

Recruitment mechanisms in North Sea plaice *Pleuronectes platessa*

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ABSTRACT: Recruitment mechanisms in a number of 0-group plaice nurseries in northwestern Europe were analysed. In all areas the same pattern of abundance of 0-group plaice emerged: increasing densities during the period of settlement followed by a continuous decrease during the rest of the season. Differences in timing of settlement in combination with differences in water temperature resulted in a wide range of mean length (30 to 78 mm) in the various areas by the end of August. Growth always appeared to be optimal within the constraints of the prevailing water temperature. Predation is evidently the main mortality factor and the same 2 types of predators were found everywhere: crustaceans in spring and migratory fish in summer and autumn. The impact of predation by crustaceans in spring varied among areas and appeared to depend on local temperature conditions. In areas characterized by low temperatures in spring no impact on the year-class strength was found, whereas in areas with high temperatures in spring, crustaceans affected recruitment. Either a reduction or a generation of variation in recruitment of plaice was observed, depending on the minimum temperature in the nursery in winter, which affects migration and/or mortality of the shrimps. Fish predation in summer and autumn appeared to have little impact on the recruitment of plaice, because variations in year-class strength were not affected by this type of predation.

INTRODUCTION

The processes determining recruitment of juvenile fish to the parent stock are a major topic in fisheries research (May 1984). Large year-to-year fluctuations in recruitment are commonly observed, and Beverton (1984) suggested that the degree of variation in recruitment in North Atlantic fish species may be inversely related to the degree of 'concentration' during early life phases. At first glance, a 'concentration' of small juveniles in a restricted area would seem to evoke mainly negative effects: increased risk of competition for food and increased vulnerability to predation and diseases.

Bergman et al. (1988) considered Beverton's hypothesis for plaice, a species characterized by low interannual variation in recruitment (Beverton 1961, Bannister et al. 1974, Bannister 1978, Rauck & Zijlstra 1978), in terms of seeking special nursery areas during early phases of life. Despite the concentration of the juveniles, food conditions always appeared to be optimal. As a result of the sheltered location of the nursery areas, predation pressure also seemed to be low com-

pared with more exposed open sea areas and to be rather constant between years (Bergman et al. 1988).

In the areas considered, the Wadden Sea and some British bays, the major causes of mortality were shown to be slightly different. Predation by shrimps appeared to be common, but in British bays predation by a variety of fish species, including cannibalism, in summer and autumn contributed significantly to the observed mortality (Bergman et al. 1988). In other coastal nursery areas, such as Swedish bays, predation on juvenile plaice by both epibenthic crustaceans (shrimps and crabs) and by fish has also been found (Pihl 1982, 1989a). Although the overall recruitment of plaice to the North Sea shows a low interannual coefficient of variation of about 40 %, which has been attributed to the regulating effect of shrimp predation in the main nursery area, the Wadden Sea (van der Veer 1986, van der Veer & Bergman 1987, Bergman et al. 1988), the coefficient of variation differed between nursery areas.

In this paper, the population dynamics of 0-group plaice *Pleuronectes platessa* L. in a number of nursery

areas in northwestern Europe are compared with respect to recruitment mechanisms and underlying abiotic and biotic key-factors.

MATERIAL AND METHODS

Description of nursery areas. The shallow nursery areas considered in this study are shown in Fig. 1. The Dutch Wadden Sea is part of the coastal estuary system along the western and northern coasts of Denmark, the Federal Republic of Germany and the Netherlands. It is

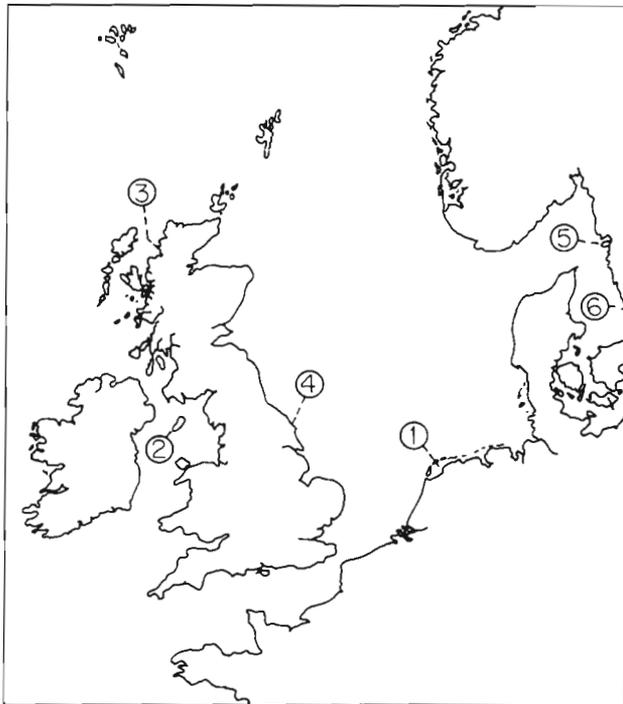


Fig. 1. Location of 0-group plaice nursery areas studied around the North Sea. 1: Dutch Wadden Sea; 2: Port Erin; 3: Loch Ewe; 4: Filey Bay; 5: Gullmar Bay; 6: Laholm Bay

bordered towards the North Sea by a number of barrier islands and sand banks. The area of the Dutch part is about 2780 km² of which about 1340 km² consists of mainly sandy tidal flats (Bergman et al. 1989). Studies on 0-group plaice were carried out between 1973 and 1982 at the Balgzand, a large tidal flat area of 52 km² located in the southwestern part of the Wadden Sea, isolated by deep gullies from other tidal flats.

