Process of estuarine colonization by 0-group sole (*Solea solea*): hydrological conditions, behaviour, and feeding activity in the Vilaine estuary

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The influence of environmental factors on the estuarine settlement and the behaviour of sole late larvae was examined by sampling which was stratified either by transects or by depth, photoperiod, and tidal conditions at one station. The initiation of inshore migration is controlled by the thermohaline conditions in the bay which depend on river flow, tidal cycle, and wind regime. Their fluctuations in abundance seem to be linked less to predator-prey relationships than to water density variations which induce spatial segregation of the sole and potential predators like ctenophora and scyphomedusae. In the estuary, late larvae exhibit a vertical migratory behaviour in relation to photoperiod with excursions up into the water column during the night. This diurnal rhythm is endogenous and is not related to feeding activity which is itself linked to tidal conditions and to predation on epi- and endo-benthic fauna.

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Introduction

The common sole, *Solea solea*, is a predominant species, economically and biologically, in the fish communities of the French Atlantic coast. It is especially abundant in estuarine systems which are ideal foraging habitats for the young individuals. For some pleuronectiform species like the plaice, *Pleuronectes platessa*, the transport mechanisms of the metamorphosing larvae from the open sea towards nursery areas have been described, in particular along the North Sea coast (Creutzberg et al., 1978; Rijnsdorp et al., 1985). For the sole, little information is available on this migratory phase during which they change their morphology and their behaviour while they leave coastal waters to colonize estuarine areas (Lagardère, 1982; Le, 1983).

This study, which is included in the National Research Programme into the Determinism of Recruitment (PNDR), seeks to determine, on a seasonal basis, those ecological parameters which induce late-larval sole to enter a macrotidal estuary; to study the influence of environmental conditions on their behaviour, and finally, to ascertain whether they exhibit any particular biological rhythm.

Methods

In the bay and estuary of the Vilaine where the freshwater flow is controlled by a barrage, 0-group sole were regularly sampled at 13 stations from April to June in

![Figure 1. Location of the transects and the station (no. 11) selected for sampling sessions.](image-url)
1987 (Fig. 1) with a small beam trawl (1 m wide by 0.3 m high, 4.1 m in length) equipped with a tickler chain and fitted with a 5 mm mesh at its mouth and a 1.5 mm mesh at its codend.

To study sole behaviour, one station (no. 11) was chosen in the main channel of the estuary and was then sampled for two months in 1986 (from late April to late June) in eight different tidal conditions from spring to neap tides (Fig. 2). Each sampling session was 27 hours’ long and included nine sets of samples taken at 3 h intervals. Samples were taken from two trawlers of shallow draught which, in addition to the small beam trawl already described, were equipped with two glass-eel tow nets rigged on a 6 m boom to capture the sole in the water column. Each glass-eel tow net is a conical cylinder net with a 1.2 m long anterior truncated cone of 1.2 m diameter at the mouth and 0.35 m diameter at its codend; its mesh size is 1.8 mm. The cone leads into a 0.4 m long cylinder of a mesh size of 1.5 mm. These nets have a filtering area of 2.87 m², i.e. a ratio R of 2.54 times the mouth area (Smith et al., 1968). Flow rate and hence volume filtered was measured with a centrally mounted TSK flow meter. Filtration efficiency, estimated according to Smith et al. (1968), is about 95% except when the net is clogged due to swarms of ctenophores and medusae.

At each time of sampling, the glass-eel tow nets were rigged on either side of the trawler and towed simultaneously for 10 min, first at a depth of 1 m below the surface and then at a depth of 3 m. Then the bottom trawl was shot twice and towed for 500 m (thus the total area fished on each occasion was 1000 m²). Abiotic parameters were recorded every 3 h: temperature and salinity at depth intervals of 1 m and current velocity at the three sampling levels (currents will be regarded as positive when they flow downstream and negative upstream).

