Recruitment in flatfish, with special emphasis on North Atlantic species: Progress made by the Flatfish Symposia

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(AP)

In summarizing the main results on recruitment that emerged from the series of
Flatfish Symposia, two aspects were distinguished: mean level and interannual
variability. Recruitment to a stock appears to be related to the quantity of juvenile
nursery habitats, suggesting that either larval supply or the carrying capacity of
the nurseries is the limiting factor. However, available information on growth of 0-group
flatfish suggests that the carrying capacity of nursery areas is never reached. Variability
in year-class strength is generated during the pelagic egg and larval stage, probably by
variations in the hydrodynamic circulation and in the mortality rates of eggs and
larvae. Density-dependent processes seem to occur only during the juvenile stages,
particularly in respect of growth. However, no impact on recruitment variability has
been found. Density-dependent mortality during the phase shortly after settlement
dampens the interannual recruitment variability. There is no evidence of density-
dependent effects in the adult phase at present, but these may have been important at
lower levels of exploitation. The importance of the factors determining recruitment
vary not only among species, but also over the species' range. It is suggested that
damping processes can only occur in the demersal stage, implying that variability in
year-class strength can only decrease in fish species with a demersal stage. If true,
ultimate variability in recruitment in fish species will be related to the relative duration
of the pelagic and demersal stages.

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Introduction

Flatfish are distributed over virtually all latitudes
(Pauly, 1994) and therefore present an attractive group
for the study of geographic variation in recruitment
processes. Most species are characterized by pelagic egg
and larval stages and demersal juvenile and adult stages.
Juveniles are often concentrated in restricted shallow
"nursery" areas, where they offer excellent opportunities
to carry out quantitative studies.

Studies on the early life history of flatfish started with
the work of Pearcy (1962) on winter flounder (*Pseudo-
pleuronectes americanus* (Walbaum)) on the east coast of
the United States. This pioneering work was followed up
by classical studies in Great Britain, particularly on

plaice (*Pleuronectes platessa* L.). These concentrated
initially on the demersal juvenile stage (e.g., Riley *et al.*,
1981; Edwards and Steele, 1968; Lockwood, 1974), but
later focused also on the pelagic egg and larval phase
(e.g., Talbot, 1978; Harding *et al.*, 1978). Zijlstra (1972)
emphasized the importance of the Wadden Sea estuaries
along the Dutch, German, and Danish coasts as nursery
areas for plaice and sole (*Solea solea* (L.)). His publi-
cation formed the first in a series on these species in
continental Europe (e.g., Kuipers, 1977; De Vlas, 1979;
Zijlstra and Witte, 1985; Berghahn, 1987; Rijnsdorp
et al., 1985; Van der Veer, 1986; Pihl, 1990; Hovenkamp,
1992).

In the mid-1980s, extensive investigations indicated
that year-class strength in plaice was determined during

the early pelagic stages (Zijlstra and Witte, 1985; Van der Veer, 1986). However, it remained unclear whether similar conclusions were valid for other species and areas. At the 1988 ICES Symposium on "The Early Life History of Fish" in Bergen, the idea originated to organize a flatfish symposium aimed at making an inventory of the present state of knowledge. The late Ray Beverton strongly supported the plan and he took a lead as a member of the organizing committee. The First Flatfish Symposium in 1990 with the theme "Life Cycle", was followed up by a Second in 1993 on "Recruitment" and a Third in 1996 on "System Dynamics of Flatfish". Simultaneously, other forums were organized, such as the International Symposium on North Pacific Flatfish in 1994 (Anon., 1995). But even after three decades of investigation, the central question in flatfish biology remains: what causes variability in year-class strength?

We review the progress made over the last decade in solving the recruitment problem, with a main focus on North Atlantic flatfish species. Firstly, we discuss the factors determining the mean level of recruitment. Secondly, the processes affecting variability in recruitment are analysed. And finally, a synthesis of the available information is presented.

Definitions

Recruitment is defined as the number of individuals that reach a particular age to join a specific part of the population (e.g., the mature population). It is thus a number that varies from year to year. We use recruitment process to cover everything that affects survival between spawning (or even before that: maturation) and the stage of life where year-class strength is more or less fixed. We distinguish two important aspects: the actual number of recruits and the (interannual) variability therein. We use recruitment level to identify the ultimate number of a specific year class that survives to attain sexual maturity and joins the reproductive population. In addition, indices of the number of juveniles of a specific year class surviving between spawning and recruitment are called year-class strength estimates. The interannual variability in recruitment can be standardized by expressing it as coefficient of variation.

Two sets of factors may be distinguished: variability generating or controlling factors and variability damping or regulating factors. Controlling factors enhance the variability in year-class strength, and are reflected by an increase in the coefficient of variation at a particular life stage compared with a previous stage. Regulating factors reduce variability in year-class strength and ultimately in recruitment. These show up as a decrease in the coefficient of variation at a certain life stage compared with a previous stage (Fig. 1). Correlations
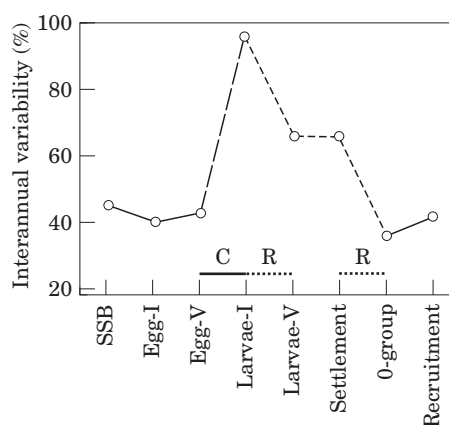

Figure 1. Sequence of variability generating or controlling factors (C) and variability damping or regulating factors (R) illustrated by changes in the coefficient of variation in abundance during early life history of plaice (*Pleuronectes platessa*) (data after Van der Veer, 1986).

between abundance estimates at various life stages and recruitment reveal when year-class strength is determined and fixed.