The British bays are situated along the coast of Great Britain and Isle of Man. Port Erin is a small bay with a sandy sediment. Studies on plaice were carried out between 1963 and 1965. Loch Ewe is a sea loch on the west coast with a surface area of ca 0.3 km². Studies on plaice were carried out from 1964 to 1967. Filey Bay is a rather isolated bay surrounded by rocks situated on the

east coast with a surface area of about 9 km². The sediment of the enclosed bay consists of sand and gravel. Plaice investigations were carried out in 1968 and 1969.

The nursery areas studied on the Swedish west coast are located in the eastern Skagerrak and the eastern Kattegat. In the Skagerrak the nursery areas consisted mainly of small bays ranging in area from 0.01 to 0.04 km². They are situated in an archipelago and protected from wind and wave exposure. Gullmar Bay has a sandy-silt sediment. In the Kattegat the nurseries are large, open and highly exposed sandy areas. The study area Laholm Bay has a surface area of 70 km². Studies on plaice were carried out in Gullmar Bay from 1977 to 1988 and in Laholm Bay from the 1930's by the Danish and Swedish Fishery Boards.

Data analysis. The data analysed in this paper have been published previously, although with a different purpose. Not all available information on 0-group plaice has been incorporated; only longer time series and data sets with a frequent sampling intensity were analysed. Data concerning the Dutch Wadden Sea have been published by Kuipers (1977), Zijlstra et al. (1982), van der Veer (1986) and Bergman et al. (1988). For the British bays, data on Port Erin were taken from Riley & Corlett (1966), on Loch Ewe from Edwards & Steele (1968) and Steele & Edwards (1970) and on Filey Bay from Lockwood (1972, 1974). Data concerning the bays on the Swedish west coast, Laholm Bay and Gullmar Bay, were taken from Pihl & Rosenberg (1982), Nielsen & Bagge (1985) and Pihl (1989a, b). In most areas sampling was done by 2 or 4 m beam trawls. In shallow waters a push net (some British bays) or a drop trap (Swedish bays) was used.

All data were analysed on abundance estimates. Although different nets and net efficiencies were used, no conversion of the original data was applied. When possible, growth conditions of the 0-group plaice were analysed by comparing observed growth in the field with 'simulated' growth using an experimentally established growth model obtained under optimal food conditions describing maximal growth in relation to temperature (Fonds unpubl., in van der Veer 1986):

$$\Delta L = 1.3T + 1.7 \text{ (mm mo}^{-1}\text{)} \quad (1)$$

in which ΔL = length increase in mm mo⁻¹; T = prevailing mean water temperature (°C). Mortality estimates were standardized by computing instantaneous mortality rate Z (d⁻¹) according to:

$$Z = 1/t \ln (N_0/N_t) \quad (\text{d}^{-1}) \quad (2)$$

in which t = time interval in days between N₀ and N_t; N₀ and N_t = abundance estimates at respectively times 0 and t. Interannual variation in abundance and mortality rate was expressed as the coefficient of variation (Coef):

$$\text{Coef} = (\text{SD}/\text{Mean}) \cdot 100 \quad (\%) \quad (3)$$

in which Mean = mean abundance; SD = standard deviation of the observations.

RESULTS

Seasonal abundance

Settlement near and inside the Wadden Sea occurred almost exclusively in shallow areas. In the Wadden Sea settlement is restricted to the tidal flat areas (Zijlstra et al. 1982, van der Veer & Bergman 1986). Mass settlement on the beaches of the Dutch coast has been observed down to a depth of 3 m (Fig. 2). During settlement in the Wadden Sea, plaice showed an

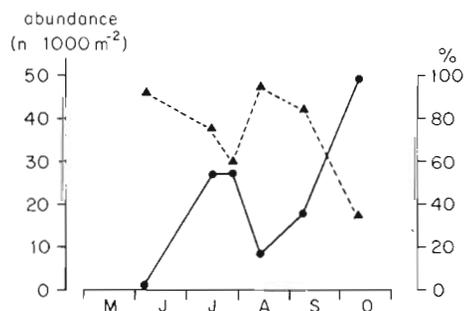


Fig. 2. *Pleuronectes platessa*. Density (●) of 0-group plaice (ind. 1000m⁻²) along the Dutch coast between IJmuiden and Den Helder in 1978, together with the percentage (▲) of the total catch found at depths < 3 m. After van Beek (unpubl.) (Netherlands Institute for Fishery Investigations, IJmuiden)

increase in abundance from March onwards to peak numbers in May of between 150 and 500 ind. 1000m⁻² (Fig. 3). Thereafter, a sharp drop in numbers followed, to densities of between 75 and 150 ind. 1000m⁻². When water temperatures dropped in autumn 0-group plaice left the tidal flats and probably migrated to deeper waters, as seen in Fig. 2 which shows increasing numbers in the coastal zone, i. e. > 3 m depth from August onwards. During the first year of life, plaice did not show any depth-related distribution pattern inside the Wadden Sea. However they migrated onto the tidal flats at high water in their search for food (Kuipers 1973, 1977). At low water, they were found in small gullies and deeper tidal channels (Kuipers 1973, van der Veer & Bergman 1986).

