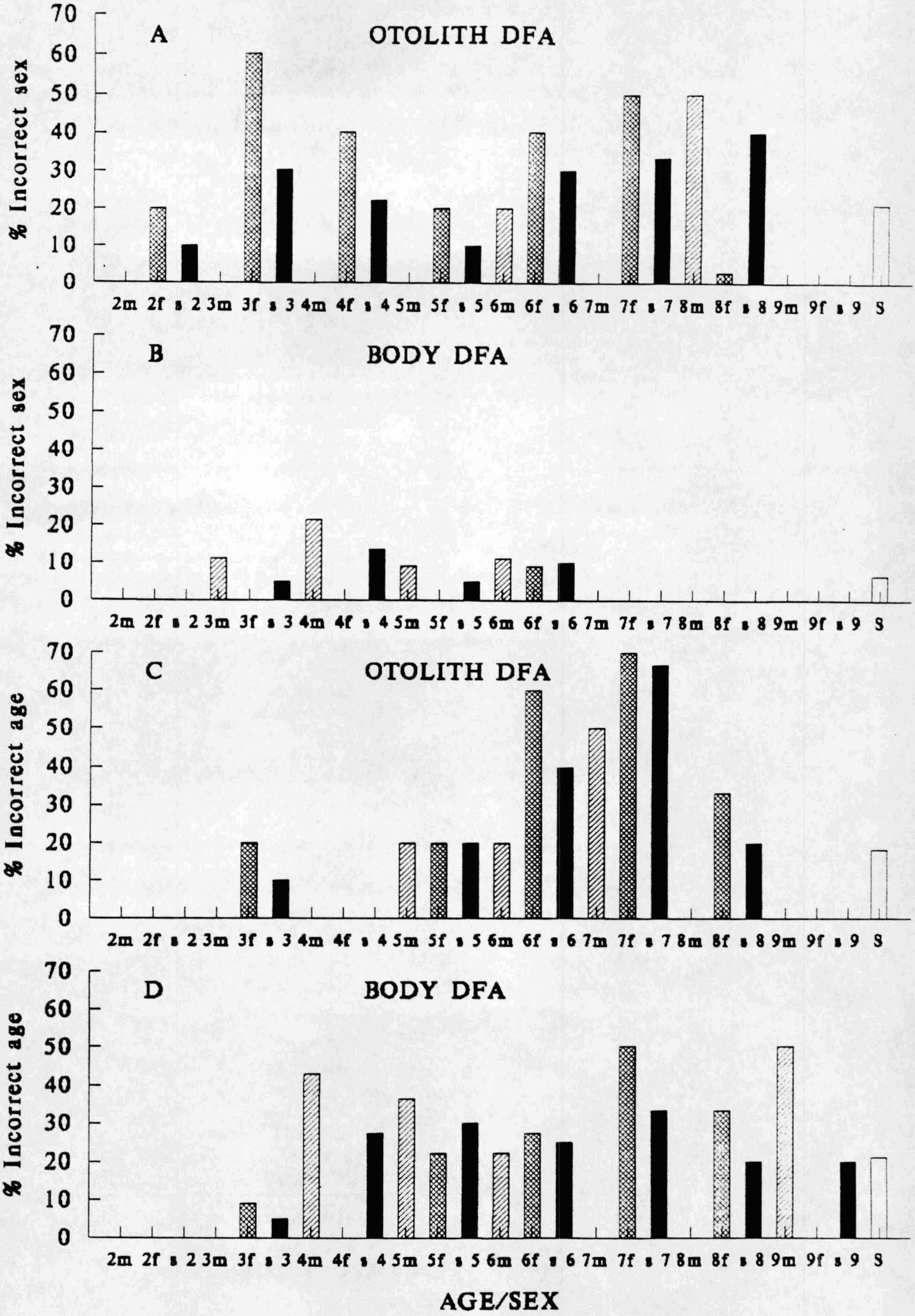
Gulrib et al. FIG. 6A-



Gulbvik et al. FIG. 7A-F



Gutwk et al. FIG. 8A-



Gutork et al. FIG 9 A-B