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Physical influences on the stock dynamics of plaice and sole in the North Sea*

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SUMMARY: A review of the literature on influences of physical factors on plaice and sole stresses the prominent role of water temperature in all life stages of the species. For plaice, e.g., water temperatures on the spawning grounds are inversely correlated with year-class strength, and growth depends primarily on temperatures. In many instances, however, direct and indirect effects are hard to disentangle and to quantify for use in models, e.g. for stock assessment and prediction (SAP). Hydrodynamic circulation influences the egg and larvae distributions. Existing models reveal the drift variability to be of the same magnitude as year to year variations of larval abundance just before immigration. An improved modelling of the processes could combine recent circulation and transport models incorporating physical/biological properties of the eggs and larvae. It is suggested that future research focuses on this approach. The course of irradiation during spring and its influence on mortality of the 0-groups of both species in the nursery deserves further studies if it is to be useful for SAP.

Key words: plaice, Pleuronectes platessa, sole, Solea solea, life history, temperature, irradiation, hydrodynamic circulation.

INTRODUCTION

A hundred years ago the International Council for the Exploration of the Sea (ICES) was founded. One of the aims of its exploration of the sea was to find causes of the variabilities in catches of e.g. North Sea plaice (*Pleuronectes platessa* L.) and sole (*Solea solea* L.). Environmental factors were thought to govern the fish abundances. Measuring the variability of the factors was supposed to make the variations in fish stocks predictable for a rational exploitation of the sea (e.g. Herwig *et al.,* 1905). Besides piling up a lot of knowledge on plaice and sole, the investigations since those times revealed that the relations between fish and the environment are much more complicated than thought earlier.

During early life history, effects of the physical environment on stocks will be most pronounced while during later stages rather a 'fine-tuning' of population numbers can be expected (van der Veer, 1986). Recruitment, i.e. the entry of newcomers into a defined compartment of the adult or fished stock, will thus mainly be controlled during early life. Recruitment, on the other hand, is the crucial unknown in stock management and thus of the outmost practical importance. If it fluctuates with some parameters of the physical environment, it may be principally unpredictable. There may, however, be some longer-term cycles ('decadal' or 'multidecadal'; Rothschild, 2000). In this case, the identification of the phase of such a cycle could help substantially in defining the target biomass for rebuilding a stock, or in the interpretation of the stock-recruitment relationship for the definition of

management reference points. As an example, O'Brian *et al.* (2000) assume North Sea cod to be in a phase of low recruitment due to a period of high water temperatures. Yndestad (2001) describes cyclic fluctuations in Northeast Arctic cod biomass and suggests that a long-term management strategy should cope with this partly predictable phenomenon.

Until now, relationships between fish and their environment were not used in stock assessment methods for flatfishes of the North Sea (Daan, 1997; Anonymous, 2001). The EU Concerted Action "Sustainable fisheries. How can the scientific basis for fish stock assessments and predictions be improved? (SAP)" examined how existing oceanographical, climatological, and biological knowledge can be better utilised for assessment and prediction purposes for European fisheries under a precautionary approach.

While scrutinising the literature on potentially useful scientific knowledge we identified quite a lot of influences of physical parameter described qualitatively, but far fewer influences described quantitatively which might be used later on in assessment and predictions. Based largely on these literature reviews, this paper compiles information on the influence of physical parameters on different life stages of North Sea plaice and sole with their life cycle as a guiding line. The first task of the concerted action SAP was to identify main causes for shortcomings in present assessments. This paper demonstrates important gaps in the knowledge of physical influences on especially the plaice, which belongs to the most investigated species in European waters, and suggests further investigations to fill the gaps. The next step should be to consider practical techniques for utilising this new knowledge in the management process.

ON THE LIFE CYCLES OF PLAICE AND SOLE

Plaice

North Sea plaice (*Pleuronectes platessa* L.) spawns in the offshore waters of the English Channel and the southern North Sea (Fig. 1, Harding *et al.*, 1978). The spawning intensity differs locally and in time (Talbot, 1978). In the North Sea, three main spawning areas seem to exist: off Borkum, in the Southern Bight, and off Flamborough (Harding *et al.*, 1978). In the Southern Bight, the spawning
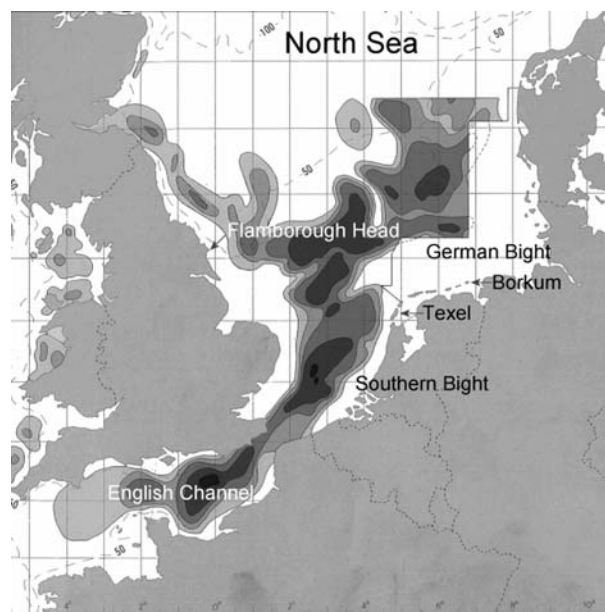

Fig. 1. – Spawning areas of plaice in the North Sea (from MAFF 1981).

season lasts from mid-December to early March, in the other areas it starts and ends up to one month later.

The eggs drift parallel to the coasts with the residual currents in the surface layer. Egg development lasts 15 to 30 days (Harding *et al.*, 1978). The larval stages take another 60 to 90 days in the surface water, which slowly disperses the larvae towards the coasts. Before metamorphosis the larvae reach the near-shore areas and tidal inlets which will be the nursery areas of the 0-group fishes (van Beek *et al.*, 1989).

Immigration and settlement during the latest larval stage and metamorphosis to early 0-group plaice are well documented (see e.g. Rijnsdorp *et al.*, 1985; Bergman *et al.*, 1989; Boehlert and Mundy, 1988). The most important nursery areas of North Sea plaice are the Wadden Seas of the Dutch and German coasts (Zijlstra, 1972; van Beek *et al.*, 1989). For roughly the first year of their life juvenile plaice stay in or close to the inshore and Wadden Sea nurseries in tidal and intertidal zones (Ansell and Gibson, 1990).

