Assessment of golden redfish (*Sebastes marinus* L) in Icelandic waters*

HÖSKULDUR BJÖRNSSON and THORSTEINN SIGURDSSON

Marine Research Institute, 101 Reykjavik, Iceland. E-mail: hoski@hafro.is

SUMMARY: Assessment of redfish has traditionally suffered from the inability to age the fish. For golden redfish in Icelandic waters, length distributions and abundance indices are available both from commercial catch and from surveys, particularly a groundfish survey in March. This paper addresses the use of an age- and length-based cohort model for the assessment of redfish, where all selection curves depend on the length of the fish and information on age is not a prerequisite but can be utilised if available. In the last few years it appears that ageing of this species has been successful and in this paper we compare assessment results of a model that incorporates age information with those that do not. Finally, we calculate yield per recruit, $F_{\text{max}}$ and $F_{11}$, for the stock. Stock size, catch and fishing mortality are then simulated 10 years ahead using different catch control laws.

Key words: assessment, redfish, length-based methods, population models.

INTRODUCTION

The genus *Sebastes* is very common and widely distributed in the North Atlantic. It is found off the coast of Britain, along the Norwegian coast, in the Barents Sea and Spitzergen, off the Faroe Island, off Iceland, off East and West Greenland, and along the east coast of North America from Baffin Island south to Cape Cod (Magnússon and Magnússon, 1995).

Of the three exploited species in the North Atlantic, golden redfish (*Sebastes marinus*) has the longest history of exploitation. Golden redfish in Icelandic waters is considered to belong to the same stock as that from East Greenland and the Faroe Islands (ICES, 1983). In the twenties, substantial redfish fishery started in the North Atlantic and golden redfish has been caught in the Greenland-Iceland-Faroe area since around 1930 (Magnússon, 1956). Before World War II, the redfish catch peaked at 105 thousand tonnes in 1938, where 65 thousand tonnes came from the E. Greenland-Iceland-Faroe Islands area (EGIF). After the war, the catches increased again, exceeding 230 thousand tonnes in 1955, of which about 75% was taken from the EGIF stocks. Since then, the total catch taken from the stocks has decreased, and was 77 thousand tonnes in 1999 (Fig. 1).

Reliable information on the species composition of the redfish catches is limited prior to 1965, but there are indications that the majority of the redfish caught in that period originated from *S. marinus*. The total estimated catch from the EGIF *S. marinus* stock in different ICES areas varies (Fig. 2), the catch prior to 1965 being estimated by assuming that catch composition from a given fishing area, fishing

*Received October 9, 2000. Accepted March 21, 2002.*
depth and fishing nation remained the same as it was in the period from 1965–1975 when data are available on the catch composition.

During the last few decades the most important fishing grounds for *S. marinus* have been off South-west and west Iceland. Another important fishing area is the “Rosengarten”, between Iceland and the Faroe Islands, where the fishery extends to the shelf of the Faroe Islands. The catches in these areas have, however, declined in recent years (ICES, 2000).

Off East Greenland, catches have declined drastically during the last few decades. The average annual catch in the nineties was below 1000 tonnes, compared to 60 thousands tonnes in 1976 and 15 to 31 thousands tonnes during the period 1978 to 1983 (Fig. 2). Surveys in Greenland waters show negligible abundance of both juvenile and adult *S. marinus* in recent years, confirming the poor state of *S. marinus* in this area (ICES, 2000).

Assessing this stock has been problematic for a number of reasons. The species is long-lived, and ageing it has been difficult. Moreover, as mentioned above, the catch of *S. marinus* and *S. mentella* has historically been mixed together. In spite of this, ICES assessment on this stock was at times age-based (VPA; ICES, 1992), but such methods were later abandoned, because the age determinations were inconsistent with information on recruitment variability seen in the length distributions from surveys (ICES, 1995). In recent years, age-based methods have therefore been replaced by CPUE-based methods but also with methods using various available data (ICES, 1995). The type of data needed to apply to these “age-based” models can vary, but a catch history and some time series of abundance indices is always needed. Catch in number-at-age is usually not required for these methods, although some recent implementations of these techniques...
are starting to incorporate such information. Stefánsson and Sigurðsson (1997) presented one such model on golden redfish, utilising survey indices and length distributions from survey and commercial catch, as well as available age recordings.