Recruitment level

Rijnsdorp *et al.* (1992) found a positive relationship between relative recruitment, both mean and maximum, and the approximate surface area of the nursery grounds for a number of sole stocks (Fig. 2). This intraspecific "nursery size hypothesis" appears to be valid also for plaice: the abundance of 0-group for different populations around the North Sea shows a positive relationship to the size of the nursery area (Fig. 3). Recently, Steinarsson and co-workers (unpubl.) carried out a similar analysis for subpopulations of plaice around Iceland and found a positive relationship between size of the nursery area and adult stock size (Fig. 4). Rijnsdorp *et al.* (1992) further suggested that the "nursery size hypothesis" might also be valid for interspecific differences between flatfish species. In examining the abundance of flatfish species in the North Sea, Gibson (1994) indeed found a significant positive correlation between the habitat requirements of juveniles in terms of depth range and their abundance (Fig. 5). The hypothesis might also explain why turbot (*Scophthalmus maximus* (L.)) and brill (*Scophthalmus rhombus* (L.)) are relatively rare species in the North Sea (Daan *et al.*, 1990), since their nursery areas are restricted to a narrow band along sandy beaches with a water depth of less than 1 m (Riley *et al.*, 1981). Obviously, the information available strongly supports the "nursery size hypothesis" not only as explanation of intraspecific but also of interspecific differences in recruitment.

Figure 3. Relationship between average year-class strength in 0-group plaice (*Pleuronectes platessa*) in August (mean ± s.e.) and surface area of the nursery grounds for different areas around the North Sea (data after [1] Edwards and Steele, 1968; [2] Lockwood, 1974; [3] Zijlstra *et al.*, 1982; [4] Pihl, 1990; and [5] Mengedoht, 1995).
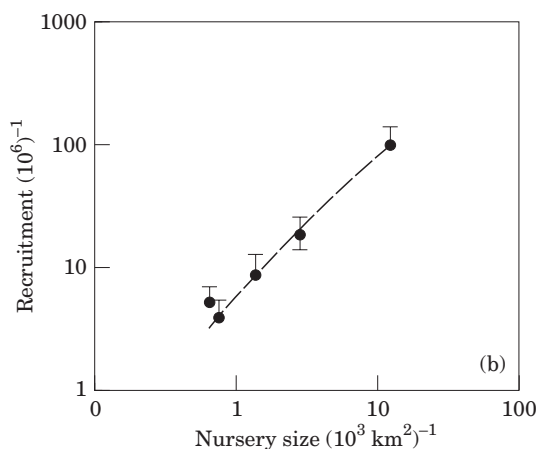

Figure 2. Sole *Solea solea* stocks in ICES Subareas IV and VII. (a) Location of stocks and nursery areas. (b) Relationship between average recruitment (geometric mean ± s.e.) and surface area of the nursery grounds (data after Rijnsdorp *et al.*, 1992).

The positive relationship between recruitment and nursery size raises the question whether nursery areas may ever become saturated with settling larvae and reach their "carrying capacity". In this context, carrying capacity is defined according to MacCall's theoretical basin model (1990) as the population density of a habitat at which the *per capita* population growth rate is zero. Studies on individual growth of juveniles have yielded contradictory results. Data on growth rate of 0-group plaice and sole generally failed to show an effect of population density. Spatial growth differences could be attributed to different origin of the settlers and its effects on timing of settlement in relation to distance to the spawning grounds (Karakiri *et al.*, 1991), while interannual growth variations could be explained by differences in temperature regimes (Edwards and Steele, 1968; Zijlstra *et al.*, 1982; Van der Veer, 1986; Bergman
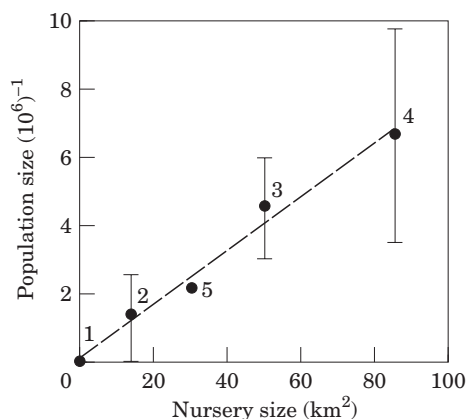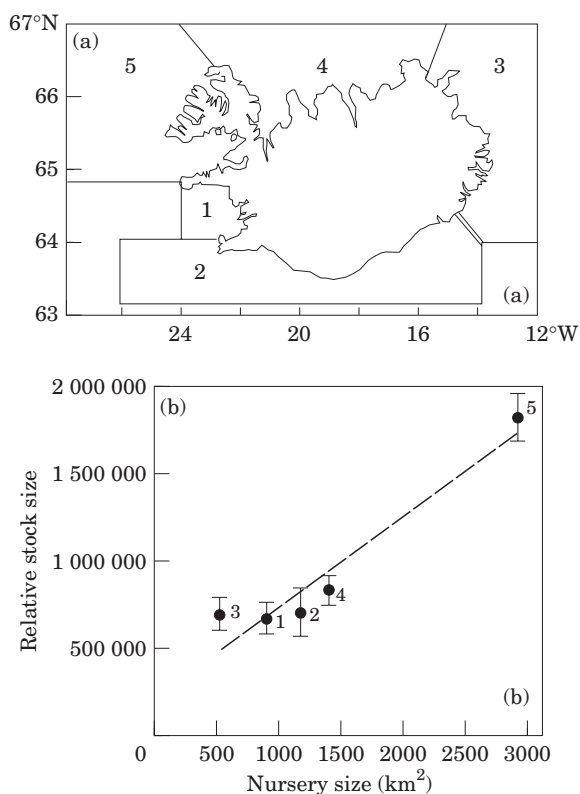

