



SCIENTIFIC COUNCIL MEETING - SEPTEMBER 1998

Growth and Maturation of Haddock (*Melanogrammus aeglefinus*) in Icelandic Waters

by

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Abstract

Growth and maturation of haddock in Icelandic waters have shown considerable spatial and temporal variation in the past several decades. After 1988 haddock have matured much earlier than in earlier decades and haddock in some areas appear to mature young and also show stunted growth. The paper compares possible reasons for this phenomenon and evaluates different models of the growth-maturation process through the use of otolith radii and length at age as well as biological samples from groundfish surveys and commercial catches. It is found that there is considerable spatial and temporal variation in growth and maturity. Some of the variability may be due to some form of competition among yearclasses whereas there are also indications of a link between growth and maturation in certain areas.

1 Introduction

Considerable changes have been observed in growth and maturation of haddock in Icelandic waters in the period from 1970 to 1998 (Anon (1998)). In particular, observations in the commercial catches of an increase in the proportion of young mature fish (Table 1, from Anon (1998)) along with considerable variation in observed mean weight at age (Table 2, from Anon (1998)) is of considerable interest. If the variation in growth is density-linked, this could potentially be of importance for the utilisation of the stock (Beverton 1992) and might have an effect on predictions of medium-term yield from the stock (Helser and Brodziak 1998).

Given that the proportion mature at age is an important determinant of spawning stock biomass, there is considerable interest in determining whether the changes in maturity at age are real factors affecting the spawning potential or artifacts of sampling as has been seen for some species (e.g. cod, as in Stefansson (1992)).

There appear to be small areas where haddock grow much less than in other areas (Jdnsson and Gudfinnsson 1998), indicating small-scale variation in growth and thus possibly also in maturation. It follows that it is important to consider the spatial variation and that selection of different areas for analysis may well lead to different results concerning what factors are important when considering growth.

In other areas considerable research has been undertaken to elucidate which factors are important in the growth-maturation process for haddock. Research on haddock in captivity, described by Hislop *et al.* (1978), mainly focuses on fecundity, indicating that fecundity is increased with increased food supply. The evidence for food supply increasing the proportion of fish spawning is, however, too scant for firm conclusions. In the North Sea it is well known that haddock recruitment is highly variable (Hislop 1988), with size and age composition varying between years. Furthermore, Hislop (1988) found that fish maturing young (age 2) produce smaller and lighter eggs than older fish.

Work on haddock in the Barents Sea, (Sonina 1981; Kovtsova 1987) indicates that there is considerable variability in length and weight at age from one year class to another. Variation in growth rate appears to be dependent on food supply, population density and other environmental factors such as temperature, may also be important. The faster growing fish appear to mature younger, and in fact an increased growth rate may not only lead to fish maturing younger but also smaller. The notion that growth rate depends on calorific value of food supply ((Sonina 1981)) will not be considered in the present paper.

It is quite plausible that growth of haddock may be density dependent, particularly since the yearclass size tends to vary by several orders of magnitude for this species. This effect seems to be present in the Barents Sea (Sonina 1981) where growth appears to depend on the total population numbers, rather than only that of the year class. Similarly, in the North Sea in the 1960's, large yearclasses initially showed low growth (as did the subsequent year class) but after the youngest ages growth increased and became comparable with much smaller year classes (Jones 1983; Cushing 1984; Hislop 1996). This may well indicate that competition effects from an abundant yearclass only affect smaller and younger fish. In particular it was found that the year classes from the years before the large year classes grew rapidly despite spending all but the first year in a period of high haddock abundance, (Hislop 1996). In the Barents Sea, during the period from 1962-1986, the highest growth was observed in the 1982 yearclass, despite 1982 being a strong yearclass, as the population biomass was low (Kovtsova 1987).

Naturally various environmental factors may be of importance in determining the growth of haddock as that of any fish species. In particular, Cushing (1984) related the timing of the Calanus spring bloom with gadoid recruitment - later spring outburst of Calanus provides gadoids with a greater food supply. Cushing (1984) did not find conclusive evidence of a corresponding relationship between haddock and Calanus but suggested that haddock may be affected by cod through predation and competition.

Although density dependence is a plausible mechanism, it is by no means universal, as it has been found that mean lengths-at-age of haddock in the North Sea in

the 1960's were comparable with those of the 1950's (higher than 1920's) despite the stock biomass being considerably higher (Jones 1983). Indications for density dependent growth have been reported for haddock on Georges Bank (Ross and Nelson 1992), but investigations of density dependent growth are hampered by the fact that several mechanisms can sometimes result in the same measurements. Notably, enhanced survival of small fish in good yearclasses may give the appearance of density dependent growth within a yearclass (Bromley 1989).

In the Barents Sea, there are indications that growth rate rather than length was the important factor in maturation (Sonina 1981). Fast growing fish mature younger and smaller than slow growing fish which mature older and at a greater length. If fish grow more slowly after maturation, as energy is required for reproduction, a faster growing population will mature younger and shorter and subsequently may be smaller. Haddock in warmer water grow faster, which may be a reason why the North Sea haddock population (Hislop *et al.* 1978) matures younger and shorter than Icelandic haddock which in turn matures younger and shorter than Barents Sea haddock.

It is thus possible that a considerable portion of the variation could be due to environmental factors, such as warmer water producing a larger year class which are able to mature faster (and therefore at a shorter length). In the Arcto-Boreal waters warmer water also tends to imply more food and faster growth.

The questions raised above for haddock are to some extent of a general ecological nature and it is of some interest to note which factors play a role for other species, in order to shed some light on which effects might be expected for haddock in Icelandic waters. Considerable research has been conducted on North Sea plaice in order to understand and link the growth and maturation processes (Rijnsdorp 1992). For this species, length and age at maturity have changed this century with fish maturing younger and smaller. It is not clear whether this is a genotypic or phenotypic change, but several aspects are of interest. For example, if the maturation process takes more than 1 year then early growth appears to be more influential than growth in the year immediately prior to maturation. The entire growth history is therefore important for plaice with immature female plaice smaller than mature plaice, both in the year of sampling and earlier.

In addition to flatfish, the growth and maturation of salmonids has been extensively studied, both in captivity and in the wild. For male salmon parr it appears that there is a minimum length for maturation and early maturity follows faster average growth (Myers *et al.* 1986). Another aspect in this case is that after gonadal development, mature fish appear to grow slower than immature fish of the same age (Myers *et al.* 1986). Previous changes in growth thus appear to explain changes in the proportion mature from year to year.

Naturally, these growth and maturity variations are due to some physiological variations which stem in one way or another from the past and present environment in accordance with the response dictated genetically. It has been found that higher fat levels and/or early (within a year) replenishment of fat stores leads to early maturation in salmon (Rowe *et al.* 1991). It is therefore quite plausible that the onset of maturity is in some way linked to feeding in some earlier periods. For salmon it has thus been found that the timing of growth within a year is

important and fast growth in late winter or early spring leads to maturation but fast growth in late spring or summer does not (Rowe and Thorpe 1990). The conclusion from these studies appears to be that if the growing season starts too late, then there will be insufficient time to acquire reserves for spawning, (Rowe and Thorpe 1990).

There are of course other factors such as increased daylight, water temperature and food supply or decreased density which may increase the proportion mature and affect growth. For example, Millar (1990) and Millar and Myers (1990), investigating cod off Newfoundland, found that temperature and density were important factors in describing growth, but links to food supply have not been found in this area. Similarly, Jakobsson *et al.* (1993) report on density-related factors in the growth and maturation of summer-spawning herring in Icelandic waters. In this context, however, it must be noted that Rijnsdorp *et al.* (1991) found no evidence of density dependent growth, of juveniles or adults, in the North Sea for plaice, sole or cod and therefore density dependent growth does not appear to be a common phenomenon.

