

*Theme Session Y*

The effects of fishing on the genetic composition of living marine resources

Maturation characteristics in Norwegian spring-spawning herring  
before, during, and after a major population collapse

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The immense Norwegian spring-spawning herring (*Clupea harengus*) population collapsed to the state of commercial extinction in the late 1960s, probably largely due to overfishing; the stock has fully recovered since the 1980s. It is known that the collapse strongly affected maturation characteristics. However, the long-term patterns of maturation in this stock have remained largely undescribed. Using discriminant analysis and artificial neural networks, the age at maturation for individual fish can be predicted from routine scale measurements. We applied these methods to historical data on herring scales available from 1935 up to the present, in order to (1) describe the long-term variability in both age and length at 50% maturity, and (2) compute new, revised maturity ogives for the stock over the same period with temporal resolution of one year. This new information, with improved temporal resolution, enables comparisons of maturation characteristics before, during, and after the population collapse. As a further step, in order to increase our understanding of the potential impact of commercial fisheries on the genetic composition of fish stocks, we aim to disentangle genetic from phenotypic aspects of maturation.

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## Introduction

The world's largest single stock of herring (*Clupea harengus*) is that of Norwegian spring-spawning herring, occurring in the Norwegian Sea and Barents Sea. Over the past centuries, this stock of very high commercial significance showed substantial fluctuations in abundance (e.g. Hjort 1914; Devold 1963; Toresen & Østvedt 2000). The most dramatic of these occurred when from abundantly high levels in the 1940s, the population declined throughout the 1950s and 1960s until it collapsed to the state of commercial extinction in the late 1960s. It remained at extremely low levels throughout the 1970s. With the remarkably strong 1983 year-class the biomass increased rapidly, and at present the stock is considered fully recovered again (Toresen & Østvedt 2000). It is now well accepted that climatic factors have a large impact on the fluctuations in abundance (Toresen & Østvedt 2000; cf. Corten 2001). However, the causes of the collapse in the 1960s have been, and still are a topic of debate. It was probably due to a combination of unfavourable climatic conditions and overfishing of both the adult and juvenile components of the stock; but to what extent these three factors contributed to it is unknown (Dragesund & Ulltang 1978; Hamre 1990; Toresen 2002).

Recently, increasing concern has been raised about the potential selective forces that commercial fisheries pose on exploited fish stocks, in particular on life-history characteristics related with maturation (Browman 2000; Law 2000; Heino & Godø 2002). Both age and size at maturation are tightly linked to lifetime fecundity of individuals (Stearns 1992; Bernardo 1993), and therefore to stock productivity; it is therefore of high importance to assess these parameters in commercially exploited fish stocks (Marshall et al. 1998; Murawski et al. 2001). As an example, size and age at maturation changed considerably over the past decades in North Sea plaice (*Pleuronectes platessa*: Rijnsdorp 1993), Northeast Arctic cod (*Gadus morhua*: Godø 2000; Heino et al. 2002), and Northwest Atlantic cod stocks (Barot et al. 2002).

For Norwegian spring-spawning herring it is known that the stock collapse strongly affected maturation characteristics (Toresen 1990). However, due to logistic restrictions (Barros & Holst 1995) the long-term patterns of maturation in this stock have remained largely undescribed, and are particularly poorly known for the most recent three decades. This paper aims at describing this missing information. We used artificial neural networks and discriminant analysis to predict age at maturation from routine scale measurements (Engelhard et al. submitted). We applied these methods to the historical data on herring scales collected by the Institute of Marine Research, Bergen, Norway, from 1935 up to the present. Based on these data the present paper (1) describes the long-term variability in maturation characteristics for the year-classes 1930-1992, and (2) examines for differences in maturation characteristics between the periods before, during, and after the collapse.

## Methods

### *Data collection*

The study is based on mature individuals of Norwegian spring-spawning herring, collected by the Institute of Marine Research between 1935 and 2000 at the spawning grounds during the months January, February and March. Samples of 100-200 herring were collected from drift-net, beach-seine, purse-seine, and trawl catches, caught by either commercial or research vessels. For each fish, standard measurements were taken including body mass, length, sex, and maturity stage. When available, up to four scales were collected from the skin just behind the operculum, along the lateral body line. Scales were mounted on microscopic glass plates coated with gelatine and thus conserved for later analysis. By

microscopic examination of the scales, the age was determined based on the total number of growth layers.

For the majority of fish collected between 1935 and 1973, experienced scale readers moreover determined the age at maturation based on observations of each of the growth layers in the scales (Lea 1928, 1929; Runnström 1936). This implied the distinction between (1) ‘coastal’ rings corresponding to the juvenile stage (rather narrow to very wide summer zones divided by either diffuse or sharp winter rings), (2) ‘oceanic’ rings corresponding with the late immature stage when the animals live in the Norwegian Sea (wide summer zones divided by diffuse winter rings), and (3) ‘spawning’ rings corresponding to years during which the herring spawned (narrow to very narrow outer summer zones divided by sharp winter rings). However, for practical reasons this direct observation of age at maturation was discontinued in 1974, to be replaced by a supposedly more objective method of scale measurement.