In the North Western Working group of ICES, which deals with this *S. marinus* stock, a stock production model was applied to the stock in 2001 (ICES, 2001). The model, called ASPIC (Prager, 1994; Prager, 2000), fits a non-equilibrium logistic (Schaefer) production model to catch and effort data. Testing of the model with several different settings of input parameters did not give any solutions considered to be sensible (ICES, 2001).

In the last two assessments of this stock the so-called BORMICON model (BORreal MIgration and CONsumption model) has been used (ICES, 2000; Anon, 2001) and is introduced in this paper.

**AVAILABLE DATA**

**Landings data**

Prior to 1965, the data on landings were based on various assumptions (see introduction), while from 1965 the data originate from ICES.

**CPUE and biological samples from the catch**

Length measurements from the commercial catch are available back to the seventies. In recent years length determinations have been completed by inspectors aboard fishing vessels as well as from landings. Length distributions indicate that the selection curve of the commercial fleet rises from 0 to 1 between 30 and 35 cm (Fig. 3). In recent years discard of redfish around 30 cm has been of concern.

Otoliths from commercial catch have been sampled routinely since 1995 (see below).

Since 1991 all Icelandic trawlers have been required to return logbooks, where among other data they register location, duration and the catch composition for each tow. Before this regulation, approximately 50% of the trawlers returned these logbooks. These data are used to calculate CPUE indices as well as the spatial distribution of the commercial catch. Figure 4 shows CPUE estimated from all tows where golden redfish accounted for more than 10% of the total catch.

**Annual groundfish survey in March**

The Icelandic groundfish survey (Pálsson *et al.*, 1989), commenced in 1985 and has been executed annually in March since then. The survey covers Icelandic water shallower than 500 m, and was designed with special emphasis on cod and haddock, so important distribution areas of stocks may not be adequately covered. However, the survey seems to reflect the status of many other stocks, and abundance indices from the survey are the most impor-
tant source of data for assessment of these stocks, including golden redfish. Abundance indices from the survey are calculated as stratified means, corrected with the ratio between the survey area and the area towed in the survey (ICES, 2001).

Length distributions from the survey indicate that golden redfish recruitment is highly variable, the recruits being mainly in the northern area. (Figs. 5 and 6). A large yearclass is seen as a clear, consistent peak in the length distributions. The peaks in the length distributions seem to indicate relatively strong 1985 and 1990 yearclasses, first noticed as 1 year old and then clearly in several subsequent years. However, between these abundant yearclasses there appear to be years with almost no recruitment. The survey also indicates a slow growth rate for this redfish species, or approximately 2-2.5 cm per year in the first years. It also shows that annual growth from 0-group to 2 years old is variable, where the difference in average length at age 2 for the 1985 and 1990 yearclasses is 1 cm.

Abundance of golden redfish in the groundfish survey decreased constantly from 1985 to 1994 but since then it has been gradually increasing. (Fig. 7).

**Annual groundfish survey in October**

The autumn survey began in 1996. The survey stretches out to deeper water than the March survey or to approximately 1500 m versus 500 m respectively. However, since golden redfish is not common below 500 m, the October survey is comparable to the March survey regarding golden redfish and is considered to be an important additional source of information.

Indices obtained in the autumn survey indicate a continuous increase in the stock size from 1996 to 1999 (Fig. 7).

**Annual deep water shrimp survey**

A survey for the deep water shrimp stock has been carried out in July to August annually since
1987. The survey area covers most of the area between 200 and 600 m depth from north-west to east Iceland. In some years, fairly large numbers of small golden redfish have been caught in this survey. The length distributions indicate that the same large yearclasses as seen in the groundfish survey (1985 and 1990) are also dominant in the shrimp survey.

Bycatch of small redfish by the shrimp fleet has been of concern, but in the last few years the fleet has been required to use grids that allow fish to escape and thus reduce the bycatch.

0-group survey

This survey has been carried out annually in August since 1970, but its coverage was reduced in 1996, limiting the survey area only to Icelandic waters. The survey is described in Vilhjálmssson and Friðgeirsson (1976). A major problem in getting abundance indices for golden redfish from this particular survey is the difficulty involved in distinguishing golden redfish from deep water redfish. Therefore, the obtained index consists of a mixture
of two species in which it is difficult to verify to what extent it represent the number of 0-group golden redfish.