About one and a half year after being spawned, the I-group starts to migrate into deeper water for further development. After continuous migration towards the distribution areas of their spawning substock, fishes older than age VI are found deeper than 20 m. First maturation starts with age II for males, and age IV for females (Wimpenny, 1953; Rijnsdorp, 1989).
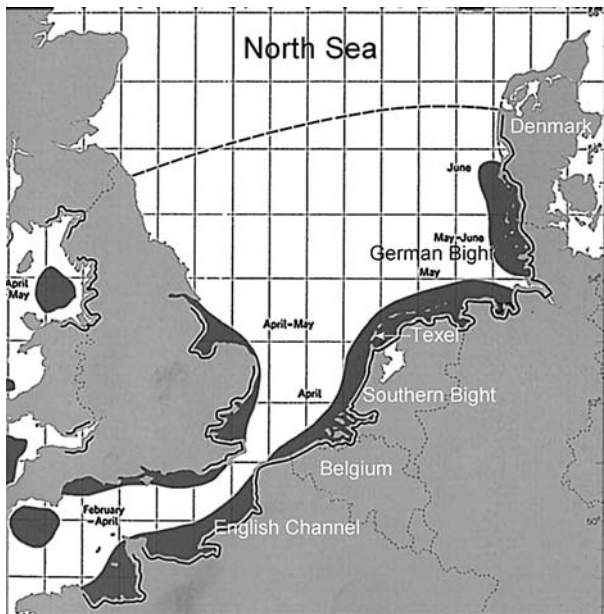
Fig. 2. – Spawning areas and times of sole in the North Sea (from MAFF 1981)

Sole

Sole (*Solea solea* L.) lives in the southern half of the North Sea at the northern edge of its total distribution area (Rijnsdorp *et al.*, 1992). It spawns in the southern North Sea and the English Channel with certain hot spots along the Belgian coast, off Texel, and in the German Bight mainly in the near-shore areas, but also offshore (Fig. 2; van Beek *et al.*, 1989). The main spawning time is from April to July.

During approximately four weeks, the eggs and larvae drift into the nursery areas and start their settlement within a month after fertilisation and become demersal (van Beek *et al.*, 1989). The nursery areas are distributed along the coast from south of the Schelde estuary to the southwestern Danish waters. The density of the juveniles is rather variable in the nursery areas (van Beek *et al.*, 1989). Compared to plaice, the younger sole prefer slightly deeper water. After a nursery period of about eleven months the I-group sole migrate offshore into deeper waters (see e.g. Fig. 6). Between age III and age V they recruit into their local spawning substocks (Rijnsdorp *et al.*, 1992).

North Sea sole is mainly abundant south of a line from Flamborough Head to the Danish Coast dominantly in waters of depth to about 40 m (Rijnsdorp *et al.*, 1992). When water temperature decreases during winter, sole starts to migrate into deeper waters of the Southern Bight. During strong cooling periods the fish forms strong concentrations in small deep areas (van Beek, 1997).

INFLUENCES OF PHYSICAL PARAMETERS

It is obvious from these life cycles that different physical parameters may influence the distribution and abundance of North Sea plaice and sole in every stage of development. Talbot (1978) described that, besides predation, water drift and temperature variability as well as wind influence the mortality of the plaice progeny during their first life stages. Gibson (1994) named the major factors contributing to growth and survival of juvenile stages of flatfish to be food, predators, temperature, salinity, oxygen, habitat structure, water depth, and hydrodynamics. The first three factors should be the most important. Dethlefsen *et al.* (1996 a) and Steeger *et al.* (2001) stated that solar radiation can be important for survival of early life stages of the two species.

Water depth determines the distribution of juvenile plaice and sole (Wimpenny, 1953; van Beek *et al.*, 1989), thus being a very important environmental parameter (Gibson, 1994). However, it is a constant factor, as are the sediments as a habitat structure (Gibson, 1994). Except for some cases in the eighties, oxygen depletion is not a critical factor in the southern North Sea. Especially during the drift and nursery phases sole and plaice live in near-surface waters with optimum oxygen supply. Therefore, these parameters will not be discussed in this paper.

On maturation and spawning

In the areas indicated in Figure 1, spawning of plaice occurs from late December to early May. Generally, the southern regions of the plaice distribution area are warmer than the northern regions during the three months before spawning. The spawning time of southern North Sea plaice precedes that of the northern areas by about one month (Rijnsdorp and Vethaak, 1997). Therefore, gonadal maturation, which starts around July of the year before (Rijnsdorp, 1989), seems to be influenced by the local ambient temperatures during ripening. Species-specific temperature sums [K × days] required for the maturation process explain the regional differences in the mean spawning time of North Sea plaice and sole as related to the local mean water temperatures (Lange and Greve, 1997). The end of Southern North Sea plaice spawning time is significantly correlated with the year-to-year changes of the local mean winter water temperatures (Fig. 3; Lange *et al.*, 2001). For the other plaice spawning groups and
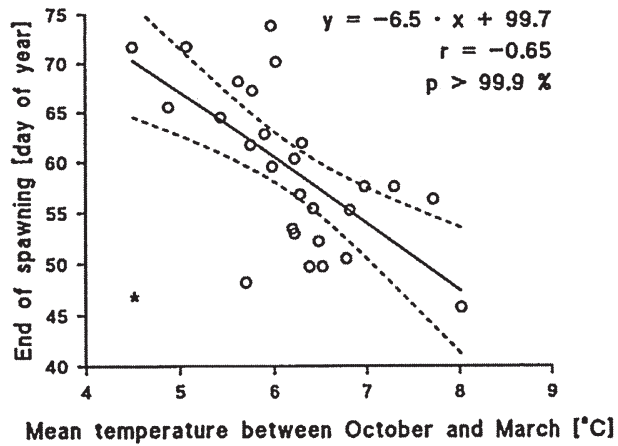
FIG. 3. – Spawning of Southern Bight plaice as a function of mean temperatures between October and March through 1966-1994 (the 1969-value is considered as outlier) (from Lange *et al.* 2001).

for sole the corresponding relations have to be investigated.

Temperature dependence of maturation was used to calculate theoretical spawning times in the North Sea on the basis of surface temperature anomalies (Dippner, 1997). A strong correlation of the North Atlantic Oscillation index (NAO) with the North Sea surface temperatures exists, especially for the winter NAO and the southern North Sea areas during January to April (Loewe, 1996). The differences in predicted spawning time between NAO high and NAO low index situations vary from about 3 weeks to more than 8 weeks from northwest to southeast in the plaice and sole distribution/spawning area (Fig. 4; Dippner, 1997). Lower NAO indices result in lower North Sea surface temperatures and thus in spawning time delay.
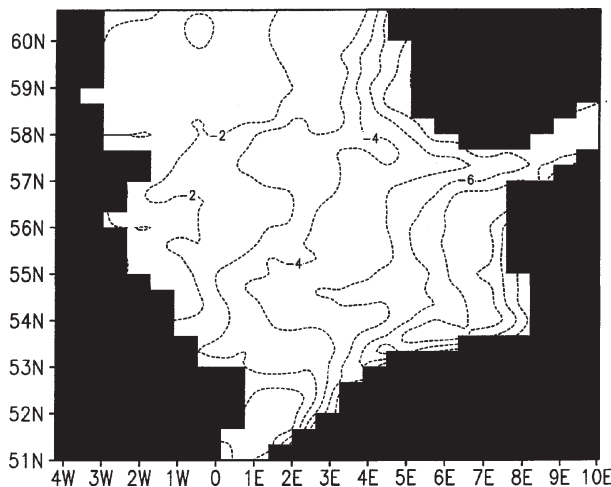

FIG. 4. – Differences in theoretical spawning time in weeks between high and low NAO index (from Dippner 1997).