The new method (described by Barros & Holst 1995) involves the measurement of the total radius of the scale and of the radius of each annual growth layer up to the 9th along a line running from the focus to the edge of the scale, by means of a stereomicroscope fitted with an ocular micrometer. All scales collected since 1974 have been measured in this way; in addition, a substantial number of the old scales collected between 1935 and 1973 have recently been re-examined, and the growth layers measured exactly according to the new method.

#### *Predicting age at maturation from scale measurements*

We used two methods to predict age at maturation from these scale measurements (Engelhard et al. submitted). These were discriminant analysis (DA), a conventional statistical procedure; and the relatively new methodology of artificial neural networks (NN), trained by backpropagation (Rumelhart et al. 1986). The prediction parameters in both methods were established based on the historical collection of scales where both age at maturation had been directly observed by scale readers, and in addition, growth layers had been measured (i.e. sampled between 1935 and 1973;  $n = 45\,386$  individuals). The two classification procedures were then applied to predict age at maturation for all individuals where scale growth layers have been measured (i.e. the complete time series from 1935 to 2000;  $n = 116\,479$  individuals). The use of both methods to classify age at maturation from such routine measurements in the herring scale was described and evaluated in a companion paper (Engelhard et al. submitted). Age at maturation, which may vary from 3 to 9 years in Norwegian spring-spawning herring, was predicted at the exact, correct value (as observed by scale readers) in 68.0% and 66.6% of cases using DA or NN, respectively. Prediction errors were more than 1 year in only 5.2% of cases (DA) or 2.9% of cases (NN). Moreover, prediction errors were highly symmetric around the observed values for age at maturation, resulting in very little under- or overestimation; overall, age at maturation may have been marginally underestimated using DA (1.1% of mean age at maturation) or marginally overestimated using NN (0.2% of mean age at maturation).

#### *Maturity ogives*

Maturity ogives, describing the proportions of individuals mature at a given age, were derived based on the entire sample of herring individuals where age at maturation had been predicted from scale measurements using either DA or NN analysis. Again, two alternative approaches were used (see below); this paper therefore gives a fourfold presentation of the maturity ogives.

First, we applied Gulland’s (1964) method, which allows the estimation of ogives if only data on mature fish are available, and is based on the relative abundances of recruit spawners and repeat spawners of given ages in the adult population. The iterative procedure is started in the year during which the last fish of a year-class considered have reached maturity, i.e. when no immature fish are left (which

is usually at the age of 9 in the study population). The immature part of that year-class in the previous year therefore consisted of fish that would all mature one year later, and is thus equal to the proportion of recruit spawners among the combined sample of recruit and repeat spawners one year later. Going backwards in time, the proportions of immature fish can thus be back-projected for all previous ages relevant for maturation (ages of 3 to 8 years for most year-classes of Norwegian spring-spawning herring). One important assumption in Gulland's (1964) method is, that annual survival is equal for immature and mature fish of a given age. However, it is likely that this assumption was to some extent violated in the study population, since the majority of Norwegian spring-spawning herring fisheries has traditionally targeted the spawning (adult) stock. Higher mortality in mature when compared to immature herring results in under-representation of early-maturing individuals among repeat spawners at higher ages, and therefore, in an underestimation of maturity for low ages.

Second, we used a direct method to derive the proportions mature-at-age, by computing which proportions of all sampled individuals known to be alive at a given age relevant for maturation, were either immature or mature (based on age at maturation predicted using either DA or NN). This method assumes that individuals maturing at either early or late ages have equal probabilities of being represented in the data. However, as the sampling typically occurred at the spawning areas, early-maturing individuals were probably more likely to be represented in our sample than late-maturing fish, and therefore might be over-represented. This violation in the second method could have resulted in an overestimation of maturity for low ages.

As Gulland's method and the direct method as applied here would lead to biases in ogives that are in opposite directions, it is likely that the true maturity ogives are intermediate between those presented here.

#### *Age at 50% maturity*

Based on the maturity ogives computed according to the four methods as described above, the age at 50% maturity (A50) was computed using logistic regressions of maturity stage (0 immature, 1 mature) with age, for each of the examined year-classes separately.

