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Seasonal Patterns in the Fish and Crustacean Community of a Turbid Temperate Estuary (Zeeschelde Estuary, Belgium)

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Fish and crustaceans were sampled for 1 year in the upper reaches of a temperate estuary characterized by high turbidity and a tidal range of up to 5 m. Samples were taken in the cooling-water circuit of the Doel Nuclear Power station (Zeeschelde, Belgium). Between July 1994 and June 1995, 55 fish species, two shrimp species and four crab species were recorded. The fish community was composed of 36 marine species, 16 freshwater species and three diadromous species. Shrimps, Gobiidae and Clupeidae dominated the samples both in numbers and biomass. An exceptionally clear seasonal succession was observed in the species composition. It is argued that young fish and crustaceans use the highly turbid Zeeschelde Estuary as a refuge from predators.

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Introduction

Communities of fish and crustaceans inhabiting estuaries represent a combination of freshwater and marine species both living at the edge of their distribution, estuarine resident and migrating species passing the estuary on their way to the spawning grounds (Claridge *et al.*, 1986; Wheeler, 1988; Day *et al.*, 1989; Potter *et al.*, 1990; Potter *et al.*, 1997). The spatial organization of estuarine species communities is highly correlated with salinity and substratum type (Henderson, 1989; Hamerlynck *et al.*, 1993). The temporal structure is often the result of seasonal migrations of young fish and crustaceans moving between coast and adjacent estuaries (McLusky, 1989; Robertson & Duke, 1990b). Most species spawn in deeper offshore waters which may be favourable for egg survival and dispersion (Blaber, 1997). After hatching, larvae are drifted to the coastal and estuarine nurseries where they become mobile and then migrate to shallow and turbid areas using the tides as a means of transport (McLusky, 1989; Daan *et al.*, 1990). For temperate estuaries, this pattern of movements results in consecutive migration waves of juveniles of marine fish, crabs and shrimps (Wharfe *et al.*, 1984; Claridge *et al.*, 1986; Pomfret *et al.*, 1991; Potter *et al.*, 1997). In tropical estuaries, seasonality in species communities is less apparent (Day *et al.*, 1989;

Laroche *et al.*, 1997) and sometimes masked by large variances in catch data (Robertson & Duke, 1990a). It has, however, been widely recognized that both temperate and tropical estuaries and inshore areas act as nurseries as they provide almost unlimited food resources (Day *et al.*, 1989) and offer shelter from predators (Cyrus & Blaber, 1992; Ruiz *et al.*, 1993).

Seasonal changes in the structure of the fish and crustacean communities in a highly turbid temperate estuary [Zeeschelde Estuary, Belgium (Figure 1)] are the focus of this study. Therefore, sampling was conducted for 1 year in a power station cooling-water inlet providing a wealth of regular data. This alternative fishing technique was most convenient in an area where trawling and netting are difficult because of extreme tides, heavy shipping and harbour activities, and unexpected weather conditions. The nature of these migrations is further discussed by questioning whether or not the upper reaches of the Zeeschelde are a nursery area offering enhanced protection.

Material and methods

Sampling site and sampling regime

The lower Schelde Estuary (Westerschelde) is situated between the Belgian–Dutch border and the North Sea (Figure 1) and has a complex morphology of gullies,