In the samples, which were fixed in 5% formalin, pleuronectiform fishes were identified, counted, and measured. Their abundance was converted into numbers per 1000 m² for the bottom samples and per 1000 m³ for the water column ones. Gut contents were analysed with an estimation of state of fullness (empty; half-full; full) and identification of prey items. Their potential predators were identified, counted, and the gut contents of the ctenophora were examined.

Results

Hydrological conditions during inshore migration of sole and its biological characteristics

The date of the first observation of sole late larvae in the estuary differs according to the year: they appeared

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at the end of April in 1986 and in mid-April in 1987. Analysis of the hydroclimatic data can help to explain these differences (Fig. 3).

In 1986, during the first spring tides period, although the river flow rate was low, cold freshwater (corresponding to exceptional snowfall) was pushed seaward by regular offshore winds (N–NE) blowing at a speed of 3 to 7.5 m s$^{-1}$. In such conditions, a hydrographic front with a high density stratification occurred at the mouth of the estuary (Fig. 4) and no young sole were observed upstream. During the second spring tides, in spite of a high freshwater discharge due to heavy rainfall between 14 and 22 April, water mass exchanges were induced by regular westerly winds blowing at high speeds (4 to 9 m s$^{-1}$): the first settlement of the 0-group sole occurred at the end of April.

In early April 1987 (Fig. 3), a low river flow associated with a constant southwesterly wind (4 m s$^{-1}$) resulted in mixing in the bay and estuarine water masses and no front was detected in the area (Fig. 4). The first sole influx was observed as early as 15 April.

When unfavourable conditions occur in the estuary (as in 1986), we suppose the young sole remain in the bay, at the mouth of the outer estuary where the depth is less than 5 m: indeed, in this area, concentrations of sole were observed in early April 1987 before their penetration into the estuary.

The interannual comparison of the length frequency distribution of these initial immigrants (Fig. 5) shows a significant difference in their mean size, the fish entering the estuary in April being smaller in 1986 ($10.56 \pm 1.66$ mm) than in 1987 ($11.21 \pm 2.58$ mm) ($t = 2.35$, $p < 0.05$).

Variations of late larvae abundance in the estuary

In spring 1986, comparison of the changes in water density with the levels of abundance of late larvae at station 11 (Fig. 6) shows that the first appearance of the

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**Figure 4.** Spatial variation of the water stratification index (ID) in the Vilaine ecosystem in early April 1986 and 1987.

**Figure 5.** Length-frequency distribution of young sole captured in the estuary in late April 1986 and mid-April 1987.

**Figure 6.** Variations in the abundance of sole late larvae and their potential predators in relation to water density fluctuations in April 1986 at station no. 11.
larvae coincides with an increase in density. The water density \(\sigma_t\) reached 18.8 (at 12°C, 25 ppt salinity) which is closer to average marine conditions \(\sigma_t; 27.2\) at 9.6°C, 35.2 ppt; Camus et al., 1987). Larval abundance decreases when the river is again in spate as on 5 May when, after a week of heavy rain, \(\sigma_t\) reduced to 15.1 (at 12.3°C, 20.3 ppt). Later, in early June, the new decrease of late larvae density does not correspond to unfavourable water conditions but to their transformation into juveniles which are not considered in this analysis. From mid-June, there is no further influx of late larvae to the estuary and all the sole are juveniles more than 20 mm in length. These variations indicate that the early stages of sole (metamorphosing sole) are susceptible to water quality and move into the estuarine ecosystem in accordance with the water mass displacement which is mainly governed by the river flow.

An examination of the pattern of sole late larvae distribution in relation to water density from April to June in the estuarine area (Fig. 7) leads to the observation that these young stages are concentrated in water masses in which density \(\sigma_t\) varies between 19 and 23 and few are present in cold/euhaline \(\sigma_t > 25\) or warm/messo-oligohaline \(\sigma_t < 17\) conditions. These conditions are not the same as those for the oldest sole (juveniles of more than 20 mm long) which in May are mainly concentrated in water masses where density is between 16 and 23 (with a maximum of 17), while in June, the peak of their abundance is located near the barrage where water density is low \(\sigma_t = 11\) with 630 soles 1000 m\(^{-2}\). This change corresponds to their progressive adaptation to estuarine conditions.

