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FISH STOCK ASSESSMENTS AND PREDICTIONS: INTEGRATING RELEVANT KNOWLEDGE.
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Scientific knowledge of biological processes that are potentially useful in fish stock predictions*

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SUMMARY: Based on an extensive review of available knowledge, several sources of information have been identified as potentially useful in fish stock predictions. They refer to a variety of biological processes of importance for stock dynamics, e.g. growth, maturation and egg production as well as early and juvenile life stage survival and subsequent recruitment, for which examples are given. Environmental variables impacting these processes were derived, ranging from simple statistical exploratory analyses to complex process studies for various stocks in different sea areas. Causal relationships are understood to varying degrees and in several cases the identified variables may only be taken as proxies for processes not investigated in detail yet. Besides the explanatory power of relevant variables, their predictability and related predictive time frames are of major importance for a potential application in stock predictions. These criteria in particular may hamper implementation in the foreseeable future in several cases. However, the information may still be highly relevant for a) hindcasting stock developments that are so far not fully understood, b) defining stock projection scenarios for simulation of different fishery management strategies under varying environmental conditions and considering species interactions and c) elucidating areas of future research to further enhance our predictive capabilities.

Key words: environmental variability, spawning stock, species interactions, fish stock predictions.

INTRODUCTION

The handling of uncertainties in fish stock assessment and management is crucial for the implementation of the precautionary approach to fisheries management and has been addressed in various recent research activities. This includes implementation of enhanced statistical analyses, formulation of improved stock assessment models considering uncertainty of input data in model output as well as extensive application of risk analyses in stock predictions (see International Symposium on "Fisheries Management under Uncertainty", Bergen 1997, ICES Symposium "Confronting Uncertainty in the

Evaluation and Implementation of Fisheries Management Systems" Cape Town 1998). Less attention has been given to the reduction of uncertainty in stock assessment and thereby improvement of our ability to predict short- and long-term stock developments under different exploitation strategies (Laevastu, 1993; Ulltang, 1996 and 1998). Reducing uncertainty in stock assessment requires an improved understanding of underlying population dynamic processes and their subsequent integration into assessment and prediction models, considering progress made in handling uncertainty. At present the capabilities are limited to conducting realistic medium- to long-term stock and catch projections under different fisheries management directives, environmental perturbations and species interac-

tions. The determination of biological reference points and a sustainable fisheries management is correspondingly difficult. Also short-term predictions, though depending more on adequate monitoring techniques of the present stock status, may be improved substantially by including environmental processes affecting individual growth and maturation, intra- and interspecific interactions, stock recruitment and fishing efficiency. As a consequence the EU project "Sustainable fisheries. How can the scientific basis for fish stock assessments and predictions be improved?" (SAP) was initiated to facilitate progress in this direction. The main objective of the project was to determine, whether existing scientific knowledge can be better utilised for reducing the uncertainties and increasing the time horizon of fish stock assessments (Ulltang, this volume). Brander (this volume) addresses in his contribution the basic questions why: do we need improved stock predictions, what may they look like and what general information is needed to conduct them.

Based on extensive reviews of available biological knowledge conducted within the project, the present contribution follows up on this, summarising and discussing possibilities identified for an improvement of stock predictions. It is not intended to prove that reducing uncertainty is the only way to proceed in fisheries science and management; there is no doubt that also management procedures have to be improved to make them more robust to uncertainties in stock predictions (e.g. Walters and Collie, 1988; Hilborn *et al.*, 2001). However, given the substantial research effort directed to basic fish biology and the impact of environmental factors on fish stock dynamics within the last 20 years, it appears to be worthwhile to review results having the potential to improve stock assessments and predictions, especially with the aim of dis-entangling the impact of the spawning stock and environmental factors on recruitment success.

This review attempts to follow the success of a year-class during ontogeny from spawner abundance through the egg and larval to the juvenile stage according to Paulik's (1973) framework for examining the entire life history process. This concept is broadly accepted (Rothschild, 1986; Ulltang, 1996), but has not really been implemented yet (Rothschild, 2000). Exceptions may be salmon stocks, for which the concept was originally developed (e.g. Larkin and Hourston, 1964; Larkin *et al.*, 1964), which however are characterised by relatively unique reproductive strategies. Breaking down the

life cycle into several successive life stages requires detailed investigations on growth, maturation and viable egg production of adult fish as well as on survival of eggs, larvae and juveniles in relation to prevailing oceanographic conditions and species interaction. This approach has seldom been employed in marine fish stocks. Notable examples include plaice in the North Sea and the Irish Sea (e.g. Beverton and Iles, 1992; Nash, 1988), walleye pollock in the North Pacific (e.g. Kendall *et al.,* 1996; Megrey *et al.*, 1996), anchovy in the Benguela Current (e.g. Painting *et al.*, 1998), cod in the Barents Sea (e.g. Sundby *et al.*, 1989) and the Central Baltic (Köster *et al.*, this volume). In all these cases, however, attempts are still ongoing, with the major problem in all systems being a lack of extended time series information for key processes and the variety and complexity of the processes involved. Consequently, this review does not concentrate on one of these stocks as an illustrative example, but compiles information from various research activities on different species and stocks. Baltic fish stocks are certainly over-represented here, which reflects our personal involvement in studying these stocks rather than any specifically advanced stage of research.

By following this approach, it can be shown that suitable information is available for improving fish stock predictions in several cases, although only selected processes are well enough understood for immediate implementation in the assessment work, even in the best studied stocks. For processes not yet fully understood, adequate proxies can be identified in a considerable number of cases. However, in addition to sufficient explanatory power, the predictability of environmental variables as proxies is of major importance for a potential application in fish stock predictions. Consequently, we address the applicability of identified variables to present short-term prediction and medium- to long-term projection methodologies and discuss the potential benefit of their implementation.

BIOLOGICAL PROCESSES AFFECTING SURVIVAL DURING DIFFERENT LIFE STAGES

A simplified schematic presentation of a fish's life cycle is given in Figure 1. This figure is based on Paulik's (1973) multi-stage spawner-recruit relationship, separating the life cycle into the following phases:
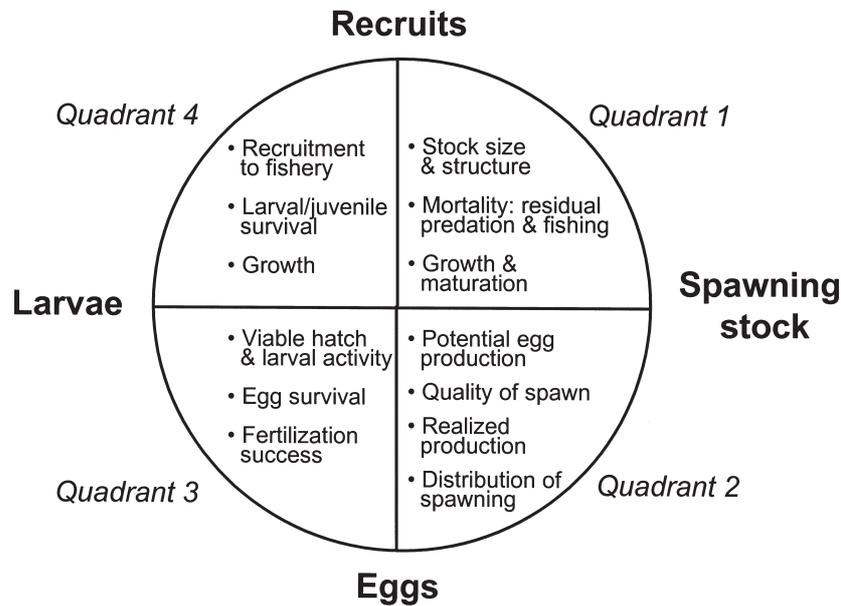
FIG. 1. – The life cycle of fish with different processes affecting developmental success from one stage to the next (in clockwise direction), based on Paulik's multi-stage spawner recruit relationship (Paulik 1973) modified after Ulltang (1996).

- from recruitment to the fishery to recruitment to the spawning stock,
  - from spawning stock to actual egg production,
  - from egg to larval production,
  - from larval production to recruitment.

The first quadrant comprises basically the traditional work areas of stock assessment (Ulltang, 1996): i) historical and present stock sizes and stock structures according to age or size, ii) mortality rates caused by predation or other natural causes as well as fishery, and iii) growth rates and proportion that are sexually mature at age or size.

The second quadrant covers research areas that are currently major areas of interest (for review see Trippel *et al.*, 1997): i) how well can we estimate the potential egg production or an equivalent measure of the stock's reproductive potential, ii) how is offspring survival related to who is participating in spawning (i.e. the relationship between quality of spawn and fish size, condition and spawning experience), iii) how high is the actual egg production compared to the potential and what causes deviations, and iv) leading into the 3rd quadrant, where and when does spawning happen and what is the impact on offspring survival probability?

The third quadrant covers the egg stage to larval hatch with key rates being i) fertilisation rate, ii) egg development and survival rates, and iii) viable hatch, all in relation to ambient environmental conditions. The egg stage has been commonly ignored in both

assessment and recruitment related research activities throughout the last two decades, apart from recent research efforts aimed at the viability of spawning products in dependence of parental characteristics (e.g. Chambers, 1997; Trippel, 1998) and application of the egg production method to determine spawning stock sizes (e.g. Lasker, 1985).

The fourth quadrant comprises the survival from the larval stage to recruitment, which is the traditional recruitment research area. It was in general believed that especially in this stage population regulation takes place (for review see Heath, 1992 and Rothschild, 2000) with key processes being i) feeding success and related growth rates, and ii) mortality caused by starvation and predation and the role of physical forcing conditions in modulating these processes. Recruitment to the fishery is added in our review as an additional process, which actually accounts for difficulties in estimating recruitment reliably before a year-class enters the fishery, rather than a biologically sensitive development into another life stage.

From recruits to spawning stock

Effect of habitat suitability on abundance indices

Stock assessment methodologies rely in several assessments heavily on catch rates from commercial fishing fleets to tune Virtual Population Analyses

(VPA). The catchability of the fish by these fleets is an important variable, yet limited process knowledge is available to describe how catchability varies over time with stock distribution or environmental factors. Below we describe two examples of how failures to quantify changes in catchability during stock declines can bias perceptions of stock status.

Investigations on northern cod off Canada demonstrated that the area occupied by the stock was reduced considerably when the stock declined (Atkinson *et al.*, 1997). A positive relation between the area occupied by a stock and abundance has been reported before (e.g. Winters and Wheeler, 1985; Rose and Leggett, 1991), and is no great problem for assessing the stock size if the fish distribute uniformly over the stock area (Swain and Sinclair, 1994). However, in reality a uniform distribution is seldom encountered (Paloheimo and Dickie, 1964), as habitat selection regularly occurs (MacCall, 1990). In the case of northern cod, a reduction in the suitable habitat took place concurrent with decreasing stock size (O'Driscoll *et al.*, 2000). This resulted in a shift in distribution to remaining areas with high habitat suitability sustaining high densities and commercial catch rates in these areas. Only after the stock size had fallen to a very low level did the decline in abundance become visible from commercial catch rates in these areas of stock concentration.