Bohlin *et al.* (1994), analysing sea trout, found that maturing male parr were bigger the previous year than non-maturing fish. After maturation, immature fish grew faster than mature. After maturation, salmon and sea trout somatic growth slows but for plaice there is a time delay (Rijnsdorp 1992). This may be related to differences in time scale of maturation between the species. Plaice being affected by growth history and salmon by more recent growth.

2 Conceptual models

The basic purpose of the present paper is to throw some light on the relationship between growth and maturation. A fundamental problem in this is that the mature fish which spawn at a given age may have matured for the first time either in the same or any earlier season.

Various models can be envisaged for the interrelationship between the maturation process and growth. This topic has been given consideration in the fisheries literature as well as in the general ecological literature, where models for reproductive tactics have been given considerable attention (e.g. Wootton (1992)).

The timing of the onset of maturity may be thought of and modelled in widely different ways. One such approach is taken in Beverton *et al.* (1993) and Vilhjalmsón (1994) where "maturation cohorts" are studied. A maturation cohort is defined as the group of fish of a certain yearclass which mature at the same age. This approach is inherently reasonable if maturation is e.g. defined through a genetic trait so that maturation at a certain age defines a group of individuals which have certain population characteristics different from those maturing at a different age. In this setting the maturation process can be thought of as a driving force which will affect e.g. maturity-dependent growth etc. Some studies have in fact shown that the age of maturation is at least partially under genetic control for some teleosts such as chinook salmon, *Oncorhynchus tshawytscha* (Hankin *et al.* 1993).

On the other hand, it has been found that maturation-related factors may vary in response to nongenetic effects. In particular, it has been found in laboratory experiments that increased food supply may change haddock fecundity and the proportion of spawners (Hislop *et al.* 1978). In the field it has been suggested that maturity at age in Barents Sea haddock may change in response to growth conditions as a result of changes in population abundance, food availability and temperature (Sonina 1981; Kovtsova 1987; Kovtsova 1993). Similarly, for southwest Scotian shelf haddock, length at 50% maturity has been found to vary with a significant positive correlation to biomass (Waiwood 1989). According to these theories, early maturation would be a consequence of increased growth of immature fish. If this is the case then maturation is more appropriately modelled as a consequence of other factors rather than as a driving force. If reduced growth is a consequence of the maturation process, it is possible that, in the von Bertalanffy model, early maturation simply shows up as a higher K-value and lower L-infinity.

Related work on other species of fish indicates that the feeding level at an early stage is an important factor in deciding whether fish mature early. For example, it has been found that salmon maturation may be delayed through reduced feeding (Rowe and Thorpe 1990; Thorpe *et al.* 1990) or starvation (Reimers *et al.* 1993). Indications are found in these investigations that an early reduced feeding level may initially result in slower growth, which leads to a lower proportion maturing.

The starved salmon have then been found to be able to compensate later on for the initial reduced growth, as they have not spent energy on gonad production and therefore not suffered reduced growth as a final consequence.

Although fecundity will not be considered per se in this paper, it is of interest to note that very similar results have been found concerning the effects of reduced feeding levels on fecundity and egg size. Research on rainbow trout (*Salmo gairdneri*) and brook trout (*Salmo trutta*) indicates that lowered rations correspond to lower fecundities, later maturation and smaller eggs (Springate *et al.* 1985; Vladyakov 1956). Similar conclusions have been drawn for the three-spined stickleback (*Gasterosteus aculeatus*), where it has been seen that lower food levels reduce the percentage of fish that mature (Wootton 1973) and the fecundity of the convict cichlid (*Cichlasoma nigrofasciatum*) was reduced when given low rations (Townshend and Wootton 1984). Rijnsdorp *et al.* (1991) illustrates for plaice (*Pleuronectes platessa*), that when somatic growth of plaice increases by 25%, the percentage of mature fish increases by 10%, for sole (*Solea solea*) the absolute ovary weight increases as the condition factor increases but maturation does not seem linked to growth. For cod, however, the results of Rijnsdorp *et al.* (1991) were conflicting in that the somatic growth seemed to vary randomly with no relation to maturity, but the fecundity seemed to increase as the spawning stock decreased.

Finally, (Hodder 1963; Hodder 1965) found that environmental factors such as temperature may affect the fecundity of the Grand Bank haddock.

All of these results point in the same general direction: Well fed fish seem to mature earlier, producing more eggs and larger eggs. An appropriate model

should therefore be able to predict that fish which initially grow fast mature early.

The other side of the coin concerns the effect that maturation has on subsequent growth. Many studies are available on this topic and the basic conclusion seems to be that fish will try to maintain a minimum egg weight to body weight ratio. Good growth prior to spawning will correspond to sufficient energy accumulation that the fish will not lose somatic weight, whereas if the fish does not acquire enough food prior to spawning, it will lose weight when developing gonads. Such results have been obtained in controlled experiments with the three-spined stickleback (Wootton and Evans 1975) where the total production, i.e. egg production plus somatic growth was a function of the amount of food consumed. Similarly, there are indications that, in cod (*Gadus morhua*), small vitellogenic oocytes (constituting the annual potential fecundity in a determinate spawner) are produced at low cost but that favorable conditions are used to regulate the energy-expensive process of increasing egg size (Kjesbu *et al.* 1991). Also the results confirmed earlier results that appetite dropped during the spawning period and that the female cod are dependent on reserves of protein and fat (withdrawn from the muscle and liver, respectively) to promote gonadal maturation. The net effect of early maturation is not obvious, as for example Atlantic salmon, *Salmo salar*, have in some instances been found to be able to regain the weight lost due to early maturation and in fact reach the same weight as their immature siblings.

The above considerations indicate that a highly plausible model for the growth and maturation process would be one where increased growth at an early stage affects maturation which again affects later growth. There are also strong indications of a need to consider not only maturation and weight but also to consider fecundity along with egg size when looking at the relationship between spawning stock biomass and the number of surviving offspring.

3 Materials

To study the growth/maturation relationships one would ideally use experiments where individual fish are tracked and measured throughout their lifetime (Hawkins *et al.* 1967). A related approach is to use maturation cohorts along with back-calculated individual length (or weight) at age. Otoliths have been extensively used as indicators of historical growth of individual fish. Although the approach has often proved useful, several authors have found problems with techniques of backcalculation. For example, poor environmental conditions may lead to slow somatic growth but continued otolith growth resulting in the observation that slow growing fish have relatively larger otoliths. These confounding issues are commonly described as bias (Campana 1990) or as a change in the relation between scale/otolith and body growth (Thompson 1929).

On the other hand, the primary problem with using the basic concept of maturation cohorts is, of course, that the timing of onset of maturity is not readily known with annual spawners such as haddock. In order to define a maturation cohort, some indicator in the otolith is required, and although such indicators have been found in Arcto-Norwegian cod (Beverton *et al.* 1993), such indicators

have yet to be quantified for haddock in Icelandic waters. If such a signal exists in the otolith, it should be possible to extract from the otolith growth curves.

In the present analysis, individual haddock otoliths were scanned (Fig. 1) and radii measured in three different directions from the center or the first annual ring, to the outer annuli. A total of 236 sliced otoliths were available for this analysis, where the emphasis was on samples containing the abundant 1989 and 1990 yearclass, off the western part of the south coast of Iceland. Further biological data available on each individual haddock includes length, sex, maturity and age.