In British bays seasonal settlement of 0-group plaice (Fig. 4) was observed in shallow waters at depth ranging from a few cm down to 2 to 4 m (Riley & Corlett 1966, Macer 1967, Edwards & Steele 1968, Lockwood 1972, Poxton et al. 1982). In Port Erin Bay, settlement occurred in May and June. Maximum numbers were found in June–July. Between years there was a large variation in peak abundance ranging from 100 to 500 ind. per standard tow. Thereafter, a continuous decline in abundance was observed in all years to densities less than 100 per tow in September. In Loch Ewe, settling was slightly earlier, from April to June. After the first individuals appeared, total numbers increased in all years up to maximum numbers in June–July between 35 × 10³ in 1968 and 170 × 10³ in 1966. Again, a drop in numbers followed, from September onwards, to between 3 × 10³ and 11 × 10³ individuals. During most of the growing season, the fish were restricted to depths

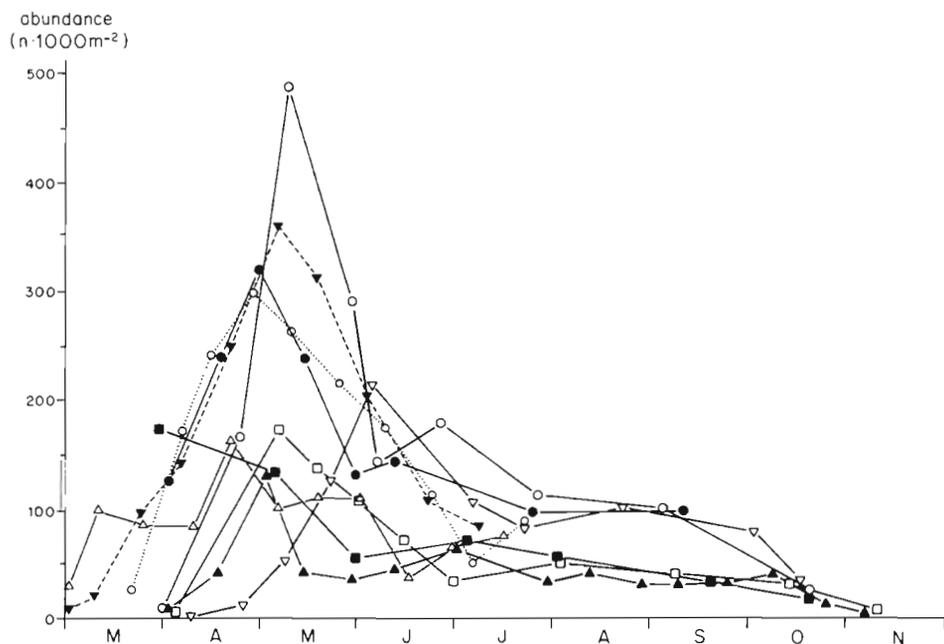


Fig. 3. *Pleuronectes platessa*. Mean density of 0-group plaice (ind. 1000m⁻²) in the Dutch Wadden Sea at the Balgzand in 1973 to 1982, after Zijlstra et al. (1982) and van der Veer (1986). (▽) 1973; (▲) 1975; (□) 1976; (■) 1977; (○) 1978; (●) 1979; (△) 1980; (▼) 1981; (○...○) 1982

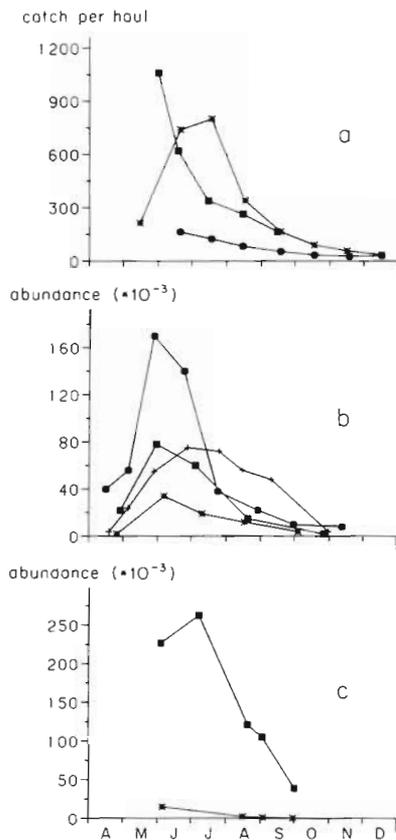


Fig. 4. *Pleuronectes platessa*. Abundance of 0-group plaice in British bays. (a) Port Erin, after Riley & Corlett (1966): (*) 1963; (●) 1964; (■) 1965. (b) Loch Ewe, after Steele & Edwards (1970): (●) 1965; (■) 1966; (+) 1967; (*) 1968. (c) Filey Bay, after Lockwood 1972: (■) 1968; (*) 1969 ($\times 10^{-6}$)

< 4 m. By the end of September, the population was found in the deeper part of the bay, probably as a result of migration (Steele & Edwards 1970). In Filey Bay, settlement was observed between May and early July. After immigration of the first larvae, densities increased, reaching peak numbers between 20×10^3 and 260×10^3 ind. in July and August, followed by a decrease to $< 30 \times 10^3$. There were some indications that plaice in Filey Bay were distributed over depth according to size, although the phenomenon was not always quite clear (Lockwood 1972).

Settlement on the Swedish west coast was generally observed during April and May (Fig. 5). In 1979 the start of the settlement was delayed by about 1 mo, probably related to the severe preceding winter. Fish settled in waters less than 1 m deep. In Gullmar Bay, peak abundance during settling, usually in late May, was estimated at between 0.2 and 2.8 ind. m^{-2} at 0 to 0.7 m depth. In late summer (August–September), the abundance was between 0.1 and 0.2 ind. m^{-2} . In Laholm Bay, densities of 0-group plaice in July were