#### *Length at 50% maturity*

As the data only included mature herring individuals, length frequency distributions of both mature and immature individuals were reconstructed by back-calculations, based on length at catch ( $L_c$ ), total scale radius ( $S_c$ ), and the radius of the scale at age  $i$  ( $S_i$ ). We used the following formula to back-calculate length  $L_i$  at the earlier age  $i$  (proportional length back-calculation, equation [10] as recommended by Francis 1990; modified from Hile 1941):

$$L_i = \frac{a}{b} + (L_c + \frac{a}{b}) (S_i / S_c)$$

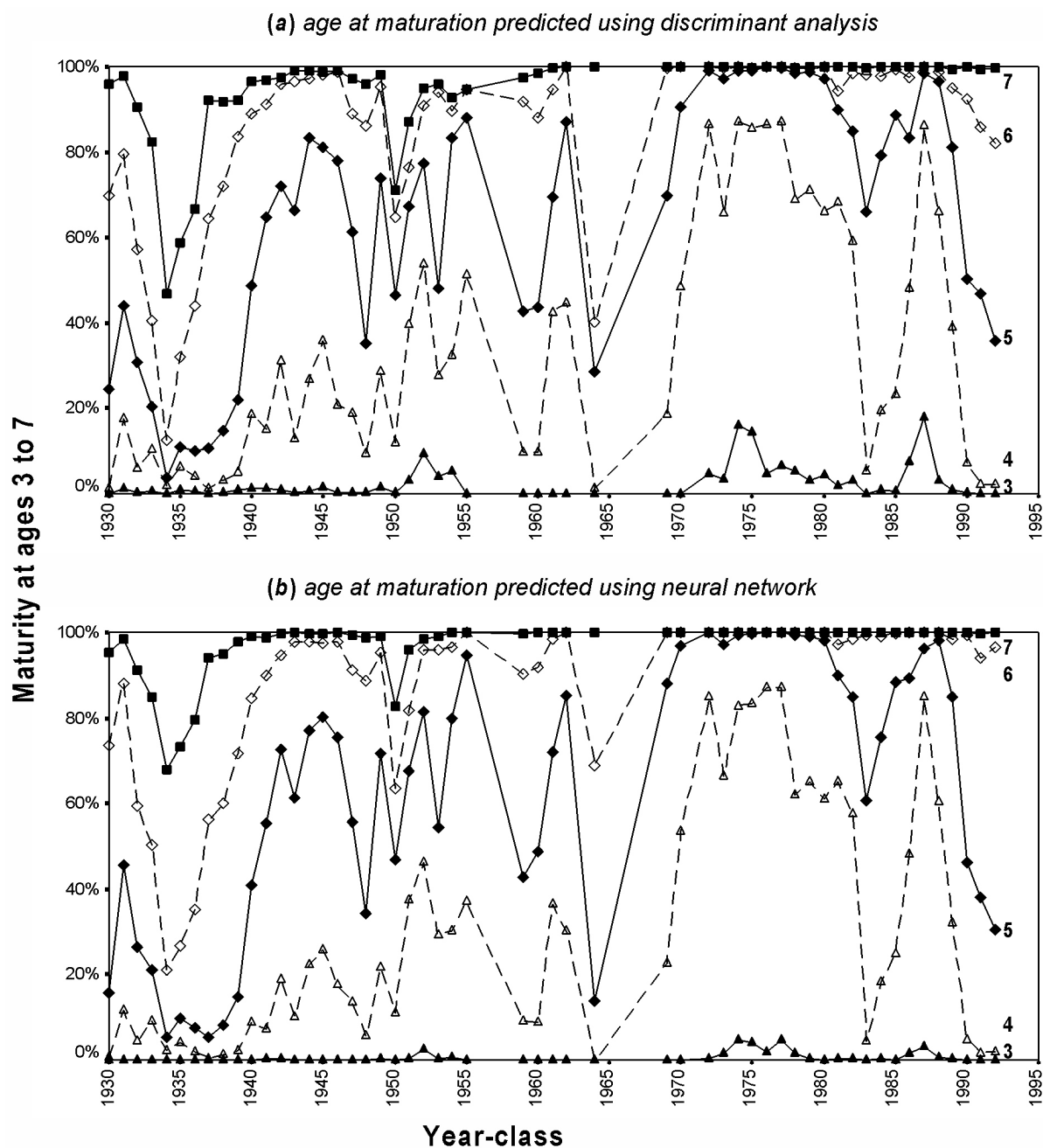
where  $a$  and  $b$  are the intercept and regression coefficient, respectively, of the linear regression of total scale radius on body length ( $a = 0.949$ ,  $b = 0.209$ ).

Length frequency distributions were thus computed for immatures and matures (maturity stage of individuals at a given age based on age at maturation as predicted using either DA or NN). By means of logistic regressions of maturity stage with length, the length at 50% maturity (L50) was then estimated for each of the considered year-classes separately.

The statistical analyses were carried out using the SPSS 10.0.7 package (SPSS Inc., 1989-1999).