Data on haddock from the March groundfish survey in Icelandic waters (Pálsson *et al.* 1989) is used to obtain various indicators of mean length and maturity for different areas and age groups. The survey covers the marine area around Iceland, down to 500m, which includes the entire distribution area of haddock.

4 Analysis

In order to indicate whether (and how) otolith growth relates to somatic growth, the measured otolith radii need to be compared to actual fish length. This is done through plots and simple anova models. The first step in this process is to determine whether and how the otolith radii are linked to length.

Although conversion factors and backcalculations can be used to estimate true historical length at previous ages, this is not necessary. Rather, as the annual otolith increments are linked to growth (possibly in a nonlinear fashion), and the whole point is to explain the growth-maturation link, the otolith radii are used as a proxy for growth and used directly for comparing growth and maturation. This direct use of the otolith dimensions avoids problems involved in backcalculations.

If there is a growth-maturation link, then certain patterns of individual growth curves should correspond to certain maturation patterns and, conversely, it may be expected that fish which matured in a certain year should be distinguishable through their growth curves. As a first step, therefore, the growth curves of otolith radii are grouped together into groups of similar historical growth using cluster analysis.

Data from the groundfish survey in Icelandic waters is analysed simply by using sampled otolith, age, length and maturity data in order to obtain such information as length at age, maturity at age etc.

The emphasis is on female haddock for most of the analysis, although some comparisons will also be made for males. Although the females may be more important in terms of the spawning potential, changes in growth of males will affect the total yields of haddock and thus may affect future predictions of yield potential from the stock. As seen in Tables 6-6, temporal variation in maturity at age is much greater for males than females.

A point worth noting is that it may be easier to find a cause for fish staying immature rather than searching for the cause of maturation. In particular, the immature fish at a certain age have been immature for their entire lifespan, whereas it is not known when the mature fish changed their status.

5 Results

5.1 Relating otolith growth and somatic growth

The most suitable direction of measurement of otolith radii was taken to be the longest (to the right (R) in Fig. 1), as it correlated the closest with length at catch (Table 6). However, the shorter side of the lateral axis correlated better with the length at catch of the 3 and 4 year old immature fish. If this is due to the problem of otolith deposition continuing after the cessation of somatic growth then it may be the more appropriate direction.

Although the distance from age 1 to the border of the otolith is the best predictor of length, age is a significant addition to an ANOVA model describing length as a function of otolith size and fish age (Table 6). This implies that there is unexplained variation in the way otolith radii and fish length increase, not explained by a simple linear link between the two.

The fact that the distance from age 1 to border is better than the distance from the center is useful since there are problems in deciding where the "centre" of the otolith is.

5.2 Spatial and density-related variation in growth

Earlier results indicate that there may be small areas where haddock grow much less than in other areas (Jdnsson and Gudfinnsson 1998). This is also seen from the groundfish survey, where there are highly significant variations in length at age at different stations (Table 9). In order to avoid the effects of intra-haul correlations (Pennington and Vlstad 1994), an analysis of variance was done based on the median length at age 3 for those stations where age 3 haddock had occurred every one of the years 1992-97.

A two-way anova with a year and station effect yielded highly significant results in both variables (Table 10). A more detailed analysis of the local growth phenomenon can be undertaken based on an inshore survey off the south coast where more stations are taken in a small area.

It follows that it is important to consider the spatial variation and that selection of different areas for analysis may well lead to different results concerning which factors are important when considering growth.

Growth curves based on the entire survey area are shown in fig 2. For the total area it is seen that the abundant 1989 yearclass is followed by the slower-growing 1990 and 1991 yearclasses. This would seem to indicate that possible competition may slow somewhat the growth of yearclasses which follow a large yearclass, in accordance with results obtained in the North Sea (Jones 1983; Cushing 1984; Hislop 1996).

For the spawning area a very different pattern emerges, as seen in fig 3 and the indications are not nearly as clear as for the total area. The cause of this difference is not apparent, but it is quite possible that varying migration patterns may lead to very different and possibly constant or randomly varying mean length at age on the spawning grounds, even when the actual growth of individuals in the total population varies considerably.

5.3 Formal statistical tests of growth and maturity relationships

The otolith data can be used to investigate the differences in historical growth of different groups of fish. A simple t-test on the growth in the penultimate year yields a significant difference between the haddock which were mature and those which were immature at age 4 ($p=0.012$, based on those caught and sex staged at age 4). Those caught at age 3 did not show a significant difference in the penultimate growth ($p=0.30$).

An analysis of variance indicates that when all data is used, the yearclasses have significantly different (otolith) growth from age 3 to age 4 ($p(0.001)$). This result necessarily complicates the interpretation, since maturity stage, age and yearclass are somewhat confounded. When only age 4 is considered, however, the data consist entirely of the 1990 yearclass and the growth from age 3 to age 4 is significantly different for the different maturity stages with mature females growing faster.

The differences in (otolith) growth by area can be tested with an ANOVA of age 3 to age 4 growth on area (statistical rectangle). This gives a marginally significant difference ($p=0.09$).

Similarly, there is a difference in otolith radius between mature and immature haddock with immature shorter for both age 3 and 4, significantly so for age 4 ($p=0.20$ and $p=0.02$ for ages 3 and 4, respectively).

5.4 Isolating growth groups

The cluster analysis is applied to individual data on otolith radii from age 1 to the border of the otolith. A dendrogram describing such an analysis of otolith growth zones up to age three (based on fish age three or older) is given as Fig. 4 and up to age four in Fig. 5.

This analysis groups individual fish into groups which describe similar (otolith) growth histories. If there is a relationship between growth history and maturation, then the growth groups should show different maturity patterns.

5.5 Comparing maturation of growth groups

The cluster analysis is used to group the individual haddock into 5 groups. The mean length at age in each group is plotted in Figs. 6-7.

It is seen in these growth curves that some clusters with similar final mean radii have different histories. In particular the cluster of predominantly 1990 cohort grew faster younger, but had significantly lower growth than the 1989 cohort between ages 3 and 4. The reason for this appears to be that the year 1992 was a year of rapid growth with the 1989 cohort having fast growth from age 3 to 4 and the 1990 cohort rapid growth at age 2-3.

In this context it should be noted that the year 1992 corresponds to the change in age of maturity of Icelandic haddock, as observed in the catch data (Table 1).

Also given in these figures is the proportion mature in the final age group shown. It is seen that the immature fish are concentrated in the lower curves and the top curves are based on only mature fish. This would appear to be a fairly strong indication of a link between the growth history and the maturation of female haddock.

It is thus seen that the cluster analysis of growth appears to distinguish between different maturation regimes in that immature female haddock tend to have had slower growth than the mature females.

Further to this, there is a separation of fish from different yearclasses into these clusters. This is seen in Table 6 which gives the proportional composition of yearclasses in each cluster. This is a confirmation of the difference in growth of these different yearclasses seen above in the groundfish survey data (Fig 2).

In addition to the above analysis where only complete data up to a given age is used, it is possible to extend the methodology to include all available data. In particular, since the cluster analysis is based on Euclidean distance (mean across ages), these can be computed between growth curves which have a different number of age groups. Having grouped such growth curves, the proportion mature can be computed for every year on every growth curve, by considering those fish which were caught at that age on that growth curve. These analyses are presented in Figs. 8- 9.

The same effect can be seen from Fig. 9 as from the growth and maturity figures to ages 3 and 4. Here, there is a tendency for the immature fish to concentrate on the lower growth curves and the highest proportions mature are found on the top curve. It should be noted that the sample size in each cell is fairly small (Table 6).