The length-frequency distribution of sole (Fig. 8) from late April to mid-June indicates that inshore migration of newly settled fish does not occur in a single wave but can last more than one month with repetitive peaks, the new immigrants mixing with the oldest ones.

The temporal changes in the abundance of the postlarvae and potential predators such as ctenophores \((Pleurobrachia pileus)\) and scyphomedusae \((Aurelia aurita)\) (Fig. 6) show that peaks in abundance of sole late larvae are followed by peaks in abundance of both predator taxa. These reciprocal oscillations may be interpreted as evidence of predatory regulation of sole early life stages by the gelatinous predators. Such regulation has been described for the larval herring population in Kiel Bight (Möller, 1984) and for plaice and flounder larvae in the Wadden Sea (van der Veer, 1985) where young fish up to 12 mm were found in the digestive contents of \(Pleurobrachia pileus\). In the Vilaine ecosystem, analysis of stomach contents of these predators revealed no soles but rather copepods which are the main component of the estuarine plankton. Examination of the spatial distribution of these different taxa in Vilaine bay and estuary in April and May 1987 (Fig. 9) shows that they are located in distinct water masses, the young sole being upstream and the gelatinous predators downstream. Such spatial segregation was observed by Frank and Leggett (1985) in coastal Newfound-land between the abundance of gelatinous predators and ichthyoplankton.

**Vertical migration of postlarvae and their feeding activity**

Observations of the vertical distribution of the late larvae during two of the eight sampling sessions (for the six others, sole was scarce) show that they exhibit a
pronounced behavioural response to photoperiod: they remain on the bottom throughout the day and migrate vertically into the water column at night (Fig. 10). The hydrographic conditions in the Vilaine estuary are controlled by the barrage discharge and so tidal effects on the vertical migration of sole larvae are minimal. Nightly excursion into the water column occurs at both ebb and flood tides but the magnitude of migration, in terms of abundance of larvae migrating towards the surface, seems to be linked to the current velocity and direction. The number of larvae migrating increases as current speed reduces with few or no sole late larvae to be found in the water column when the currents are strong and oriented downstream. Such adaptation to the current conditions allow young soles to remain in the estuary. In the Wadden Sea, Rijnsdorp et al. (1985) indicated that plaice larvae are more “likely pelagic during flood than during ebb tides and that this tendency is more pronounced at night than during the day”. For sole, no vertical migration was observed during the day, even when the current conditions were favourable. Such a pattern of cyclical vertical distribution has been described for the metamorphosing English sole (*Parophrys vetulus*) in Yaquina Bay (Oregon) by Boehlert and Mundy (1987).

The diurnal pattern of migration of early life stages of sole in the Vilaine estuary does not depend on their feeding rhythm (Fig. 11) which follows the tidal rhythm. Although food is continuously observed in the digestive contents, they seem to feed according to a semi-diurnal pattern, mainly during day and night flood tides. Their prey belong to the supra-benthic meiofauna with harpacticoid copepods as the main component of their diet. Plankton are negligible as a food resource for late

Figure 8. Length-frequency distributions observed at station no. 11 in spring 1986.

Figure 9. Spatial distribution of young sole and their potential predators in April and May 1987. MED. = medusae, CTEN. = ctenophores.
larvae which consume them mainly at the beginning of their inshore migration (10% of the food composition in April) (Fig. 12).

Discussion
For species which spawn offshore and which have an estuarine-dependent cycle, Boehlert and Mundy (1988) recognize two principal phases of movement necessary for their recruitment to estuaries: nearshore accumulation of the larvae which is essentially passive, then an estuarine recruitment which is the result of active behaviour adapted to the environment. According to Miller (1988), "the stages in the transition from passive to active migration depend upon increased agility, and would be expected to vary among species and the particular current regime". For fish larvae, the first stage of the migration from the open sea to the nursery areas has often been explained as passive transport by drift; such a mechanism involves planktonic larval stages of weak swimming ability (Cushing, 1975; Miller et al., 1984; Boehlert and Mundy, 1987).