This problem is not restricted to the northern cod, but has also been observed for other fish stocks, e.g. the cod in the Central Baltic. Concurrently to a decline in stock size since the early 1980s, the majority of the stock are concentrated in western distribution areas (e.g. Köster *et al.*, 2001a). An International Bottom Trawl Survey, applying an area stratified sampling scheme, picked up the decline rather early (Sparholt and Tomkiewicz, 2000). Catch rates from commercial fishing fleets (ICES, 1999a and 2000a), however, did not reflect the reduction in stock biomass very well (Fig. 2a) and were consequently also not used as tuning indices in the assessment (ICES, 2000a).

Investigations on habitat preferences and threshold values in the Baltic (Tomkiewicz *et al.*, 1998; Neuenfeldt, 2002), suggested that the adult cod stock concentrates in areas with salinities of >10 PSU. When these salinities are not available or not accessible due to low oxygen concentrations in the bottom water as occurring in the eastern Central Baltic (ICES Sub-division 26 and 28), cod prefer at least salinities of >8 PSU. Independent of salinity, cod avoid water layers with oxygen concentrations of <2.5 ml/l, which corresponds to the threshold described for Gulf of St. Lawrence cod (D'Amours, 1993).

Based on these threshold levels, annual values for habitat area have been defined for Baltic cod and multiplied with the corresponding CPUE data from the commercial fleets This product provides a reasonable index of stock size, indicating trends in development rather similar to other indices (Fig. 2b). Thus, when accounting for shifts in distribution and concentration during time periods of reducing habitat suitability, applicability of commercial CPUE data is obviously improved. In principal this is well known (e.g. Swain and Sinclair, 1994) and can also easily be seen from mapping CPUE data (Hilborn and Walters, 1992). However, it is seldom accounted for in stock assessment, probably because a variety of other processes are known to affect the catchability and catch rates of commercial fleets, which are difficult to separate from environmental impact (for review see Hilborn and Walters, 1992).

In theory, habitat association between fish stocks and hydrographic variables will affect research survey catch rates as well (e.g. Perry and Smith, 1994), even if a stratified random sampling design is utilised and the stratification does not sufficiently consider the factors influencing the distribution patterns. Some examples show that accounting for changes in habitat characteristics improves research survey results, i.e.
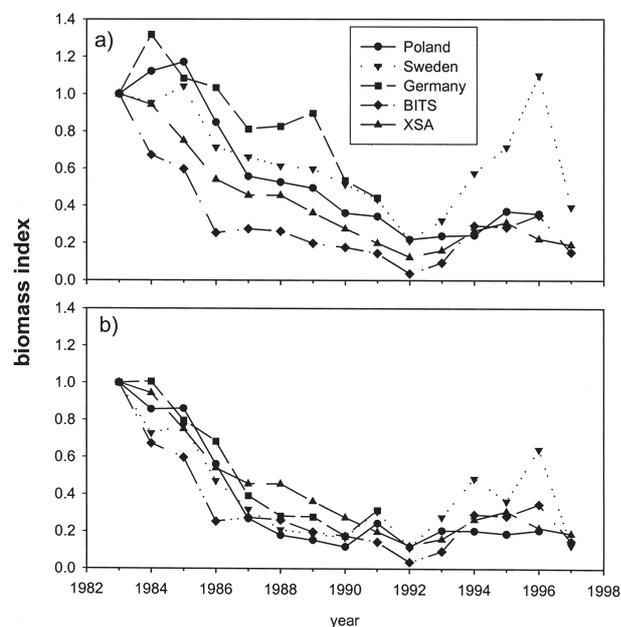

FIG. 2. – Relative catch rates of cod by commercial national trawler fleets in the Central Baltic in comparison to catch rates of the Baltic International Trawl Survey (BITS) and stock biomass from standard XSA assessment (ICES, 2000); (a) uncorrected and (b) corrected for habitat areas affecting the catchability.

removes a considerable part of the normally encountered year effect (Smith and Page, 1996). Swain *et al.* (2000) also found significant relationships between bottom trawl survey catch rates of cod in the Southern Gulf of St. Lawrence and ambient temperature as well as depth distribution. Tests with calibration of SPA or residuals from multiplicative models, including year-class, age and cumulative mortality as terms, did not support the hypothesis that these relations resulted from effects on catchability. Swain *et al.* (2000) conclude that adjustments for effects on catchability should be based on relationships with inconsistencies in survey catch rates, instead of direct relationships with the catch rates. These corrections still fail to account for changes in trawl catchability due to pelagic orientation (e.g. in areas of low oxygen concentration), direct impact of hydrographic factors on swimming activity and net avoidance or other changes in fish behaviour relative to the trawl (for review see Godø, 1998).

Starvation as a cause of mortality

Habitat quality may not only affect the distribution, but also the nutritional condition of the fish and in severe cases also their mortality. Pronounced fluctuations in nutritional condition of cod in Canadian waters led to the initiation of experiments on the impact of starvation on mortality in comparison to condition indices monitored in the field (Lambert and Dutil, 1997a). Especially during the spawning season, some cod in the wild population were obviously in a condition corresponding to those deceased in the experiments (Fig. 3). During the feeding season, the situation was different, but most cod were still unable to obtain condition factors reached in the experiment under food satiation.

Inter-annual variability in feeding success is evident from available time series of condition indices for St. Lawrence cod (Dutil *et al.*, 1999). Dutil and Lambert (2000), summarising available data, concluded that mortality from poor condition contributed to the decrease in productivity of the northern Gulf of St. Lawrence cod in the late 1980s and early 1990s. Given a highly significant relationship between simple condition indices (Fulton's condition factor and hepatosomatic index) and biochemical composition as well as energy content, a simple monitoring of the energy reserves of cod stocks appears to be possible (Lambert and Dutil, 1997b). Even if starvation as a cause of natural mortality is more frequently encountered in freshwater fish (e.g.
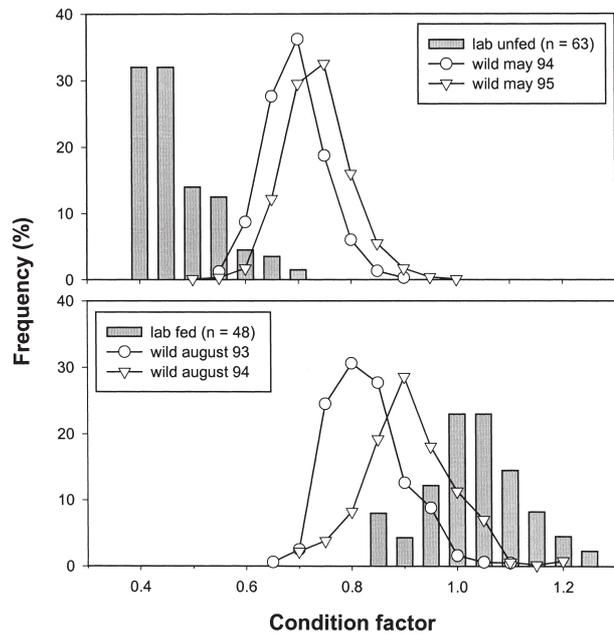

FIG. 3. – Distribution of the condition factor (according to Fulton) of wild northern Gulf of St. Lawrence cod captured in spring (May) at their yearly minimum and in summer (August) near their maximum condition period in comparison to condition factors of cod kept in the laboratory under controlled feeding conditions (starved or fed) (adapted from Fig. 6 in Lambert and Dutil, 1997).

Adams *et al.*, 1985; Griffiths and Kirkwood, 1995) than in marine fish stocks (e.g. Myers and Cadigan, 1995), the introduction of a monitoring system appears to be worthwhile as energy reserves in a population will affect growth, maturation and egg production, all processes influencing the reproductive success of a stock.

Predation

Another cause of mortality is predation. Within the last 20 years considerable effort has been directed to modelling predator-prey interactions, as it has been realised that for small pelagic prey species predation mortality often exceeds fishing mortality (see Bax, 1998 for review). According to Hollowed *et al.* (2000), multispecies models may be classified into: i) those handling environment and/or lower trophic levels as aggregate (e.g. ECOPATH-ECOSIM) and dynamic system models (BORMICON or MULTSPEC) and ii) those considering a sub-set of species interactions as multispecies production and dynamic multispecies models (e.g. MSVPA). Predation mortalities of specific age-groups can be estimated by dynamic models, e.g. the MSVPA based on the traditional VPA approach (for review see Magnusson, 1995) and more advanced statistically based

models such as BORMICON (Stefánsson and Páls-son, 1998). In a number of regular stock assessments and predictions, these age-specific predation mortalities have been incorporated (e.g. ICES, 2000a).

The necessity for including predation in medium- to long-term projections (e.g. Bax, 1998) and the determination of biological reference points has been widely accepted (e.g. Gislason, 1999). However, short-term inter-annual variability in predation mortality is assumed to be limited, making the incorporation of these fluctuations in short-term predictions unnecessary (but see Stephenson (1997) for another view). Although we believe that for the majority of the assessed species, this might be correct, we doubt that it is true for prey species in systems with few dominating and largely fluctuating predator species, e.g. capelin in the North Atlantic (Mehl, 1989; Carscadden *et al.*, 2001) and sprat in the Baltic (Sparholt, 1994).

Predation mortalities of Baltic sprat caused by cod show a substantial inter-annual variation in young age-groups, while the variability for older age-groups is more limited (Fig. 4). Highest inter-annual variability is encountered in periods of pronounced changes in predator stock sizes at low prey abundance at the beginning of the time series (ICES, 2000a). The predation mortalities are estimated by MSVPA allowing for inter-annual fluctuations in predator consumption rates in dependence of ambient temperatures and predator weight at age (ICES,

1999b). Variability in prey weight at age is incorporated as well, but prey suitability coefficients (Sparre, 1991) are kept constant over time, which probably dampens out inter-annual fluctuations in predation mortalities (see below).

The conclusion to be drawn from the example is that in relatively simple systems with one key predator undergoing large stock fluctuations, predation mortality of major prey species cannot simply be kept constant in short-term predictions, but could be coupled to the abundance of the predator and potentially alternative prey. A more elaborate procedure is the utilisation of forecast versions of existing multispecies models (e.g. MSFOR: Sparre, 1991).

Weight at age

Besides inter-annual variation in mortality rates, significant year to year changes in weight at age are frequently observed (e.g. Nakken, 1994; Shelton *et al.*, 1999). A dramatic example with severe socio-economic consequences is the Baltic herring (Raid and Lankov, 1995, Cardinale and Arrhenius, 2000), which has shown a decline in weight at age by more than 50% in all age-groups since the beginning of the 1980s (ICES, 2000a). A similar decrease has been observed for Baltic sprat, starting later (ICES, 2000a).