Since there is a limited total number of otoliths and maturity data, these become quite sparse when estimating the proportion mature for each age on each growth curve. More data is therefore required before firm conclusions can be drawn, although the indications of the growth-maturity relationship are strong from these plots.

6 Conclusions and discussion

Otoliths provide valuable information on the growth history of individual fish. The otolith radius is, however, not simply a function of the length of the fish, since the age of the fish is a significant additional regression variable. The relationship appears to be nonlinear and other explanatory variables may need to be included. It is an important area of future research to establish the relationship between otolith (or scale) growth and somatic growth, in order to better predict the various effects in terms of yield and biomass.

When the entire area around Iceland is considered, it would appear that an abundant yearclass affects the growth of the two subsequent yearclasses. The first abundant yearclass does not seem affected by its own abundance, however, possibly reinforcing earlier conclusions that density dependence takes the form of reduced growth due to total numbers in the population rather than the numbers in the cohort. This sort of effect will have some effect on predictions of medium- and long-term yield from the stock and needs to be taken into account when such predictions are made.

As with other haddock populations (such as the North Sea and Barents Sea) age at maturation - and subsequently length at maturation is variable.

Cluster analysis of otolith growth curves indicates that maturation is linked to the growth history and that otolith growth can be used to explain some of the variation in the maturation process. In particular, there are indications that immature individuals tend to have grown according to lower growth curves than the mature individuals.

A considerable portion of the changes in observed proportion mature in the population is due to variable maturation of males. This indicates a need to compute "female" biomass rather than "spawning" biomass in assessments.

Further research should be conducted into the growth-maturation link for male haddock as such factors may be important when predicting medium- or long-term yields from the stock.

This paper has largely ignored the precise form of the relationship between otolith radii and growth, since for the purpose of the present analysis it is sufficient to consider solely the otolith radii. It is, however, of considerable interest to establish the appropriate relationship in order to convert the otolith size as precisely as possible to historical fish length. There is a case to be made to consider also the relationship between fish length and scale radii in order to determine which type of back calculation is likely to have higher predictive power in terms of length. In many ways the scale growth is expected to be more tightly linked to the body growth of the individual fish and may potentially be a better indicator of historical growth, although the otoliths of haddock tend to be easier to read than the scales and are therefore routinely collected.

The present analysis clearly demonstrates variation in growth history. In order to estimate the proportion mature at every age on several growth curves, which

is needed to understand the link between maturity and growth, a considerable body of data is required. The present results can be seen as a first formulation of hypotheses, which need to be verified on different data sets, from other time periods.

In particular, it would be of considerable interest to determine whether maturation can be linked to changes in growth in the year before maturation rather than simply overall faster growth. For such comparisons more growth curves need to be studied, since the simple grouping into 5 growth curves used here tends to group these into curves which do not often intersect. A finer grouping, allowing for more detail in the growth curves, requires considerably more data.

Since there is little if any indication of reduced growth of females after maturation, such factors, if they exist, would primarily be expected for males. This indicates a need for analysis of male growth, since such an effect will affect the potential yield from the stock.

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Year	2	3	4	5	6	7	8	9
1978	0.00	0.13	0.30	0.46	0.68	0.86	0.96	1.00
1979	0.00	0.13	0.30	0.46	0.68	0.86	0.96	1.00
1980	0.00	0.13	0.30	0.46	0.68	0.86	0.96	1.00
1981	0.00	0.13	0.30	0.46	0.68	0.86	0.96	1.00
1982	0.00	0.13	0.30	0.46	0.68	0.86	0.96	1.00
1983	0.00	0.13	0.30	0.46	0.68	0.86	0.96	1.00
1984	0.00	0.13	0.30	0.46	0.68	0.86	0.96	1.00
1985	0.01	0.10	0.40	0.43	0.72	0.67	0.92	0.89
1986	0.02	0.19	0.43	0.66	0.83	0.87	0.95	0.99
1987	0.02	0.11	0.41	0.52	0.79	0.78	1.00	0.96
1988	0.01	0.22	0.38	0.77	0.79	0.93	0.90	1.00
1989	0.04	0.20	0.53	0.72	0.80	1.00	1.00	1.00
1990	0.11	0.28	0.59	0.81	0.84	0.92	0.90	1.00
1991	0.04	0.20	0.58	0.75	0.82	0.91	0.94	1.00
1992	0.04	0.14	0.42	0.77	0.86	0.87	0.71	1.00
1993	0.12	0.33	0.47	0.66	0.88	0.97	0.93	0.85
1994	0.25	0.32	0.57	0.78	0.86	1.00	0.90	1.00
1995	0.16	0.49	0.43	0.78	0.83	0.69	1.00	1.00
1996	0.17	0.36	0.58	0.65	0.78	0.73	0.96	0.98
1997	0.09	0.44	0.66	0.71	0.75	0.86	0.89	1.00
1998	0.03	0.48	0.68	0.78	0.76	0.85	0.91	1.00

Table 1: Iceland haddock. Proportion mature by age and year as used in stock assessments..

Year	2	3	4	5	6	7	8	9
1978	620	960	1410	2030	2910	3800	4560	4720
1979	620	960	1410	2030	2910	3800	4560	4720
1980	837	831	1306	2207	2738	3188	3843	4506
1981	584	693	1081	1656	2283	3214	3409	4046
1982	330	819	1365	1649	2329	3012	3384	3965
1983	655	958	1436	1827	2355	2834	3569	4308
1984	980	1041	1476	2105	2460	3028	3014	3807
1985	599	1002	1783	2201	2727	3431	3783	4070
1986	867	1187	1755	2377	2710	3591	3760	4135
1987	446	1048	1629	2373	2984	3550	4483	4667
1988	468	808	1474	2230	2934	3545	3769	4574
1989	745	856	1170	2010	2879	4109	4035	4706
1990	357	716	1039	1542	2403	3458	4186	4969
1991	409	868	1111	1546	2035	2849	3464	4642
1992	320	856	1253	1597	2088	2529	3133	4022
1993	420	756	1372	1870	2360	2888	2975	3442
1994	568	720	1058	1742	2380	2785	3447	3156
1995	457	874	1145	1366	2079	2853	3251	3899
1996	387	841	1189	1528	1816	2641	3499	3526
1997	450	829	1192	1663	1934	2360	3059	3010

Table 2: Iceland haddock. Mean weight at age as used in stock assessments.

Age	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997
1	0	0	0	0	0	0	13	0	0	0
2	3	4	10	5	5	12	32	17	0	11
3	30	21	32	17	21	30	27	33	10	32
4	59	56	67	51	44	53	60	34	15	45
5	85	78	84	68	84	65	78	75	37	55
6	85	87	88	83	91	89	93	86	55	73
7	92	100	100	92	96	100	100	100	70	80
8	98	100	67	0	80	92	80	100	82	93

Table 3: Percentage mature by age based on male haddock caught in March groundfish survey

Age	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997
1	0	0	0	0	0	0	0	0	0	20
2	2	13	52	17	18	46	48	32	0	43
3	47	46	68	45	49	64	58	39	15	61
4	81	69	82	89	67	68	81	52	32	59
5	94	90	88	83	95	84	88	81	52	75
6	100	90	90	90	97	100	90	78	76	83
7	100	100	100	96	100	100	100	100	87	90
8	100	100	67		100	90	75		92	

Table 4: Percentage mature by age based on male haddock caught in March groundfish survey (spawning ground)

Age	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997
1	0	0	0	0	0	0	0	0	0	10
2	0	0	2	0	0	0	0	0	0	0
3	8	8	16	4	7	10	15	10	7	17
4	23	31	33	24	12	14	28	10	17	28
5	51	51	64	53	47	36	59	48	35	37
6	72	73	75	67	83	71	71	62	64	60
7	86	100	83	79	76	75	100	50	67	73
8	81	100	100	50	83	81	100		67	88