Figure 10. Vertical distribution of sole late larvae during the 28-29 April and 27-28 May sampling sessions. For each series of diagrams, on the right axis: current velocity; on the left axis: sole density (ET = ebb tide; LT = low tide; FT = flood tide; HT = high tide. Black bars indicate periods of darkness).
For sole which spawn in the Bay of Biscay (about 100 km offshore), the migration of early life stages cannot be ascribed to a typical passive drift. Koutsikopoulos and Herbland (1987) demonstrated important spatial stability of the pelagic stages in the spawning area with no dispersion of the egg and larvae and suggested that transport to the nursery areas is effected during late larval stages by active behaviour, since no onshore-oriented residual circulation occurred on the spawning grounds.

Recent data on water circulation in the bay of Vilaine (De Nadaillac and Breton, 1986) suggest that when they enter this region, the late larvae are in a hydrological environment favourable to their inshore migration. It was demonstrated that, in the bay, tidal currents have a weak impact on water mass exchanges and residual circulation is mainly dominated by the wind with bottom currents oriented landward. For metamorphosing larvae, this pattern of water circulation with an increase of the amount of oceanic water entering the bay under wind stress (essentially onshore winds), is certainly the main feature contributing to their inshore transportation. In the Marennes-Oleron region where tidal action is predominant, the role played by bottom currents on the young stage transport has already been indicated by Le (1983). For sole, it is possible that the metamorphosing larvae carry out passive but selective horizontal movements using bottom currents to reach the mouth of the estuary where they accumulate. Such a pattern of migration has previously been described for other pleuronectiforms like plaice in North Sea areas (Rijnsdorp et al., 1985; Creutzberg et al., 1978).

The second stage of migration, which is estuarine penetration and settlement, is clearly an active transport. For sole in the Vilaine estuary, the first incursion is controlled by hydroclimatic conditions, i.e. river flow and wind regime. If, as in 1986, an offshore wind is associated with a high freshwater discharge, a hydrographic front occurs at the mouth of the estuary which presents an obstacle for early life stages whose diurnal pattern of vertical migrations prevents them from passing through. As size differences were observed between sole which were trapped at the mouth of the estuary until the end of April 1986 and those which entered the estuary in early April 1987, we suggested that such differences may be attributed to lack of access to preferred feeding areas when a front occurs. This hydrographic structure which is an uncertain phenomenon controlled by the climate, can be considered as one of the “point source” stimuli suggested by Boehlert and Mundy (1988) and may have an impact on the success or failure of the estuarine settlement of sole.

Settlement of metamorphosing sole extends over about 1.5 months with high abundance of metamorphosing individuals generally occurring on spring tides and low densities on the next neap tides. These oscillations suggest that estuarine migration may be linked to the lunar cycle: new immigrants mixing with previously settled ones. Such pulses of fish linked to the spring-neap tide cycles were observed in Parophrys vetulus recruitment by Boehlert and Mundy (1987). At each abundance peak, we observed that young sole entered the estuary at all depths, with no size difference between sole collected in the water column and on the estuarine settlement of sole.

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bottom. This vertical distribution, which disappears in June, when late-larvae influxes have ceased, corresponds to a typical circadian rhythm with night excursions in the water column associated with low current velocities. Champalbert et al. (1987) showed that this rhythmic activity is an endogenous phenomenon which persists for several days when sole late larvae are reared in complete darkness, light acting as a zeitgeber. Diel rhythms are known in other euryhaline species such as plaice, flounder, or English sole with nocturnal vertical migration on flood tides (Arnold and Cook, 1984; Weinstein et al., 1980; Creutzberg et al., 1978; Rijnsdorp et al., 1985; Boehlert and Mundy, 1988). Although sole late larvae may be partly flushed downstream on night ebb tides as Rijnsdorp et al. (1985) described for the plaice, on balance, these migrations are positive and in favour of their retention in the estuary since their period on the bottom is longer than their occurrence in the water column.