Generally, this is in accordance with the delayed start and end of plaice and sole spawning at lower water temperatures, as reported by Rijnsdorp and Vethaak (1997), and with the earlier peak spawning in the warmer years 1989 and 1990 found by van der Land (1991). The fact that spawning times did not change substantially during the period 1960 to 1995 corresponds with the small surface temperature changes without any trend during that period (Becker and Wegner, 1993; Becker and Pauly, 1996).

During the period 1960 to 1995, however, the first maturation in both species shifted to lower ages and smaller sizes (Rijnsdorp and Vethaak, 1997). Increased fishing pressure and increased biological productivity in the coastal waters due to eutrophication seemed to be the reason for that development, but no significant relation between maturation parameters and water temperatures was found.

For spawning, maturing plaice in the southern North Sea generally migrate in a southwesterly direction (in the western areas in a northerly direction). Spent fish return to the northeast (to the south, respectively). Selective use of the tidal current supports the fish in their migrations (Cushing, 1990). Further on, the fish make use of variable depths with different current velocities in each tidal cycle (Cushing, 1990). They seem to compensate current variability induced by atmospheric influences by choosing the water depth with the most suitable current. Therefore, the spawning migration of plaice and sole can only be minimally influenced by residual current variability.

The spawning migration of the mature plaice leads to spawning concentrations in waters some miles off the coasts (Rijnsdorp, 1989). With maximum salinity and minimum turbulence as well as minimum turbidity (Cushing, 1990) these offshore waters are the optimum environment for the developing eggs. In contrast to the shallower near-shore waters, the time ranges of meteorologically induced changes and salinity variability in offshore waters are of the order of a few days to months. Therefore, at least some of the eggs spawned during a season of about a quarter of a year will be likely to find a suitable environment for development. Whereas an average male plaice is in spawning condition for at least 11 weeks during the whole period, an average female produces several batches of eggs during a five-week period of the peak spawning time (Rijnsdorp, 1989). To what extent physical influences trigger this batch production is unknown.

According to Simpson (1959), the Borkum area produces the highest proportion of young plaice and the Flamborough area the lowest, while the Southern Bight is intermediate. In contrast, the annual egg production numbers calculated by Harding *et al.* (1978) show the Southern Bight to be the most important area. However, the plaice egg distributions were centered in the warmer offshore water entering the southern North Sea through the English Channel (e.g. Coombs *et al.*, 1990). The total southern North Sea spawning places with their maximum distances from each other of about 250 km are inside the spatial scales of recruitment correlations which were estimated as approximately 500 km for marine species (Myers *et al.*, 1997).

The spawning area of North Sea plaice in total remained nearly unchanged over the years of investigations (Harding *et al.*, 1978; Rijnsdorp, 1989), while the hot spots may change from year to year (see the differences in the ranking of the spawning grounds between Simpson (1959) and Harding *et al.* (1978)).

On the egg stages

The mortality of plaice eggs drifting with the residual surface current varies interannually between 2% and 13% per day (Harding *et al.*, 1978; van der Land, 1991). For sole the respective figures are 15% to 55% per day during the egg development (Anonymous, 1986). The mortality rate is influenced by different factors: predation, temperature and other physical parameters, malformation, etc. Due to the linkages of the factors to each other, the individual role of the components for the drifting eggs are hard to distinguish.

In general, temperature is a limiting factor for the development of sole eggs (Irvin, 1974). Experiments on egg mortality/survival resulted in a temperature tolerance range of 8°C to 16°C (Irvin, 1974) which corresponds to the normal ambient temperatures (10°C to 15°C; van Beek *et al.*, 1989). Rijnsdorp and Vingerhoed (1994) observed relationships between plaice and sole egg mortality and water temperature. As temperatures were inside the tolerance ranges, indirect temperature influence was supposed to act via predation: increasing temperature will lead to an increasing daily rate of food consumption of the predators leading to an increasing egg mortality (Rijnsdorp and Vingerhoed, 1994; van der Land, 1991).

For plaice eggs the tolerance range is between 2°C and 8°C. Better survival rates are associated with water temperature at the lower end of the range in the spawning season (Harding *et al.*, 1978).

Physical properties of plaice eggs were determined by Coombs *et al.* (1990). The given passive vertical ascent of 5.2 m/h indicates an ascending time from fertilisation in 20-40 m water depths (Muus and Nielsen, 1999) to the surface of at least a few hours. Thus, the eggs with very low mechanical resistance during the first hours after fertilisation (Pommeranz, 1974) are exposed only to reduced mechanical stress during this critical phase. As they grow older the crushing resistance of the eggs increases and causes diminished mortality by breakers in the near surface layer. Thus, Pommeranz (1974) estimated only small mortality by wave action, and Coombs *et al.* (1990) suggested effects of rough weather on egg mortality only in some years.

Lethal effects from the ultraviolet component of daylight were experimentally shown from certain light intensities upwards (Pommeranz, 1974). However, the southern North Sea egg distribution areas get light intensity less than the supposed tolerance limit during the spawning and egg development period. By experiments Dethlefsen *et al.* (1996a) found a dosage-dependent increase in malformation and mortality, small changes in DNA integrity, and reduced buoyancy of plaice eggs with slightly increased solar UV-B irradiation dosages. Due to its important ecological impact, especially the influence on buoyancy needs further investigations.

Cameron *et al.* (1992) observed high degrees of malformation in eggs from the Southern and German Bight in 1987, while the 1986 samples showed a much lower degree of malformation. This was unexpected because the 1986 water temperatures were far below those of 1987. Besides temperature, different environmental influences including UV-B radiation should have caused the differences in malformation. Generally, with 11% malformation plaice eggs always showed the lowest rates when compared with other species sampled during the winter surveys; during summer surveys sole eggs showed the lowest malformation rate (4%) of all species (Cameron *et al.*, 1992).

The numbers of malformed eggs of certain fish species (incl. plaice) in the German Bight decrease with the distance to the coast, which is explained as the influence of pollutants in the coastal waters (Dethlefsen *et al.*, 1996 b; von Westernhagen and Dethlefsen, 1997). Additionally, the occurrence of malformed embryos is significantly negatively cor-

related with water temperature (von Westernhagen and Dethlefsen, 1997). However, the increase in malformation (and succeeding mortality) with low water temperatures is adverse to the observation of reduced egg mortality at low temperatures (van der Land, 1991; Rijnsdorp and Vingerhoed, 1994).