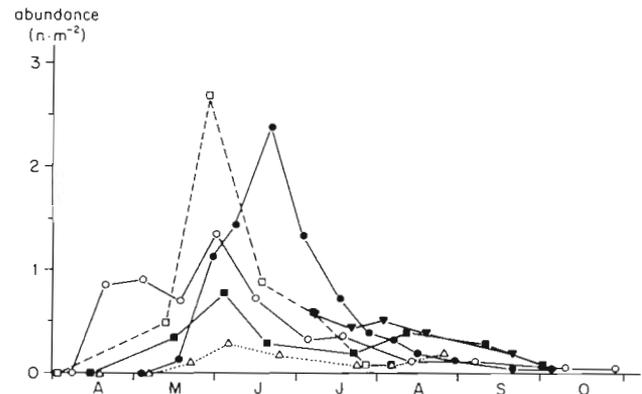


Fig. 5. *Pleuronectes platessa*. Abundance of 0-group plaice (ind. m^{-2}) in Gullmar Bay, Sweden, after Pihl (1989a, b). (▼—▼) 1977; (○—○) 1978; (●—●) 1979; (△---△) 1980; (■—■) 1981; (□—□) 1982

estimated at 0.1 to 0.5 ind. m^{-2} at a water depth of 1.5 m (Pihl 1989 b). In late summer densities had decreased to between 0.01 and 0.1 ind. m^{-2} . In autumn, the fish migrated to deeper water.

In all nursery areas the seasonal abundance of 0-group plaice showed a similar pattern: increasing densities in spring until the end of settlement followed by a continuous decline during the rest of the season.

Growth

Table 1 summarizes the size ranges of mean length in 0-group plaice for the various nursery areas at settlement and by the end of the growing season. The differences between the various areas appear to reflect differences in water temperature in the nursery areas

Table 1. *Pleuronectes platessa*. Between-year variation in mean length (mm) of 0-group plaice in the various nursery areas at settlement and at the beginning of August

Area	Years of observation	Mean size range	
		Settlement	1 Aug
Balgzand	1973–1982	10–15	63–78
Loch Ewe	1965–1968	10–20	45–52
Filey Bay	1968–1969	10–20	30–35
Gullmar Bay	1977–1982	14–16	50–70

(Fig. 6) as well as in the length of growth season. Seasonal variations in mean temperature were largest in the Wadden Sea and in Gullmar Bay, whereas in British bays the seasonal differences in temperature were much reduced. As a consequence of the lower summer temperatures, growth in British bays would be expected to be lower. Although the temperature regimes in the Wadden Sea and Gullmar Bay were

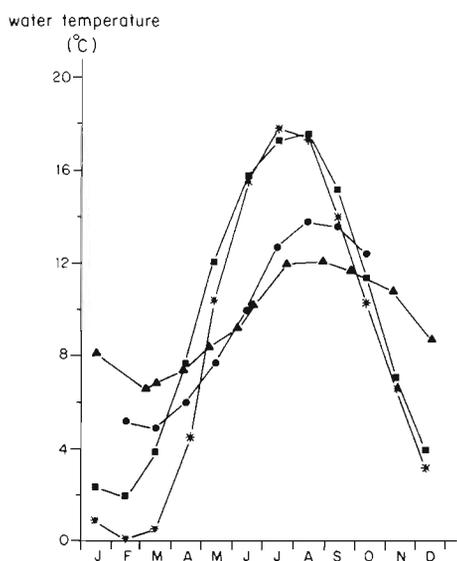


Fig. 6. Mean water temperature (°C) in: (■) Dutch Wadden Sea, after Netherlands Institute for Fishery Investigations (unpubl.); (●) British Bays, Filey Bay, after Lockwood (1972); (▲) Loch Ewe, after Steele & Baird (1968); (*) Swedish Bays, after Pihl (unpubl.)

similar, the larger size of plaice in the Wadden Sea by the end of the season could be explained by the earlier arrival time of the larvae.

The food conditions in the various nursery areas can be addressed by comparing observed length increase in the field with expected length increase, applying the experimentally obtained relationship between optimum growth and temperature (Eq. 1) (Fig. 7). The observed increase in mean length in the field might be an underestimate of the real growth in some areas (British bays), since catch data were not always corrected for net efficiency. However, catch efficiency decreases with increasing fish length (Kuipers 1975) and within the size range of the 0-group plaice the error will be negligible.

Growth in the Wadden Sea was more rapid during the early phase but dropped off in August. There is no indication that fluctuations in abundance over the years influenced this pattern. For Port Erin Bay, no growth and temperature data were available. Temperature data for Loch Ewe have only been published for 1965 (Steele & Baird 1968). Edwards & Steele (1968) observed growth differences between years and they