## Results

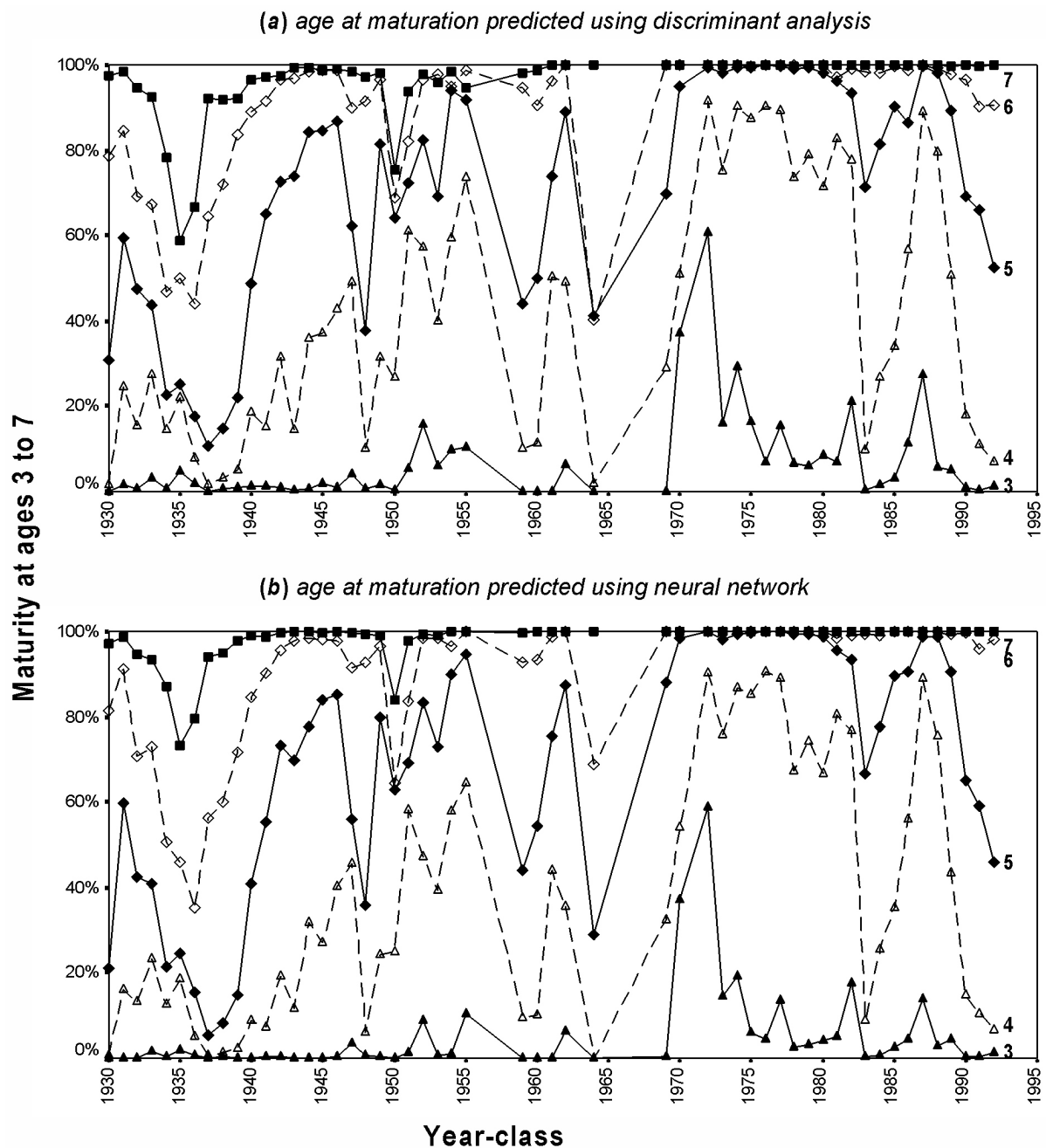
Maturity ogives, lengths and ages at 50% maturity were computed for 54 year-classes (1930-1955, 1959-1962, 1964, 1969-1970, and 1972-1992). The sample sizes for these year-classes averaged 2009 individuals (median 973, range 63 to 14 635 individuals). Sample sizes for the remaining nine year-classes (1956-1958, 1963, 1965-1968, and 1971) were either very low, incomplete, or limited to very few ages (average 69, median 40, range 12 to 210 individuals); these year-classes were omitted from the analyses of maturation characteristics.



**Figure 1 a,b** The proportions of individuals mature at ages 3 to 7 for the year-classes 1930-1992, as computed using Gulland's (1964) method and based on predictions of age at maturation made using discriminant analysis (*upper graph*) or neural network analysis (*lower graph*). The ages 3 to 7 are represented, respectively, by filled and unfilled triangles, filled and unfilled diamonds, and filled squares (see also numbers at right-hand side of graph).