**Age readings**

As mentioned earlier, age readings of redfish have been considered unreliable (ICES, 1996) and age-based assessment methods have therefore been discarded for assessment of the EGIF golden redfish stock (ICES, 1992b). The strong 1985-yearclass, first seen in the spring survey in 1986 with a modal length of about 7.5 cm, made further investigation of growth and ageing methods possible. Length distributions from the March survey indicate that adjacent yearclasses are much smaller than the 1985 yearclass, giving a possibility to follow the 1985 yearclass closely. In 1995 a systematic sampling programme for golden redfish otoliths was started, both from the commercial catch and the surveys. Different age reading methods were tested and the results from the Icelandic age reader were compared to ageing made by Norwegian age readers. Based on this comparison between readers and a protocol in which the same reader repeatedly read the same otoliths, the most consistent age reading method was to “break and burn” the otoliths before counting the annual rings. When reading the age, the reader knew the fish length but not the sampling year.

In conjunction with length distributions from commercial catches, available age recordings have been used to calculate annual catch in numbers by age (Figure 8). As expected, the 1985 yearclass has been dominating in the catches during the last few years and in 1999 the 1985 yearclass accounted for almost 42% of the total catch in ICES Division Va. The results of the age recordings confirm the survey finding that the recruitment of the stock is highly variable.

Annual catch in number-at-age from 1995 to 2000 is plotted on a logarithmic scale in Figure 9. The ageing data for each yearclass cannot be used to determine the total mortality (Z) as there are only a few years with data available for each yearclass and relatively few otoliths have been read for the older age groups, which are fully recruited to the fishable stock. Therefore, total mortality was estimated using the following model:

\[ N_{age,year} = \alpha_{yearclass} e^{-Z_{age}} \text{ or } \log(N_{age,year}) = \beta_{yearclass} Z_{age} \]

This model estimates the total mortality (Z), if applied to fully recruited fish during years with reasonably stable effort. The parameters \( \beta_{yearclass} \) are needed to correct for variability in yearclass strength but the parameter Z which is common for all yearclasses and age groups is the parameter of interest. The model fitted belongs to the Poisson family of GLM models using the log link function (McCullagh and Nelder 1989). The Poisson model is considered appropriate since an insufficient number of otoliths is an important source of error for the older age groups.

The estimated value of Z was 0.24 for the age range 15 to 30 years but 0.18 for the age range 20 to 30 years. This is contrary to expectations, as the total mortality calculated in this way would be expected to decrease when younger age groups are included.
DESCRIPTION OF THE BORMICON MODEL

The BORMICON model is a simulation model developed at the MRI Iceland, described in Stefánsson and Pálsson (1997), Stefánsson (1998), Anon. (1997) and Björnsson (1998). The model is designed as multispecies-multiarea model but can also be used as a single species model. In recent years development of the model has also taken place in Norway (Froysa et.al., 2002) and currently the model is being developed under a grant from the EU (Anon., 2001b).

The characteristics that distinguish the model from most stock assessment models is that both age and length are modelled, which requires modelling of the fish growth. This is done by calculating the mean growth for each length group, using a parametric growth equation and then updating the length distributions according to the calculated mean growth, by allowing a certain proportion of the fish to have no growth, a proportion to grow one length group, a proportion two length groups, etc. How these proportions are selected affects the spread of the length distributions but the following two equations must always be satisfied:

\[ \sum p_{il} = 1, \quad \text{and} \quad \sum i p_{il} = \mu_l \]

Here \( \mu \) is the calculated mean growth and \( p_{il} \) is the proportion of fishes in length group \( l \) growing \( i \) length groups.

The proportions are selected from a beta-binomial distribution, i.e. a binomial distribution \( f(n,p) \) where \( n \) is the maximum number of length groups that a fish can grow in one time interval and the probability \( p \) comes from a beta distribution, described by parameters \( \alpha \) and \( \beta \) (Stefánsson, 2001). As in all discrete probability distributions the condition \( \sum p_i = 1 \) is automatically satisfied. The mean of this distribution is given by

\[ \mu_l = \frac{n\alpha}{\alpha + \beta} = \sum_{i=0}^{n} p_{il} \]

For a given value of the parameter \( \beta \) the parameter \( \alpha \) is selected, so \( \mu_l = G_l \) where \( G_l \) is the mean growth as calculated by the parametric growth equation. The parameter \( \beta \), which can be estimated or specified in the input files, affects the spread of the length distribution.