Although spawned in positions to start their development under optimum environmental conditions and to find the plankton spring outburst as soon as they reach their larval stages (Cushing, 1990), the variability of the residual current due to meteorological parameters causes larger rates of egg mortality (van der Veer *et al.*, 1998). Van der Veer *et al.* (1998) estimated parts of the impact of interannual circulation variability on the eggs and larvae dispersal of Southern Bight plaice which were transported as passive tracers in a realistic 2D circulation model using observed wind and pressure fields. As the most important conclusion the authors found that the interannual variability in transport from the spawning ground to the waters off the nursery areas is of the same magnitude as the interannual variability in larval abundance, i.e. interannual changes in hydrodynamic circulation are large enough to explain the interannual variability in larval year class strength (van der Veer *et al.*, 1998).

On larvae

The positions of spawning grounds of plaice and the nurseries on the continental coast require a transport into the northeast and east direction. While this is indeed the direction of the residual currents, the speed of these currents is too low to explain the time of arrival on the easternmore parts of the coast; rather, the westerly winds prevailing in the respective season must be forcing the transport (Rauck, 1974). Thus, it is an obvious question whether more or stronger westerly winds could improve the transport and lead to higher settlement, i.e. higher recruitment. However, a positive relationship between the occurrence of westerly winds and plaice recruitment could not be shown (Rauck, 1974). A further recent analysis of over 40 years' data did not show a different pattern of weekly mean wind vectors at Helgoland for years of high or low recruitment (Damm, unpublished).

The hydrodynamical drift simulation mentioned above was able to model the dispersal of plaice larvae from spawning in the Southern Bight mainly into the Marsdiep in accordance with the observations (van der Veer *et al.*, 1998). Differences in peak occurrence time between observation and model results seem to originate from the simplification to take eggs and larvae as passive tracer. Nevertheless, the strong variation of tracer distributions was of the same magnitude as the observed variability in larvae abundances. This indicated that the horizontal drift induced by the momentary wind fields was a severe influence on larval mortality (van der Veer *et al.*, 1998). Also, the influences of temperature, directly via survival rate or/and indirectly via metabolism and predation, can be enlarged or diminished by the hydrodynamics. This and the active swimming of the larvae (Ryland, 1963) should be part of future larvae drift modeling.

The numerous investigations on the transport mechanisms of the larval plaice immigrating (and metamorphosing) from their coastal zone distributions into the Wadden Sea nursery areas lead to different hypotheses. The first one considers an active use of selective horizontal tidal transport by the immigrating larvae. Reaching the coastal areas, plaice larvae show a tendency to move towards the bottom (Harding and Talbot, 1973). From there they pass from the open sea outside the island chain through the inlets onto the tidal flats, where they settle. There is evidence that this onshore transport is actively supported by behavioural features of the larvae: resting on the seabed during ebb tide and rising into the water column during flood ('selective tidal transport'; Rijnsdorp *et al.*, 1985; Bergman *et al.*, 1989). The active component seems to increase the further inshore the larvae come, whereas in the outer parts of the channels larvae move passively like suspended matter. The larval immigration into the later nursery areas is at least partly supported by a current phenomenon. A mechanism detected by Dietrich (1953) off the island of Texel generates a temporary landward bottom current; he suggested that this might be meaningful for the transport of larvae and suspended matter. The process is driven by a temporary layering and needs the existence of low-salinity surface water and a certain pattern of the local tidal streams. According to Dietrich (1953), there should be a second locality with the required properties off the North-Frisian Islands at the Danish-German border. The effect was explicitly mentioned by Cushing (1972) as a transport mechanism for metamorphosing plaice, where he coined the term 'gates' for the respective localities. The phenomenon was detected by Dietrich (1953) during a phase of calm weather in 1952. It appears likely that it can be destroyed by strong winds, for

which fact Cushing (1990) collected evidence from Visser (1977). Rijnsdorp *et al.* (1985), however, gave little importance to the 'gates' since they cover only small stretches of the coast.

In the second hypothesis the larvae are transported passively by the tidal current into their settlement areas. From the patchy larval distribution with plankton inside the Wadden Sea areas, Bergman *et al.* (1989) concluded that the larvae reach the tidal basins with the North Sea water entering with each flood tide. The magnitude of local larval supply depends either on the amount of "new" North Sea water during each flood tide or on the amount of retained North Sea water during ebb tide (Bergman *et al.*, 1989).

Hovenkamp (1991), investigating larval immigration in the Marsdiep inlet south of Texel, could not find relationships between the amount of larval immigration and local wind stress during the immigration periods in 1987-89. Thus, it appears that wind influence on plaice larval immigration is not a straightforward matter in the North Sea. The analysis of the wind vectors of Helgoland with respect to recruitment in the German Bight (Damm, unpublished) supports this. In other areas (Skagerrak-Kattegat: Nielsen *et al.*, 1998; Barents Sea: Kovtsova and Boitsov, 1995), it was easier to detect some plausible relationships.

Differences in the origin of the plaice larvae immigrating into the western Wadden Sea seem to depend on the water temperature: during a cold year most larvae are thought to come from the Western Channel; during warmer years they originate from more northerly spawning grounds, as supported by the wind components for the single years (Hovenkamp, 1991). This result is in contrast to the "normal" drift way: warmer years have intensified transports through the Channel into the North Sea and along the Dutch coast.

The mean abundances of plaice larvae as calculated from the larvae numbers of the flood tides over the whole period of immigration are in strong relation to the indices of year class strength in the nursery area (van der Veer, 1986).

By means of tidal currents and/or the 'Dietrich mechanism', the larvae reach the area of settlement and metamorphosis from late February to early May, depending on the area. The number of larvae locally settling depends on the "new" North Sea water retained in the tidal basins (Bergman *et al.*, 1989) or on the varying abundance of larvae in the near shore areas due to the hydrodynamic transportation (van

der Veer, 1986). In the Wadden Sea the larvae accumulate onto tidal flats which act as a trap for the settling larvae probably due to favourable food conditions (Creutzberg *et al.*, 1978).

Along the French Channel coast, sole-settlement depends on salinity range and "minimum" temperatures (11°C; Marchand, 1991).

Fish larvae are predators as well as prey. The amount that can be consumed of a certain prey depends not only on the absolute abundance of predator and prey species (and the effect of competitors) but also on the degree of overlap of the two in space and time. In the case of larvae, the respective window in terms of space may be as small as the size of plankton patches (Bailey, 1994). Temperature may be an agent here: if two populations (predator and prey or predator and competitor) are in a process of development, as occurs with fish larvae in spring, the species-specific temperature dependence of the production rates will govern the timing of overlap (van der Land, 1991).