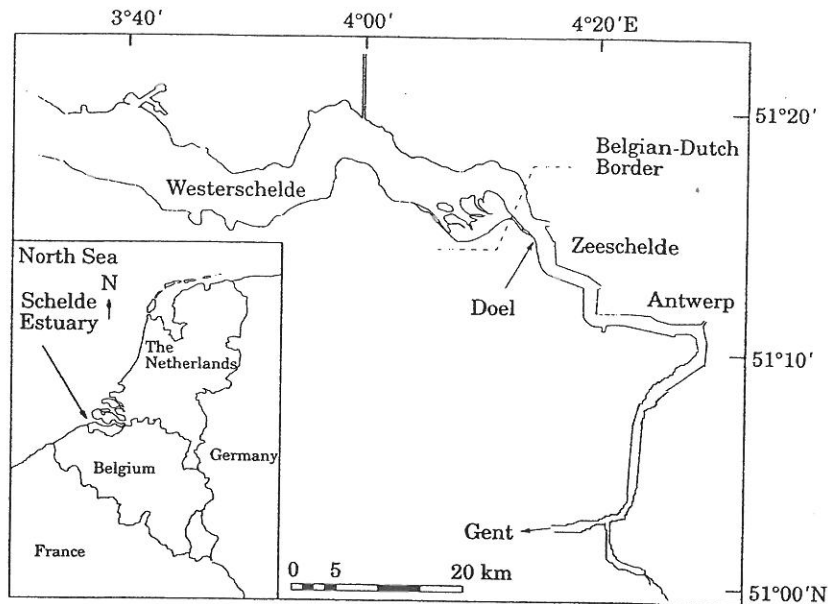


FIGURE 1. A map showing the Zeeschelde Estuary (Belgium) and the location at which fish and crustaceans were sampled (Nuclear Power Plant Doel).

sandflats and channels (Claessens, 1988). The upper estuary (Zeeschelde) (Figure 1) consists of freshwater between Gent and Antwerp and brackish water between Antwerp and the Dutch–Belgian border (Figure 1). The mean freshwater discharge is $105 \text{ m}^3 \text{ s}^{-1}$ (Heip, 1988). Mean tidal range at Doel is 4.85 m (Claessens, 1988).

Samples of fish, shrimps and crabs were collected semi-weekly from the cooling-water intake screens of the Nuclear Power Plant Doel, located in the brackish part of the Zeeschelde (Figure 1). Sampling started in July 1994 and finished in June 1995. The cooling-water intake is situated 2 m above the bottom and withdraws $25.1 \text{ m}^3 \text{ s}^{-1}$ water corresponding to 0.35% of the local Zeeschelde flow. Since the mesh size of the intake screens is 4 mm, neither larvae nor smaller crustaceans such as Mysidaceae could be sampled. Approximately $8 \times 10^6 \text{ m}^3$ cooling water was monitored in 135 samples.

Fish and crustaceans were separated from debris, identified to species level, counted, measured and preserved in 7% formaldehyde. The genus *Pomatoschistus* was identified according to Hamerlynck (1990). Subsamples were taken for large catches of fish or crustaceans by dividing the total catch in equal parts. For each species, biomass (ashfree dry weight) was calculated using length-biomass regressions (Hostens & Hamerlynck, unpubl.; Maes, unpubl.).

During sampling the following environmental variables were measured using a water quality multiprobe logger (Hydrolab, Datasonde 3): temperature, °C;

salinity; dissolved oxygen concentration, mg l^{-1} ; and turbidity, NTU.

Data analysis

Abundance data (numbers $\times 10^{-3} \text{ m}^{-3}$ cooling-water sampled) and biomass data ($\text{g ADW} \times 10^{-3} \text{ m}^{-3}$ cooling-water sampled) were root–root transformed prior to statistical analysis (Field *et al.*, 1982). To study the temporal community structure, correlation biplots, based on principal component analysis (PCA), were used to project n-dimensional data in two-dimensions (Ter Braak, 1994). Variables (species) are represented as species vectors; samples as points. The species vectors are pointing towards samples when reaching their maximum abundance or biomass. Eigenvalues indicate the amount of variability expressed by each principal component.