For herring, three different hypotheses have been put forward for explanation. First of all, a decrease
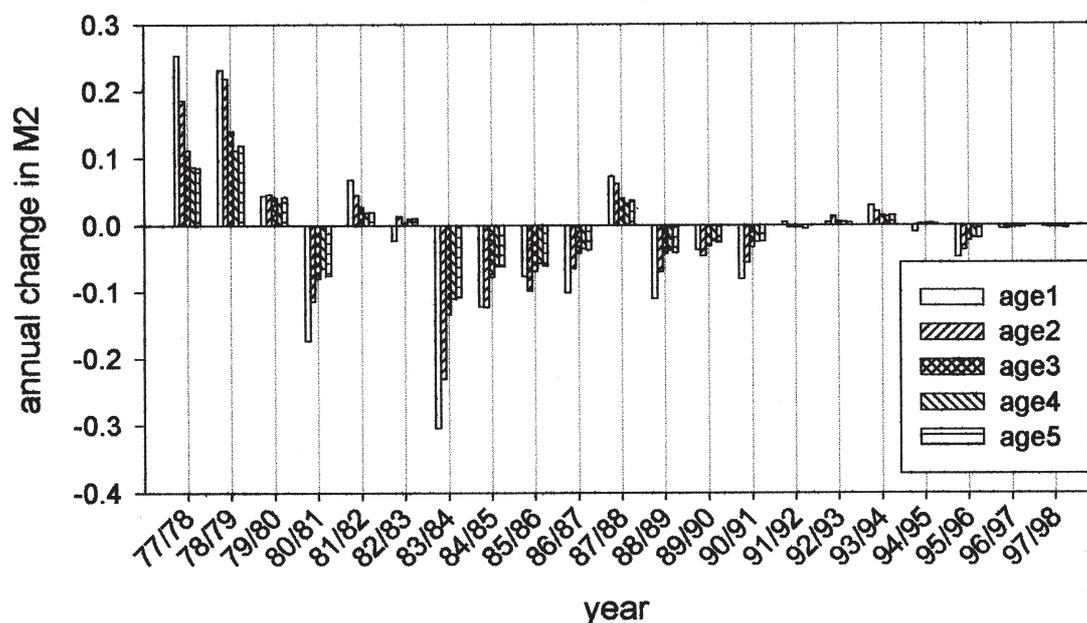

FIG. 4. – Annual change in predation mortality rates (M2; per year) of Central Baltic sprat according to age-group as derived from MSVPA runs (ICES, 1999b).
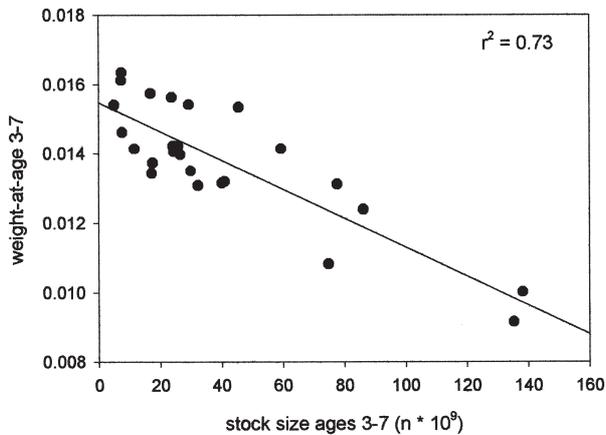
FIG. 5. – Relationship between weight at age and stock size of sprat in the Baltic (from ICES, 2000).

in size specific predation by cod is apparent (Beyer and Lassen, 1994), which will primarily provide a relief to the smallest herring of an age-group, which is more vulnerable to predation by cod than larger ones. Secondly, as the herring assessment unit in the Baltic consists of a considerable number of sub-stocks with different growth rates (e.g. Ojaveer, 1989), a shift in dominance of these different sub-stocks has been suggested (Sparholt, 1994). Thirdly, a shortage of food supply accelerated by increasing competition with the rapidly increasing sprat stock was hypothesised (Cardinale and Arrhenius, 2000).

For sprat the explanation is easier than for herring, as the decline in weight at age started at low predator abundance and additionally the suitability of sprat as prey of cod does not change very much with age (ICES, 1997). Furthermore, there exist no such clearly distinct sub-stocks of sprat in the Baltic and those which could be separated (Ojaveer, 1989) show relatively similar growth changes as obvious from area-specific data compiled by ICES (1999b). With respect to the third hypothesis, weight at age is significantly correlated to the food availability per sprat and daily rations (Möllmann unpubl. data) estimated on the basis of stomach content data and ambient temperatures applying a general model of gastric evacuation (Möllmann and Köster, 1999). Based on this exploratory analysis, we suggest using a relationship between weight at age and stock size for prediction purposes (Fig. 5). For herring a similar relationship including sprat as a competitor was established by Cardinale and Arrhenius (2000).

Utilising these types of relationship is of course a short-cut, as growth depends-besides prey availability in quantitative and qualitative terms-on a

series of other processes, i.e. feeding intensity, assimilation, metabolism, transformation and excretion with all rates being controlled by ambient temperature. Michalsen et al. (1998) give a good example of the complexity: in situations in which the ambient temperature decreases, the metabolic processes slow down, reducing growth rates regardless of prey availability. On the other hand, if the food supply is limited, growth rates may be higher at lower temperatures than in warmer areas, due to reduced metabolic costs.

In an attempt to predict weight at age, Shelton et al. (1999) included, besides an area and an age effect, the area covered by cold water ($<0°C$) on the Newfoundland shelf (CIL) in a general linear model. Although the environmental variable improved the predictive capabilities of the model, the explained part of the variance is limited and the applicability in stock predictions is hampered by the uncertainty in predicting water conditions more than one year ahead, i.e. a significant autocorrelation in the CIL exists only for a lag of 1 year. However, Brander (2000) resolved a significant relationship between weight at age 3 and bottom temperature anomaly during first year of life in North Sea cod. The relationship between mean weight at age of a cohort and temperature experienced during the first year of life exists up to age 6, suggesting that predictions of weight at age over a longer time span may be possible (Brander, 2000).

Growth and thus weight at age is sex specific in various fish species, e.g. North Sea plaice (Bannister, 1977). Further evidence exists that growth also differs between immature and mature fish (STORE, 2001). While the latter is probably of limited importance for the estimation of the spawning stock biomass in fish stocks consisting of several adult age-groups, the sex specific growth has implications for the calculation of the female spawning stock biomass and the potential egg production of the stock. It is presently common practice in fish stock assessment to apply sex unspecific weight and maturity at age data, although sex specific information is recorded in several monitoring programs and could be used to test the validity of the approach (e.g. Jakobsen and Ajaid, 1999).

Maturation

Growth affects not only the size at age, but also the likelihood of attaining sexual maturity at a given age or size (e.g. Nikolsky, 1962; Dragesund et al.,

1980; Hutchings, 1997). A declining age and length at sexual maturity has been observed for most gadoid stocks in the Northwest Atlantic since the 1970s (Trippel *et al.*, 1997), but also for stocks in the Northeast Atlantic (e.g. Jørgensen, 1990). This has been explained by higher growth rates and better nutritional condition at smaller size, due to increased food supply per individual at low stock levels (Trippel, 1995). However, a genetic selection of early maturing fish under heavy fishing pressure is another potential explanation (Trippel, 1995).

Not only the sexual but also the gonadal maturation process is affected by the nutritional condition of the fish. Laboratory studies conducted with Northwest Atlantic cod showed that individuals in poor condition will skip spawning (Burton *et al.*, 1997), a fact which has also been reported for other species kept in captivity (Burton and Idler, 1987; Bromley *et al.*, 2000). Also on a population level evidence for skipped spawning exists for Northeast Arctic cod (Marshall *et al.*, 1998): in 1987 cod were on average in poor condition according to their hepatosomatic index, resulting in lower percentages of smaller cod attaining sexual maturity as well as a high proportion of fish in size classes corresponding to repeat spawners not participating in the spawning. In contrast in 1993, a year characterised by good nutritional conditions, the expected regular pattern was observed. Marshall *et al.* (1998) and Yaragina and Marshall (2000) have demonstrated that liver condition of Northeast Arctic cod is coupled with prey availability, especially with the size of the capelin stock (Fig. 6).

Apart from using condition indices at age to estimate proportions of fish participating in spawning (Marshall *et al.*, 2000), the liver condition index has been utilised to estimate the liver energy content of mature females in the stock (TLE) as a proxy for the total egg production (Marshall *et al.*, 1999). This proxy shows only a rough general agreement with changes in the spawning stock biomass over time (Fig. 7). Both values were high at the beginning of the time series (from 1947-1951) and low in the second half of the 1980s, associated with the collapse of the capelin stock (Marshall *et al.*, 2000). Outside these time periods the variation in SSB and TLE appears to be largely independent. Construction of bioenergetic proxies for egg production is in essence replacing the quantity of spawner biomass by a measure of quantity and quality (Marshall *et al.*, 2000), which is justified by the relationships established between fecundity and nutritional condition of females described within the following section.

A relationship between recruitment and body size characteristics of the adults has also been established for haddock on the Scotian Shelf (Marshall and Frank, 1999a). This shows that even in data-poor stocks, improved estimates of the reproductive potential can be obtained through relatively minor modifications to existing data. For example, the age-diversity index for Icelandic cod, estimated from the VPA numbers at age, shows a higher correlation with recruitment than spawner biomass (Marteinsdottir and Thorarinsson, 1998).
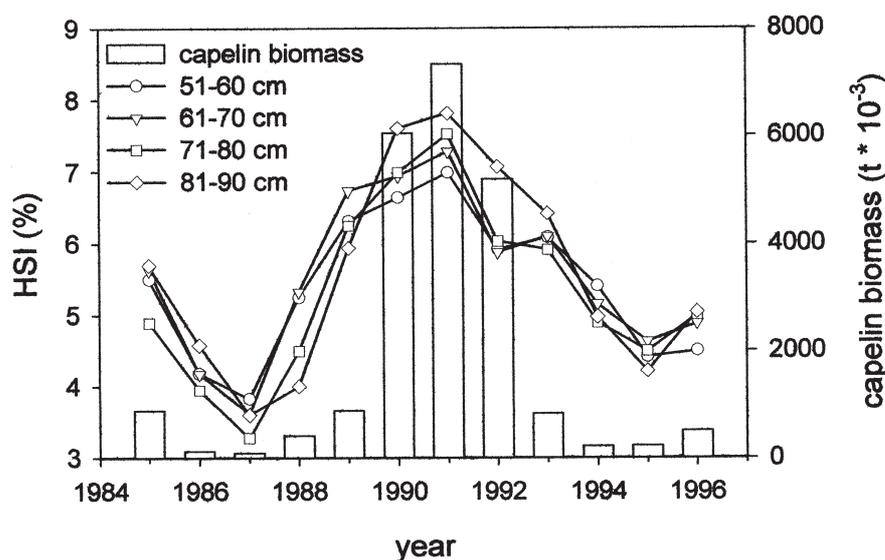

FIG. 6. – Time series of hepatosomatic index (HSI) for Northeast Arctic cod in different length classes in comparison to Barents Sea capelin biomass (adapted from Fig. 2 in Marshall *et al.*, 1998).
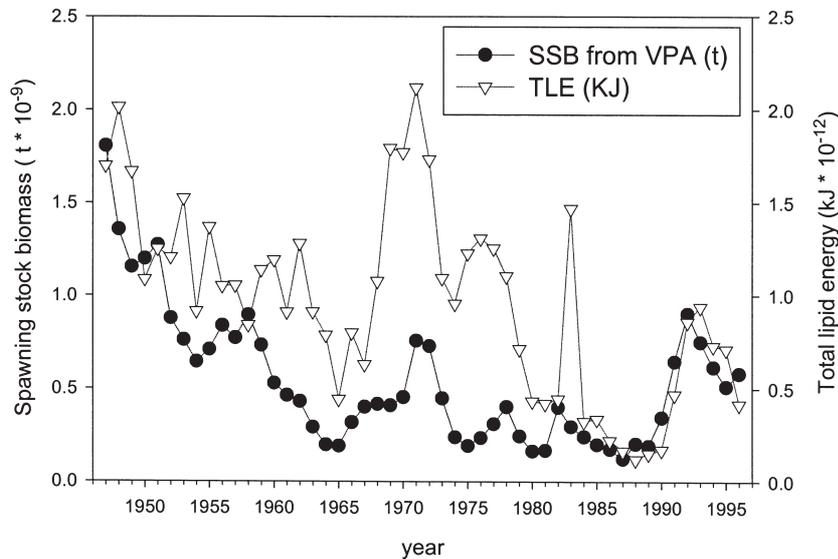
FIG. 7. – Time series of total lipid energy content (TLE) of Northeast Arctic cod females and spawning stock biomass (SSB) (adapted from Fig. 3 in Marshall *et al.*, 2000).