Figure 4. Plaice (*Pleuronectes platessa*) populations around Iceland. (a) Subdivisions used. (b) Relationship between stock biomass (mean ± s.e.) estimated from CPUE multiplied by the surface area of the <100 m zone and the depth zone <20 m (as a measure of nursery size), 1985–1997 (data from Steinarsson, unpubl.).
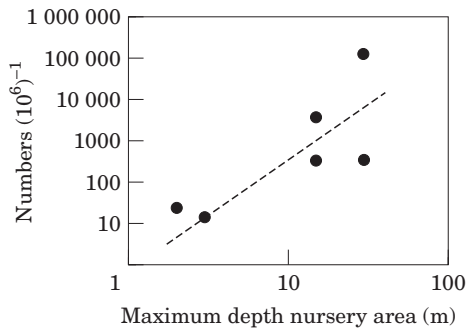
Figure 5. Relationship between stock numbers and maximum depth distribution as a measure of habitat size in North Sea flatfish species (data after Gibson, 1994).
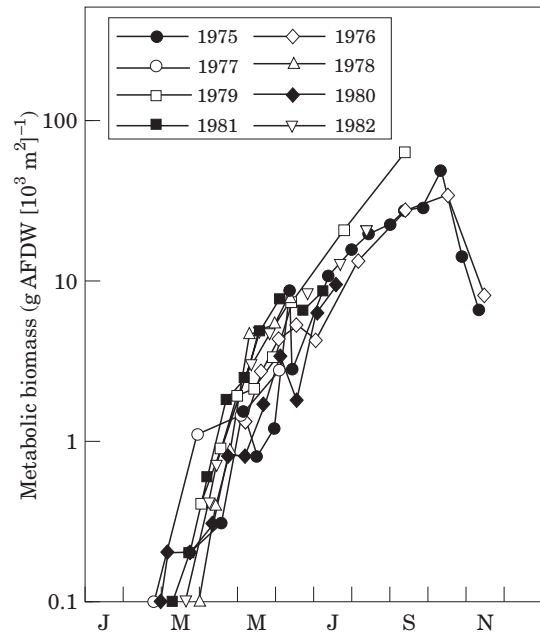

Figure 6. Seasonal pattern in metabolic biomass of 0-group plaice (*Pleuronectes platessa*) at the Balgzand, 1975–1982. For each survey, individual biomass per 0.5 mm size class interval [W (g)=0.0019 L^3 (cm); Fonds *et al.*, 1992] was converted into metabolic biomass (MB=W$^{0.8}$), multiplied by the number of individuals of that size, and summed over all size classes.

et al., 1988; Van der Veer *et al.*, 1990; Rogers, 1994; Nash *et al.*, 1994; Jager *et al.*, 1995). Only Modin and Pihl (1994) were able to show that density-dependent growth in 0-group plaice did occur at extremely high densities. Also, I- and II-group plaice have shown depressed growth rates during periods of high abundance (Rijnsdorp and Van Leeuwen, 1992, 1996).

Studies on population growth of juveniles are scarce. Zijlstra *et al.* (1982) and Van der Veer (1986) provide information for 0-group plaice in the Dutch Wadden Sea for a number of years (Fig. 6). Population growth is expressed as the change in total individual metabolic biomasses (W$^{0.8}$), because the relationship between energy requirements and metabolic biomass is linear in contrast to that with biomass (Fonds *et al.*, 1992). In all years, population biomass increases after settlement in spring until emigration starts in autumn and does not level off during the summer period. The increase during the growing season implies that the *per capita* population growth rate remains positive, suggesting that the carrying capacity is never reached.

It should be noted that interpretation of these growth studies may be biased. Firstly, ambient temperatures cannot be estimated with high accuracy and the true effect may therefore be underestimated. Secondly, field studies have not addressed the potential effects of variations in abundance on the distribution of a year class over primary and marginal habitat. If a larger part of the population of a strong year class moves into a marginal habitat where it experiences lower growth rates and higher mortality rates, a study that is confined to the primary habitat may give a biased signal of the population-regulating processes. Thirdly, the lack of evidence for density-dependent growth in juveniles may be due to other disturbing factors. For example, eutrophication may have resulted in an increased production of suitable benthic food. There are indeed indications that growth rates were lower during the

pre-eutrophication period (Rijnsdorp and Van Leeuwen, 1992; Gibson, 1994). There is ample evidence that food availability and quality is an important factor in determining growth (Rijnsdorp and Van Beek, 1991; Van der Veer and Witte, 1993; Berghahn *et al.*, 1995). Although the information is restricted to a few species only, the data do support the suggestion by Gibson (1994) that saturation of nursery grounds is rare or non-existent, implying that fluctuations in larval supply might be the key factor. Local physical and morphological conditions will determine the passive transport and the ultimate supply of larvae to the nurseries (Rijnsdorp *et al.*, 1985; Bergman *et al.*, 1989). A larger nursery area may be expected to trap on average a larger number of settling larvae.

On a global scale, Pauly (1994) observes a decrease in biomass – and hence recruitment – of flatfish from temperate to tropical areas. He suggests that flatfish are overadapted to feeding on zoobenthic infauna and epifauna, and that, in combination with a decreasing trend in importance of the benthic system towards the tropics, food-limitation might increase with decreasing latitude. This would explain lower biomass values. In contrast to Gibson (1994), Pauly (1994) implicitly assumes that the carrying capacity of the nursery acts as a limiting factor and that it decreases towards the tropics.