*Comparison between methods*

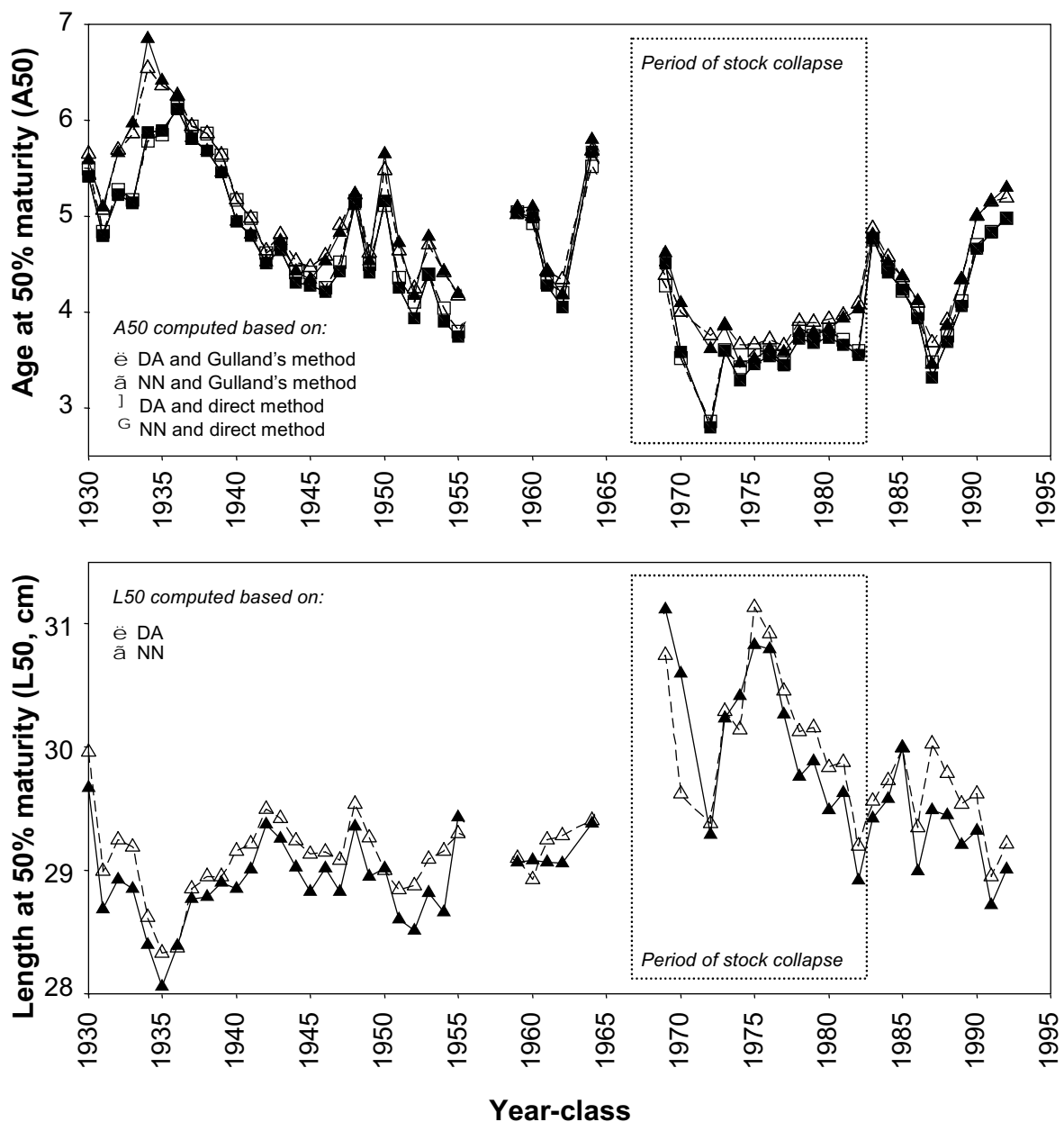
If age at maturation was predicted from scale measurements using either discriminant analysis (DA) or neural network analysis (NN), then this resulted in marginally different estimations of maturity ogives (compare Figure 1a with 1b, and compare Figure 2a with 2b), ages at 50% maturity ( $A_{50}$ , Figure 3a), and lengths at 50% maturity ( $L_{50}$ , Figure 3b). In particular, the use of DA resulted in slightly lower estimates of  $L_{50}$  than in the case of NN (Figure 3b; mean difference 0.17 cm). Otherwise, the use of either DA or NN did not appear to result in any considerable biases in estimates of life-history characteristics.



**Figure 2 a,b** The proportions of individuals mature at ages 3 to 7 for the year-classes 1930-1992, as computed using the direct method and based on predictions of age at maturation made using discriminant analysis (*upper graph*) or neural network analysis (*lower graph*). The ages 3 to 7 are represented, respectively, by filled and unfilled triangles, filled and unfilled diamonds, and filled squares (see also numbers at right-hand side of graph).