Results

Environmental data

Minimum and maximum temperatures recorded in the Zeeschelde ranged from 4.9 °C in February to 24.8 °C in August. Mean salinity and oxygen concentrations were 7.99 and 4.59 mg l^{-1} , respectively. Maximum salinities were measured in summer and minimum salinities in winter. The oxygen concentration showed an opposite pattern with maxima in winter and minima in summer when the oxygen concentration dropped just below 2 mg l^{-1} . Secchi

disc depths were on average 19.6 cm and never exceeded 48 cm. Mean turbidity was 165 NTU. *hoof*

Species number and composition

In total, 55 fish species and six crustacean species were caught. Of the fish species, 36 were marine migrants and 16 species typically occur in fresh water (Table 1). Both groups included species that spend part of the life in estuaries as well as species occasionally entering estuaries. None of the species were strictly estuarine dependent i.e. they can spawn and mature in either fully marine or in freshwater environments. *Anguilla anguilla* was the only catadromous species while *Lampetra fluviatilis* and *Alosa fallax* are anadromous (Table 1). Crustaceans caught at Doel included two shrimp species and four crab species (Table 2). It was noted that except for *Carcinus maenas* all crab species were exotics. A living specimen of the blue crab *Callinectes sapidus* was recorded for the first time in Belgium.

Abundance and biomass data

In terms of numbers, eight species made up >95% of the total catches. The most abundant species were the shrimps *Palaemonetes varians* (37.4%) and *Crangon crangon* (29.8%). The most numerous fish species were gobies [*Pomatoschistus microps* (12.6%), *P. minutus* (7.8%) and *P. lozanoi* (1.0%)], Clupeidae [*Clupea harengus* (6.4%) and *Sprattus sprattus* (1.7%)] and the pipefish *Syngnathus rostellatus* (2.5%). In terms of biomass the same species, with addition of *Dicentrarchus labrax* and *Pleuronectes flesus*, dominated the community; *C. harengus*, 29.2%; *P. varians*, 18.0%; *P. minutus*, 17.7%; *C. crangon*, 10.6%; *S. sprattus*, 7.5%; and *P. microps*, 5.0%; *D. labrax*, 4.5%; *P. flesus*, 1.9%; and *S. rostellatus*, 1.0%.

Seasonal community structure

The seasonal changes in the community of fish and crustaceans were analysed using correlations biplots based on PCA. Principal component analysis with abundance data yielded the same information as PCA based on biomass data. Therefore only the correlation biplot with biomass data is shown in Figure 2. The total amount of variability explained by the first two eigenvalues corresponding to the first two principal components was 45.5%. Only species representing >0.1% of the total catches were included in the analysis. Including more species only affected the total variability expressed by the eigenvalues but did not change community structure.

The analysis placed all samples on a circle [Figure 2(a)]. Samples taken in the same month were closely located to each other in the biplot and arranged in a clear seasonal succession [Figure 2(b)]. Five groups of species were more or less separated by the analysis:

Group A [*Rhithropanopeus harrisi*] comprised only one species, an exotic crab species which has recently settled in the Zeeschelde.

Group B [*C. maenas*, *S. rostellatus*, *C. crangon*] occurring mainly in late summer and early fall (August, September) when temperature and salinity were both high.

Group C [*P. minutus*, *P. lozanoi*, *P. microps*] scoring highest biomass in fall (October, November).

Group D [*D. labrax*, *C. harengus*, *S. sprattus*] of which most individuals were caught in December. High numbers of larvae of both Clupeidae reached the Zeeschelde starting from May but were not quantified.

Group E [*Liza ramada*, *L. fluviatilis*, *Gasterosteus aculeatus*, *Pleuronectes flesus*] with species mainly sampled in winter and early spring (January, February, March, April) when high oxygen concentrations were recorded. In this period, numbers of freshwater species caught at Doel were relatively high. Not only *G. aculeatus*, but also *Rhoeus sericeus*, *Gymnocephalus cernuus* and *Abramis brama* took advantage of decreased salinities during winter and early spring.

The period between March and June was characterized by low abundance and biomass. Three species namely *A. anguilla*, *Stizostedion lucioperca* and *P. varians* were poorly represented by the analysis and could therefore not be placed in a species set. The proper reconstruction of *P. varians* was obstructed by two abundance maxima (April and August). *Anguilla anguilla* and *S. lucioperca* are present throughout the year with no marked abundance maximum.