Recruitment variability

Variability in recruitment is generally much larger than variability in spawning stock biomass or potential egg production, because the adult population incorporates members of several year classes. The implication is that variability-generating processes operate between spawning and recruitment. The evidence for variability-generating and variability-damping factors during different life stages within a population is discussed separately. Subsequently, the single stock approach will be expanded to differences between populations of the same species over its geographical range of distribution, and between species.

Variability-generating factors

The adult stage

For individual stocks, first maturation occurs within a specific size range. After spawning, the energy lost by reproductive investment has to be compensated for first before surplus energy may be used for growth. Since fecundity is size-specific, the number of eggs produced during consecutive spawning events will increase. Egg size may also increase with increasing body size and age. Furthermore, female plaice appears to start spawning earlier in the season as they grow older (Rijnsdorp, 1989). There is no indication whether sex ratio or size composition of the males affects spawning success. At the population level, total reproductive investment depends on sex ratio, size composition, and absolute numbers involved, but information on fertilization rate and interannual variability therein is lacking (Rijnsdorp, 1994).

Rijnsdorp (1994) provided evidence that variability-generating processes may occur in the adult phase. The interannual variability in size-specific fecundity varies in different species between 5% and 25%. Furthermore, exploitation may strongly modify the adult population in terms of absolute numbers, sex ratio, size composition, spawning season, and egg quality (size). Although the importance of maternal effects on reproductive potential has often been stressed (Solemdal, 1997), convincing evidence that these contribute strongly to generating interannual variability in recruitment is still lacking. Interannual variability in the number of fertilized eggs might be generated compared to a simple measure of spawning stock biomass by variations in any of the aspects mentioned above, but field evidence for major shifts is lacking. Rijnsdorp (1994) concludes that time series of recruitment so far do not provide evidence that these factors are important.

Pelagic egg and larval stage

Leggett and DeBlois (1994) provide a review of the timing of year-class formation in marine fish. Their
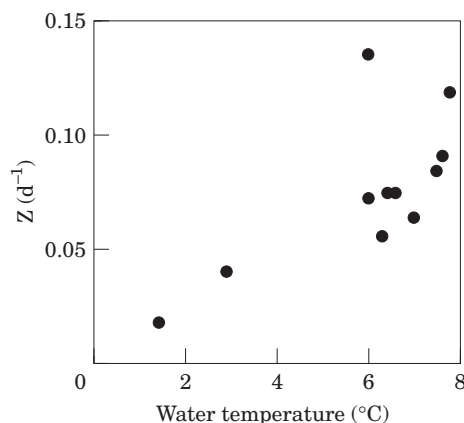
Figure 7. Relationship between mean daily mortality and water temperature of plaice (*Pleuronectes platessa*) eggs during development in the Southern Bight of the North Sea (data after Harding *et al.*, 1978).

findings were consistent with Gulland's (1965) hypothesis of a coarse control during the period of egg and larval drift, suggesting that variability-generating processes operate during this period. Most studies focused on the possible role of food and predation as controlling factors. Notwithstanding the conflicting and often indirect nature of the information (Leggett and DeBlois, 1994), the hypothesis that year-class strength in marine fish larvae is determined by starvation and predation in the egg and larval stages could not be rejected.

In a zoogeographic study on recruitment variation in dab (*Limanda limanda* (L.)), the available evidence also points to critical events during the pelagic stage, suggesting that year-class strength might even be determined during the egg stage (Henderson, 1998). As in plaice (Van der Veer, 1986), a negative relationship between year-class strength and water temperature at the time of spawning was observed. Henderson (1998) assumed that pathogens may be important in determining egg mortality. Support for his hypothesis is provided by the significant positive correlation between egg mortality in plaice and sole and water temperature (Fig. 7), while prevalence of malformations in flatfish eggs was negatively correlated with water temperature (Dethlefsen *et al.*, 1996). Based on laboratory experiments, Fonds (1995) also suggested that the observed negative relationship between survival of plaice eggs and water temperature might be caused by a reduced activity of pathogenic bacteria at low temperatures.

Recently, the role of hydrodynamics in explaining interannual variability in flatfish recruitment has been given attention (Pepin *et al.*, 1995; Werner *et al.*, 1997). In their review, Werner *et al.* (1997) were not able to provide explicit links between physical variability and recruitment, despite a large number of studies for a variety of marine fish populations. On interannual time
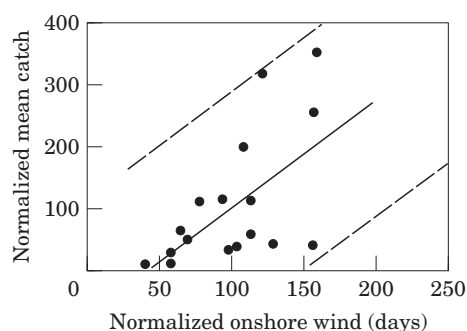
Figure 8. Correlation between year-class strength of turbot (*Scophthalmus maximus*) around the coast of England and Wales and offshore winds. Dashed lines indicate 95% confidence limits (data after Riley *et al.*, 1981).