Table 5: Percentage mature by age based on female haddock caught in March groundfish survey

Age	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997
1	0	0	0	0	0	0	0	0	0	0
2	0	0	13	0	0	0	0	0	0	0
3	15	16	39	15	18	28	31	15	15	24
4	40	46	55	49	45	34	59	25	24	47
5	70	71	70	63	71	64	74	69	50	50
6	87	75	82	72	85	75	82	67	67	80
7	98	100	93	95	83	100	100	0	55	79
8	93	100	100	50	88	80	100		100	100

Table 6: Percentage mature by age based on female haddock caught in March groundfish survey (spawning ground)

	L		R		D	
	centre	age 1	centre	age 1	centre	age 1
length	0.845	0.848	0.866	0.902	0.838	
length (imm)	0.865	0.856	0.750	0.861	0.833	
length (mat)	0.727	0.736	0.791	0.846	0.762	

Table 7: Correlations between length at catch and otolith radii in three different directions (left, right and down) and from the center or border of age 1 radius.

Term	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
ln(radii)	1	5.514	5.514	732.626	0
age	1	0.126	0.126	16.745	0.00008
Residuals	111	0.835	0.007		

Table 8: ANOVA results from describing log-length of haddock as a function of log-otolith radius and age.

Station	92	93	94	95	96	97
31701	41.5	37.0	34.0	36.0	38.0	32.0
31712	40.5	37.0	37.0	37.0	38.0	33.0
31912	32.0	31.0	31.0	30.0	36.0	34.5
32011	32.0	31.0	32.0	34.0	33.5	37.0
32012	34.0	30.0	31.0	33.0	32.0	34.0
32111	33.5	33.0	35.0	34.0	30.0	31.5
36411	45.5	37.0	34.0	39.0	40.0	37.0
36501	40.0	37.0	33.5	35.0	36.0	38.0
36511	40.0	40.0	31.0	34.0	34.0	33.0
37201	36.5	33.0	37.0	35.5	37.0	36.0
37311	33.0	36.0	35.5	36.0	42.0	35.0
37312	33.0	38.0	35.0	41.0	41.0	37.5

Table 9: Median length of haddock at age 3 by station and year, for groundfish survey stations with otolith samples in all years from 1992-1997.

Term	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
factor(c(y))	5	71.4	14.27	2.101	0.07904
factor(c(r))	11	310.1	28.19	4.150	0.00018
Residuals	55	373.6	6.79		

Table 10: ANOVA results from describing median length of haddock at age 3 as a station and year effect.

Group	Yearclass				
	1986	1987	1988	1989	1990
1	.	.	6	56	38
2	5	.	.	45	50
3	.	4	.	33	62
4	.	10	10	50	30
5	.	.	.	29	71

Table 11: Year class composition of clusters derived from dendrograms of otolith growth curves up to age 4.

Group	Age					
	2	3	4	5	6	7
1	0(2)	25(4)	80(10)	100(5)	100(1)	100(1)
2	0(5)	38(8)	91(11)	100(4)	.	100(1)
3	.	50(2)	100(10)	100(8)	100(1)	.
4	0(2)	17(6)	67(3)	100(4)	.	.
5	0(1)

Table 12: Percentage mature at age (size of sample) in each cluster derived from dendrogram of otolith growth curves using data from all available haddock.



Fig. 1. Haddock otolith with measured directions indicated, left (L), down (D) and right (R).

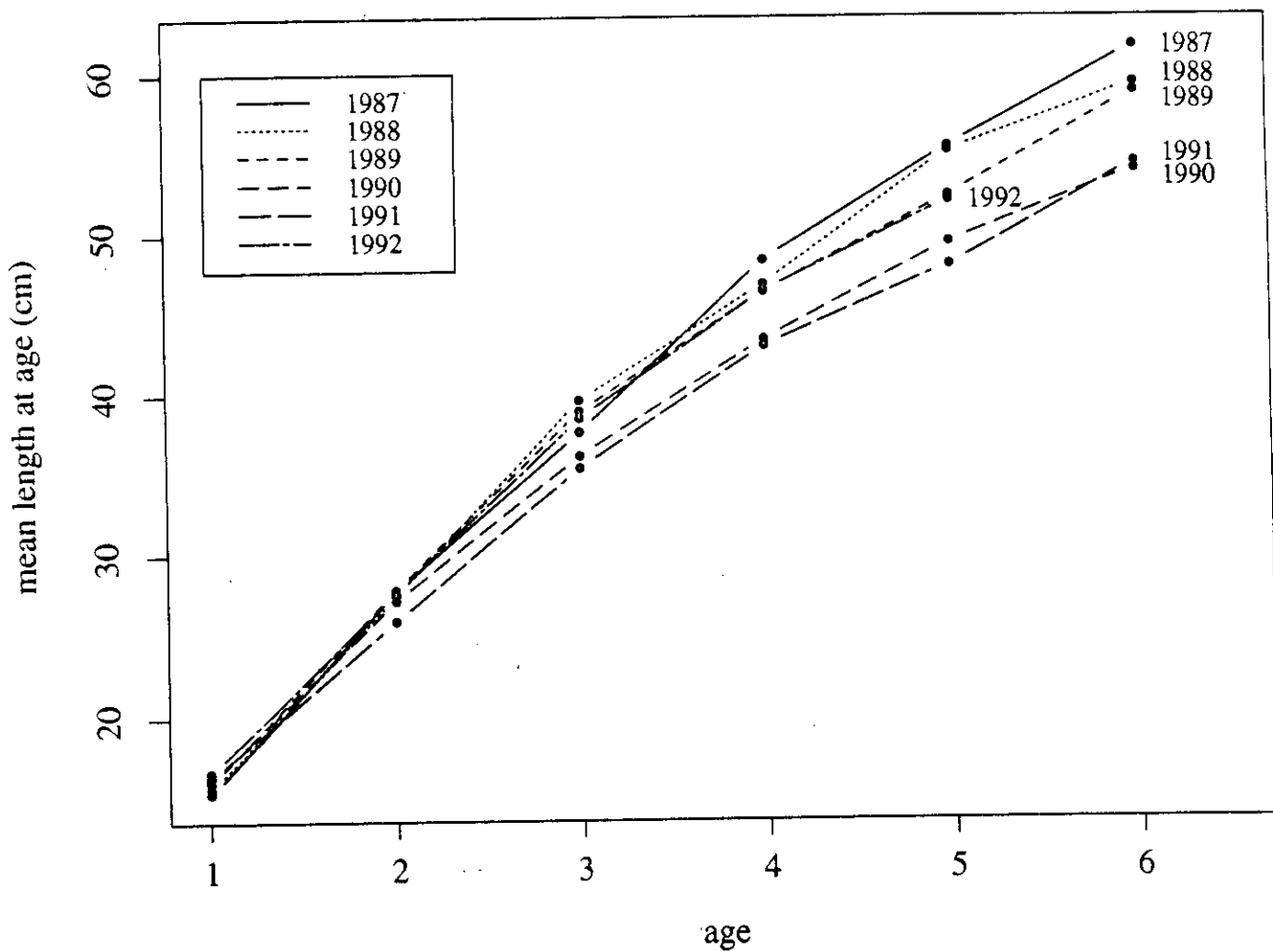


Fig. 2. Mean length of female haddock from groundfish survey. Entire area used in the analysis.