The dominant species reached maximum abundance in the following chronological order starting from July: (1) Young of *C. maenas*; (2) Young of *P. varians*; (3) *S. rostellatus*; (4) Young of *C. crangon*; (5) Young of *P. microps*; (6) Young of *P. lozanoi*; (7) Young of *P. minutus*; (8) Juvenile *C. harengus*; (9) Juvenile *S. sprattus*; (10) Recently metamorphosed *L. fluviatilis*; (11) *P. flesus*; (12) Spring stock of *P. varians*.

Discussion

Sampling method

Sampling in power station cooling-water inlets has been successfully used to study fish and crustacean faunas of temperate estuaries and coasts (Van den

TABLE 1. Species list, mean abundance (numbers $\times 10^{-3} \text{ m}^{-3}$ cooling-water sampled) and standard deviation (SD) of fish sampled in the cooling-water of the Nuclear Power Plant Doel over the period July 1994–June 1995

Scientific name	Common name	Mean	\pm SD
Anadromous species			
<i>Lampetra fluviatilis</i> (L.)	River lamprey	0.06	0.14
<i>Alosa fallax</i> (Lacepède, 1803)	Twaiite shad	<0.01	<0.01
Catadromous species			
<i>Anguilla anguilla</i> (L.)	Eel	0.16	0.15
Freshwater species			
<i>Abramis brama</i> (L.)	Bream	<0.01	<0.01
<i>Carassius auratus</i> (L.)	Goldfish	<0.01	<0.01
<i>Carassius carassius</i> (L.)	Crucian carp	<0.01	<0.01
<i>Cyprinus carpio</i> (L.)	Carp	<0.01	<0.01
<i>Leuciscus leuciscus</i> (L.)	Dace	<0.01	<0.01
<i>Leucaspis delineatus</i> (Heckel, 1843)	Moderlieschen	<0.01	<0.01
<i>Rhoeus sericeus</i> (Pallas, 1776)	Bitterling	0.02	0.07
<i>Rutilus rutilus</i> (L.)	Roach	0.02	0.05
<i>Tinca tinca</i> (L.)	Tench	<0.01	<0.01
<i>Gasterosteus aculeatus</i> (L.)	Three-spined stickleback	0.19	0.30
<i>Pungitius pungitius</i> (L.)	Ten-spined stickleback	0.01	0.02
<i>Cottus gobio</i> (L.)	Bullhead	<0.01	<0.01
<i>Lepomis gibbosus</i> (L.)	Pumpkinseed	<0.01	<0.01
<i>Gymnocephalus cernuus</i> (L.)	Ruffe	<0.01	<0.01
<i>Perca fluviatilis</i> (L.)	Perch	0.06	0.09
<i>Stizostedion lucioperca</i> (L.)	Pikeperch	0.16	0.37
Marine species			
<i>Clupea harengus</i> (L.)	Herring	37.48	92.09
<i>Sprattus sprattus</i> (L.)	Sprat	10.00	36.30
<i>Engraulis encrasicolus</i> (L.)	Anchovy	0.05	0.36
<i>Osmerus eperlanus</i> (L.)	Smelt	0.06	0.10
<i>Ciliata mustela</i> (L.)	Five-bearded rockling	<0.01	<0.01
<i>Gadus morhua</i> (L.)	Cod	<0.01	<0.01
<i>Merlangius merlangus</i> (L.)	Whiting	<0.01	<0.01
<i>Trisopterus luscus</i> (L.)	Bib	<0.01	<0.01
<i>Raniceps raninus</i> (L.)	Tadpole-fish	<0.01	<0.01
<i>Atherina presbyter</i> (Cuvier, 1829)	Sand-smelt	<0.01	<0.01
<i>Spinachia spinachia</i> (L.)	Fifteen-spined stickleback	<0.01	<0.01
<i>Syngnathus acus</i> (L.)	Greater pipefish	<0.01	<0.01
<i>Syngnathus rostellatus</i> (Nilsson, 1855)	Nilsson's pipefish	14.47	44.25
<i>Eutrigla gurnardus</i> (L.)	Grey gurnard	<0.01	<0.01
<i>Trigla lucerna</i> (L.)	Tub gurnard	<0.01	<0.01
<i>Myoxocephalus scorpius</i> (L.)	Bull-rout	<0.01	<0.01
<i>Agonus cataphractus</i> (L.)	Hook-nose	<0.01	<0.01
<i>Cyclopterus lumpus</i> (L.)	Lumpsucker	<0.01	<0.01
<i>Liparis liparis</i> (L.)	Sea snail	<0.01	<0.01
<i>Dicentrarchus labrax</i> (L.)	Bass	2.00	3.36
<i>Trachurus trachurus</i> (L.)	Horse mackerel	0.04	0.43
<i>Liza ramada</i> (Risso, 1826)	Thin-lipped grey mullet	0.03	0.06
<i>Pholis gunnellus</i> (L.)	Butterfish	<0.01	<0.01
<i>Zoarces viviparus</i> (L.)	Eelpout	<0.01	<0.01
<i>Anmodytes tobianus</i> (L.)	Sandeel	0.01	0.06
<i>Hyperoplus lanceolatus</i> (Le Sauvage, 1824)	Greater Sandeel	<0.01	<0.01
<i>Callionymus lyra</i> (L.)	Dragonet	<0.01	<0.01
<i>Pomatoschistus lozanoi</i> (de Buen, 1923)	Lozano's goby	6.20	19.01
<i>Pomatoschistus microps</i> (Krøer, 1838)	Common goby	46.29	85.82
<i>Pomatoschistus minutus</i> (Pallas, 1770)	Sand goby	74.33	164.89
<i>Scomber scombrus</i> (Linnaeus 1758)	Mackerel	<0.01	<0.01
<i>Scophthalmus rhombus</i> (L.)	Brill	<0.01	<0.01
<i>Limanda limanda</i> (L.)	Dab	0.01	0.05
<i>Pleuronectes flesus</i> (L.)	Flounder	0.45	1.46
<i>Pleuronectes platessa</i> (L.)	Plaice	<0.01	<0.01
<i>Solea solea</i> (L.)	Sole	0.03	0.07