scales, they listed wind as the most intensively studied abiotic factor contributing to recruitment variability. Using wind as a measure of transport, Riley *et al.* (1981) found a significant positive correlation between the year-class strength of turbot around the coast of England and Wales and offshore winds (Fig. 8). Also in the petrale sole (*Eopsetta jordani* (Lockington)) along the northeast Pacific Ocean, variation in year-class strength was associated with oceanographic conditions during the pelagic larval stages (Castillo *et al.*, 1994). Coombs *et al.* (1990) suggest that weather conditions during embryonic development might significantly influence recruitment strength of North Sea plaice, rough weather supposedly leading to increased egg mortality. Recently, Nielsen *et al.* (1998) showed that year-class strength of plaice along the Danish Kattegat coast was related to prevailing wind conditions, suggesting that recruitment to the area depends on egg and larval transport from the Skagerrak. Further support for the importance of transport in determining year-class strength was provided by Van der Veer *et al.* (1998) in an analysis of the impact of interannual variability in hydrodynamic circulation on egg and larval transport of plaice in the southern North Sea. Simulations with a realistic 2D circulation model were compared with observed larval concentrations in the coastal zone. Results showed that interannual variability in transport was in the same order as observed in year-class strength. The authors concluded that the variability in circulation patterns during the early pelagic stages in the open sea might be a key factor. A similar suggestion was already made a few decades ago by Talbot (1976, 1978).

Demersal juvenile stage

Metamorphosis and settlement of flatfish larvae has been considered to be a key process in determining recruitment. The change from a symmetrical pelagic larva to a demersal flatfish requires extensive functional

changes, involving flattening of the body, strong development of the unpaired fins, often a marked reduction of the paired fins, eye migration, and changes in pigmentation (Fuiman, 1997; Osse, 1997). Especially the rewiring and recalibration of vision during eye migration will strongly affect food detection (Osse *et al.*, 1997) and maybe also predator avoidance. Although Creutzberg *et al.* (1978) indeed found that almost 100% of the settling plaice larvae had empty stomachs, starvation was not causing additional mortality but was merely a key factor in the settlement process. Starving larvae remained swimming until favourable benthic food conditions were encountered. Then the larvae settled and remained demersal. Also the positive linear relationship between abundance of pelagic plaice larvae and subsequently settled juveniles (Van der Veer, 1986) suggests the absence of either a starvation- or predation-induced variability-generating process.

Variability-generating processes during this phase can be introduced by variability in either mortality or the length of the period, or by a combination of these two factors. Van der Veer *et al.* (1994) reviewed the impact of juvenile growth on recruitment in flatfish, which might be caused either by size-selective mortality and/or by size-dependent onset of maturation. Although interannual variability existed in both factors, there was no indication that these processes were important. In a recent paper on size-selective predation on 0-group flatfish, this conclusion was confirmed (Van der Veer *et al.*, 1997).

Bailey (1994) discussed the impact of predation on recruitment variability in flatfish. Fluctuating numbers of predators are considered to be the most likely condition leading to increasing variability in recruitment, since predator population dynamics might be influenced by factors other than prey abundance. Iles and Beverton (1991) and Beverton and Iles (1992a, b) could not find any indication of variability-generating factors in a systematic analysis of mortality rates in juvenile flatfish in European waters. Bailey (1994) confirmed this general conclusion, but provided evidence that the situation might be different under exceptional conditions. In plaice, strong year classes are associated with cold winters (Brander and Houghton, 1982; Van der Veer, 1986; Van der Veer and Witte, 1999) and it has been argued that the extremely strong 1963 year class may have been partly caused by a release from predation by crustaceans in the nursery (Van der Veer and Bergman, 1987). Beukema (1991, 1992) observed a delay of about 1 month in the arrival of crustaceans after a cold winter. Other indirect support arises from observations by Pihl (1990) in plaice nurseries along the Swedish west coast. In these areas, with large year-to-year variability in winter temperature and hence in predator abundance, variability in year-class strength increased during the first year of life (Van der Veer *et al.*, 1990). Adverse

environmental conditions may also occur in the demersal stage. In North Sea sole, low winter temperatures caused high mortality in all demersal stages (Woodhead, 1964). Mortality between the 0- and I-group was negatively correlated with winter temperature, generating a larger variability in I-group abundance in the more northerly situated nursery areas only (Van Beek et al., 1989; Rijnsdorp et al., 1992).

Overall, there is no strong evidence that variability-generating processes in the demersal juvenile stage are common and of importance. Only in areas with cold and strongly varying winter temperatures might fluctuating numbers of predators induce interannual variability in year-class strength.

Variability-damping factors

A first approach to check the presence of regulating factors is to investigate stock-recruitment data. Iles (1994) showed in a review of 20 flatfish stocks that in six cases there was a significant non-linear stock-recruitment relationship. This evidence for density dependence was strengthened by the fact that for eight additional stocks a model of constant recruitment was favoured over a model in which recruitment was directly proportional to stock size. The identification of the form of the relationship has considerable potential for insight in population-regulating mechanisms (Iles and Beverton, 1999). A further analysis by Beverton (1995) in relation to his "concentration hypothesis" yielded strong evidence that there are critical periods in both the adult and juvenile stage that are of primary importance in regulating recruitment.

The adult stage

Regulating processes may operate through density-dependent adult mortality, growth, maturation, and/or fecundity. Data on density-dependent adult mortality are virtually absent. Predation would seem to become less important with increasing fish size. The general size rules in predator–prey relationships indicate that mortality through cannibalism in the adult phase is unlikely. Whereas optimum prey size appears to be in general about one-third of the predator size, the length at first maturity is at half the asymptotic maximum length in most flatfish species (Beverton, 1992).