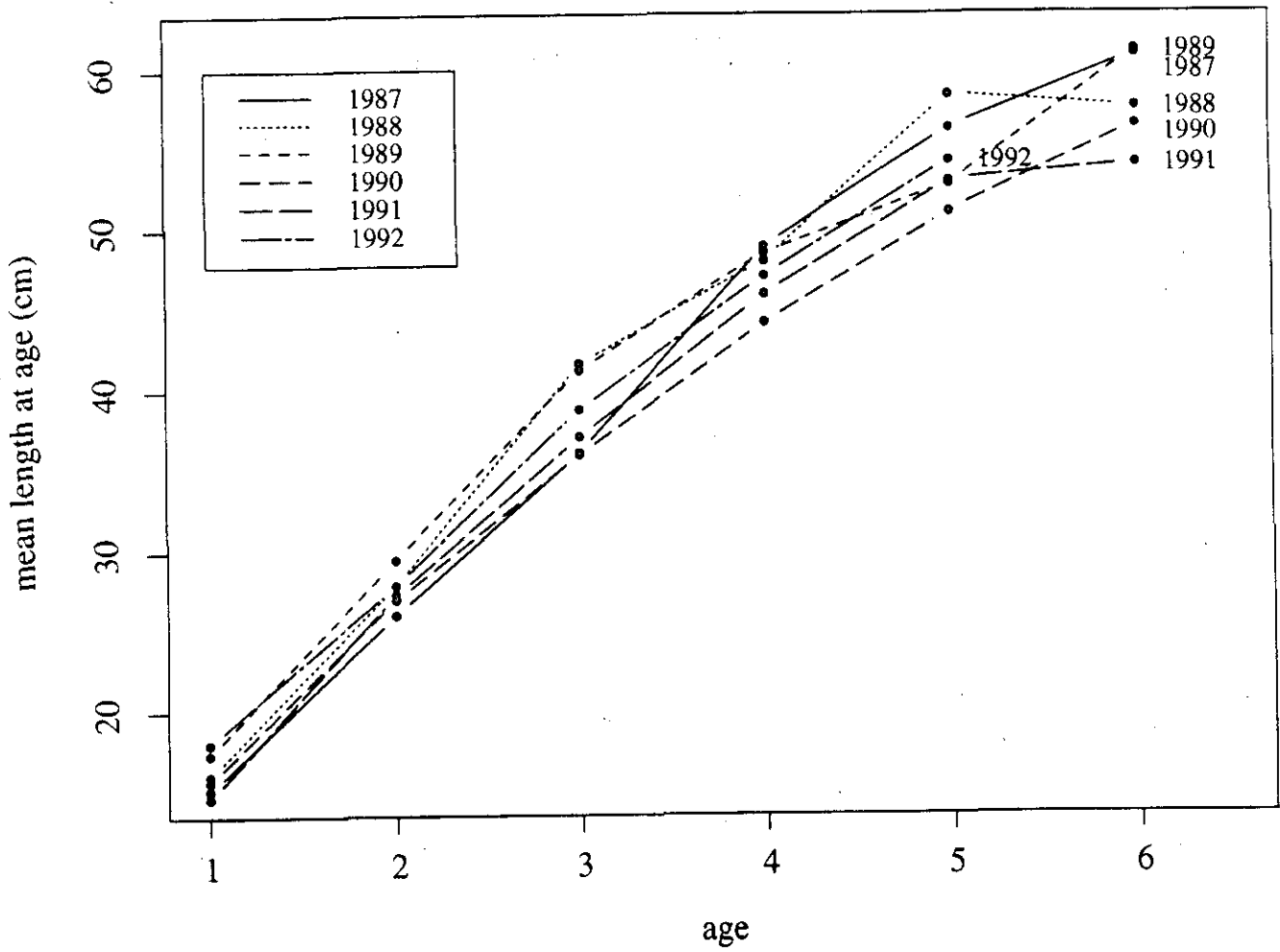


Fig. 3. Mean length of females haddock from groundfish survey. Spawning area used in the analysis.

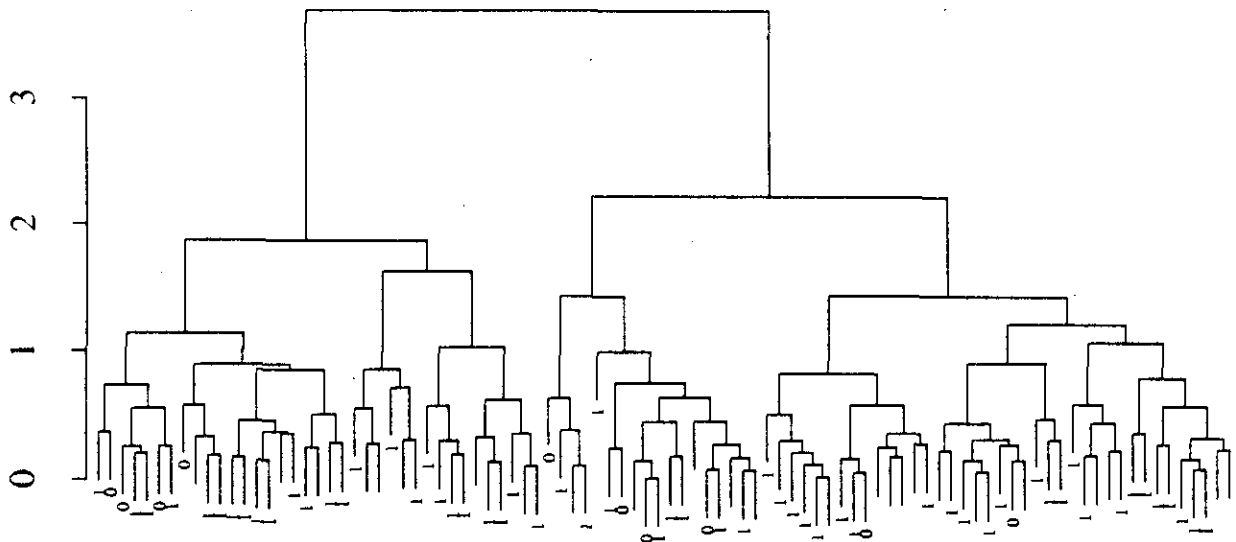


Fig. 4. Dendrogram illustrating relationship between growth curves of otolith radii using data from haddock caught at age 3 or older.

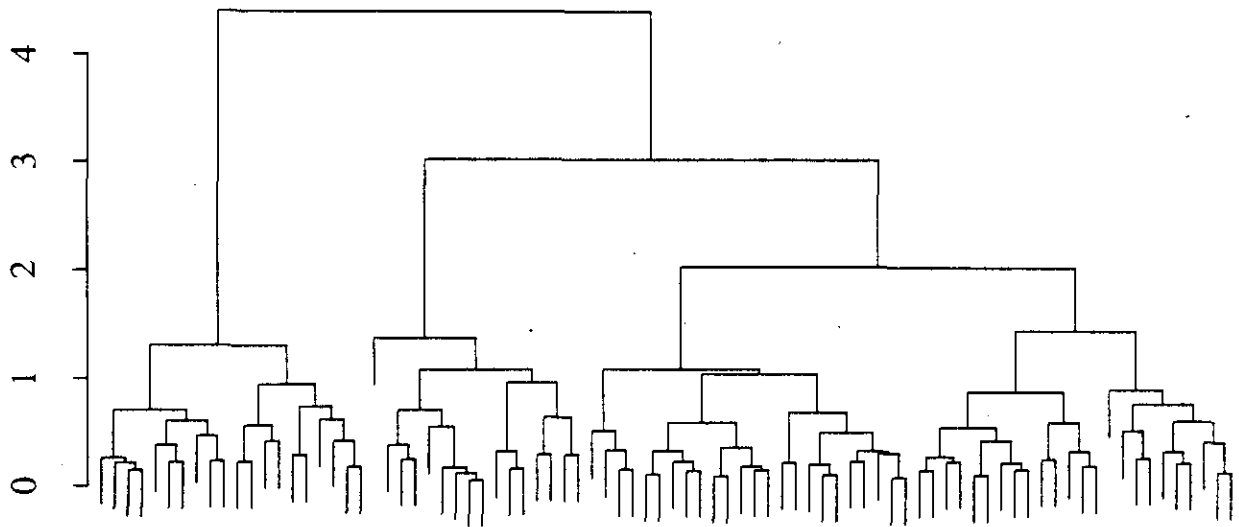


Fig. 5. Dendrogram illustrating relationship between growth curves of otolith radii using data from haddock caught at age 4 or older.