All fleets (predators) in the model have size-based preference for their preys and can affect mean weight and length at age of the population if the difference in preference is large within age groups. A fleet is modelled so that either the total catch or the total effort in each area and time interval is specified. In the redfish assessment described in next section, the amount caught by the commercial fleet is specified but the survey is modelled as a fleet with a constant effort.

The first step in the calculations of catch in numbers by age and length is to calculate the “modelled CPUE” for each fleet:

\[ \text{Fig. 9. – Ln of catch at age for golden redfish in ICES division Va. The yearclasses are indicated on the figure.} \]
where $S_{\text{prey},l}$ is the selection of prey of length $l$, $N_{\text{prey},l}$ number of and $W_{\text{prey},l}$ mean weight of prey of length $l$. The total catch of each length group of each prey is then calculated from

$$C_{\text{prey},l} = \frac{S_{\text{prey},l}N_{\text{prey},l}W_{\text{prey},l}}{CPUE_{\text{mod}}}$$

where $C_{\text{prey},l}$ is the amount caught by the fleet of lengthgroup $l$ of prey and $C$ is the total amount caught by the fleet, either specified or calculated from $C = E \cdot CPUE_{\text{mod}}$, where $E$ is the specified effort.

The model does not use catch in number directly as input data, but instead length distributions, age samples and other data used to calculate catch in numbers. An objective function that is a measure of the discrepancy between model and data is calculated and minimised by changing selected parameters in the model.

Various types of data can be used in the objective function, for example length distributions, age-length keys, survey indices by length or age, CPUE data, mean length and/or weight at age and stomach content data. The model can be used in situations where data are not sampled regularly enough to calculate annual catch in numbers by age, or where age readings are not considered reliable.

The model has two alternative optimising algorithms linked to it, simulated annealing (Corona et al., 1987) and the algorithm of Hooke and Jeeves (1961). Simulated annealing is more robust and can find the global optimum where there are multiple optima, but the number of iterations needed is 2-3 orders of magnitude larger than when the Hooke and Jeeves algorithm is used. Neither of the algorithms returns estimates of the Hessian matrix but work is ongoing to link a quasi-Newton optimising algorithms to the model, as well as an optimising algorithm that starts with simulated annealing but converts to Hooke and Jeeves, and then a quasi-Newton algorithm when the optimum is approached. (Anon., 2001b).

DESCRIPTION OF REDFISH ASSESSMENT

Golden redfish is a slow-growing, long-lived species, so many years (20 to 30) pass from the time when a yearclass is born until it has mostly disappeared from the catch. Therefore, the simulation time needs to be long but difficulties arise due to limited data prior to 1985, when the groundfish survey began. In the assessment described here, the simulation was started in 1970 but other data than catch are limited for the first decade. Since the species grows slowly (2 cm per year), the time steps used in the simulation can be relatively large, so six-month time steps were selected. The age range used is 0 to 30 years, with the oldest age treated as a plus group. The length at recruitment is estimated, and is allowed to be different prior to 1990 than later, to reflect that the 1990 yearclass seems to be larger than the 1985 yearclass at the same age. Mean growth is calculated by von Bertalanffy’s equation.

Choice of natural mortality was a problem as usual in stock assessments. It is known that small redfish are preyed on by cod (Magnússon and Pálsson, 1989). Medium and large redfish, however, are not easily eaten by demersal fishes but predation by sperm whales (Martin and Clarke, 1986) could affect this part of the population. Other causes of natural mortality, including spawning stress, are on the other hand likely to become important for the older age groups (Beverton and Holt, 1957). There are indications that natural mortality, due to both predation and spawning stress is related to size rather than age (Hampton, 2000; Froysa et al., 2002). Natural mortality of a long-lived species like golden redfish can be expected to be low. Model runs using the values 0.05 and 0.1 for ages 8 and older are presented in this paper. Higher values are used for the youngest age-groups but the natural mortality of these age groups is aliased with the selection pattern of the survey, so constant natural mortality for all age groups would have given nearly identical results.

The commercial catch is modelled as one fleet with a selection pattern described by a logistic function and total catch in tonnes specified for each time period. The survey, however, is modelled as a fleet with constant effort and a nonparametric selection pattern that is estimated separately for each length group.