Growth, maturation, and fecundity are intricately linked within the energy budget of a fish, where the amount of surplus energy plays a crucial role (Rijnsdorp, 1989, 1993). Factors affecting surplus energy, such as intra- and interspecific competition and environmental conditions (especially food availability and temperature) will also affect the allocation of energy over somatic growth and reproduction. On an annual basis, surplus energy is a continuously increasing function of body size, and reproductive investment is a function of body weight. Reproductive effort is not only determined by egg numbers, but also by egg size. Egg size shows in general an inverse trend during the spawning season of an individual fish and a positive trend with increasing fish size (Solemdal, 1997). Annual variations in surplus energy in the adult phase will be reflected in both somatic growth and corresponding reproductive effort. The most extreme trade-off between somatic growth and reproduction exist when adults skip a spawning season (intermittent spawning).

Regulating processes should become particularly evident at high levels of abundance or biomass. However, most information available is derived from commercially important populations which appear to have been reduced by fishing below the threshold at which food supply per fish becomes limiting (Rijnsdorp, 1994). At such reduced levels of abundance, regulatory processes can no longer be detected. The analysis of available information from the early years of exploitation (Rijnsdorp, 1994) suggests that density-dependent growth has occurred in the past. The feature of intermittent spawning has also been suggested, at least in fish inhabiting colder waters. On the other hand, size-specific fecundity appeared to be stable over a broad range of population abundance and may only decrease at very high values. The mechanisms involved are further complicated by the trade-off between egg numbers and egg size. Overall, Rijnsdorp (1994) concluded that density-dependent ripening and absolute fecundity, mediated through density-dependent growth, may regulate recruitment at high levels of population abundance.

Pelagic egg and larval stage

Information on regulating processes operating during egg and larval development are scarce. Predation-induced mortality by planktivorous fish has been identified as a main source of mortality (Pommeranz, 1981; Daan et al., 1985; Ellis and Nash, 1997).

No evidence for regulatory processes has been found in the egg stage. Observations on plaice and sole eggs (Harding et al., 1978; Van der Land, 1991) indicate mortality to be independent of density (Fig. 9a). In both species, mortality is related to water temperature (Van der Land, 1991; Rijnsdorp and Vingerhoed, 1994). However, stage-specific cumulative mortality rates will be less dependent on temperature because of the levelling out effect of temperature on daily growth and daily mortality rates (Pepin, 1991).

Also during larval development, data suggesting the existence of major regulatory processes are lacking. The available quantitative information for plaice (Harding et al., 1978) suggests a negative correlation (not significant; $r_s = -0.40$; $n = 4$) between larval abundance and
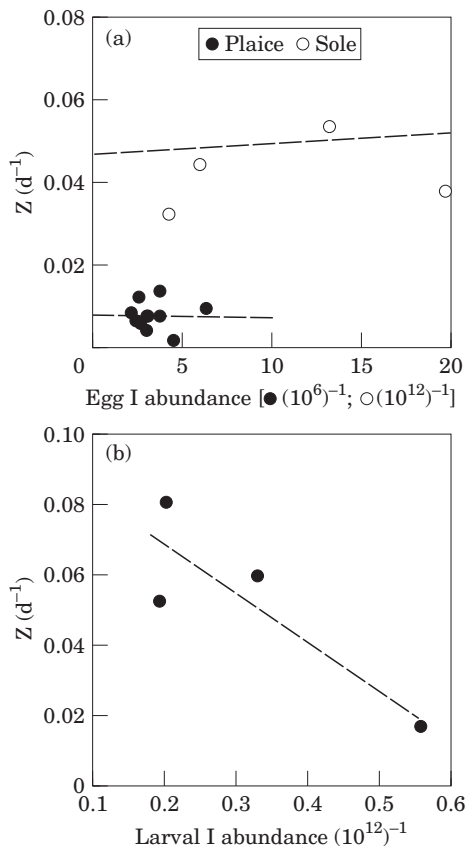
Figure 9. Relationship between daily mortality (Z) and abundance of pelagic first egg and larval stages of plaice (*Pleuronectes platessa*) (data after Harding *et al.*, 1978) and sole (*Solea solea*) (data after Van der Land, 1991) in the Southern Bight of the North Sea. (a) Eggs of stage I. (b) Larvae of stage I.

mortality (Fig. 9b), indicating a variability-generating rather than damping process.

Demersal juvenile stage

Regulating processes operating during the juvenile stage could act either on stage duration through density-dependent growth (for review, see Van der Veer *et al.*, 1994) or on survival through density-dependent mortality. Extensive research on plaice has revealed the general picture that mean length of juveniles is reduced at high densities as observed during the pre-war period and during the time of the two exceptionally strong year classes of 1963 and 1985 (Rijnsdorp and Van Leeuwen, 1992, 1996). In contrast, there is no evidence for density-dependent growth of 0-group plaice in the nursery areas along the European coast (Zijlstra *et al.*, 1982; Van der Veer, 1986; Bergman *et al.*, 1988; Van der Veer *et al.*, 1990; Mengedoht, 1995). However, this lack of evidence may be due to our inability to estimate precisely the

effect of differences in ambient temperatures on growth rate and to possible bias in the field studies (Van der Veer *et al.*, 1997).

Population regulation through density-dependent mortality has also been observed. In Japanese flounder [*Paralichthys olivaceus* (Temminck and Schlegel)], cannibalism of I- and II-group on 0-group is an important source of mortality (Furuta, 1996). A comparison of mortality rates of demersal 0-group plaice, dab, and turbot in European waters yielded significant density-dependent effects (Iles and Beverton, 1991; Beverton and Iles, 1992a, b). Predation is probably the most important source of mortality, since a variety of crustaceans, fish, and birds have been found to prey upon juvenile flatfish (for review, see Van der Veer *et al.*, 1997). At least for predation by crustaceans, density-dependent effects were generated by both a functional and a numerical response of the predator (Van der Veer and Bergman, 1987).