In late larval cohorts which settled in the estuary, we observed a superimposition of two different rhythms: a circadian activity which favours their upstream migration and their estuarine retention, and a cirri-tidal one for their feeding activity. This phenomenon corresponds to the occurrence of the “appetitive behaviour” which is observed in metamorphosing larvae of pleuroeonciforms when they enter nearshore and estuarine areas (Boehlert and Mundy, 1988). According to these authors (1987), “a suite of stimuli associated with tidal flux acts as a zeitgeber to superimpose a cirri-tidal rhythm upon the circadian rhythm which already may be present”. In juvenile pleuroeonciform species, tidal and cirri-tidal migration patterns linked to the availability of the intertidal feeding grounds have been described either under controlled conditions in laboratory, or in their natural environments and are characteristic of their adaptation to estuarine areas (Kuipers, 1973; Le, 1983; Gibson, 1984; van der Veer and Bergman, 1986). In subtidal areas, Kruuk (1963), de Groot (1971) and Lagardère (1987) showed sole juveniles to have a daily activity rhythm with nocturnal food intake; these rhythmic activities demonstrate that the sole has a great ability to adjust its behaviour to the characteristics of the environment.

In the Vilaine region, abrupt decreases of metamorphosing sole abundance from late April to early June, correspond to outbursts of predatory cnidaria. Swarms of Aurelia aurita and Pleurobrachia pileus have often been described in nearshore and estuarine areas (Fraser, 1970; Möller, 1980a; van der Veer and Sadee, 1984; van der Veer and Oorthuysen, 1985; Papathanassiou et al., 1987). In Scottish waters, Fraser (1970) indicated the regular appearances of P. pileus were correlated to scarcity or exclusion of other planktonic components. This gelatinous eutrophore dominated the water over large areas. In our study, we also observed this phenomenon. The reciprocal oscillations we observed are similar to those described by several authors who interpreted them as predator–prey interactions since A. aurita and P. pileus have both been confirmed as larval flatfish predators (Greve, 1972; Bailey, 1984; Bailey and Batty, 1984; Purcell, 1985; van der Veer, 1985). So in the present study, abrupt population decrease of sole may be partly caused by these predators.

However, we think these predator–prey relationships are not the main factor responsible for these oscillations. We did not observe spatial overlap of sole and their predators which were spatially segregated. Young sole concentrations were located more upstream than those of A. aurita and P. pileus. The occupation of two distinct water masses by predators and their prey, which has been observed and discussed by Frank and Leggett (1985), may be one possible interpretation of our data.

Another argument in favour of the second hypothesis concerns the size and behaviour of the metamorphosing larvae. Several authors demonstrated that for cruising raptorial predators like medusae, increased larval size and swimming activity results in declining vulnerability to capture, with improved detection of predators and better escape ability (Bailey and Houde, 1987). P. pileus, an ambush raptorial predator drifting passively, feeds mainly on copepods (Fraser, 1970; Möller, 1980b). For flatfish larvae, Bailey (1984) demonstrated that the escape speed of flounder increases from 26.7 mm s⁻¹ at the yolk sac stage (4 mm) to 89.7 mm s⁻¹ at 7 mm feeding stage. Bailey and Batty (1984) showed that capture success by predators declines with increasing larval size, especially for flounder and plaice larvae. We think that this phenomenon is more marked in metamorphosing stages. Furthermore A. aurita and P. pileus are planktonic organisms and we observed that metamorphosing sole larvae spend most of the time on the bottom.

In the Wadden Sea, van der Veer and Bergman (1987) demonstrated that a suprabenthic predator like Crangon crangon causes significant mortality of 0-group plaice (<30 mm). For sole, a similar pattern of predation might be expected in our study area as the brown shrimp population occurs in high densities.

So for sole, during the transition from larval to juvenile stage, we suggest that their increasing swimming speed, and their vertical and horizontal distribution patterns in the estuarine area do not favour encounters with potential planktonic predators, but do enhance their vulnerability to suprabenthic predators. These conditions are certainly different to those on spawning grounds and should be considered in relation to larval mortality and to recruitment.

References