Larval plaice are known to feed dominantly on the appendicularian *Oikopleura* (Cushing, 1990). Sandeel (*Ammodytes marinus*) larvae, which co-occur with plaice larvae in the Southern North Sea, share the same prey (Wyatt, 1974). The sandeel larvae appear later and their abundance is more sharply peaked; it is therefore unlikely that the timing of overlap is crucial. Furthermore, Ryland (1964) estimated abundant *Oikopleura* reserves for both species. Wyatt (1974) notes that in 1963 *Oikopleura* was scarce and the plaice larvae switched to a completely different diet (however, figures given by Harding (1974) do not support this lack of appendicularians). Anyway, 1963 was a year with low larval mortality (Bannister *et al.*, 1974) and high recruitment. Thus, it can be questioned whether food and competition for food in general are key factors for the survival of plaice larvae.

The larval development of flatfish is in response to temperature: at the population level, the mean metamorphic age and size increase inversely to temperature. The effect on size is not as strong as on age, and the data are less convincing (Chambers and Leggett, 1992). Due to Hovenkamp and Witte (1991), somatic growth rates of plaice larvae are strongly related to water temperature. The development seems to be more related to temperature than to size. A similar qualitative relation for sole in the Bay of Biscay was confirmed by Boulhic *et al.* (1992). Differences in the duration of the larval period were to a certain

extent related to the water temperature: the larvae of the cold spawning season 1987 were less developed at the same age as the larvae of the less cold seasons 1988 and 1989.

There is a significant negative correlation in plaice larvae between surface temperature and the occurrence of malformation (von Westernhagen and Dethlefsen, 1997). Unfortunately, the –lesser– influence of salinity, oxygen, and different pollutants in malformation are included in the relation and cannot be separated. In shallow nursery areas the combined physical disturbance on the bottom sediment from tidal and wind-induced waves and currents ('exposure') might influence the settling behaviour and the survival of the metamorphosed plaice (Pihl and van der Veer, 1992).

On early juveniles

A population control by density-regulated mortality (Rauck and Zijlstra, 1978) dampens the high interannual fluctuations in larval abundances (van der Veer, 1986). However, the fluctuations of population densities in the nursery areas do not mirror the plaice reproductive variability (Rijnsdorp et al., 1991). The contribution of the different parts of the continental nursery areas to the overall abundance index of 0-group plaice appear to be relatively stable (van Beek et al., 1989). The distribution of the juvenile sole within the continental nursery areas is rather variable; the yearly contributions of the areas to the 0-group production change remarkably (van Beek et al., 1989).

The year class strength of plaice is inversely related to water temperature at the spawning ground (van der Veer and Witte, 1999); the abundance of 0-group plaice in the German Bight is negatively correlated with temperature during gonadal maturation and during the first egg stages (Lange and Greve, 1997). Delay in spawning time and development caused by low temperature gives better survival chances when entering the nursery areas due to the more delayed predator development (van der Veer and Witte, 1999).

Directly after settlement young plaice start to use the tidal movement actively to disperse onto the tidal flats for feeding (van der Veer and Bergman, 1986). The individuals which even move into the intertidal zone seem to exploit the food resource at any given tidal level (Ansell and Gibson, 1990). Therefore, food scarcity for juvenile plaice (and sole) seldom occurs.

Density-dependent effects in growth due to food limitation seem to be restricted to only minor parts of the plaice population; differences in mean length between the nursery areas are largely explainable by differences in the time of larval immigration in combination with the local water temperatures (van der Veer et al., 1990). The growth of both plaice and sole on the nursery grounds is not food-limited according to Millner and Whiting (1996). On the other hand, Berghahn et al. (1995) found individual and local growth rates of 0-group plaice determined by differences in food quantity and quality due to bottom conditions. According to Gibson (1994), changes in food abundance can affect settlement and distribution pattern.

The increase in benthic production in the nurseries does not effect the growth rates of either species (Millner and Whiting, 1996). A long-term trend in mean length-at-age data is not stated for either of the 0-groups (Millner and Whiting, 1996). An inverse relationship between length and abundance of 0-group plaice seems to be determined by the temperature during egg stage (Zijlstra & Witte. 1982).

Two main predator groups on early juvenile plaice cause substantial mortality (van der Veer et al., 1990): while fish predation during summer and autumn has only little impact on the recruitment, the influence of the predatory crustaceans brown shrimp and shore crab on the just settled fish is temperature-dependent during spring. After severe winters the numbers of predatory crustaceans are reduced, and the early juveniles grow to sizes which are too large for the recovered crustacean stocks in June (van der Veer et al., 2000 b) because the brown shrimp, e.g., has only a limited food size window (van der Veer et al., 1994).

During late spring and early summer extreme climatic conditions may cause serious damage to the juvenile stages of plaice and sole. Large parts of the recruits remain on the flats or in small pools and do not leave with the ebb tide (Berghahn, 1983; Champalbert and Marchand, 1993). Even in pools with less than 5 cm water cover they are able to survive dug into the upper sediment layer. Resulting from low water at times of high insolation, nearly cloudless sky, light winds, and a successive heating-up to temperatures higher than 20°C (monthly average 10-13°C, observed maximum 28-32°C), an escape reaction occurs which has been called "exodus" (Berghahn, 1983). Following an exodus, large numbers of dead individuals were found whose metabo-
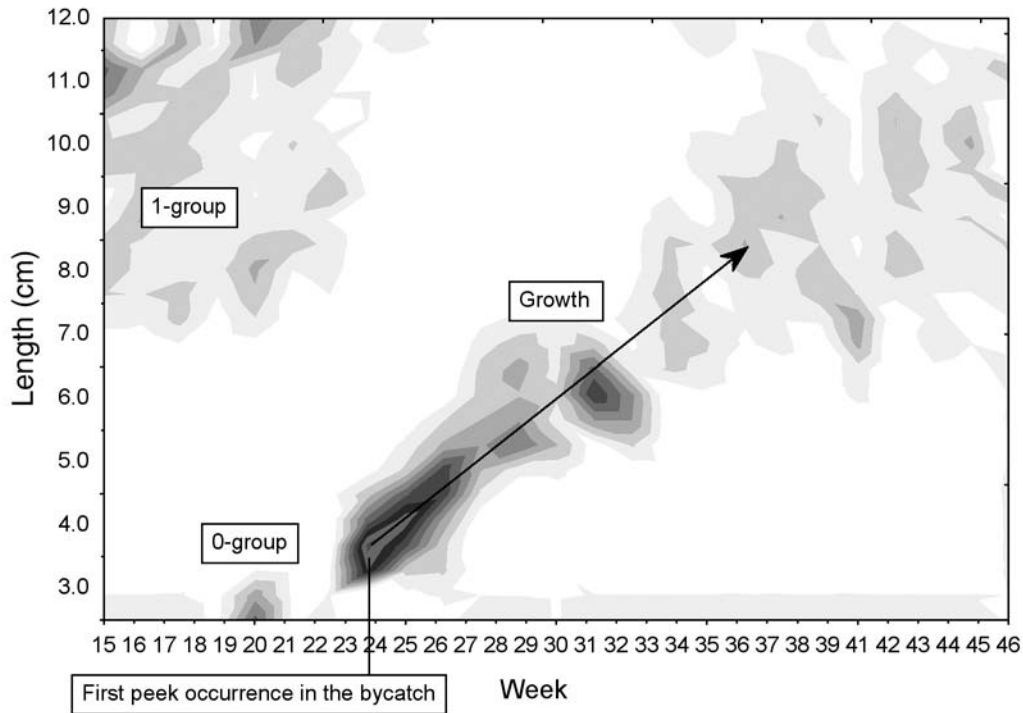
FIG. 5. – Occurrence and length of plaice in the bycatch of German shrimp fishery, Büsum 1965.