From spawning stock to egg production

Potential fecundity

It is commonly accepted that the fecundity of individual female fish of the same size drawn from a spawning population within a spawning season shows considerable deviations (e.g. Hislop *et al.*, 1978; Kjesbu and Holm, 1994; Rijnsdorp, 1994). There is strong evidence that the individual fecundity is influenced by the availability of food (Woodhead and Woodhead, 1965; Kjesbu and Holm, 1994) or stock density (Bagenal, 1973; Rijnsdorp, 1994). The dependence of fecundity on nutritional condition reported by Tyler and Dunn (1976) for winter flounder and by Kjesbu *et al.* (1991) for cod has lately been confirmed for yellow perch from Lake Erie (Henderson *et al.*, 2000). For cod from the Gulf of St. Lawrence, Lambert and Dutil (2000) demonstrated that not only the realised fecundity, but also the average egg dry weight is related to the nutritional status of the female. Kjesbu *et al.* (1998), synthesising available information on potential fecundity of the Northeast Arctic cod stock, revealed significant positive relationships between potential fecundity and environmental temperature as well as the availability of capelin per maturing cod.

An analysis of individual fecundity data of Baltic cod sampled within the last two decades (Kraus *et al.*, 2000) revealed significant inter-annual variations in the relative potential fecundity, but not between different spawning grounds or between early and late spawning fish. Growth anomaly on a population level, i.e. the increase in weight at age during the preceding feeding and winter season, in combination with the corresponding ambient temperatures, explained 66% of the annual variance in relative fecundity (Kraus *et al.*, 2000).

For many stocks, these detailed data on reproduction do not exist. Furthermore, existing sampling programmes often do not collect basic data such as age-specific values of the mature proportion and weight. Treating any of these terms as constants will decrease the accuracy of the resulting estimate of reproductive potential. This is particularly true for stocks exhibiting large interannual variability in condition, because besides maturity (see above) and fecundity, condition affects also atresia (Kjesbu *et al.*, 1991), egg (e.g. Chambers and Waiwood, 1996) and larval quality (e.g. Marteinsdottir and Steinarsson, 1998) simultaneously.

Realised fecundity

The potential fecundity may considerably overestimate the actual fecundity due to resorption of oocytes during the prolonged spawning time of multiple batch spawners. The estimation of actual fecundity is especially difficult in fish species that are indeterminate spawners, i.e. that produce multiple batches of eggs in one spawning season with successive recruitment of vitellogenic oocytes (Alheit, 1989). Although the daily egg production method (Lasker, 1985) is regularly applied for

pelagic fish species (e.g. anchovies, sardines, horse mackerel) to estimate the size of the spawning stock (e.g. ICES, 2000b), in most cases little information on intra- and inter-annual variability in spawning frequency of batch spawning species and relative fecundity is available (but note recent efforts by ICES, 2000c and ICES, 2000d). In particular intra- and inter-annual variability in prevalence and intensity of atresia is seldom studied. Exceptions are the northern anchovy off California and the Cape anchovy in the southern Benguela, for which studies have demonstrated that ovarian atresia occurs in cases of unsatisfied metabolic requirements (Hunter and Goldberg, 1980; Melo, 1994). This may even result in ceased spawning activity for the remainder of the season (Hunter and Macewicz, 1985), a process that has also been described for other fish species, such as turbot (Bromley et al., 2000).

A complete resorption of ripening oocytes has been described by Bell et al. (1992) for orange roughy individuals having a lowered condition compared to reproductive females. Orange roughy is like cod a group synchronous (determinate) spawner. Nevertheless, Kjesbu et al. (1991) observed in an experimental study with Atlantic cod that a significant reduction in potential fecundity due to atresia in the prespawning ovary is not very common, except for fish in very poor condition. This result was confirmed by Kjesbu et al. (1998), also for spawning individuals, although a lack of contrast in condition may have led to an underestimation of the occurrence and especially the proportion of affected oocytes.

In order to test the reliability of the spawning stock biomass and estimates of potential egg production by the population as a measure of actual egg production for Baltic cod, Köster et al. (this volume) conducted comparisons with the actual egg production as determined from ichthyoplankton surveys at peak spawning time. The SSB estimated by an area dis-aggregated MSVPA (Köster et al., 2001a) for Sub-division 25, i.e. the area that currently contains the only important spawning ground, applying a maturity ogive invariate with time (as utilised up to 1996 in the assessment), revealed no correlation with actual production of the youngest egg stage. Applying year- or period-specific maturity ogives as applied in the present assessment resulted in a significant correlation, but with considerable variability ($r^2 = 0.30$). In contrast, both the female SSB and the predicted potential egg production are more closely correlated to the actual daily egg production.

The potential egg production explains slightly more variability ($r^2 = 0.63$ compared to 0.61), but the female SSB appears to be already a reasonable measure of egg production, given that reliable sex ratios and sex-specific maturity ogives are implemented (Tomkiewicz et al., 1997).

Quality of spawning products and timing of spawning activity

Not only the quantity spawned, but also who is spawning matters for the survival probability of the offspring (for review see Trippel et al., 1997; Solemdal, 1997). For Central Baltic cod, laboratory experiments demonstrated that egg size depends on female size (Nissling and Vallin, 1996), with larval length and growth depending on egg size (Nissling et al., 1998). This confirms results obtained for different species, i.e. Atlantic cod (e.g. Grauman, 1965; Kjesbu, 1989; Marteinsdottir and Steinarsson, 1998), herring (Blaxter and Hempel, 1963) and walleye pollock (Hinckley, 1990).

Larger egg and larval size is commonly related to higher survival probability, with larger larvae having a better ability to avoid predators (e.g. Miller et al., 1988), larger energy reserves and higher growth rates (Blaxter and Hempel, 1963; Webb and Weihs, 1986) and ability to utilise a wider variety of food organisms (e.g. Hunter, 1981; Knutsen and Tilseth, 1985). In the Baltic, there is an additional impact of egg size on survival, as egg size is related to buoyancy (Vallin and Nissling, 2000), with higher buoyancy allowing development in less dense water above the commonly oxygen depleted bottom water (Wieland et al., 1994).

A difference in egg size and egg quality between first-time and repeat spawners is well accepted, with the offspring of first-time spawners being in general less viable (Solemdal et al., 1995; Kjesbu et al., 1996; Trippel, 1998). Evidence exists that fertilisation success depends as well on female size (Buckley et al. 1991; Solemdal et al., 1995), but not on male size (Rakitin et al., 1999). The latter authors concluded from their and previous findings of Trippel and Neilson (1992) that there is no need to adjust spawning stock reproductive potential due to the variation of sperm quality with male age/size.

Male condition had an impact on fertilisation success (Ratikin et al., 1999) and further evidence exists that male stock characteristics may bocome more important in sub-optimal environments, i.e. low salinity in estuarine systems (STORE, 2001). Given

the decline in age and size at sexual maturity through time in a considerable number of Atlantic fish stocks and an often truncated age/size structure of the stocks (Trippel, 1995), the above findings suggest that the conventional spawning stock biomass, even when calculated with regularly updated maturity ogives, does not reflect the reproductive potential of the stock adequately (Trippel *et al*., 1997).

Apart from an age/size dependence of egg size and viability, a decline in egg size with continuation of spawning activity has been demonstrated for different cod stocks (Kjesbu, 1989; Kjesbu *et al*., 1996; Trippel, 1998; Vallin and Nissling, 2000). First-time spawners show in general a decrease in egg size right from the beginning of the spawning activity, while repeat spawners show a parabolic shape in egg size with a peak relatively early in the spawning season (Kjesbu *et al*., 1996; Vallin and Nissling, 2000). In addition, spawning activity of larger females starts earlier than that of smaller ones (Kjesbu *et al*., 1996; Trippel *et al*., 1997; Tomkiewicz and Köster, 1999), indicating that most viable eggs are spawned relatively early in the spawning season.

Timing of spawning has implications on the survival probability of the offspring, and environmental conditions conducive for egg and larval survival may drastically change throughout the spawning season. For example, early spawned cod eggs in the Baltic encounter on average better oxygen conditions than later spawned ones, due to a continued oxygen consumption in the water layers of egg development after inflows of oxygenated water at the beginning of the year (MacKenzie *et al*., 1996). On the other hand, early spawned cod eggs will experience higher predation pressure, due to increased temporal and spatial overlap between sprat as predators and eggs as prey (Köster and Möllmann, 2000a).

With respect to food availability, an early spawning resulted historically in a temporal overlap of cod larvae with the nauplii and early copepodites of the copepod *Pseudocalanus elongatus*, which is a major prey of cod larvae in the Baltic (Zuzarte *et al*., 1996). However, due to a pronounced decline in the standing stock and production of *P. elongatus* within the 1990s (e.g. Dippner *et al*., 2000; Möllmann *et al*., 2000), the prey availability in spring/early summer has decreased from a food unlimited situation to a food limited one (Hinrichsen *et al*., 2002a). The development of key zooplankton species in the Baltic appears to be coupled with large-scale climatic forcing (Dippner *et al*., 2000, Hänninen *et al*., 2000),

which simultaneously affects the survival of cod offspring, suggesting an integrated approach in projecting stock development that considers maternal characteristics as well as environmental processes.