Intra- and interspecific variation

The analysis of variability-generating and variability-damping processes so far does not take into account that species vary in life history traits over their range of distribution (e.g. Leggett and Carscadden, 1978; Houde, 1989) and, therefore, their likely susceptibility to different control mechanisms. Miller *et al.* (1991), in applying this reasoning, developed a hypothesis, which has been later referred to as the "species range hypothesis" (Leggett and Frank, 1997). The underlying assumptions are: (1) species differ in life history traits, and therefore in susceptibility to different controls on recruitment, and (2) species life history traits vary over their range of distribution, and therefore controlling factors differ over both latitudinal and inshore–offshore gradients. Using latitudinal and inshore–offshore gradients in food, predation, and abiotic factors, these assumptions lead to the hypothesis that factors controlling recruitment of a species vary over its range with the following implications: (1) abiotic factors are most important at the edges of the range; (2) predation plus abiotic factors control recruitment at the polar edge of the range; (3) food plus abiotic factors control recruitment at the equatorial edge.

Miller *et al.* (1991) predicted that recruitment would be most variable at the polar edge of the species range, least near the centre of the range, and be intermediate near the equatorial edge (Fig. 10). However, they emphasized that the latitudinal pattern might be modified or obscured in the case of migratory species and that inshore–offshore environmental gradients may swamp latitudinal effects.

A first attempt to falsify the species range hypothesis was made by Walsh (1994). His analysis of recruitment variability in populations of long rough dab
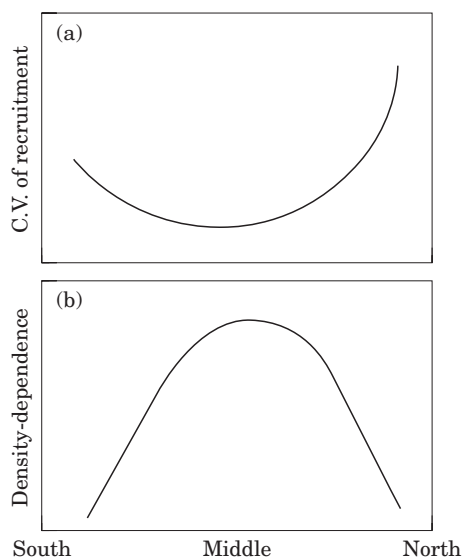
Figure 10. Schematic representation (redrawn after Leggett and Frank, 1997) of the species range hypothesis of Miller et al. (1991) with respect to: (a) coefficient of variation in recruitment, (b) importance of density-dependent processes.
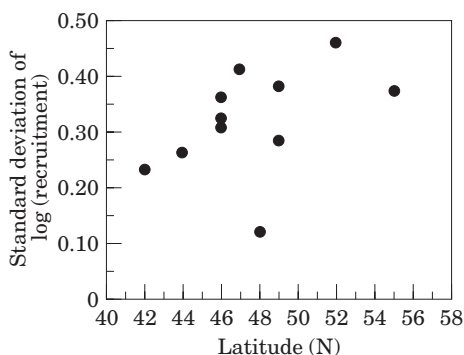

Figure 11. Latitudinal recruitment variability of age-4 long rough dab (American plaice) *Hippoglossoides platessoides* in the western and eastern North Atlantic expressed as the standard deviation of the residuals of detrended log (base 10) recruitment (data after Walsh, 1994).

(=American plaice) (*Hippoglossoides platessoides* (Fabricius)) showed an increasing south to north latitudinal gradient without a valley in the centre (Fig. 11), and on this basis at least part of the hypothesis would have to be rejected. Leggett and Frank (1997) expanded the validation by including a variety of North Atlantic flatfish species, based on stock and recruitment data compiled by Myers et al. (1995). The results were generally inconsistent with the species range hypothesis and they concluded that recruitment variability is dominated by density-independent factors operating at a local scale on the egg and larval stages. Neither Walsh (1994) nor Leggett and Frank (1997) considered

inshore–offshore gradients. Philippart et al. (1998), in an analysis of latitudinal variation in recruitment in north-west Europe based on other data sources, observed patterns of variation which also did not correspond with the expectation. However, they suggested that other sources of variation might have masked the expected patterns, such as different sampling methods, average age at recruitment, inshore–offshore gradients, and shifts in species ranges over time.

The basic assumption that species differ in susceptibility to different controls on recruitment still seems valid. In a recent paper, Tanaka et al. (1997) present an overview of latitudinal differences in life history traits in Japanese flounder, in combination with seasonal differences in food availability and potential predators. The abundance of mysids, one of the main food sources, decreased markedly in the southern range at increasing temperatures. Abundance of predatory shrimps showed a reverse trend with highest densities at the northern edge. Miller et al. (1991) based their hypothesis on likely trends in food availability, predation pressure, and abiotic factors. These factors are most likely to act only in the juvenile stage, while year-class strength appears to be established already in the pelagic phase (Leggett and Frank, 1997). This suggests that the species range hypothesis does not apply to the main factors causing the coarse control, but to the subsequent fine control. The dominance of density-independent factors operating at a local scale on the egg and larval stages stresses the importance of hydrodynamic circulation as a key factor in determining year-class strength (Leggett and Frank, 1997). It is noteworthy that the Japanese flounder spawns closer to the inshore nursery area than most species, and thus may escape many of the vagaries caused by long migration ways to the nurseries (Minami and Tanaka, 1992).

If hydrodynamic circulation represents a key factor, it can be hypothesized that recruitment variability depends on pelagic stage duration as a forcing factor. Since egg and larval development is strongly affected by temperature, the implication is that recruitment variability over the range of a species should be inversely correlated with temperature, as observed for long rough dab (Fig. 11). Furthermore, a large portion of the patterns observed by Leggett and Frank (1997) for plaice and sole might be explained this way. Exceptions may be found in areas where temperature is inversely correlated with hydroclimate for migration, e.g., stronger shoreward currents in colder years (Miller et al., 1984).