lism was probably not able to adapt to the rapidly changed temperatures or which were damaged by high doses of UV-B radiation. Apart from this damage, reduced or failed food consumption can be suspected as a reason for increased mortality rates (14% to 27%) due to sublethal radiation and heat (Berghahn *et al.*, 1993). High temperatures, UV-B radiation, and starvation were also suspected to be the cause for hyaline rings on the otoliths of plaice (Berghahn and Karakiri, 1990; Berghahn, 2000) since laboratory experiments have shown that hyaline rings can be produced by high doses of UV-B radiation. Later in the year, even at above-average temperatures, these effects become less significant due to the greater water depth which the juveniles then prefer.

Immigration from the flats and pools into the deeper channels, either as an exodus or in a more steady form of migration, takes the juveniles into the fishing grounds of the shrimp fishery. Here, similar trends can be observed for the commencement times of two events: the first peak of young plaice in the by-catch of the shrimp fishery (Fig. 5) and the 'maximum' offshore water temperatures (t > 14°C) from the 21st week onwards (Purps *et al.*, 1999). Since 1982, peak occurrence was observed earlier in the year (Fig. 6). The time of the first peak occurrence of young plaice in the by-catch (Fig. 6) and the mean
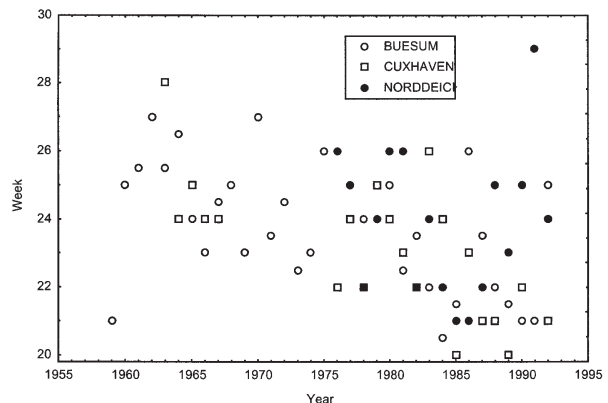

FIG. 6. – Time of first peak occurrence of young plaice in the bycatch of the German shrimp fishery, sampled at 3 landing sites.

length of 0-group, respectively, are correlated significantly (r = 0.674, r² = 0.454, p < 0.001). This means that smaller fishes occur earlier in the shrimp fishery due to advanced exodus. Young fish remaining on the flats avoid the contact with certain predators. Thus, they are able to grow up until they have reached a size where they fit less into the size spectrum of their predators and also have a higher velocity in order to escape.

VPA estimates of the 0-group juveniles of plaice and sole in the North Sea showed a trend that is similar to the trend of the index of the North Atlantic Oscillation (NAO) (Figs. 7 and 8; Purps *et al.*,
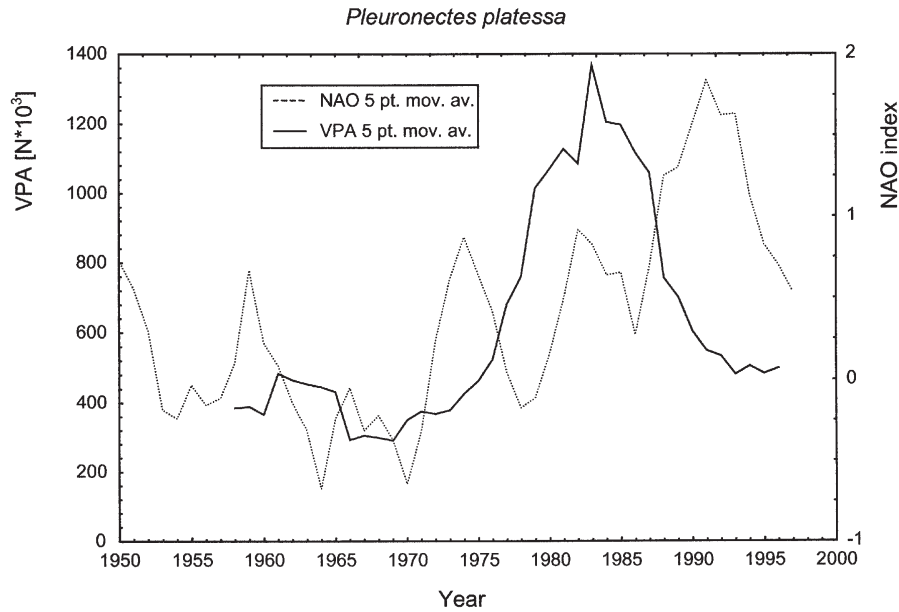
Pleuronectes platessa
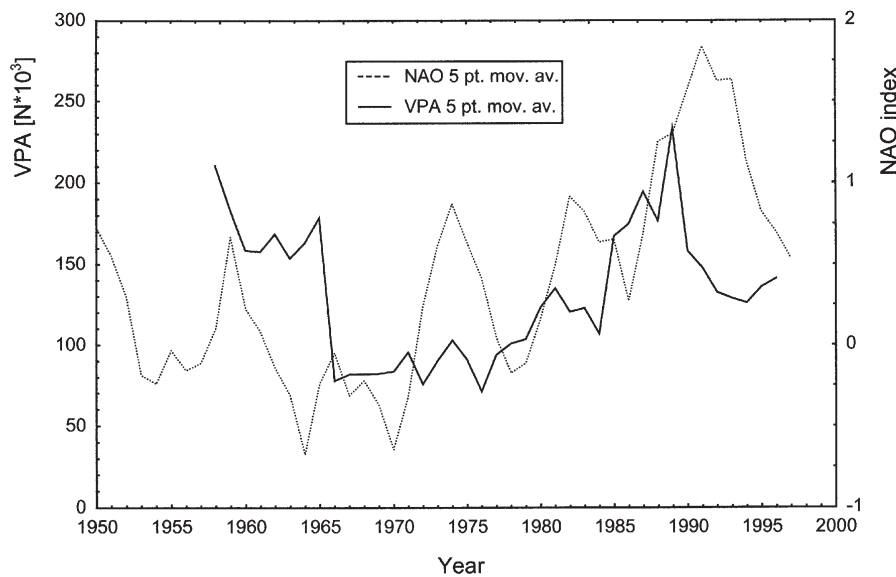
FIG. 7. – Trends of NAO and plaice 0-group VPA