From egg to larval production

Fertilisation success

In estuarine systems, low salinity effects the fertilisation of marine fish species (Solemdal, 1970; Westin and Nissling, 1991). For Baltic cod, a minimum salinity of 11 psu is required for activation of spermatozoa and thus successful fertilisation (Westin and Nissling, 1991). This reduces spawning success in northeastern areas of the Baltic and has consequently been incorporated into indices describing environmental conditions that allow successful egg development (see below). Apart from estuarine systems, however, the percentage of unfertilised eggs found in field studies appears to be low (e.g. Brodeur *et al*., 1996). This corresponds to the conclusion drawn above, that there is no evidence for a need to adjust spawning stock reproductive potential due to the variation in sperm quality with male age/size.

Egg survival

Egg mortalities tend to be high in marine fish species (e.g. McGurk, 1986; Houde, 1989a; Pepin, 1991). Inter-annual variability in egg survival has been described for some stocks as relatively low, e.g. walleye pollock (Brodeur *et al*., 1996), or highly fluctuating, e.g. the northern anchovy population off California (Lasker, 1985). In the latter case, the varying mortality rates were attributed to predation, e.g. cannibalism, as well as oceanographic processes, e.g. offshore transport (Lasker, 1985). In fact, there is considerable evidence that predation by invertebrates and fish can be a major source of mortality of pelagic and demersal fish eggs (for review see Heath, 1992; Leggett and DeBlois, 1994: newest evidence Swain and Sinclair, 2000). However, adequate field studies to quantify the impact of predation on egg and larval survival are difficult to design (Bailey and Houde, 1989). In reality this has never been achieved for marine fish stocks. In the best case, estimates for single spawning grounds have been determined, in general for demersal spawners like herring which have the advantage that eggs are deposited in a single batch (Heath 1992). For pelag-

ic spawners, average egg mortality rates caused by cannibalism have been estimated in some cases, e.g. for Californian (Hunter and Kimbrell, 1980) and Peruvian anchovy (Santander *et al.*, 1983). Notable exceptions are walleye pollock (Brodeur and Bailey, 1996; Brodeur *et al.*, 1996) as well as Baltic cod and sprat (Köster et al. 2000a, b), for which predation pressure by different predator species has been estimated, also resolving inter-annual variability to a certain extent. Variability in the predation process caused by hydrographic processes forcing predator and prey overlap (e.g. Garrison *et al.*, 2000; Köster and Möllmann, 2000b) or predator response to changing prey composition, sizes and densities are in general not well enough understood to incorporate these processes in recruitment models, although intelligent use of mesocosm studies has increased our knowledge with respect to latter processes (see Paradis *et al.*, 1996).

The direct impact of oceanographic processes on egg development is well known with respect to the dependence of egg development rates on temperature (e.g. Thompson and Riley, 1981; LeClus and Malan, 1995; Pepin *et al.*, 1997), with some studies considering also additional variables, e.g. salinity and oxygen concentration (Nissling and Westin, 1991; Wieland *et al.*, 1994). The impact of ambient temperature on egg mortality rates has also been established for some species (e.g. Thompson *et al.*, 1981; Iversen and Danielsen, 1994). However, studies applying these laboratory measurements to the field are scarce, although evidence on lethal temperatures in-situ exists for several stocks (see Houde, 1989a). The impact of temperature on size at hatch is still under discussion (Chambers, 1997) and is probably a dome shaped relationship (Pepin *et al.*, 1997). Other oceanographic processes affecting mortality are physical damage through storm activity (e.g. Morrison *et al.*, 1990), and more indirect advective losses (e.g. Painting *et al.*, 1998).

Apart from these exogenous factors, endogenous processes affect egg survival as well: i) chromosome aberrations during embryonic development that occur commonly and are in several cases lethal (Kjørsvik *et al.*, 1994), ii) contamination by toxicants in polluted areas increasing embryonic abnormalities (e.g. Cameron *et al.*, 1989), iii) toxic algal blooms affecting egg mortality (Aneer, 1985) and iv) endogene parasites affecting egg survival (e.g. Pedersen and Køie, 1994). However, in all cases we know, the variable impact on egg or larval survival in the field has not been quantified and causing

endogenous factors are seldom identified. This makes incorporation into stock assessment presently impossible and although evidence exists that variable egg mortality may substantially affect recruitment (e.g. Koslow *et al.*, 1985), relatively few recruitment studies address this life stage explicitly. One example is cod in the Central Baltic. As described above, low salinity affects the fertilisation success of marine fish species. For cod in the Central Baltic this leads to the definition of one of the threshold values of the so called 'reproductive volume' (RV) (Plikshs *et al.*, 1993), i.e. the water volume available for successful cod egg development. The other thresholds indicate minimum oxygen and temperature requirements for egg survival (>2 ml/l oxygen concentration and 1.5°C). Comparing the potential egg production of the cod stock in the three historically most important spawning grounds (Köster *et al.*, 2001b) with the RV at spawning time (MacKenzie *et al.*, 2000), suggests that a large portion of the egg production has been spawned in unsuitable environments in the Gdansk Deep and the Gotland Basin, especially in the early 1980s (Fig. 8). Clearly, these types of mis-match between spawning effort and environmental conditions allowing a successful reproduction need to be considered when predicting future stock development on medium- to long-term scales.

This leads to the question of how predictable the RV actually is. The magnitude of the RV depends first of all on the occurrence and magnitude of inflows of saline, oxygenated water from the North Sea/Skagerrak (Hinrichsen *et al.*, 2002b), in the majority of the cases taking place in winter (Matthäus and Franck, 1992). As the Baltic is characterised by a series of deep basins separated by shallow sills, an inflow will usually fill up the first basin only, with little or no transport in an eastern direction. Only if the inflow has an unusual magnitude or more likely if the advected water is replaced by an even denser water mass in a subsequent inflow or a subsequent inflow of less dense water glides over the earlier inflown water, the eastern Baltic basins will benefit from the water exchange. The first basin, i.e. the Bornholm Basin, benefits from smaller regular inflows, sustaining annual egg development, although in varying quantities (MacKenzie *et al.*, 2000). Hydrographic monitoring and the unique topography make predictions of RV in a given year in all basins rather accurate (Hinrichsen *et al.*, 2002b). As a secondary effect of large inflows into the Bornholm Basin, it is likely that a certain
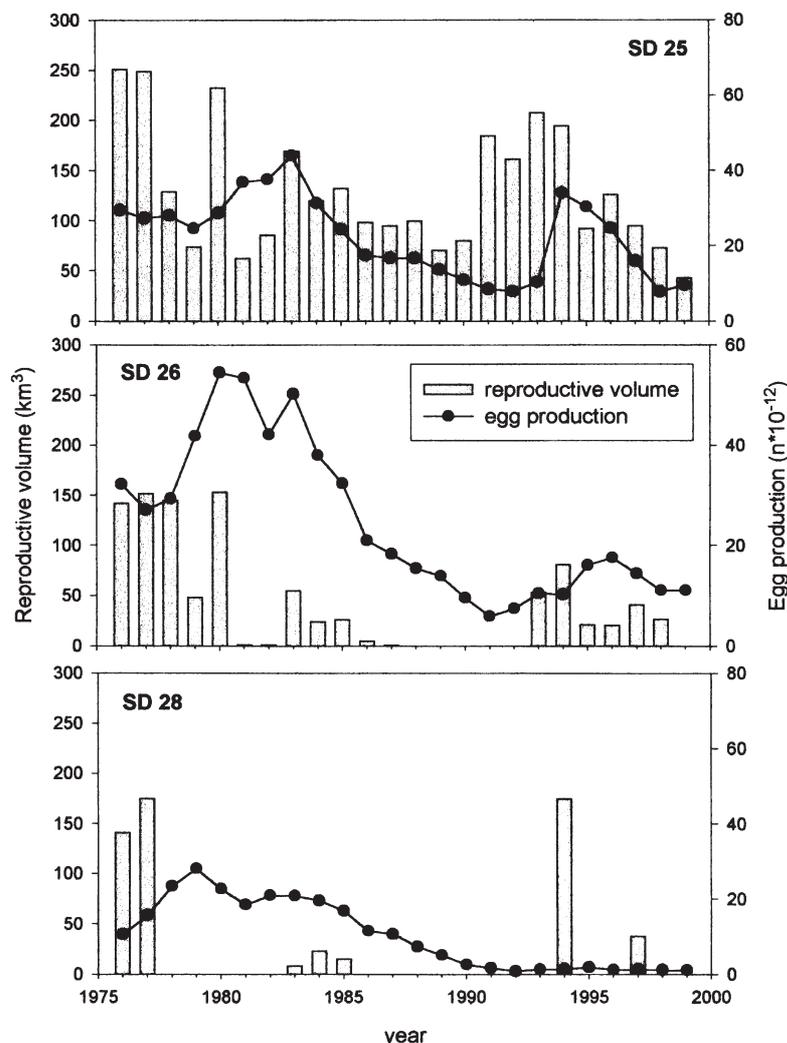
FIG. 8. – Time series of potential egg production of cod in different ICES Sub-divisions (SD) of the Central Baltic in comparison to the available reproductive volume sustaining egg development.

amount of saline and oxygenated water is transported to the east until the next year. In turn, without an inflow into the Bornholm Basin in the last year, a significant transport of oxygenated water to the east in a given year is unlikely. Predictions beyond this time frame are hardly possible as long as large-scale atmospheric processes responsible for inflow events (Hinrichsen *et al.*, 2002b) are not predictable.

As cod recruits to the fishery in the Central Baltic at an age of 2, reasonable predictions are limited to the time frame of three years ahead. In a given assessment year n, the recruiting year-class strength n-2 can be derived from trawl surveys, n-1 recruiting next year from observed RV and SSB as well as larval surveys (see below), n recruiting in two years from observed RV and predicted SSB, and n+1 recruiting in three years from predicted RV and predicted SSB. Furthermore, cod egg survival in rela-

tion to the oxygen condition can be modelled in a more realistic way than utilising RV (Köster *et al.*, 2001b) and depends on other causes as well (Sparholt, 1996; Köster *et al.*, this volume). This will not, however, affect the outlined extended short-term prediction scheme and also consequences for medium- to long-term projections are still valid, as all major processes involved depend on the spawning stock (abundance of mature females according to ages/sizes, weight at age, average fecundity) and regularly monitored hydrographic conditions.

Spatial variability in survival to the larval stage

Based on the case study described above, one might conclude that the spatial variation in environmental factors affecting cod egg survival in the Baltic is so large that it is relatively easy to resolve

environmental effects, compared to other sea areas. However, spatial variability in survival probability of offspring has been detected in other fish stocks as well (e.g. Rose *et al*., 1999). Simulations of survival success of haddock egg production in different areas off Scotland (Heath and Gallego, 1998) suggest considerable deviations in survival to the larval stage depending on where the egg production originates. Results suggest that 13.6% of the egg production west of Scotland generates 24% of the surviving larvae at 7 mm length. These modelling and simulation studies therefore suggest that spatial variation in environmental conditions might affect egg and larval survival in other areas, but direct field evidence is presently lacking.