TABLE 2. Species list, mean abundance (numbers $\times 10^{-3} \text{ m}^{-3}$ cooling-water sampled) and standard deviation (SD) of crustaceans sampled in the cooling-water of the Nuclear Power Plant Doel over the period July 1994–June 1995

Scientific name	Common name	Mean	\pm SD
<i>Crangon crangon</i> (Linnaeus, 1758)	Common shrimp	175.32	383.73
<i>Palaemonetes varians</i> (Leach, 1814)	Palaemonid shrimp	219.88	333.05
<i>Eriocheir sinensis</i> (H. Milne Edwards, 1854)	Chinese mitten crab	<0.01	<0.01
<i>Callinectes sapidus</i> (Rathbun, 1896)	Blue crab	<0.01	<0.01
<i>Rhithropanopeus harrisi</i> (Gould, 1841)	Dwarf crab	0.24	0.60
<i>Carcinus maenas</i> (L.)	Shore crab	0.71	2.04

Broek, 1979; Hadderingh *et al.*, 1983; Wharfe *et al.*, 1984; Claridge *et al.*, 1986; Turnpenny, 1988; Henderson, 1989). This method offers a useful means to obtain regular, quantitative samples, irrespective of weather conditions. The inlet is a fixed point in the water column accelerating fish that are near or almost upon the intake into the openings. Unlike beam trawling, power stations sample pelagic, demersal and benthic species as they are a pitfall for organisms walking over the substrate and a suction trap for swimmers (Henderson *et al.*, 1992). Since larger fish probably escape from the apertures, the method is designed for smaller fish species and juveniles. Although specimens >50 cm of *S. lucioperca* and *A. anguilla* have been captured at Doel, the quantitative estimate of their abundance as well as of the abundance of larger Salmonidae and Clupeidae such as the anadromous *A. fallax* may be biased. It is however unlikely that the community structure would have been affected by the presumed absence of large individuals in this data since juveniles form a greater part of estuarine fish communities (Day *et al.*, 1989).