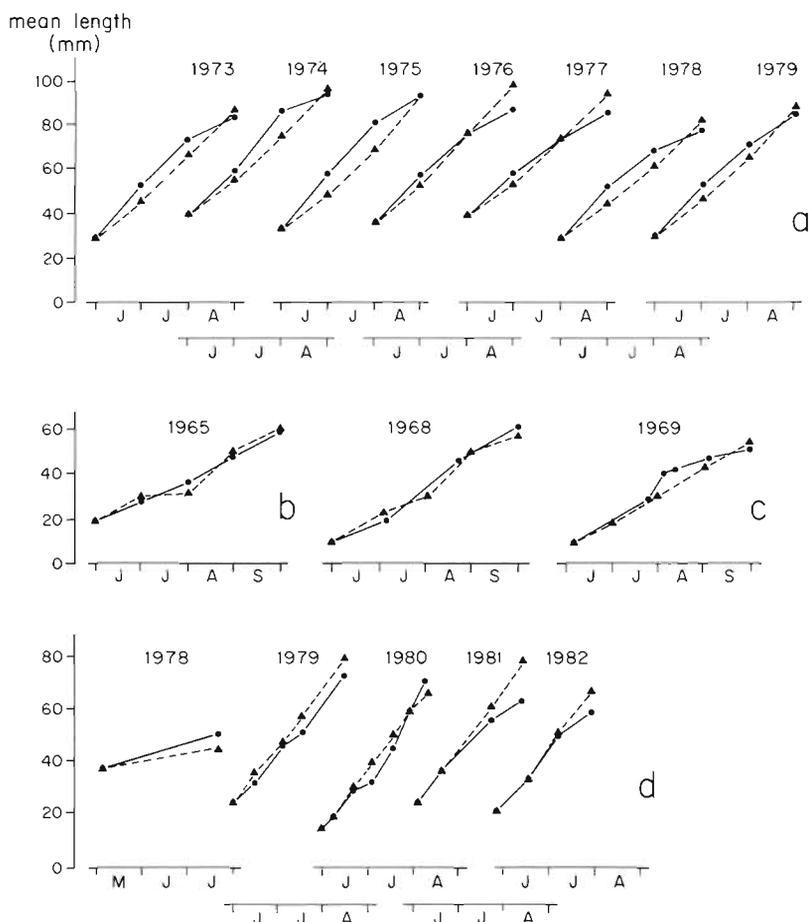


Fig. 7. *Pleuronectes platessa*. Mean length (●—●) of 0-group plaice (mm) compared with 'simulated' maximal growth (▲—▲) according to a growth model obtained under optimal food conditions in the laboratory, after Fonds in van der Veer (1986). (a) Dutch Wadden Sea, Balgzand area 1973 to 1979; (b) British bays, Loch Ewe in 1965; (c) British bays, Filey Bay in 1968 and 1969; (d) Swedish bays, Gullmar Bay in 1978 to 1982

suggested that these were density-dependent, implying food limitation of the 0-group fish. However, 1965 yielded the most abundant year-class and growth was similar to expectations on the basis of the temperature regime. It therefore seems more likely that the observed variation between years is related to differences in temperature in combination with differences in timing of settling (van der Veer 1986). For Filey Bay the observed differences in growth between 1968 and 1969 could be fully explained by differences in water temperature between the years. Also, in Gullmar Bay, the observed growth rate did not deviate from the expected growth over most of the season, indicating no food limitation.

Mortality

Table 2 lists the predators of 0-group plaice in the various nursery areas as revealed by stomach content analysis. In all areas, crustaceans were found to prey upon plaice (Edwards & Steele 1968, van der Veer & Bergman 1987, Pihl 1989a, unpubl.). Crustacean preda-

Table 2. Predators of 0-group plaice in the various nursery areas as revealed by stomach content analysis (* rare; ** common) for spring and summer-autumn separately. For references see text

Species	Wadden Sea	British bays	Swedish bays
Spring			
Brown shrimp	**	*	**
Shore crab	**		**
Summer and autumn			
I, II-group plaice	*	*	
Other flatfish sp.		**	
Bass	*		
Lesser weever		**	
Young coalfish		**	
Young cod		**	**
Skate		**	

tion is restricted to plaice up to a size of 3 cm (van der Veer & Bergman 1987) and will therefore operate in spring. Fish were also found to prey upon larger sized plaice in summer and autumn in all areas. Depending on the area, the significance of the different predator species varied. In the Wadden Sea, cannibalism hardly occurs (de Vlas 1979), and most fish species that have been identified as predators of plaice are absent or only present in very low densities (e. g. bass) on the tidal flats (van der Veer 1986). In British bays, mortality by fish species, including cannibalism, was more impor-

tant. In Port Erin, predation by dabs, flounder, turbot, lesser weever and young coalfish was important, as was cannibalism (Riley & Corlett 1966). In Loch Ewe, more than 50 % of the young cod had plaice remains in their stomach, suggesting that this species was the main predator. Other predators were the lesser weever and skate. Cannibalism by I- and II-group plaice was considered less important (Edwards & Steele 1970). In Swedish bays juvenile cod was also identified as a predator in late summer and autumn (Pihl 1982).

Mortality rates after settlement varied during the season (Table 3). In the Wadden Sea, mortality rates were relatively low. Only during a short period after settling from April to June were mortality rates up to 0.04 d^{-1} found, caused largely by shrimp predation (van der Veer & Bergman 1987), and shown to be density-dependent (van der Veer 1986). Thereafter, mortality rates dropped to a mean of 0.004 d^{-1} during the period July to September. In British bays, mortality between July and September appears to be higher than in the Wadden Sea area (mean = 0.019 d^{-1}), although the water temperature was lower. In Swedish bays (Gullmar Bay), mean mortality rate over the years was slightly higher than in British bays, with a mean of 0.024 d^{-1} . In both British and Swedish bays this mortality did not show a significant relationship with density.

Recruitment mechanisms

The fluctuations in recruitment in the various nursery areas were analysed by estimating the coefficient of variation in abundance and mortality during the early life history, based on the data presented in the previous sections. In all areas, the same 2 processes could be distinguished: a period of predation by crustaceans in spring until the fish reach a size of 3 cm (van der Veer & Bergman 1987) and a period of predation by fish in summer and autumn. Fig. 8 shows these 2 periods for the different nursery areas, estimated on the basis of growth and water temperature data. Although there will be some variation between years, 0-group plaice reach a mean size of about 3 cm around 1 July. Thereafter, they have become too large for predation by crustaceans (van der Veer & Bergman 1987). Thus, the impact of the 2 types of predators was evaluated by comparing the variation at the peak of settlement with the variation on 1 July and 1 September (Table 4). The data sets on abundance in Swedish bays (Figs. 9 and 10) were obtained from Pihl (1989a, b).