From larval production to recruits

Survival during the larval stage

Larval growth and survival, both processes being inter-linked (for review see Houde, 1997), may be determined by a variety of exogenous factors including the quality and quantity of food, temperature or other physical factors, diseases and infections by parasites, pollution and of course predation. In our contribution, we do not intend to cover these processes in detail (for review see Heath, 1992; Chambers and Trippel, 1997). Instead we concentrate in the following sections firstly on the utilisation of larval surveys to predict recruitment. Secondly outline how hydrodynamic modelling may improve the strength of the predictions. Thirdly, we describe how coupled hydro- and trophodynamic models may be utilised to simulate reproductive success from egg production to the juvenile stage. Finally, before covering the juvenile stage in more detail, we will discuss the potential benefit of including environmental factors affecting the larval stage in recruitment models.

Larval abundance as a predictor of recruitment

Larval surveys have the potential to predict cod recruitment in the Baltic, as demonstrated by a significant linear relationship between larval abundance and 0-group recruitment for cod in Sub-division 25, containing presently the only important spawning area (Köster *et al*., 2001b). Larval abundance explains 64% of the variability in recruitment, but with a significant positive intercept, caused mainly by very low larval abundance in the early

1990s, although recruitment was around average compared to the years 1986-1996. This inconsistency is caused by a shift in peak spawning activity from the second half of May 1989 to the end of July in 1996 (Wieland *et al*., 2000), which was realised too late to adapt the survey timing. This clearly indicates that ichthyoplankton surveys during traditional peak spawning times are insufficient to get a reliable estimate of larval abundance in case of variable or shifting spawning times. Relationships between temperature and timing of gonadal maturation (Hutchings and Myers, 1994; Carscadden *et al*., 2001) may be used to direct the effort of the ichthyoplankton surveys if survey dates are flexible; otherwise a full coverage of the spawning time is needed. However, spatial differences in temperature may also affect the distribution of the spawning effort, e.g. for anchovy and sardines in the Southern Benguela system (LeClus, 1990).

Additionally to timing and location of the spawning activity, variable transport of eggs and larvae caused by large-scale atmospheric forcing may significantly affect the distribution of larvae (e.g. Hermann *et al*., 1996; Shannon, 1998). In fact, the latter process may be why Köster *et al*. (this volume) were unable to find a relationship between Baltic sprat larval abundance and recruitment based on the ichthyoplankton surveys. Given a shallower distribution of larger sprat larvae in the water column compared to cod (Wieland and Zuzarte, 1991), wind driven transport out of the survey area may regularly occur. Hydrodynamic modelling revealed that advective losses hardly occur at low to moderate wind speed (the normal situation at peak spawning time of sprat) but may reach the order of 25% at higher wind forcing (STORE, 2001). Given the maximum current velocities and the topography in the Central Baltic, the impact of advection is probably relatively low compared to other areas, for example characterised by shelf-edge jet currents (e.g. Shannon, 1998).

Considering the prerequisite to cover times and areas of late larval occurrence adequately and considering the impact of advection, it is clear that recruitment forecasting from larval surveys has seldom been employed in stock assessment and attempts have largely been unsuccessful, although relationships between late larval abundance and recruitment have been described for a variety of stocks, e.g. for Northeast Arctic cod (Sundby *et al*., 1989), for Northern Baltic sprat and herring (Sjöstrand, 1989) and for North Sea herring (ICES, 2000e).

Simulation studies performed by Bradford (1992) and Mertz and Myers (1995), utilising published data on mortality rates of early life stages and their inter-annual variability, suggest that predictions of recruitment based on late larval abundance or larval mortality rates are in principal possible, but only with low variability in early juvenile mortality or with mortality rates correlated across stages. Nevertheless, we believe that application of advanced hydrodynamic models utilising realistic wind forcing will make it possible to correct ichthyoplankton survey results for advective gains and losses. This will not solve the problem of a temporal mis-match of surveys and larval production, nor will it solve problems caused by very narrow temporal and spatial larval survival windows that are apparent for some fish stocks (e.g. Houde 1989b). Especially the latter process needs further investigation, applying also different approaches like description of the characteristics of surviving juveniles (e.g. Fritz *et al.*, 1990; Taggart and Frank, 1990), and again hydrodynamic modelling allows one to reconstruct the physical environment which leads to increased survival success (e.g. St. John *et al.*, 2000).

Coupled hydro- and trophodynamic models

Modelling transport, growth and survival of early life stages of fish by coupled hydro- and trophodynamic models is a research area that is currently a focus of scientific interest. Several of these bio-physical models have been established, e.g. for walleye pollock (Hermann *et al.*, 1996; Hinckley *et al.*, 2000), haddock off Scotland (Heath and Gallego, 1998; Heath and Gallego, 2000), bay anchovy from Chesapeake Bay (Rose *et al.*, 1999), haddock on Browns Bank (Brickman and Frank, 2000; Brickman *et al.*, 2001) and cod in the Baltic (Hinrichsen *et al.*, 2002a). In general the hydrodynamic models using either Lagrangian particle tracking (Werner *et al.*, 1996) or advection-diffusion equation models (Lynch *et al.*, 1998) are forced by realistic atmospheric conditions and resolve the small-scale vertical and meso-scale horizontal hydro-dynamics quite well.

The biological components are more problematic: the stage dependent egg mortality is beyond predictability (Brickman and Frank, 2000), and modelling of larval growth is difficult, especially as in general prey fields are not available in sufficient temporal and spatial resolution. This leads to the following assumptions: i) prey concentration does not limit larval growth, thereby making inclusion of food-dependent feeding and growth rates redundant (Heath and Gallego, 1998), ii) mean prey densities are uniform in space and time (e.g. Herman *et al.*, 1996), iii) prey density is variable over season, but invariate over years (Tyler *et al.*, 1997), partly considering feed back by predation on prey density (Rose *et al.*, 1999), and iv) prey density is horizontally and seasonally variable, applying overall yearly weighting factors to account for inter-annual variability in integrated prey abundance (Hinrichsen *et al.*, 2002a). Depending on the magnitude of spatial, intra- and inter-annual variability in prey fields, one or the other approach may be justified, as generation of a dynamic 3-D prey field requires ultimately species and stage specific modelling of the zooplankton population dynamics (Miller *et al.*, 1998; Lynch *et al.*, 1998).

Furthermore, variability in predation pressure is not considered in any of the models yet, resulting in mortality rates being forced mainly by physical conditions affecting egg developmental rates, larval growth and in turn larval mortality rates. This presently limits the application in recruitment predictions. However, existing coupled hydro- and trophodynamic models offer a framework for testing hypotheses on various processes affecting egg, larval and juvenile survival and considering variability in environmental conditions in space and time. In particular, the identification and generation of environmental indices (e.g. upwelling, transport) representing one or a number of important processes that affect larval survival may be possible. These in turn, can then be utilised in simpler recruitment models.

Prediction of recruitment incorporating environmental variability

Environmental factors influencing recruitment have been identified in almost all fish stocks. In some cases single factors seem to explain a considerable part of the recruitment variability (e.g. Planque and Fox, 1998), however, in most cases a suite of environmental factors is involved (e.g. Megrey *et al.*, 1995; Painting *et al.*, 1998; Jarre-Teichmann *et al.*, 2000).

Walters and Collie (1988) criticised correlative environment-recruitment studies because of biases, measurement error and the high likelihood of spurious correlations. Myers (1998) reviewed the success of previously published environment-recruitment correlations when they were tested with new data.

He concluded that correlations for populations at the limit of a species range were often confirmed, while correlations near the centre of a species range frequently failed. The approach of comparing many populations of the same or similar species has been used intensively in eastern boundary upwelling systems (Bakun, 1996). In particular the optimal environmental window hypothesis relates recruitment to the environment in upwelling systems (Cury and Roy, 1989), suggesting a non-linear dome-shaped relationship between recruitment and upwelling intensity.

One of the few applications of environment-recruitment relationships in stock assessment was introduced for the anchovy in the Bay of Biscay. As the stock development and fisheries depends to a large extend on the abundance of age-group 1, prediction of recruitment is of considerable importance in the management of the fishery, similar to other anchovy stocks (e.g. Bloomer et al., 1994). The fishery on age-group 0 provides only a limited indication on the year-class strength and there exists no apparent stock-recruitment relationship (ICES, 2001). However, a close correlation of recruitment to the intensity of upwelling along the French and Spanish coast has been identified by Borja et al. (1996 and 1998). This relationship was utilised by the assessment Working Group in 1999 (ICES, 2000b) to predict the year-class strength 1998 (in combination with commercial catch data) and 1999 to be incorporated into the short-term prediction for 2000. In this prediction both year-classes were substantially underestimated, with the consequence that up-dated recruitment predictions in 2000 were not considered in short-term predictions for 2001 (ICES, 2001). Instead, alternative environmental indices were tested. A statistical model suggested by Allain et al. (2001) utilising upwelling and shelf stratification breakdown, as generated by a 3-D hydrodynamic model, performed best when updated with most data of recent years. Upwelling from March to July has a positive effect on recruitment, while the presence of a decrease in the mean stratification in June/July has a negative effect on recruitment. Integration of both variables in a multiple linear regression explains 59% (Fig. 9) of the variability in recruitment at age 0 compared to 50% using one of the available upwelling indices alone (ICES, 2001).

Tyler (1992) claimed that this type of correlation analysis may also be used in single populations if a sound conceptual framework and judicious use of statistical methods is applied. In agreement with

Megrey et al. (1996), we believe that a combination of approaches is required for the identification of major processes affecting reproductive success: i) investigation of the spatial and temporal distribution of different early life stages in relation to hypothesised key events separately, ii) testing of the underlying processes in coupled bio-physical models under various forcing conditions and iii) comparison of time series of important environmental variables with recruitment success using a suite of statistical methods. In any case, a sound estimation of the stock's reproductive effort as well as reproductive success in terms of juvenile abundance is required. Especially the latter has in quite a number of recruitment studies been taken from standard assessment output, without questioning the reliability of the estimate (see below).

The predictability of identified key environmental variables and the strength of the relationship between recruitment and these variables define the potential of reducing uncertainty in stock predictions and set their time limits (Basson, 1998). Quite clearly an improved understanding of large-scale physical atmospheric and oceanographic processes affecting local physical conditions may improve the time frame of predictions. An example is the first order autoregressive model of volume flux to the Western Barents Sea. In this model the position of the Gulf Stream off the US coast two years earlier explains 50% of the variability in temperature in the Barents Sea, an important factor for Northeast Arctic cod recruitment, growth and distribution (Ottersen et al., 2000). The predictive power is still
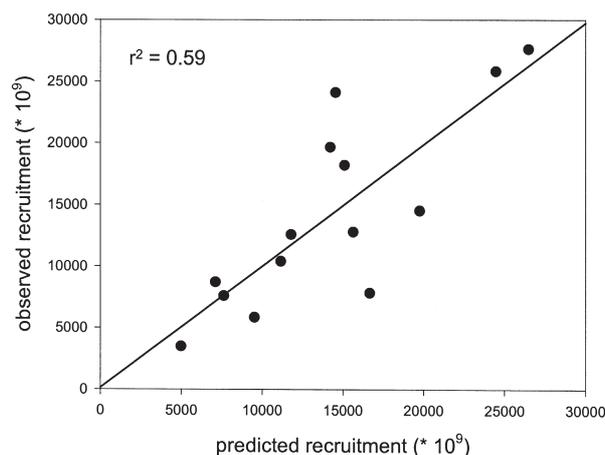

FIG. 9. – Observed vs. predicted recruitment of anchovy in the Bay of Biscay, predicted from a multiple linear regression of 0-group recruitment on upwelling intensity in March-July and an index of stratification breakdown in June/July (based on model by Allain *et al.* 2000; data from ICES, 2001).

limited and forecasting the stock development 4 years ahead (the stock recruits at age 3) would require in addition a prediction of the capelin stock development, which is currently possible 2-3 years ahead (Ulltang 1996). Nevertheless, the information could be used in medium-term projections simulating the stock development under different exploitation scenarios.