The use of either Gulland's (1964) or the direct method (see Methods section) did result in larger, albeit still reasonably small differences in estimates of maturity ogives (compare Figure 1a with 2a, and compare Figure 1b with 2b). For the higher maturation ages (5 to 9 years), there was high similarity in the proportions of mature fish as computed using these two methods. For the lower maturation ages (3 and 4 years), Gulland's method (Figure 1a,b) generally indicated relatively smaller proportions of mature individuals than the direct method did (Figure 2a,b). This resulted in estimations of age at 50% maturity (A50) that were generally higher if Gulland's method was used in comparison to the values computed using the direct method (Figure 3a).

In Figure 4 we illustrate these methodological differences by comparing values of A50 for 54 year-classes, as computed using either of these four methods. While Gulland's method resulted in higher values than the direct method did (upper two graphs), there were only very small differences in the values computed using either DA or NN (lower two graphs).



**Figure 3 a** (upper graph) Time-series on age at 50% maturity (A50) for the year-classes 1930-1992, as computed using four alternative methods (i.e. combinations of either discriminant (DA) or neural network analysis (NN), and either Gulland's or the direct method; see Methods section). **Figure 3 b** (lower graph) Time-series on length at 50% maturity (L50) for the same year-classes, as computed based on predictions of age at maturation using either DA or NN. Period of stock collapse indicated in both graphs.

**Table 1** Maturation characteristics (means  $\pm$  SD; based on values computed per year-class) in periods before, during, and after the stock collapse. Parameters include A50 computed using either of four methods, and L50 computed using either of two methods (see Methods section). We used analysis of variance to examine for overall differences in maturation characteristics between the three periods, and post-hoc comparisons with Bonferroni adjustment to examine for differences between pairs of periods (*b*, *d* and *a* refer to periods before, during and after the collapse, respectively; symbols < and > refer to directions of differences significant at  $P < 0.05$  level).

	Before <i>n</i> = 31	During <i>n</i> = 13	After <i>n</i> = 10	ANOVA <i>P</i>	Post-hoc comparisons
<i>Year-classes</i>	1930-55, 1959-62, 1964	1969-70, 1972-82	1983-92		
<i>A50, computed using:</i>					
DA and Gulland's method	5.10 $\pm$ 0.71	3.83 $\pm$ 0.31	4.49 $\pm$ 0.59	< 0.0001	<i>b</i> > <i>d</i> , <i>d</i> < <i>a</i> , <i>b</i> > <i>a</i>
NN and Gulland's method	5.13 $\pm$ 0.67	3.88 $\pm$ 0.21	4.52 $\pm$ 0.53	< 0.0001	<i>b</i> > <i>d</i> , <i>d</i> < <i>a</i> , <i>b</i> > <i>a</i>
DA and direct method	4.86 $\pm$ 0.66	3.58 $\pm$ 0.37	4.29 $\pm$ 0.54	< 0.0001	<i>b</i> > <i>d</i> , <i>d</i> < <i>a</i> , <i>b</i> > <i>a</i>
NN and direct method	4.92 $\pm$ 0.64	3.62 $\pm$ 0.32	4.33 $\pm$ 0.50	< 0.0001	<i>b</i> > <i>d</i> , <i>d</i> < <i>a</i> , <i>b</i> > <i>a</i>
<i>L50, computed using:</i>					
DA	28.9 $\pm$ 0.3	30.1 $\pm$ 0.7	29.3 $\pm$ 0.4	< 0.0001	<i>b</i> < <i>d</i> , <i>d</i> > <i>a</i> , <i>b</i> < <i>a</i>
NN	29.1 $\pm$ 0.3	30.1 $\pm$ 0.6	29.6 $\pm$ 0.3	< 0.0001	<i>b</i> < <i>d</i> , <i>d</i> > <i>a</i> , <i>b</i> < <i>a</i>

### *Maturity ogives*

The maturity ogives, as computed using these four methods, showed the same long-term patterns (see Figures 1*a,b*, 2*a,b*). For year-classes representing the 1930s to early 1960s, maturity occurred at high ages (and at particularly high ages in year-classes of the mid-1930s). The majority of fish (>75%) did not recruit to the spawning stock before reaching the age of 5, 6 or (mid-1930s) 7. By contrast, in the period of collapse (year-classes 1969 to 1982) maturity occurred at considerably earlier ages, and the majority of fish (>75%) had already recruited to the spawning stock by the age of 4. While previously only very few fish matured already at the age of 3, maturation at this early age was comparatively common in the period of collapse (note however the difference between Gulland's and the direct method; compare Figures 1*a,b* vs. 2*a,b*).

The strong 1983 year-class, which contributed most significantly to the stock's recovery, again showed slow maturation, and the majority of this year-class matured at the age of 5. Maturity-at-age in more recent year-classes has been variable, in some resembling the collapse period (1987 year-class in particular) and in others resembling the pre-collapse period (1992 year-class in particular).