The interannual coefficient in variation (Coef) in abundance at settlement was about the same among sites, between 62 and 69 %. After the period of predation by crustaceans the Coef in abundance between years had dropped to 35 % in the Wadden Sea,

Table 3. *Pleuronectes platessa*. Instantaneous mortality rate (Z , d^{-1}) of 0-group plaice between 1 July and 1 September in the Dutch Wadden Sea (after Zijlstra et al. [1982] and van der Veer [1986]), British bays (Port Erin after Riley & Corlett [1966], Loch Ewe after Steele & Edwards [1970], Filey Bay after Lockwood [1972]), and Swedish bays (after Pihl 1989a)

Year	Area	Abundance		Z_t (-)	Z (d^{-1})
		1 Jul	1 Sep		
Wadden Sea					
1973	Balgzand	125 ^a	100 ^a	0.223	0.0037
1975	Balgzand	70 ^a	50 ^a	0.336	0.0056
1976	Balgzand	55 ^a	43 ^a	0.257	0.0042
1977	Balgzand	70 ^a	50 ^a	0.336	0.0056
1978	Balgzand	150 ^a	100 ^a	0.405	0.0068
1979	Balgzand	125 ^a	95 ^a	0.274	0.0046
1980	Balgzand	70 ^a	60 ^a	0.154	0.0026
1981	Balgzand	90 ^a	75 ^a	0.182	0.0030
1982	Balgzand	80 ^a	65 ^a	0.208	0.0035
	Mean				0.0044
British bays					
1963	Port Erin	500 ^b	210 ^b	0.868	0.014
1964	Port Erin	150 ^b	70 ^b	0.762	0.013
1965	Port Erin	770 ^b	240 ^b	1.166	0.019
1965	Loch Ewe	138 ^c	22 ^c	1.836	0.031
1966	Loch Ewe	62 ^c	12 ^c	1.642	0.027
1967	Loch Ewe	70 ^c	50 ^c	0.336	0.005
1968	Loch Ewe	22 ^c	10 ^c	0.788	0.013
1968	Filey Bay	262.7 ^c	105.7 ^c	0.910	0.015
1969	Filey Bay	15.1 ^d	2.3 ^d	1.865	0.031
	Mean				0.0186
Swedish bays					
1978	Gullmar Bay	0.34 ^e	0.12 ^e	1.040	0.017
1979	Gullmar Bay	1.34 ^e	0.15 ^e	2.190	0.036
1980	Gullmar Bay	0.15 ^e	0.10 ^e	0.541	0.009
1981	Gullmar Bay	0.25 ^e	0.10 ^e	1.222	0.020
1982	Gullmar Bay	0.60 ^e	0.10 ^e	2.389	0.040
	Mean				0.0244

^a Ind. 1000 m⁻²; ^b ind. per standard haul; ^c × 10⁻³; ^d × 10⁻⁶; ^e ind. m⁻²

whereas in British bays it remained about the same, and in Swedish bays it even increased to 89 %. Predation by fishes in the second period did not affect the ultimate Coef in the Wadden Sea area. Some reduction was observed in Port Erin, but this reduction was balanced by an increase in Loch Ewe. Some reduction occurred also in Gullmar Bay. In Laholm Bay, a relatively high Coef was found in August, but no comparable data were available for the times at settlement and 1 July.

DISCUSSION

The geographic distribution of the nursery areas studied implies that they will be supplied with larvae originating from different spawning areas. The location of most of these nurseries has been more or less documented (e.g. Harding et al. 1978). A passive trans-

port of eggs and larvae by currents from the spawning areas towards the nurseries is assumed, which might be affected by wind stress as indicated for the Kattegat-Skagerrak area (Pihl 1989a). Cushing (1974, 1990) suggested that transport of larvae towards the nursery areas might be the combined effect of larval behaviour and a coastward-directed bottom current. Although this may apply to exposed coasts, Rijnsdorp et al. (1985) and Bergman et al. (1989) suggested for sheltered areas like the Wadden Sea that larvae are passively transported with the tides.

The processes operating during pelagic egg and larval drift have hardly been studied. Pommeranz (1981) and Daan et al. (1985) found modest predation by herring on pelagic eggs in the southern North Sea. However, this mortality could only explain part of the observed decline in abundance. Hovenkamp (1989, 1990) suggests the occurrence of temporary starvation of larvae, which might have an effect on survival. An

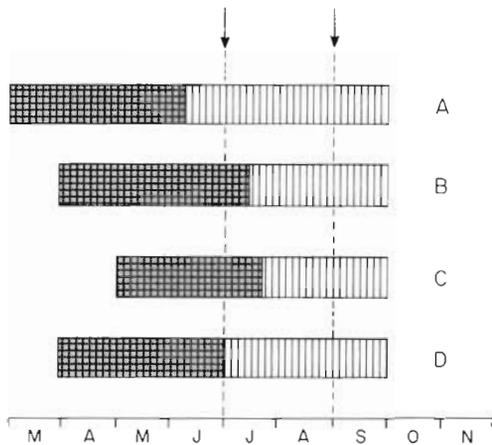


Fig. 8. *Pleuronectes platessa*. Postulated periods of predation dominated by crustaceans (cross-hatching) and by fish (vertical hatching) on 0-group plaice in the various nursery areas: (A) Dutch Wadden Sea; (B) Loch Ewe and (C) Filey Bay; (D) Swedish bays. Compiled by combining growth data (Fig. 7) with water temperature data (Fig. 6)

indirect indication of the importance of the processes operating during the pelagic phase can be obtained by comparing the coefficient of variation in abundance during these stages with those in newly settled demersal plaice in the nursery area. Van der Veer (1986) found an increase in variation between the time of egg