Apart from utilisation of established empirical environment-recruitment relationships, short-term forecasts may be based on non-parametric classification schemes (Rothschild and Mullen, 1985), as demonstrated for walleye pollock by Megrey *et al.* (1996) or cape anchovy by Painting and Korrûbel (1998).

Density dependence in the juvenile stage

While density-dependent processes are less evident in the larval stage, they are more easily detectable in the juvenile stage, especially for populations that concentrate in specific nursery areas during the first year of life (Iles and Beverton, 2000). Density dependent mortality has been identified in different flatfish species during the phase shortly after settlement, dampening the inter-annual variability in recruitment, but not explaining a significant part of the variability (Van der Veer *et al.*, 2000).

By meta-analysis, Rijnsdorp *et al.* (1992) found a positive relationship between average recruitment success and spatial extension of the nursery grounds for sole, which holds also for different plaice populations around the North Sea (Van der Veer *et al.*, 2000). Similar to flatfish, density dependent mortality has been detected in walleye pollock during the transition between the larval and the juvenile phase (Bailey *et al.*, 1996). This has been explained by increasing predation pressure on young of the year when they start schooling behaviour. Similarly, Sundby *et al.* (1989) reported density dependent mortality for juvenile Northeast Arctic cod in the transition phase from pelagic to demersal mode of life. A high predation pressure on settled juveniles also appears to be an important reason for density dependence in flatfish populations (e.g. Bailey, 1994; for review see van der Veer *et al.*, 1997).

Also temperature effects on juvenile survival, as detected for North Sea plaice (e.g. Brander and Houghton, 1982), have been explained by related changes in predation: Van der Veer and Bergman (1987) suggest a release from predation by crus-

taceans in the nursery area due to avoidance of these areas by the predator at low temperature. In general, density dependent predation on juveniles has been identified as a factor controlling recruitment success or dampening its variability (Van der Veer *et al.*, 2000); in both ways it may have a significant influence on the population dynamics of most fish stocks and thus needs to be considered in recruitment predictions.

A framework for exploring density dependent processes in the juvenile stage has been set-up by Heath and Gallego (2000) for haddock off Scotland. The basic concept with respect to egg and larval development has been described before. For the transition from pelagic to demersal phase a density dependent mortality was incorporated. This is based on the observation that a negative autocorrelation has been detected in North Sea haddock recruitment, with strong year classes inhibiting the establishment of recruitment in immediately following year-classes (Cook and Armstrong, 1986). The present model is relatively simple, assuming competition for available space on the seabed to be the regulating process, but in principal the framework is flexible to incorporate more advanced process models (Heath and Gallego, 2000). The coupled individual based and hydrodynamic model has been used to explore the effect of spawning stock size on the spatial and temporal patterns in survivorship of various developmental stages. In absence of any density dependent processes in the pelagic phase, the temporal pattern of survival from different spawning dates was independent of spawning stock abundance. During the demersal phase, however, an increased spawning stock resulted in decreased survival for later spawned cohorts, as earlier spawned individuals inhibited their settlement. This type of model, further improved with respect to biological and physical process models, has the potential to incorporate temporal and spatial dynamics in the recruitment process, allowing simulations of stock development under area- and time-specific exploitation strategies and environmental variability.

Predation mortality and abundance of pre-recruits from multispecies models

Estimating pre-recruit predation mortality and abundances by multispecies models carried into earlier age-groups has been suggested as a tool to determine the reproductive success of fish stocks (Sparholt, 1995; Ulltang, 1996). We have used this
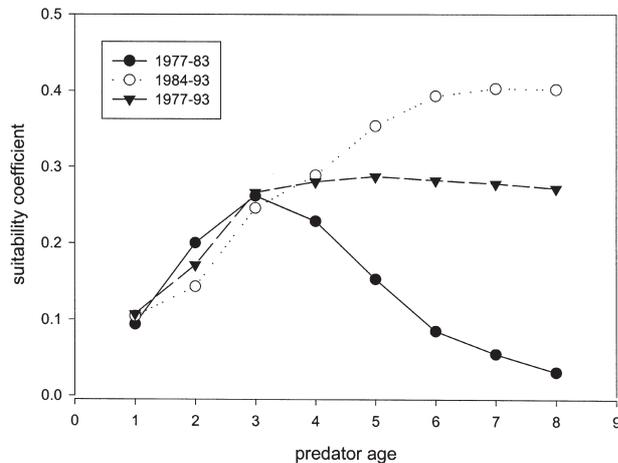
FIG. 10. – Suitability coefficients of Baltic cod age-group 0 as prey of predatory cod age-groups 1-8 (averages over quarters), determined with different sets of stomach content data: 1977-1983 encompassing the period of high and 1984-1993 the period of low occurence of cod in cod stomachs, as well as the entire period used in standard MSVPA (from ICES, 1999b).

technique for Baltic cod and sprat as well (Köster *et al.* 2001a). However, present multispecies models use constant prey-predator suitability coefficients over time (Sparre, 1991), an assumption that might lead to dampened variability in recruitment estimates.

For prey species regularly taken by a predator, the assumption of constant suitability coefficients appears to be reasonable. However, this cannot be applied to estimate the effect of cannibalism in Baltic cod, as this is relatively seldom an intensive process (Uzars and Plikshs, 2000), but may occasionally remove considerable amounts of juveniles from the population (Sparholt, 1994).

In order to test the stability of suitability coefficients, ICES (1999b) performed MSVPA runs splitting the available time series of stomach content data into an early and a late period with high and low occurrence of cannibalism respectively. The resulting average suitability values of 0-group cod are very similar in both periods for predators up to age-group 3, but increasingly different for older predators (Fig. 10). For the early period coefficients further increase with age following an asymptotic function, while for the later period an almost linear decline is encountered. We interpret this difference with a change in predator distribution: at a low stock size, the majority of the adult stock is concentrated in southern central areas, while nursery areas are located mainly in the eastern Baltic. This distribution pattern results in a more limited overlap between juvenile and predatory adult cod when the

stock size is decreasing, but a continued overlap of early and late juveniles and recruits (up to age-groups 3). Also in northern cod the intensity of cannibalism has been related to spatial overlap of young and older stages, in this case, however, related to the extension of the area occupied by the juveniles, depending on year-class strength (Anderson and Gregory, 2000).

Apart from medium- to long-term distribution changes, inter-annual variability in cannibalism may be influenced by changing hydrographic conditions as well, reported for example by Wespestad et al. (2000) for walleye pollock. Here strong year-classes are generated when juvenile pollock are transported inshore in spring, minimising the horizontal overlap to the adults, while weak year-classes are formed when transport is reduced and juveniles remain on the outer shelf in the vicinity of cannibalistic adults.

Backtracking of recruitment into the pre-recruit stage by multispecies assessment models requires that major predators, or at least those predators which exert fluctuating, substantial predation pressure, be considered in the model, and the same applies for stock predictions of the prey species. This limits the approach to relatively simple systems, with a limited number of dominating predator species, e.g. the Northeast Arctic cod, capelin and herring complex (Bogstad *et al.*, 1997), while application for the North Sea and Georges Bank is already difficult. Furthermore, backtracking might only be possible to older juvenile age-groups, as predation on smaller 0-group fish is likely to be more complex with several predatory species involved.

It should be noted that the MSVPA is only one of the available multispecies models with the potential to be utilised in estimating predation mortalities and abundances of pre-recruits (for review see Hollowed *et al.*, 2000). In comparatively simple ecosystems, simpler models for estimating predation pressure on juveniles may also be successful. An example is given by Ulltang (1996), who plotted a survival index (the ratio between observed 0-group abundance and year-class strength at age 3 from VPA) against an index of cod predator abundance (the sum of the size of three preceding year-classes at age 3). This resulted in a very close relationship for the 1980s, while including the 1970s generated a higher variability, especially in the earliest years of the time series. For other potential methods, see discussion in Ulltang (1996).

Early juvenile abundance and size as a predictor of recruitment

Young fish surveys are a common tool in stock assessment to give an indication about incoming year-class strength. Some surveys are directed to the early 0-group, still pelagic even in demersal species; examples are 0-group cod in the Barents Sea (Nakken and Raknes 1996) and around Iceland (ICES, 2000f), and herring in the North Sea (ICES, 2000e). Others are directed to early settled juveniles, such as age-group 1 cod in the Barents Sea (Jakobsen *et al.,* 1997), 0- and 1-group plaice and sole in the North Sea (ICES, 2000g), or to well established juveniles, as in the IBTS survey in the North Sea (ICES, 2000h) and the BITS survey in the Baltic (ICES, 2000i).

Besides catchability problems (e.g. Nakken and Raknes, 1996), the surveys on early juveniles and to a lesser degree also on later stages suffer, to a varying degree from intra- and inter-annual variability in the distribution of the target. Here relatively early life stages have the advantage that they still concentrate in the vicinity of spawning areas that are easier to cover than widespread distribution areas of older juveniles (for example see Helle *et al.,* 2000).

In general, sufficient knowledge is available on timing and location of spawning to apply hydrodynamic modelling approaches with realistic atmospheric forcing conditions, which may detect unusual transport situations and potentially also enable the correction of abundance indices.

Variability in survival until recruitment to the fishery is a general problem, which explains the tendency of assessment groups to utilise abundance indices of well established older juveniles, which of course reduces the lead time in stock predictions. Present short-term predictions within ICES are based on last year's assessment data, predicting next years stock and catch development. Thus, a survey in the present year assessing the year-class strength of next year's recruits satisfies basically the demand to conduct short-term predictions. To predict the surviving population size in the next but one year requires a recruitment estimate of the subsequent year-class. However, most assessment working groups consider the impact of this uncertainty as marginal, especially as they concentrate on the spawning stock size as the most important stock measure.

In fact, one might be more interested in predicting growth and maturation of the recently and presently recruiting year-classes to describe the development of the reproductive potential of the stock (see quadrant 1). In any case, there is a clear cut difference in the needs of present stock assessment and recruitment related research, though the latter may enable expansion of short-term predictions into the medium-term time frame, at least for relatively long living species, as outlined earlier. A prerequisite for such an application is the establishment of close relationships between predictor and recruitment (e.g. Walters and Collie, 1988; Bradford, 1992) and, perhaps even more important, a sufficiently stable relationship over extended time periods.