### *Age at 50% maturity*

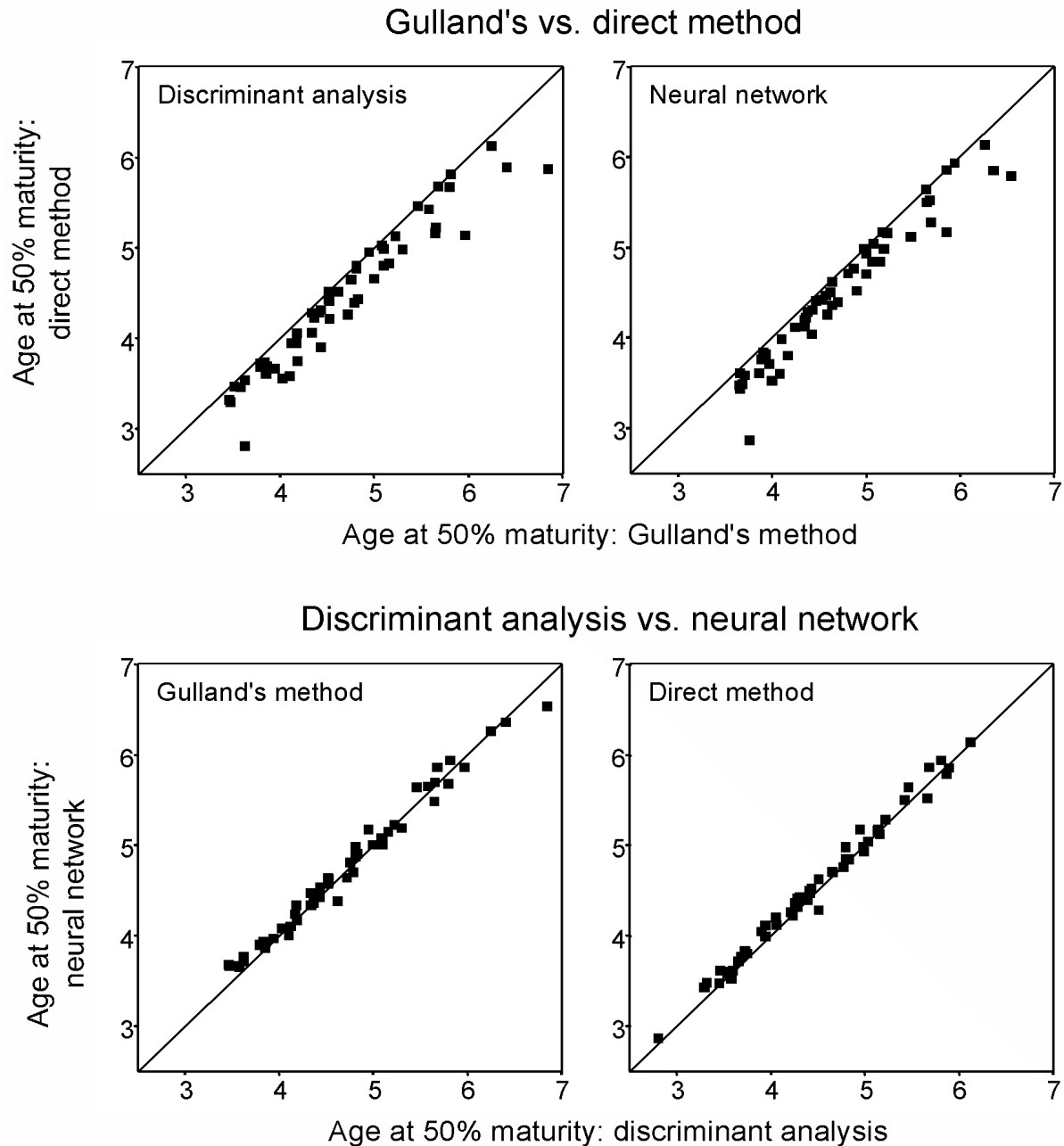
Figure 3*a* shows the time-series of the age at 50% maturity (A50) for year-classes from 1930 to 1992, as computed by means of either Gulland's or the direct method, and based on predictions of age at maturation using either DA or NN. Although the values computed using Gulland's method are generally higher than those computed using the direct method (see above), the results show the same decreasing trend from the 1930s (about 5 or 6 years) to the period of stock collapse (about 4 years), and in the post-collapse period rather irregular but again generally higher A50 values.

An analysis of variance (Table 1) shows that A50 values, computed using either of the four methods, are significantly different between year-classes representing the periods before, during and after the collapse ( $P < 0.0001$ ), and post hoc comparisons show that while values were lowest in the collapse period, present values are still significantly lower than those of the pre-collapse period (Table 1).



### Length at 50% maturity

The length at 50% maturity (L50) for the same year-classes, as based on either DA or NN analysis, is illustrated in Figure 3b. The time-series mirrors that of the age at 50% maturity, and shows that the year-classes 1969-1982 representing the period of stock collapse, on average matured at higher lengths (~30 cm) than earlier or later year-classes did (~29 cm). Although the overall differences between year-classes in L50 were relatively small (few cm), there were nevertheless significant differences in L50 values between year-classes before, during and after the collapse period (Table 1:  $P < 0.0001$ ). Current values are intermediate between those of the collapse and pre-collapse periods.