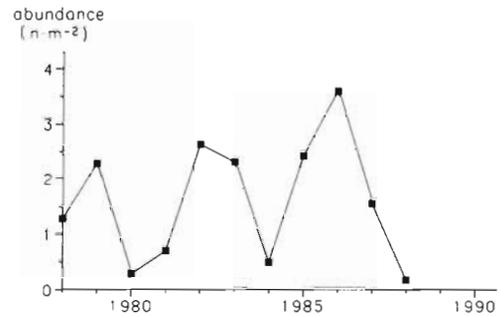


Fig. 9. *Pleuronectes platessa*. Peak abundance (ind. m^{-2}) of 0-group plaice in Gullmar Bay at settling at the end of May/early June, after Pihl (1989a)

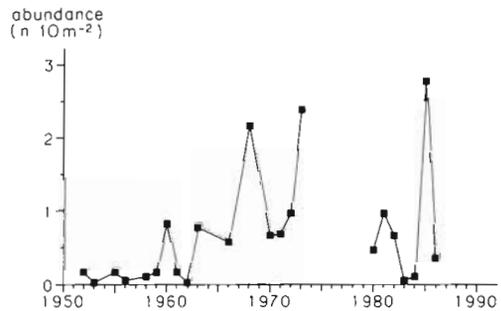


Fig. 10. *Pleuronectes platessa*. Abundance (ind. $10m^{-2}$) of 0-group plaice in Laholm Bay at the end of August, after Pihl (1989b)

Table 4. *Pleuronectes platessa*. Interannual mean, standard deviation and coefficient of variation (%) in abundance of 0-group plaice in the Wadden Sea, British bays and Swedish bays at settlement, after the period of crustacean predation at 1 July and after the period of fish predation from 1 July until 1 September (Wadden Sea after Zijlstra et al. [1982] and van der Veer [1986]; British bays: Port Erin after Riley & Corlett [1966], Loch Ewe after Steele & Edwards [1970], Filey Bay after Lockwood [1972]; and Swedish bays after Figs. 9 and 10 [Pihl 1989a, b])

Area		Abundance		
		Settlement	1 Jul	1 Sep
Balgzand	Mean	114.6 ^a	92.8 ^a	70.9
	SD	71.1	32.6	22.6
	Coef	62 %	35 %	32 %
Port Erin	Mean	693 ^b	483 ^b	173
	SD	469	325	91
	Coef	68 %	67 %	52 %
Loch Ewe	Mean	86.3 ^c	74.5 ^c	23.5
	SD	59.3	48.1	18.4
	Coef	69 %	64 %	78 %
Gullmar Bay	Mean	1.75 ^d	0.54 ^d	0.15 ^d
	SD	1.09	0.48	0.10
	Coef	62 %	89 %	67 %
Laholm Bay	Mean			0.63 ^d
	SD			0.76
	Coef			122 %
Dutch area	Coef	62 %	35 %	32 %
British bays	Coef	68-69 %	64-67 %	52-78 %
Swedish bays	Coef	62 %	89 %	67-122 %

^a Ind. $1000m^{-2}$; ^b ind. per standard haul; ^c $\times 10^{-3}$; ^d ind. m^{-2}

production and settlement of plaice in the Wadden Sea, suggesting that the year-class strength of plaice was generated during the pelagic phase. Data available for other nursery areas (Port Erin, Loch Ewe and Gullmar Bay) show a similar variation in abundance of newly-settled plaice as in the Dutch Wadden Sea: 62 to 69%.

A critical period for plaice is arrival near the coastal nursery areas and the transition from a pelagic to a demersal way of life. Coelenterates, especially the ctenophore *Pleurobrachia pileus* and the scyphomedusa *Aurelia aurita*, have been identified as potential predators on larval plaice (van der Veer 1985) and they both show an outburst off the Dutch coast in spring (van der Veer & Sadée 1984, van der Veer & Oorthuysen 1985). However, almost all larvae have arrived and settled on the tidal flats when this outburst occurs (van der Veer 1985). The process of larval arrival may be terminated by this screen of predators but these predators do not seem to have any effect on the year-class strength of plaice (van der Veer 1985). In the Kattegat-Skagerrak area, the outburst of *A. aurita* occurs in May (Henroth & Grøndahl 1983), also when most of the plaice larvae have already settled. Considering the distribution of these coelenterates in the North Sea (Möller 1980) it would seem likely that similar outbursts will occur in the other nursery areas studied, but no information is available on their timing.

Settling seems to be induced by suitable demersal food conditions (meiofauna components) for the hungry larvae (Creutzberg et al. 1978, Rijnsdorp et al. 1985, Bergman et al. 1987). Settlement seems in general to be restricted to the shallowest areas, although it may extend down to about 4 m water depth. The observed growth rates in all nurseries were similar to the expected growth rates based on laboratory experiments under optimum food conditions if the prevailing temperatures are taken into account. The suggestions of density-dependent effects due to food limitation in the nursery areas by Edwards & Steele (1968) and Lockwood (1974) are thus not supported by this analysis. Differences in mean length of plaice between the various areas are largely explained by differences in timing of larval immigration in combination with differences in water temperatures. Recently, growth of 0-group plaice in the Dutch and German Wadden Sea has been examined within small subpopulations (Berghahn 1987, Bergman et al. 1987) and even by otolith microstructure analysis (Karakiri et al. 1989). Sometimes, food limitation was found. However, this seems to be restricted to only a minor part of the population (Bergman et al. 1987), permitting a generalization of the growth analysis for the whole population in the various nurseries.