Data/constraints used in the objective function to be minimised are as follows (a-e): (a) length distributions from the commercial catch using multinomial likelihood function; (b) age length keys $P(a/L)$ from the commercial catch and the survey using multinomial likelihood function; (c) length disaggregated survey indices in 1 cm length groups using lognormal errors; (d) mean length at age from the survey and the commercial catch; and (e) under-
stocking, i.e. too small biomass to cover the specified catch in tonnes.

The total objective function to be minimised is a weighted sum of the different components. Selection of the weights is best described as *ad hoc*. Stefánsson (1998) demonstrates a possible approach for selecting the weights on different components of the objective function.

Estimated parameters are (a-e): (a) number of fishes when the simulation starts; (b) recruitment each year; (c) parameters in the growth equation; (d) parameter $\beta$ of the beta-binomial distribution controlling the spread of the length distributions; and (e) selection pattern of the commercial fleet.

The estimation can at times be difficult because some parameters or groups of parameters are correlated and the possibility of multiple optima cannot be excluded. The optimisation was started with simulated annealing to make the results less sensitive to starting values, converting to the Hooke and Jeeves algorithm when “the optimum” was approached.

Five different runs are presented here, a base case and four alternatives.

The alternatives differ from the base case by:

**Alternative 1.** $M = 0.1$ in contrast to $M = 0.05$ in the base case.

**Alternative 2.** No age data used in the objective function.

**Alternative 3.** The only data from commercial catch that are used in the objective function are age-length keys. Otherwise only survey data are used.

**Alternative 4.** The only survey indices used in the objective function are those of 10 cm and smaller fish.

Weights of different components in the objective function are either the same as in the base case, or the component is not included.

**RESULTS FROM MODEL RUNS**

**Base case**

Figures 10-14 and Table 1 summarise the results from the base case. In the prediction phase, recruitment after 1999 is assumed to be the mean of the estimated recruitment from 1992 to 1999. Figure 10a shows the estimated selection pattern of the commercial catch and the survey. The survey selection curve starts to go down for fish above 40 cm, indicating that either large redfish become less available to the survey or abundance...
of large redfish is overestimated in the model, for example by ignoring possible increased natural mortality of large redfish. The selection pattern of the commercial fleet is described by a logit function but the residuals from model fitting to the length distributions from the commercial catch do not show a trend for fish over 40 cm, supporting the hypothesis that large redfish become less available in the survey.

The estimated recruitment is shown in Figure 10d. The recruitment is highly variable with peaks in 1985 and 1990. This is in agreement with the age recordings and also with the survey results. As mentioned above, the 1985 and 1990 yearclasses seem to be much larger than other yearclasses since the groundfish survey started, but the model seems to put part of the 1990 yearclass in the 1991 yearclass. The results in Figure 10d show bad recruitment after 1991 or 96 million fishes on average. This estimate of recruitment is driven by survey data (Fig. 6). It is not clear why the model transfers part of the 1990 yearclass to the 1991 yearclass but extensive area closures to protect the incoming 1990 yearclass could be the main cause.

Figure 10b shows the estimated mean length at age as well as one standard deviation from the mean. It also shows how the commercial catch affects mean length at age in the stock. Judging from the
mean length at age, $L_\infty$ is around 45 cm when fishing effort is included, while the estimated value of $L_\infty$ is 56 cm.

In Figure 10c yield per recruit is shown as a function of fishing mortality. Yield per recruit here is calculated by simulating one yearclass of one million fishes for 40 years with a selection pattern and growth parameters, as estimated. The total yield over these 40 years is then a measure of yield per recruit. Estimates of $F_{\text{max}}(0.16)$ and $F_{0.1}(0.08)$ are shown in Figure 10c. Maximum yield per recruit is 250 g, so the mean recruitment after 1991 (96 million) can only sustain an annual catch of 24 thousand tonnes.

Fig. 12. – Results from base case. Predictions are made with fixed annual catch after the year 2000. The numbers in the figures show the catch.

Fig. 13. – Results from base case with prediction done with fishing mortality. The numbers show the fishing mortality of age 20. 0.084 is estimated $F_{0.1}$ and 0.162 estimate of $F_{\text{max}}$. 
Figure 11 shows residuals from the model fit to the survey data, demonstrating large positive residuals in some years, most notably 1990 and 1999. Survey data and model fit to them are also compared in Figure 5.