**Figure 4** Comparisons of values for age at 50% maturity (A50) as computed using four alternative combinations of methods (see Methods section). *Upper graphs*: A50 results based on Gulland's (1964) method and the direct method compared, if age at maturation is predicted using either discriminant (*top left*) or neural network analysis (*top right*). *Lower graphs*: A50 results based on discriminant and neural network analyses compared, if computed using either Gulland's method (*bottom left*) or the direct method (*bottom right*).

## Discussion

To our knowledge, this is the first paper to show maturity ogives for Norwegian spring-spawning herring with a temporal resolution of 1 year encompassing periods well before, during, and after the stock collapse. There is, however, information available on ogives with lower temporal resolution (e.g. Toresen & Østvedt 2000; ICES 2001); moreover, maturity ogives with a temporal resolution of 1 year but restricted to year-classes before the collapse (i.e., 1928-1964 year-classes) are currently being published (Toresen & Østvedt in press). In the light of the relatively limited information already available, the values presented here may serve to the understanding of changes in stock properties that may have occurred since, or have resulted from, the stock collapse.

There are wide differences in the distribution of early immature, late immature, and mature individuals of Norwegian spring-spawning herring in the Norwegian Sea and Barents Sea. Due to this spatio-temporal segregation it is difficult to establish maturity ogives directly based on the sampling of immature and mature fish, as observed proportions are unlikely to reflect the true proportions in the population. It is possible to establish maturity ogives based solely on information of adult individuals (e.g. Gulland 1964; Jørgensen 1990), and this is greatly facilitated if data on the age at maturation for large numbers of individual fish are available. Such knowledge has now become available with the application of the two methods (discriminant and neural network analysis) to classify age at maturation based on routine measurements of growth layers in herring scales (Engelhard et al. submitted).

However, the maturity ogives reported here based entirely on individuals caught as matures, will only be unbiased if there are no marked differences in annual survival between herring individuals that were either immature or mature at a given age. It is likely that this is, and usually has not been the case in the study population. The most important commercial fishery on this stock has traditionally occurred at the spawning areas, targeting the adult component. There have in addition been periods during which fisheries on juvenile herring, of various intensities, took place (small herring and fat herring fisheries, before 1971) but these mainly targeted very young fish of ages 0-3 years, below most ages relevant for maturation (Dragesund & Ulltang 1978). This implies that among individuals of any age relevant for maturation (perhaps except age 3 in some periods), mature fish probably typically suffer greater mortality than immatures, violating the assumptions required for both Gulland's (1964) method and the direct method (see Methods) as used here to compute the maturity ogives. However, we expect the biases in the ogives as obtained by both methods, to be in opposite directions, and the "true" ogives to be intermediate between those presented here in fourfold.

The key result of this study is that it confirms the strong change in maturation characteristics when the stock collapsed, as discussed previously (e.g. Toresen 1990); it shows that during the period of collapse fish matured at earlier ages (in particular at ages 3-4 rather than 5-7), that the age at 50% maturity was considerably lower and the length at 50% maturity somewhat higher than previously. It moreover shows that maturation characteristics in the current, post-collapse period are intermediate between those of the collapse and pre-collapse periods (see also Dragesund et al. 1997 on changes in biological properties in the stock). The most recent trend seen throughout the year-classes 1987-1992 gives an indication that maturation characteristics in the stock might be returning to those typical for the pre-collapse period; future analysis including the most recent year-classes (currently recruiting to the spawning stock) may either confirm or refute this tendency.

The stock collapse must have caused a relaxation of density-dependent effects, including reduced competition with conspecifics resulting in higher growth rates and condition factors (see Iles 1967; Hubold 1978; Holst 1996; and Shin & Rochet 1998 on density-dependent growth in juvenile herring); these effects were undoubtedly a main factor in the changes in maturation properties as reported here. Moreover, in the period of collapse the stock was virtually absent from the northern half of its former range (Dragesund et al. 1997; Holst & Slotte 1998). Even though the collapse coincided with a period of generally lower

temperatures (Toresen & Østvedt 2000), this more southerly distribution implied on average warmer conditions experienced by juveniles, and therefore faster growth rates and earlier maturation (Runnström 1936).

One important question now is (cf. Law 2000; Browman 2000), can the observed changes in maturation characteristics be entirely attributed to phenotypically plastic responses of the fish to changes in their biotic and physical environment? Or are these in addition due to changes in the genetic composition of the stock, resulting from the selection pressures posed on the stock by fisheries, in particular during the periods of over-exploitation? The disentanglement between the environmental influences (via phenotypic plasticity) on maturation characteristics and the potential fisheries-induced genetic change in the same key life-history parameters, comprises the next challenge.

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