Species number

Henderson (1989) observed a linear relationship between species number and latitude based on cooling-water intake data of seven English coastal power plants. In addition, the species number generally declined in estuaries with declining salinities. With respect to latitude and mean salinity of the present sampling area the maximum expected number of fish species is close to 60. Sampling at Doel yielded 55 species indicating that almost all species occurring in the Zeeschelde are caught. The capture of *L. fluviatilis*, *Osmerus eperlanus* and *A. fallax* is noteworthy, since they are indicators of good water quality (Hamerlynck *et al.*, 1993). During the late 1980s, the Zeeschelde Estuary was heavily affected by domestic and industrial wastewater (Van Eck *et al.*, 1991), but

water quality is gradually improving (Van Damme *et al.*, 1995). The authors thus expect increasing numbers of these species for the near future.

Seasonal structure of the fish and crustacean community

Principal component analysis on the sampling data showed an exceptionally clear annual pattern resulting in well-defined temporal changes in the species composition. Young of Decapoda and pipefish arrive in summer, followed by juvenile Gobiidae in late fall and O-group Clupeidae in early winter. There has been extensive literature published on temporal fish distribution of northern temperate estuaries (Iglesias, 1981; Evans & Talmark, 1984; Claridge *et al.*, 1986; Costa, 1988; Day *et al.*, 1989; Henderson, 1989; Elliott *et al.*, 1990; Potter *et al.*, 1997). The observed changes in temporal fish distribution are likely to be caused by seasonal migrations of marine fish into the brackish-water area and have been related to reproduction cycle, to variations in temperature and salinity, to food availability and to reduced predation pressure (McLusky, 1989; Blaber, 1997).

Many fish species complete their life cycle in tropical and subtropical estuaries (Blaber *et al.*, 1989; Robertson & Duke, 1990a), but there is less evidence they do so in temperate regions (Claridge *et al.*, 1986; Potter *et al.*, 1990). Although Elliott and Dewailly (1995) listed 27 species out of 186 occurring in 16 European estuaries as estuarine dependent, almost all species can mature and spawn at sea. Evidently European temperate estuaries are not critical to the survival of their visitors, except for diadromous species such as *A. anguilla* and Salmonidae and anadromous Clupeidae.

Abiotic water conditions (salinity and temperature) are often evoked as controls for seasonal patterns of species occurrence (Thiel *et al.*, 1995). Although a few environmental variables were measured during this study, correlations with seasonal fish distribution were