FIG. 8. – Trends of NAO and sole 0-group VPA

1999). As a leading parameter of the climate of the North Atlantic (Barnston and Livezey, 1987) the NAO winter index correlates strongly with periods of local weather in the North Sea (Turell and Holliday, 2001). A phase of high solar radiation intensity measured as "covered sky degrees" (Fig. 9) went along with a period of low NAO values in the 70s (Figs. 7, 8). Possibly, this had a detrimental effect on those juveniles living in the shallow pools, as UV-B stress increases in good weather conditions with low water turbulence and ebb tide (Steeger *et al.*, 2001). However, though one might expect that low NAO

phases with their higher insolation would be followed by earlier exodus events, this is not reflected in the observed data (Fig. 6), but could at best be related to a slight trend towards an earlier occurrence of higher insolation (Fig. 9). If NAO is related to recruitment success, (Figs. 7, 8), investigating the mechanism should include, in addition to temperature, wind, circulation, etc., indirect UV-B effects (Steeger *et al.*, 2001).

In the western Wadden Sea, a high density-dependent mortality of youngest plaice up to 35 mm was found during and shortly after settlement (van
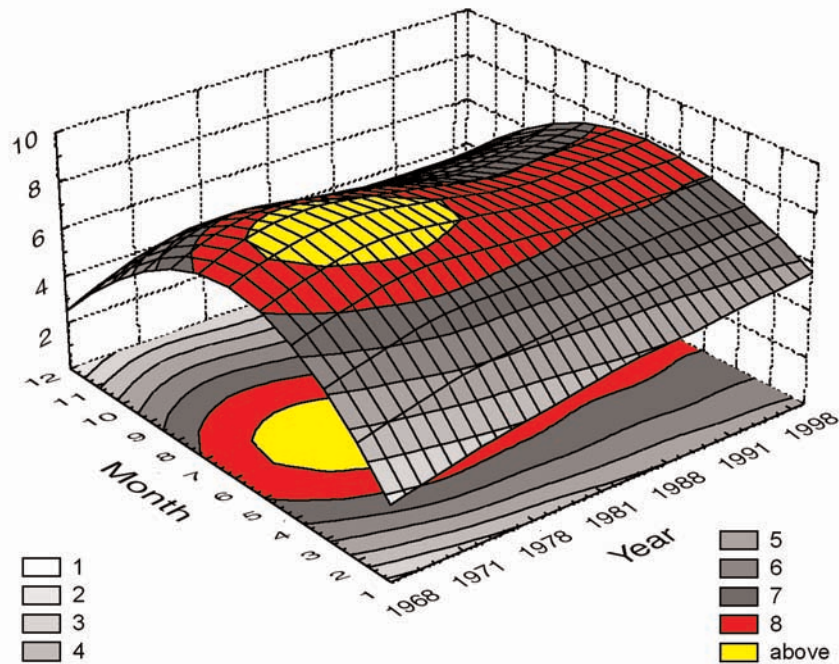
FIG. 9. – Number of days with degree of sky cover below 4/8 at Helgoland during 1966-1997

der Veer 1986). While for plaice no general temperature-dependent 0/I-group mortality seems to exist, for 0/I-group sole in the English nursery areas the survival rate appears to be inversely temperature-dependent (Millner *et al.*, 1988). However, this result may be influenced by the temperature-dependent migration of sole: with lower temperatures the I-group migrates into deeper water.

On juveniles

Despite local food limitations and hence reduced growth due to high concentrations of juvenile plaice in a restricted area, Bergman *et al.* (1988) found growth of juvenile plaice to depend only on water temperature. A formula describing the general temperature effect on growth rate of young plaice is given by Fonds *et al.* (1992). Growth data show seasonal variations which are possibly correlated with the changes in day-night cycle (Fonds, 1979). However, Rijnsdorp and van Leeuwen (1996) showed that growth changes in smaller size classes of North Sea plaice were significantly correlated with their density, eutrophication and seabed disturbances by beam trawling, but not with temperature. Thus, the temperature-growth relation of Fonds *et al.* (1992) has to be used with caution in growth models. Enhanced food availability by intensified fisheries may cause

the long-term increase in growth of 2- and 3-year old sole (de Veen, 1978 a). Changes in growth of young sole may depend on eutrophication, too; temperature seems to be a factor of lesser importance (Millner and Whiting, 1996).

Different changes in growth between the age groups of plaice and sole were observed from the late 1950s to the late 1980s. No direct long-term temperature influence was related to these changes (Rijnsdorp and van Beek, 1991). It is open to question whether, e.g., the reduced growth of the I-group during the 1980s was caused by increased density due to above average recruitment or by reduced food availability. In both cases the water temperature had an indirect influence, the dimension of which cannot be estimated at present.

Extremely low temperatures have at least two contrary indirect influences on the survival rate of the juveniles: on the one hand, low temperatures reduce the predators to a minimum, and their ensuing low abundance in the nurseries causes increased plaice survival rates (Gibson, 1994); on the other hand, during severe winters juvenile sole appear to be more vulnerable than older fish which are able to escape faster into deeper water (van Beek, 1997).

A significant negative correlation of winter temperature data with mortality rates between 0- and I-group stage of sole exists for most nursery areas in the North Sea (Gibson, 1994).

The tidal migration of plaice, starting with settlement or shortly after (Wadden Sea), is continued in all juvenile stages (de Veen, 1978 b). This is not a response to food shortage at subtidal level (Ansell and Gibson, 1990). It leads the young fish slowly into deeper water and ends with the recruiting of the maturing grown-ups into the spawning stock in greater depths (Heincke, 1913; Cushing, 1990).

A possible influence of water temperature was found in a quite different field. Van der Veer *et al.* (2000 a) compared groups of juvenile plaice, identified by meristic characters in respect to mortality and growth. They found surprisingly high differences between groups, with mortality and growth rate rising with the number of the respective character. Such meristic characters are known to vary with temperature and other environmental factors during egg and larval development (Lindsey, 1988). The year in which the samples were taken (1995), however, was unusually stable in temperature during the season of egg and larval drift (van der Veer and Witte, 1999), and the composition of incoming larvae by groups was fairly homogeneous through the season. Therefore, the findings do not point convincingly to temperature as a driving factor, but there must be some other variables besides temperature operating during early development which have significant effects on the early juveniles.