High correlations between average pelagic juvenile size and year-class strength have been identified for cod on Georges Bank (Campana, 1996), haddock on the Scotian shelf (Marshall and Frank, 1999b) and cod and haddock in the Barents Sea (Ottersen and Loeng, 2000), confirming the hypothesis that survival during the pre-recruit stage is directly related to growth rates (Anderson, 1988). Utilisation of log-transformed 0-group recruitment indices and mean length of 0-group in an autoregressive modelling revealed 60% and 65% explained variance in log year-class strength at age 3 of Northeast Arctic cod and haddock (Ottersen and Loeng, 2000). Although these coefficients of determination are reasonably large, the confidence limits of the regressions are rather wide and utilisation in recruitment predictions appears reasonable only within a long time perspective, if the basic relationships included remain stable.

PROCESSES AND VARIABLES TO BE INCORPORATED INTO STOCK PREDICTIONS

The present review has identified a series of environmental variables affecting growth, maturation and egg production, early and juvenile life stage survival and subsequent recruitment. The following section discusses the feasibility of an implementation of identified relationships to estimate input variables into short-term predictions and medium- to long-term projections, as well as shortcomings in our understanding and/or limits of predictability that hamper the incorporation in regular stock projections in foreseeable future.

Short-term predictions

The bases for short-term stock predictions are estimates of the current stock sizes. These may be

improved by considering the effect of changes in habitat suitability and shifts in the distribution of stocks when commercial or research survey catch rates are used for tuning of VPA's or related assessment models. This requires detailed knowledge about habitat preferences and behavioural response to unfavourable conditions, as well as sound information on gear selectivity and avoidance in relation to behavioural changes. Furthermore, estimates of current stock sizes may be improved and/or validated by available independent abundance indices presently not utilised, e.g. application of the egg production method for gadoids.

Recruitment estimates may also be important in short-term predictions, depending of course on the impact recruiting year-classes have on the catch and the spawning stock development. If recruits sustain a substantial part of the catch and/or get sexually mature shortly after recruiting to the fishery (e.g. anchovies), the applied recruitment estimates will affect the prediction, especially if high variability in recruitment occurs, as is typical for small pelagic fish. However, gadoids like haddock and some flat-fish stocks also show high variability in recruitment, mostly characterised by a series of relatively low year-classes and once in a while interrupted by an outstanding high year-class. In all these stocks reliable information on recruitment in the assessment and the prediction year would improve short-term predictions. Recruitment estimates may be derived by i) adequately designed late larvae or pre-recruit surveys, potentially backed-up by hydrodynamic modelling to determine advective losses and gains , ii) empirical proxies related to survival success during the early life stages (e.g. size at age), or iii) predictions based on the size/structure of the spawning stock and observed or predicted environmental conditions affecting offspring survival, similar to the procedure suggested for medium- to long-term projections (see below).

Predation mortality may be an important factor to be considered for short-term prediction of prey species in systems dominated by single or a few predatory species exhibiting large fluctuations in stock size. Especially if alternative prey species fluctuate anticyclic to the predator abundance, changes in predation mortality from year to year may be pronounced. Existing multispecies prediction programmes are able to handle this type of interaction, given that the functional response of the predator to changing prey availability is adequately described. However, changes in spatial overlap between predator and prey forced, for example, by hydrographic conditions are presently ignored. Potential candidates for the implementation of multispecies predictions are obviously small pelagics, e.g. capelin stocks, for which multispecies predictions are already partly in use (Barents Sea stock, see Bogstad and Mehl 1997). If full grown multispecies prediction models are not readily available, we can proceed through short-cuts, e.g. relating predation mortalities or indices of predation pressure to predator stock size development.

None-predatory natural mortalities are presently kept constant over the prediction period. However, if evidence of drastic environmental changes and/or pronounced fluctuations in prey abundance is observed, inter-annual variability should in principle be incorporated into short-term predictions. Allowing for inter-annual variation in residual mortality requires i) established relationships between mortality rates and health or nutritional condition in dependence of environmental variables and ii) monitoring of these environmental variables within the assessment year and a prediction for the subsequent year. These requirements, not yet met in any fish stock, will restrict the application to fish stocks which are at their limit of distribution and are thus vulnerable to changes in abiotic conditions and/or heavily dependent on single fluctuating prey taxa (e.g. gadoids in boreal systems).

Growth and maturation will respond to similar changes in environmental conditions. While substantial changes in residual mortality are relatively infrequent catastrophic events, weight at age and maturity ogives will respond more closely to environmental changes and are thus also more important candidates for dynamic inclusion in short-term predictions. Possibilities exist of making predictions of weight at age and also maturity at age operational, as clear relationships have been established between prey availability and changes in weight and proportion mature at age for some of the well studied gadoid stocks (e.g. Northeast Arctic cod). For some pelagic fish species, density dependent changes in weight at age have been resolved and consequently relationships to stock sizes, potentially including population sizes of competing species, may be utilised to predict weight at age changes (e.g. sprat and herring in the Baltic). The latter procedures in particular are short-cuts, and efforts should be allocated to implement identified processes in the forecast routines more explicitly.

Medium- to long-term projections

Medium- to long-term projections in contrast to short-term predictions depend heavily on the recruitment model employed (e.g. Gislason 1993). In ICES standard projections, recruitment is in general modelled via traditional stock-recruitment relationships. Given that recruitment depends on a combination of environmental conditions, spawning stock characteristics and species interactions, it can be expected that the predictive power of this approach is limited. Consequently, recruitment models need to be expanded to incorporate the most important processes affecting reproductive success. Among the factors and processes to be considered are: i) size, structure and condition of the spawning stock and its viable egg production, ii) temporal and spatial distribution of spawning effort, iii) impact of physical/chemical conditions on fertilisation, egg development, hatching success and larval survival, iv) food availability for larvae and juveniles in terms of quantity and quality, and v) predation pressure on all juvenile life stages. In order to do this, we are faced immediately with two major problems: various combinations of processes act in different species and even between different stocks of one species. Thus, sound conceptual models of the effects of processes are required for each stock. Secondly, changes in major environmental conditions may prove to be impossible to predict, even a generation ahead, leading to the conclusion that stochastic approaches may be the only way to proceed. However, if major changes in the environment are likely to happen, e.g. environmentally driven regime shifts (Beamish et al. 1999), or if typical cycles or general trends can be identified and the impact on specific important processes has been resolved, modelling of corresponding scenarios appears to be important.

In fish stocks exposed at times to adverse abiotic environmental conditions and/or suffering from highly variable food supply (i.e. depending on single or few fluctuating prey species), egg production may be highly variable, largely independent of the size of the spawning stock. Thus, the spawning stock biomass as an input parameter for stock-recruitment relationships should be replaced by the potential egg production as a function of stock size and structure, utilising relationships between growth, maturation rates and fecundity, all coupled to environmental conditions and/or food supply. In case of limited databases, proxies closely related to the viable egg production may be utilised instead of the estimated egg production of the population. If strong relationships exist with major prey species, for which regular assessments and predictions are conducted, existing multispecies forecast models may be modified to include identified processes.

If the reproductive potential of a stock is substantially affected by fluctuating abiotic environmental conditions, any prediction is limited to a time frame of years equivalent to the recruiting age plus one year at best, while long-term forecasts are restricted to scenario modelling, assuming trends in specific environmental conditions, empirical cycles or random variation.

In addition to the quantity, also the quality of the egg production may be modelled as a function of size/age structure of the spawning stock, spawning experience and nutritional condition of the spawning stock. Atresia is a commonly observed process in fish, which is linked to the nutritional condition of the females. The intensity and thus the impact on the actual egg production is in general not well understood and needs to be studied in more detail. Exceptions, however, exist and information on atresia has also been used as qualitative information in recruitment predictions (e.g. Cape anchovy, see Painting and Korrûbel 1998).

Temporal and spatial distribution of spawning activity, defining the environmental conditions faced by offspring, is related to an endogenous cycle, to environmental conditions during the period of oocyte ripening and to habitat preferences of the spawning fish. These processes are in principal understood for a number of fish species, but they have hardly been utilised in any stock predictions.

Fertilisation success may vary according to physical/chemical conditions on spawning grounds, first of all ambient salinity in estuarine systems. The impact of nutritional status and spawning experience on sperm quality appears to be more limited, and evidence suggesting the necessity of inclusion in recruitment models does not exist.

For egg and early larval survival, temperature may be especially important to consider in northern or southern areas of the distribution range, while salinity and oxygen cause problems mainly in stratified systems. Based on established relationships between physical factors and developmental/survival rates, considering information on temporal/spatial distribution of spawning activity, survival until the larval stage may be hindcasted and also predicted given that the environmental conditions are known.

Predation mortality on early life stages is in general not well understood and will hamper predictions if a substantial and variable impact on survival rates occurs. There is a clear necessity of substantial research input, especially with respect to the functional response of predators and the role of temporal/spatial overlap between predator and prey under varying environmental forcing conditions. For larger juveniles the traditional multispecies prediction models offer the possibility to forecast abundance and predation mortality, given that major predators are incorporated in the model and environmental variability does not seriously affect the functional response implemented, an assumption which remains to be tested.

Hatching success and larval activity are again coupled to the quality of spawning products, but also to abiotic environmental conditions during incubation. Larval feeding success is dependent on larval activity and the quantity and quality of available food as well as abiotic environmental conditions affecting capture success (e.g. turbulence, temperature). Although this area has been a focus of recruitment research for the last decades, the complex interplay between various trophodynamic processes at lower trophic levels and abiotic environmental variability made it difficult to develop hindcasting or even prediction models. Advances in hydrodynamic modelling and increased capabilities to include larvae as "intelligent" tracers into the models, and to generate at the same time the abiotic environment, are major steps to hindcast distribution pattern, identify potential and actual nursery areas and describe conditions that lead to survival success.

The implementation of advanced coupled hydro- and trophodynamic models considering, besides different early life stages, the temporal and spatial heterogeneity in the dynamics of food availability and spatial overlap to predators are major future steps in modelling recruitment processes. These models allow suggested environmental indices to be tested and new indices to be developed for use as proxies for survival probability (e.g. upwelling indices, transport rates, temperature, zooplankton abundance). However, their predictive time frame will be limited by our ability to forecast large-scale atmospheric forcing conditions, with response times in ocean characteristics being in the best cases some months. Thus, application in long-term projections will be restricted to scenario modelling approaches.

The distribution of juveniles is not only affected by advection/retention to/in nursery areas, but also by an increasing activity range with increasing size/age. Thus, the impact of habitat preferences and environmental threshold values will increasingly affect the distribution of the recruits similar to adult fish. Changing behaviour in response to environmental variability will affect catchability of commercial fishing gears and may thus violate the relationship between fishing effort and fishing mortality, which has an impact on the use of effort restrictions as a fisheries management measure. Furthermore, changes in behaviour and distribution will most likely affect the exploitation pattern, usually assumed to be constant over the prediction period.

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