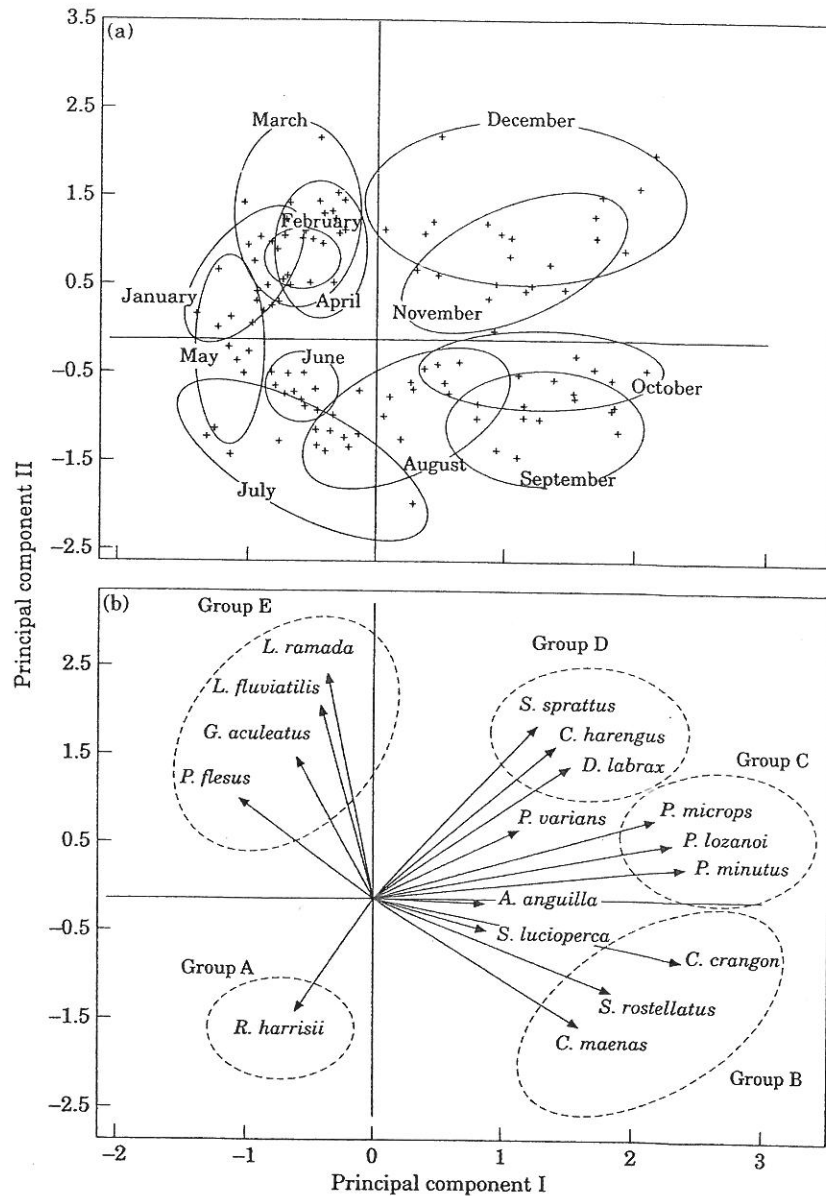


FIGURE 2. Correlation biplot based on principal component analysis. Position of the sample scores (a) and the species vectors (b) with respect to first two principal components. For a better interpretation of the biplot the sample scores are grouped by month and the species scores are multiplied by three.

R. harrisii, *Rhithropanopeus harrisii*; *C. maenas*, *Carcinus maenas*; *S. rostellatus*, *Syngnathus rostellatus*; *C. crangon*, *Crangon crangon*; *P. minutus*, *Pomatoschistus minutus*; *P. lozanoi*, *Pomatoschistus lozanoi*; *P. micros*, *Pomatoschistus micros*; *D. labrax*, *Dicentrarchus labrax*; *C. harengus*, *Clupea harengus*; *S. sprattus*, *Sprattus sprattus*; *L. ramada*, *Liza ramada*; *L. fluviatilis*, *Lampetra fluviatilis*; *G. aculeatus*, *Gasterosteus aculeatus*; *P. flesus*, *Pleuronectes flesus*; *P. varians*, *Palaemonetes varians*; *A. anguilla*, *Anguilla anguilla*; *S. lucioperca*, *Stizostedion lucioperca*.

not made because they are trivial. Euryhalinity is a precondition for estuarine visitors and inhabitants (Blaber, 1997) while temperature is probably relevant when it reaches extreme values.