Figure 12 shows the results of prediction with fixed annual catch after the year 2000 and Figure 13 the results with fixed effort after 2000. As mentioned earlier, the assumed size of the yearclasses after 1999 is the mean value for yearclasses 1992 to 1999, which is a rather pessimistic assumption as all of these yearclasses are small (Fig. 10d). However, this assumed recruitment does not affect the catchable part of the stock for the next 10 years. With these premises, an annual catch of 30,000 tonnes will most likely increase the total biomass for the next 10 years, while an annual catch of 40,000 tonnes or more will decrease it.

An important characteristic of a stock assessment model is the retrospective pattern. Figure 14 shows the retrospective pattern of the catchable biomass from the base run, terminating in 1995-2000. When looking at the figure it must be considered that all the age readings are from the years 1995 to 1999 and are much fewer in 1995 to 1996 than in 1997 to 1999. Therefore, the relative weight of data from age readings is much less when terminating in 1995 and 1996 and the results resemble more those of alternative 2, in which no age readings were incorporated in the objective function (Fig. 15a). For the runs terminating in 1997-2000 the model results are very consistent.

Comparison of alternatives and base run

Table 2 shows the distribution of the objective function for the different alternatives. As may be seen, using \( M = 0.1 \) (alternative 2) results in a slightly better fit than using \( M = 0.05 \). The other alternatives cannot be compared in terms of the total objective function as some components are ignored in each of them.

In Table 2, the values of the different components of the objective function are compared. The entities...
marked with * are those components that were not included in the total objective function. As seen, the values of the ignored components are usually quite high, which might indicate a conflict in the input data.

Figure 15a shows the development of the stock according to different alternatives using a constant catch of 44,000 tonnes per year after 2000. The recruitment after 1999 is, as in the base run, the mean of the estimated recruitment from 1992 to 1999. The base run and alternatives 1 and 2 show similar development of the stock while alternative 4 shows a more or less constant decline over the simulation period, since the estimated size of the 1990 year class is much smaller than in the other runs. In alternative 4 catch data have more weight than in the other alternatives and the 1990 year class has not yet appeared significantly in the commercial catches. Alternative 3, in which no data from the commercial catch are included, shows similar trends to the base run but the estimated stock size is always smaller. The estimated selection pattern of the commercial fleet is also quite different from the other alternatives (Fig. 16), as the length distributions from the commercial catch, which control the estimated selection pattern, are not included in alternative 3. The “real” selection pattern of the commercial fleet when hidden mortality due to the catch is taken into account could, however, be somewhere in between.

DISCUSSION AND FUTURE WORK

The results of this exercise look promising and the model used seems to be internally consistent, as demonstrated by the retrospective runs. Still, a major drawback of the results is the lack of confidence bands on stock estimates which could be obtained by using an optimising algorithm that returns an estimate of the Hessian matrix, bootstrapping of residuals (Haddon, 2001) or Bayesian analysis. Estimating the Hessian matrix for large optimisation problems can be difficult when numerical differentiation is used, though the problem could be solved by automatic differentiation (Otter Research, 2000). Bayesian analysis seems to be the most promising way to obtain confidence bands on stock estimates for models like BORMICON. This exercise on golden redfish involves estimation of selection patterns, growth parameters and recruitment from relatively limited data, so positive definiteness of the Hessian matrix is not guaranteed, even though automatic differentiation is used. Obtaining confidence bands on stock estimates is among priorities in future work on the model.

Despite these problems, a lot can be done by comparing solutions found by changing weights on different components of the objective function and varying natural mortality or other model parameters.

A potential problem with the results presented here is dependency on data from the groundfish sur-
vey, which are the only available data for the pre-recruits. Survey indices are only available since 1985, which is a short time span for such a long-lived species as redfish. In this period, only two large yearclasses have appeared, in 1985 and 1990. Their abundance in the survey is low, so either the catchability is low or the survey covers only a part of the nursery area of the stock. Future work in this context could include a comparison with data from German surveys off East Greenland as well as data from the 0 group surveys. Similar considerations apply to data from the commercial catch, which are only available for a relatively short time compared to the lifetime of the species.

ACKNOWLEDGEMENTS

We sincerely thank the two anonymous referees for their valuable criticism and Guðmundur Jóhann Óskarsson is thanked for rewording our thoughts and correcting the English.

REFERENCES


Froysa, K.G., B. Bogstadt and D.W. Skagen. – 2002. Fleksibest -