Since mortality rates generally decrease with increasing length (Cushing 1974) and the prevailing

water temperatures determine the growth rate of plaice, the latter may have an impact on the vulnerability to predation. Between July and September, plaice show a similar length increase in British bays as in Swedish waters, about 4 cm, but from a length of 20 to 60 mm compared with from 40 to 80 mm in Swedish bays. In principle, plaice in British areas are more vulnerable to predation due to their smaller size, but on the other hand predation rate per predator will be lower in British bays due to the lower mean water temperature compared with other areas.

The group of predators identified as responsible for the observed mortalities in the various nursery areas appears to be broadly similar despite differences in size and morphology of the areas: predation by crustaceans in spring and a period of fish predation later on in the season during summer and autumn. The picture is rather confusing concerning the impact of predation by crustaceans on recruitment of plaice as reflected in the fluctuations in year-class strength. Van der Veer (1986) and van der Veer & Bergman (1987) have shown that predation by crustaceans can act in a density-dependent manner not only within a year, but also between years. In British bays there is no impact of predation by crustaceans on the variation in year-class strength, while in the Wadden Sea and Skagerrak the effects are contradictory: a reduction in variation in the former and a further generation of variation in year-class strength in the latter.

Two factors seem to influence the observed pattern. The first is the absolute water temperature in the area in spring, since predation pressure is strongly dependent on temperature. In the case of the British bays, water temperature is rather low in spring, so the absence of any impact from this period of predation by crustaceans might be the result of too low a water temperature. In the 2 other areas water temperature in spring is much higher, and an impact is observed. However, the effect is reversed in the 2 areas. This is thought to be the result of a second factor, namely the temperature in winter (Fig. 11). In the Wadden Sea these fluctuations in winter between years are rather small and crustaceans normally survive the winter conditions in this area, and thus their abundance is rather constant over the years (van der Veer & Bergman 1987). As a result this process of crustacean predation can act in a density-dependent way, regulating the plaice population not only within a year but also reducing variations between years, as pointed out by van der Veer & Bergman (1987). However, in Swedish bays water temperatures in winter are lower, and values below 0°C are even found (Pihl & Rosenberg 1982). These low temperatures will affect the predatory crustaceans, either inducing mortality or forcing them to migrate to deeper waters (Pihl 1989a). In Gullmar Bay,

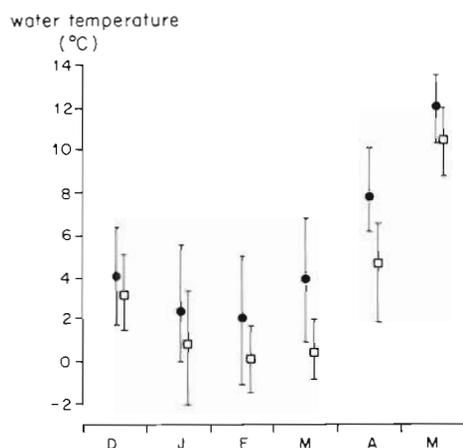


Fig. 11. Water temperatures during winter and spring in (●) the western Dutch Wadden Sea, after Netherlands Institute for Fishery Investigations (unpubl.); and (□) Swedish bays, Station Borno, after Pihl (unpubl.), together with minimum and maximum mean temperatures observed

the biomass of the predatory crustaceans *Crangon crangon* and *Carcinus maenas* was positively correlated with the winter water temperature in the area and inversely with the peak abundance of 0-group plaice in spring (Pihl 1989a). After the severe winter in 1979, the crustacean population was strongly reduced and a strong year-class of plaice was observed in Gullmar Bay (Pihl 1989a). The same was observed in the Wadden Sea area after the cold winter in 1962–1963 (Boddeke 1963). These fluctuations in abundance of the crustacean predators in Swedish bays in spring, in contrast to the Wadden Sea, prevent the density-dependent regulation of the 0-group plaice population in these areas and result in a generation in fluctuations in abundance between years after settlement.

During the period of fish predation between July and September a further decline of plaice abundance is found. Lack of long data sets complicates the interpretation of the results. Although between areas the outcome fluctuates, no clear trends can be observed in the various nursery areas, suggesting no clear influence on the recruitment of plaice. Fluctuations in abundance between years as are present in July does not seem to be affected by this type of predation, although temperatures are rather high and constant between years. The main reason might be the fact that these fish species are mainly seasonal immigrants and therefore their seasonal abundance might not directly be affected by local conditions. Moreover, year-to-year fluctuations in abundance also might prevent a regulating effect by these fishes' predation.

The picture arising from this reappraisal of data on population dynamics conflicts with that for the British bays by Lockwood (1980), who suggested the presence

of both density-dependent and density-independent processes in British nursery areas. The general hypothesis arising suggests that in all areas the same processes are operating, namely predation by crustaceans in spring and predation by fishes in summer and autumn. However, only shrimp predation in spring can affect the plaice population. The ultimate impact of this predation by crustaceans on the recruitment of plaice depends upon local temperature conditions in spring in combination with year-to-year fluctuations, which affect the abundance of the predator population. Regarding the general occurrence of crustaceans in coastal areas where juvenile flatfishes also often can be found, one might wonder whether predation by crustaceans will be a common process operating worldwide and on other 0-group flatfish species.

Brander & Houghton (1982) and van der Veer (1986) stated that year-class strength is fixed before settlement during pelagic egg and or larval stages. Processes operating after settlement were considered as a fine control after the coarse regulation during the pelagic stages (van der Veer 1986). Such a regulating mechanism corresponds with the suggestions already made by Gulland (1965). In almost all nursery areas considered, the absence of an increase in the coefficient of variation of the abundance between years supports this idea. Only in Swedish bays was a further increase in year-to-year variability observed, suggesting that in these areas year-class strength was also affected by processes operating after settlement (Pihl 1989a). However, the year-class strength generating processes in the open sea might still be considered the main factor.

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