Synthesis

In addressing variability, Heath's (1992) statement should not be forgotten that all the attention on recruitment variability masks the underlying stability of marine

populations. Slight variations in mortality over the larval stage would lead to much larger variations in recruitment than actually observed. In fact, recruitment to most populations is remarkably stable.

Variability-generating processes occur in all life stages of flatfish, but only those operating in the 3-D pelagic egg and larval stages appear to be of major importance. After settlement and transfer to the 2-D environment, regulating mechanisms dominate. This general scheme may be modified by at least four factors: fisheries, location within the range of the species, species type, and feeding type.

The main effect of fisheries appears to be that adult biomass may be reduced below the threshold at which food supply per fish is limiting (Rijnsdorp, 1994), in which case intraspecific regulating processes in the adult phase (food limitation, intermittent spawning) are no longer expected to occur. It is unclear whether this has also affected recruitment variability. The impact of the variability-generating processes in the egg and larval stages might well dominate the regulating processes in the adult stage.

Location is obviously important, because food and predators show clear trends over the distribution range of a species. Although detailed information is lacking, especially predation on early juvenile stages varies. With decreasing water temperature, the abundance of mobile epibenthic predators (crustaceans) becomes more variable (Van der Veer et al., 1990), mainly as a result of lethal winter temperatures or avoidance behaviour. The consequence is a shift from regulation to variability generation during the juvenile stage. No information is available concerning the extent to which this is also true for other sources of juvenile mortality, such as predation by larger fish, which appear to be even more capable of avoiding unfavourable environments.

Within the Pleuronectiformes, two major groups can be distinguished: those from cold waters, principally members of the Pleuronectidae, and those from warm-water habitats, including members of the Citharidae, Paralichthydae, Bothidae, Solidae, and Cynoglossidae. In temperate locations, the groups overlap. Depending on their origin in the cold or warm region, species may show a different physiological response to their environment and as a consequence differences in recruitment patterns between species and differences over the range of species are expected.

With respect to feeding, a specialization into three groups has been recognized: fish feeders, crustacean feeders, and polychaete-mollusc feeders (De Groot, 1971). Most species change their diet from zooplankton to (epi)benthic prey after settlement. The abundance in epibenthic prey (e.g. mysids; Tanaka et al., 1997) is thought to be more variable than that of benthic food items (e.g. regenerating body parts; Kuipers, 1977; De Vlas, 1979). If variable food conditions are important in generating recruitment variability, this is probably more so in species depending on epibenthic prey than in species depending on benthic prey.

Hjort (1914) put forward the hypothesis that year-class strength is controlled during the early life history, when numbers of individuals are at a maximum. Gulland (1965) suggested that the coarse control during the period of egg and larval drift was followed by a second period of fine regulation later on. The findings of Leggett and DeBlois (1994) supported this view: year-class strength in marine fish appears to be established during the pelagic egg or larval period.

According to Leggett and Frank (1997), regulation principally operates at the local (stock) scale rather than at large geographic scales. Positive correlations in recruitment time series occurred only among stocks in close geographic proximity to each other (Rijnsdorp et al., 1992; Leggett and Frank, 1997), suggesting that oceanographic conditions such as wind or sea surface temperatures are acting as forcing functions over some 100–500 km (Myers et al., 1997). This suggestion is consistent with other independent observations. Recruitment patterns in Northwest Atlantic fish stocks indicate that large-scale physical forcing, rather than local biological interactions, largely determines year-class strength (Koslow, 1984). Other analyses have also suggested that recruitment success of species in the Northeast Pacific Ocean and in the Northwest Atlantic is strongly influenced by environmental conditions (Hollowed et al., 1987; Frank, 1991; Planque and Fox, 1998). For instance, year-to-year variability in temperature has been shown to be linked with year-class strength (Frank, 1991; Planque and Fox, 1998). However, the correlations varied over the range of distribution. Positive relationships were found near the northern limits, negative relationships near the southern limits and no correlation was observed in the centre of the distribution (Frank, 1991).

A striking difference between flatfish and most other marine fish species is the relatively low recruitment variability among the former, suggesting that the degree of variation might be inversely related to the degree of concentration during early life phases (Beverton, 1984). Later, Beverton (1995) elaborated on his "concentration hypothesis" and put forward the statement that species which tend to concentrate spatially on nursery grounds during their early life may be "saturating" the carrying capacity of those habitats even when the adult population is still relatively small and not limited by their habitat. According to his view, this saturation results in density-dependent processes and explains the relatively low variability in these species. However, one might wonder whether it is the degree of concentration during early life that is responsible for the observed patterns. Regulating processes in flatfish were only observed to operate during the demersal stage and the concentration

into nursery areas coincides with the transfer from the plankton to the demersal stage. Therefore, instead of the degree of concentration, the underlying mechanism might be that regulating mechanisms only occur during demersal life stages. This might explain the apparent paradox that the lemon sole (*Microstomus kitt* L.) has a low recruitment variability even though this flatfish species does not concentrate spatially (Rae, 1970). In this respect, the results of Sundby *et al.* (1989) for cod are intriguing. Mortality in 2–3 months old juveniles in the transition of becoming demersal (but still at least partly planktonic) was density-dependent. If the implication that year-class strength variability can only decrease in fish species with a demersal stage is true, variability in recruitment in fish species will be related to the relative duration of the pelagic and demersal stages.

Acknowledgements

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