Increased estuarine productivity and food resources are linked with immigration of marine juveniles and the role of estuaries as nursery areas is documented in great detail (Haedrich, 1983; Boddeke et al., 1986;

Elliott et al., 1990; Blaber et al., 1995). However, mechanisms to find these nursery areas are poorly understood (Day et al., 1989). Indeed, juveniles of many species are probably not attracted to estuarine nursery as such but to shallow and turbid areas in general (Blaber & Blaber, 1980). Mobile fish and crustaceans appear to use these waters as a refuge from marine predators. It is experimentally proven

that animals reduce or eliminate their anti-predator behaviour under turbid conditions (Abrahams & Kattenfeld, 1997). Since this behaviour is costly, as it prevents fish from mating and foraging, a reduction in anti-predator behaviour should have a compensatory increase in feeding rates (Abrahams & Kattenfeld, 1997). It has thus been postulated that turbidity gradients existing between the sea and the adjacent estuaries, act as one of the orientation cues for juveniles migrating into estuaries (Blaber, 1997).

The number of studies on the effects of turbidity on brackish water and marine species is rather limited. The most detailed studies to date on estuarine fish distribution and turbidity have been conducted in South African and Australian estuaries (Blaber & Blaber, 1980; Cyrus & Blaber, 1992; Blaber, 1997). Evidence was presented that juveniles occurring in estuaries occupy different turbidity ranges from those of adults and it was concluded that the influence of high turbidity on fish may be linked to reduced predation pressure. Visual predators were found to be more affected by turbid water than were macrobenthic species (Hecht & van der Lingen, 1992).

The observed migration sequence of juvenile crustaceans and fish in these data, match more or less with changes in the diet of Gadidae, their major predators in the adjoining coastal area (Hamerlynck & Hostens, 1993). After feeding on copepods in May and June, the fraction of gobies and shrimps in the diet of most Gadidae increases (Hamerlynck & Hostens, 1993; Salvanes & Jarle, 1993). With increasing length of the Gadidae, the fraction of gobies in the diet decreased and the fraction of larger fish including Clupeidae and juvenile Gadidae increased (Hyslop *et al.*, 1991; Henderson *et al.*, 1992). In the highly turbid Zeeschelde estuary, numbers of *Merlangius merlangus*, *Gadus morhua* and *Trisopterus luscus* are unusually small relative to their prey, both in cooling-water samples and in additional fyke catches (Maes *et al.*, 1997). This suggests that the Zeeschelde is avoided by large numbers of piscivores and may act as a refuge for prey species.

In the absence of submerged aquatic vegetation or turbid estuarine areas *P. minutus*, *C. crangon* and young *Pleuronectes platessa* search for shelter in the shallow littoral zone during their juvenile phase (Evans, 1983). These areas are avoided by large predators probably because of their decreased foraging ability and their increased physiological stress (Ruiz *et al.*, 1993).

Seasonal changes in tropical species communities are often very complex and determined by their different breeding patterns (Davis, 1988). The complexity of fish movements in the subtropics and tropics

may be enhanced by an increased spatial habitat heterogeneity relative to temperate regions (Blaber & Milton, 1990, Robertson & Duke, 1990b). Besides turbid areas and shallows, mangroves, coral reefs and seagrass beds contribute to the protection of young fish and crustaceans from their predators (Bell *et al.*, 1984; Wright, 1986).

Though temperate zones differ from tropical regions in habitat diversity, their species apparently exhibit similar patterns of behaviour. Unless they are starved, juveniles and adults of small species evidently avoid larger predators whenever possible and prefer a nutritively-poor habitat without predators over a food-rich habitat in the presence of predators (Werner *et al.*, 1983; Manhagen, 1988; Schlosser, 1988; Abrahams & Kattenfeld, 1997).

The authors thus hypothesise that the observed seasonal structure in these data is likely to be the result of behavioural responses to changed predation risk. This behaviour is possibly size-related. Once the prey reaches a vulnerable size relative to the predator, an increased number of attacks upon the prey might be the stimulus to start migration towards protected areas. Consequently emigration to deeper and less turbid waters, when joining the adult stock, should start with larger, more mature animals. The chance to detect and escape from a predator is size-related (Taylor, 1984), resulting in a prolonged stay of younger individuals in the protected habitats.

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