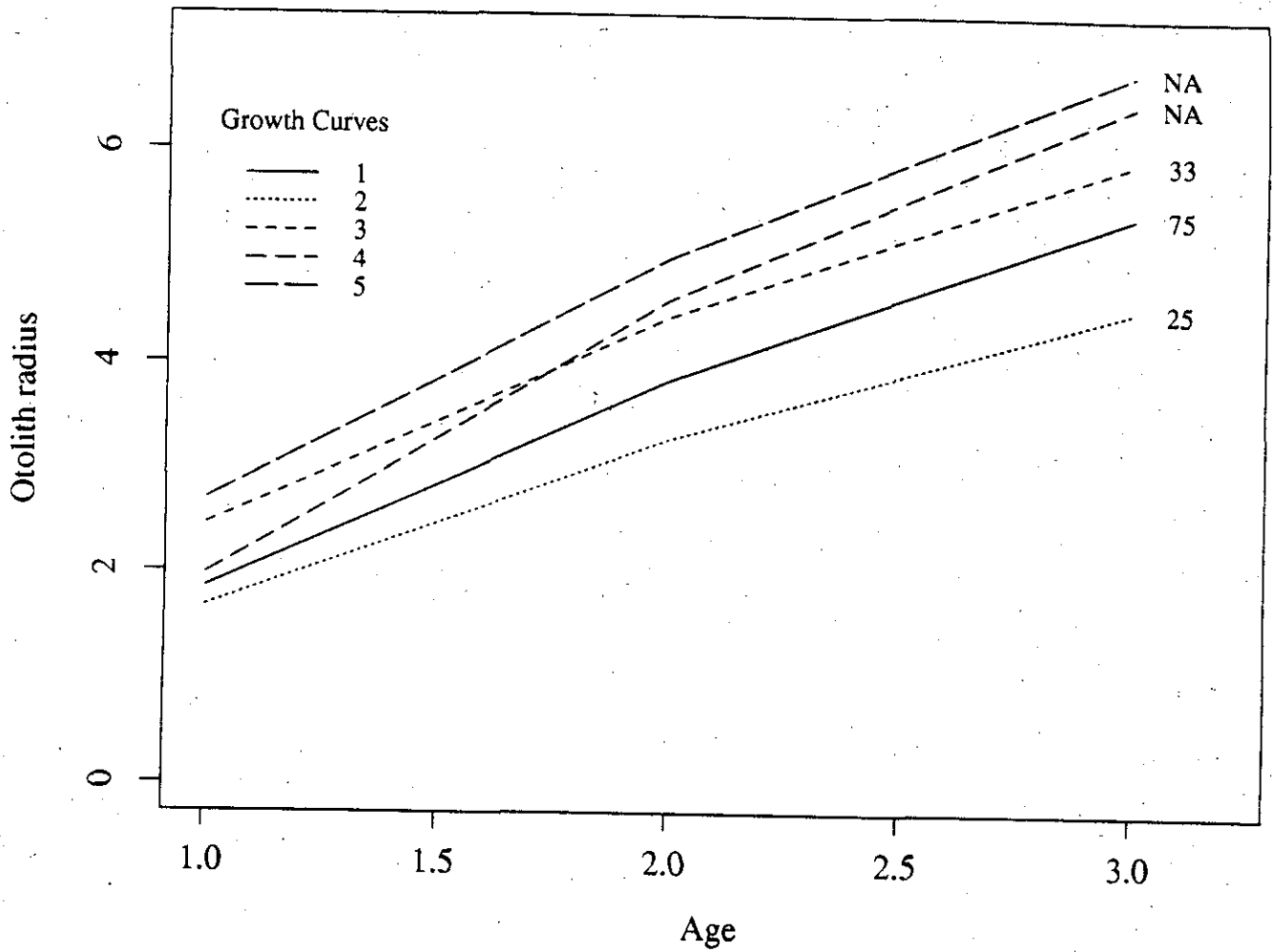


Fig. 6. Mean length in clusters based on grouping haddock based on data up to age 3. Numbers at the end of each curve denote proportion mature.