On adults

Changes in growth of plaice and sole have occurred since the 1950s with long-term trends. Catch weight-at-age of plaice and sole increased during the 1960s. The following observations did not show similar trends for both species. In plaice, a general decline up to the early 1990s in all areas suggests an environmental signal affecting all stocks which overrides the local factors such as fishing pressure and eutrophication (Millner *et al.*, 1996). In sole, more area-specific changes occurred (Millner *et al.*, 1996). A significant correlation between length and eutrophication index was found only for sole older than 6 years (Millner and Whiting, 1996). However, a general quantitative influence of the physical environment was not found (de Veen, 1978 a; Rijnsdorp and van Leeuwen, 1996).

Strong winters in the southern North Sea and in the German Bight have at least two opposing influences on the population of sole. Firstly, decreasing water temperatures force the fish preferring warmer water to move into the deeper relatively warmer

areas. Further cooling will decrease the sole's mobility and thus increase the catchability within waters with temperatures of less than 2°C (Horwood and Millner, 1998). Additionally, skin lesions lead to death and increase the mortality by up to 60% (Woodhead, 1964a, b; Rauck, 1969; van Beek, 1997). Secondly, reproduction following strong winters is mostly better than the mean recruitment (Rauck, 1969) due to reduced predators (Rijnsdorp *et al.*, 1992).

The general distribution areas of plaice and sole in their different life stages in the North Sea has remained unchanged since investigations started (Cushing, 1990). This is in accordance with the generally unchanged temperature regime as mentioned above. In the case of long-term temperature changes, Lange and Greve (1997) expected shifts in the distribution and spawning areas of the species in the North Sea in relation to changes in maturation. Differences in spawning times may occur as well.

PARAMETERS WITH "QUANTIFIED" INFLUENCE

As can be seen from this compilation, there are relatively few quantitative formulations of the physical influences investigated. Table 1 shows those which appear to be based on rather hard facts even though no relationships can be given which are apt for direct use for management and prediction purposes, but only for steps in between. Besides this scanty knowledge, the physical properties of the eggs as given by Combs *et al.* (1990) and Pommeranz (1977) are highly useful, e.g. as initial values for 3-dim drift modeling.

The much larger part of the physical influences given above is qualitatively described and cannot be easily put into a context of the assessment techniques used at the moment.

SUGGESTIONS FOR FURTHER STEPS

Variability in year-class strength of plaice and sole is generated during the pelagic egg and larval stage at least in parts by the variations in the hydrodynamic circulation (van der Veer *et al.*, 2000 c). Due to these strong influences on the later year class strength, Brander and Houghton (1982) suggested using egg surveys for first estimations of recruit numbers. A promising way to enhance the under-

TABLE 1. – Physical parameters with quantitative formulations of the influences on plaice and sole (grouping of the stages of life cycle in accordance with the text)

Parameter	influence on	described by	to use for
		Part A: Plaice	
A. 1: maturity and spawning water temperature	spawning time by age groups regional differences	Lange and Greve (1997), Rijnsdorp and Vethaak (1997) Rijnsdorp (1989)	survival model
A. 2: egg stage water temperature	mortality embryo malformation	van der Land (1991), Rijnsdorp and Vingerhoed (1994) v.Westernhagen and Dethlefsen (1997)	drift and survival model
UV-B	mortality	Dethlefsen et al. (1996)	survival model
A. 3: larval phase circulation	selective tidal transport	Rijnsdorp et al. (1985), Bergman et al. (1989)	settlement success
A. 4 and 5: 0- and 1-group water temperature	0-group year class strength	Lange and Greve (1997), van der Veer and Witte (1999)	first estimate of year class strength
water temperature	growth	Hovenkamp (1991), Bergman et al. (1988), Fonds et al. (1992)	cohort weight-at-age, size spezific mortality
		Part B: Sole	
B. 1: maturity and spawning water temperature	time of spawning	Lange & Greve (1997)	survival model
B. 2: egg stage water temperature	mortality	Irvin (1974), Anon. (1986), van der Land (1991), Rijnsdorp and Vingerhoed (1994)	drift and survival model
B. 5: juveniles water temperature	mortality between 0- and 1-group	Rijnsdorp et al. (1992)	estimation of year class strength
B. 6: adults severe winter cooling	mortality	Woodhead (1964), Horwood and Millner (1998)	estimation of stock size

standing of the regulatory mechanisms driving the distribution, abundance, as well as location and time of arrival of early stages of both species from spawning to just before settlement, could be an improved hydrodynamic model. In order to achieve progress on the studies being done so far, it seems to be necessary to include the third dimension, i.e. the distribution and migration of the studied organisms in the water column, as, e.g. Bartsch and Knust (1994 a) did.

Different model types explain parts of the variabilities in stock dynamics of plaice and sole: Rijnsdorp and Pastoors (1995) were able to simulate distributions of different plaice year classes in accordance with survey data; van der Veer et al. (1998) showed that the large interannual variability in trans-port is of the same order as the year to year variations of larval concentrations off the nursery areas; and local larval estimates were positively correlated with observed abundance. By means of a nested model system of two three-dimensional circulation models and a three-dimensional transport model Bartsch and Knust (1994 a) were able to simulate the dispersion of vertically migrating sprat larvae in the German Bight on the basis of tide, measured wind and air pressure.

We suggest a similar model configuration with the inner circulation model enlarged to the whole southern North Sea. The water density fields should be calculated by a heat transfer model (e.g. Schrum and Backhaus, 1999) on meteorological data instead of interpolated climatological densities. Larvae

should swim actively and migrate vertically in the water column. It remains to be discussed whether the necessary basic data for this model component are sufficiently covered by the literature (e.g. Ryland, 1963), or whether further accompanying field studies are necessary. Bartsch and Knust (1999 b) pointed out that especially inaccuracies in the final dispersions originate from uncertainties in the initial horizontal and vertical distributions of the eggs/larvae. As far as possible starting positions should relate to the spawning areas of the single years. There is evidence that the consideration of the physical properties of the eggs given by Coombs *et al.* (1990), of the eddy diffusivity coefficient of the eggs in the water column, of the lethal temperature and salinity limits, and of the moving of the older larvae to the lower part of the water column will improve the results.

The next step should be a modelling of the tidal transportation/inshore migration of the settling larvae onto the nursery grounds. An exchange model for this purpose was successfully run by Dick *et al.* (1999).

Investigations into juvenile stages could deal with quantifying the temperature- and irradiation-induced mortalities on the tidal flats. This would be predominantly a field study.

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