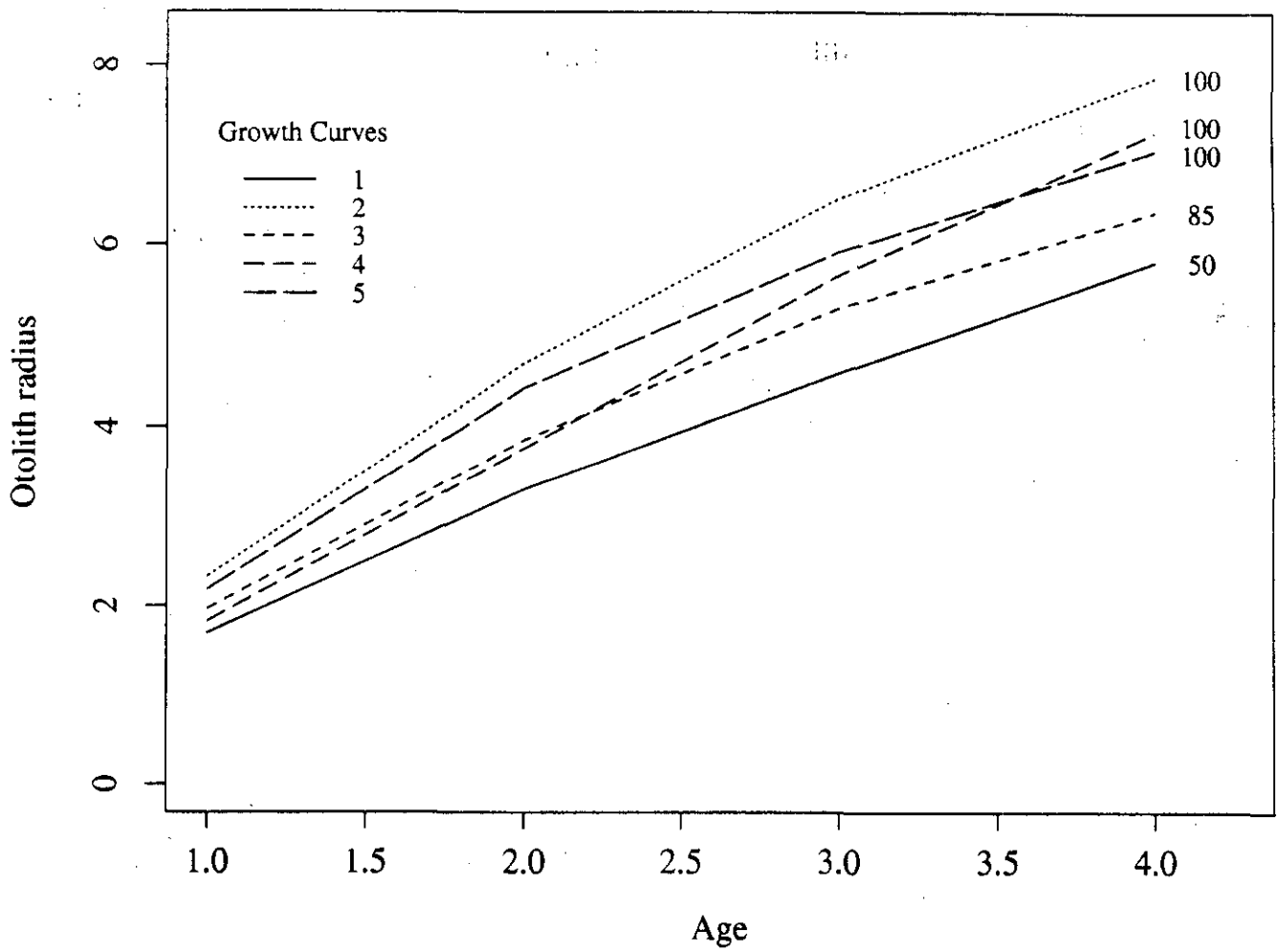


Fig. 7. Mean length in clusters based on grouping haddock based on data up to age 4. Numbers at the end of each curve denote proportion mature.

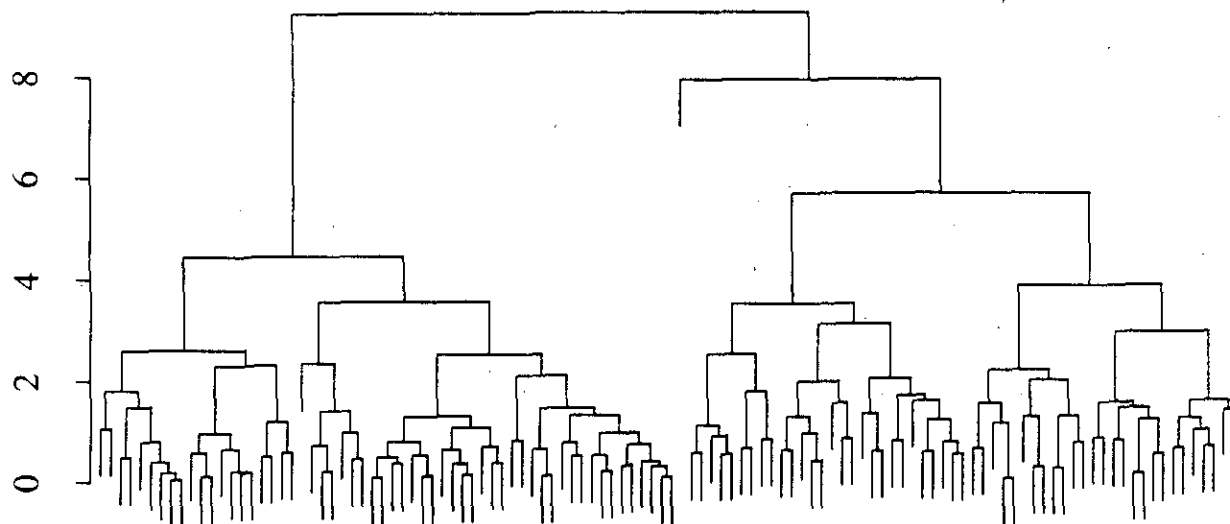


Fig. 8. Dendrogram illustrating relationship between growth curves of otolith radii using data from all available haddock.

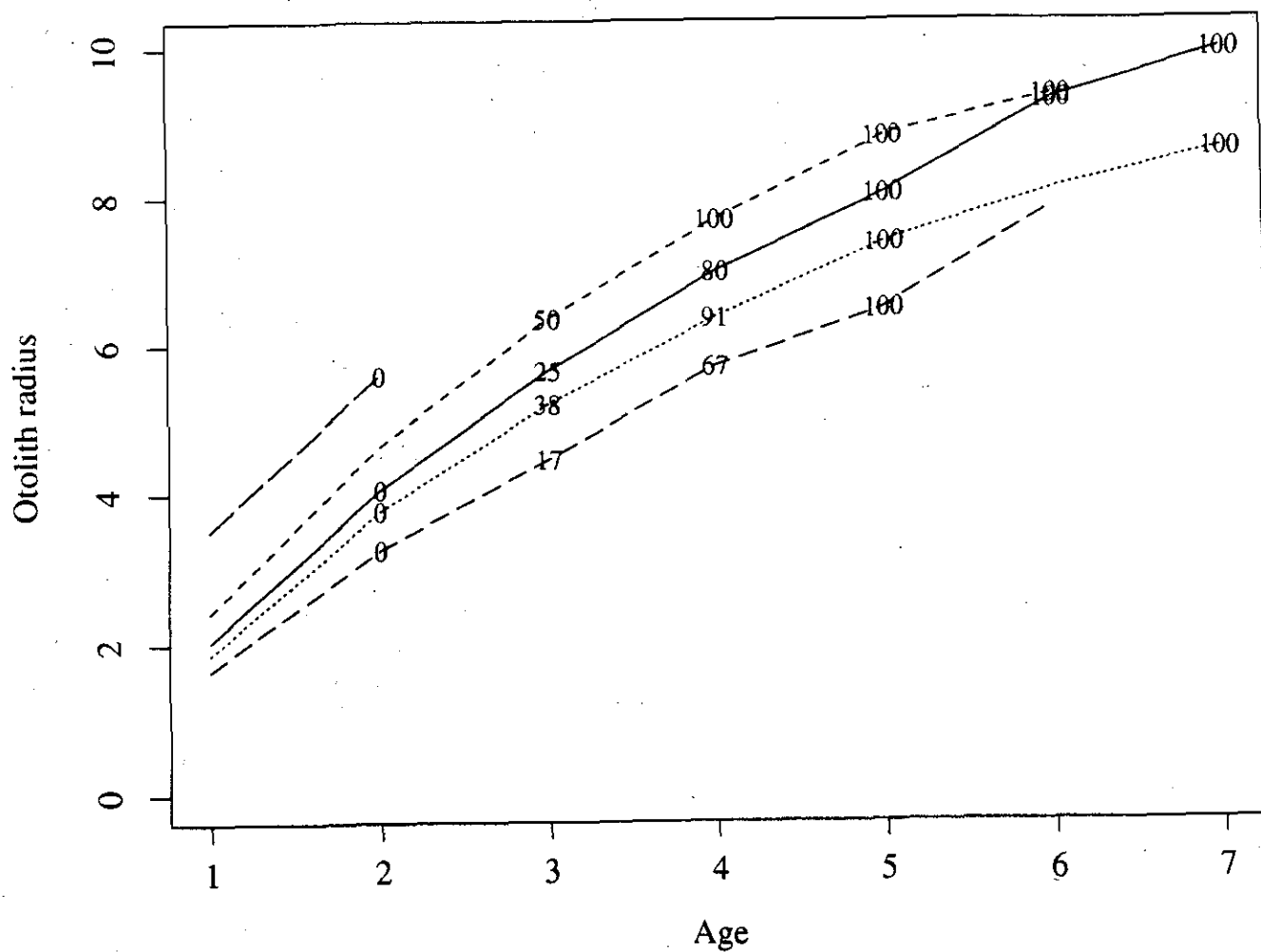


Fig. 9. Mean length in clusters based on grouping haddock based on all available data. Numbers on each curve denote proportion mature.