THE STRUCTURE OF THE FISH COMMUNITY OF THE ZEESCHELDE ESTUARY

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De structuur van de visgemeenschap van het Zeeschelde-estuarium

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Dankwoord

Zes jaar geleden ben ik aan dit doctoraat begonnen onder impuls van Dr. Paul Van Damme. Reeds toen ik in de eerste licentie zat, wist ik dat ik mijn thesis bij dit intelligente warhoofd wou en zou maken. Die licentiaatsthesis kreeg dus een uitgebreid vervolg. Tijdens die periode hebben heel wat mensen bijgedragen tot het uiteindelijke resultaat. Tot hen richt ik dit dankwoord.

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Het voorlaatste woord is weggelegd voor Arne Taillieu. Elke vis die in deze thesis vermeld staat, werd door Arne gedetermineerd, geteld, gemeten, minutieus geanalyseerd en ingegeven in tabellen en figuren. Een deel van mijn titel, mijn humor, mijn persoonlijkheid en mijn skivaardigheden heb ik zonder twijfel aan hem te danken. Een deel van de vissen die afgeschrikt worden in Doel overleven dank zij Arne. Waarvoor dank.

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Contents

Chapter 1
Introduction and Objectives

This introductory chapter reviews the use of estuaries by fishes. We examine briefly the concept of estuarine dependence and discus which factors may structure estuarine fish communities. A general description of the study site including its physicochemical characteristics and ecology is given. Finally, the main objectives of the thesis are presented.

Shallow areas, such as coastal zones, estuaries, intertidal wetlands and mangrove swamps are extensively used by many marine and freshwater fish species. These habitats are known to provide favourable conditions as they usually promote growth and recruitment to adult populations. Especially estuaries are recognized to perform a crucial role in the life-history stages of many fish species (Haedrich, 1983; Claridge *et al.*, 1986; Elliott and Dewailly, 1995; Potter *et al.*, 1997; Whitfield, 1999). They provide a migratory route for anadromous and catadromous species and an environment in which a limited number of teleosts spends the whole of their life cycle. The upper reaches are colonized by some freshwater species while lower regions are penetrated by marine stragglers. Above all however, many marine teleosts enter and remain within estuaries for a brief period of time, often in very large numbers and particularly during the early part of life cycle (Claridge *et al.*, 1986).

Seasonal, spatial and trophic changes in the structure of the fish assemblages inhabiting the upper brackishwater reaches of the Schelde estuary (Belgium) are the focus of this study. At the end of the 1980s it was believed that such a fish community was absent from this area due to water pollution. Fish catches at cooling-water filter screens, which commenced in 1991, showed the opposite. This introductory chapter presents a brief overview of the ichthyofaunal species composition in estuaries with emphasis on West European estuaries and discusses the factors structuring estuarine fish assemblages. Thereafter, the study site is presented and finally, the rationale and objectives of the thesis are given.

The composition of the estuarine ichthyofauna and estuarine dependence

The extent to which individual fish species are dependent on estuaries has been the subject of considerable research and debate (Lenanton, 1982; Elliott and Dewailly, 1995; Able and Fabahy, 1998; Whitfield, 1999). Whitfield (1999) recently proposed an acceptable terminology that categorizes the major fish groups utilizing estuaries. The estuarine fish community comprises marine migrants, marine stragglers, freshwater migrants, freshwater stragglers, estuarine residents, estuarine migrants, catadromous and anadromous species.

The majority of fish found in estuaries represent those euryhaline marine species of teleosts that enter these systems in large numbers at particular intervals of their life cycles using estuaries as nurseries (Potter *et al.*, 1990). They often migrate upstream into shallow areas where salinities are appreciably lower than full-strength seawater (Lenanton and Potter, 1987). European estuaries are known nurseries for representatives of the Clupeidae (Poxton, 1987; Elliott *et al.*, 1990), the Pleuronectidae (Bergman, 1988; Coggan and Dando, 1988; Costa, 1988; Elliott *et al.*, 1990; Kerstan, 1991), the Gobiidae (Costa and Elliott, 1991) and the Gadidae (Claridge and Potter, 1984). They are often referred to as estuarine dependent species (Elliott and Dewailly, 1995). It has been suggested, however, that the term estuarine-opportunist would be more appropriate (Lenanton and Potter, 1987) since all of these species can breed and mature at sea. While marine opportunist species make extensive use of estuaries during a least part of their life-history, marine stragglers are only recorded in small numbers, usually in the lower reaches and sometimes in the upper reaches (Whitfield, 1999). Amongst these are elasmobranch fishes as well as stenohaline teleosts.

Both estuarine residents and migrants are species of marine origin (Whitfield, 1999). While resident fishes are able to complete their entire life cycle in estuaries (for instance Syngnathidae), estuarine migrants such as the common goby *Pomatoschistus microps* are so called since they often have a marine larval phase. The number of species which spawn in temperate estuaries in the northern hemisphere is rather small (Haedrich, 1983). Claridge *et al.* (1986) found only two and possibly four species in the Severn estuary (UK) which are believed to spawn there. Spawning in estuaries causes problems with eggs swept out of the estuary by ebb tides or during heavy freshwater discharges. Hence, teleosts spawning in estuaries produce benthic eggs, which adhere to the substratum (Neira *et al.*, 1988). This situation contrasts with Australian and South African estuaries where the number of spawners is significantly greater, probably due to regular bar formations at the mouth of the estuary blocking the access to the sea (Potter *et al.*, 1990). Estuarine resident fish species are invariably small species (Whitfield, 1998) and it has been suggested that the small size of estuarine spawners would reduce their physical ability to undertake large-scale migrations to and from the sea. Predation by adult piscivorous fish populations at sea may also deter mass migrations by these species. Furthermore, typically shallow microtidal estuaries present in tropic and subtropic regions tend to favour occupation by small fish (Roberston, 1990*a*).

Some freshwater species are present throughout the year in estuaries while others enter estuaries only during brief periods when conditions are favourable. As it is the case for marine species, freshwater species can be divided in freshwater stragglers and freshwater migrants. However, due to the restricted occurrence of tidal freshwater areas and the extensive human impact on these particular ecosystems, this latter group has hardly been documented in the literature. The tidal freshwater reaches, including almost unique intertidal freshwater marshes, are nonetheless important areas for fish such as Cyprinidae and Percidae, occurring in lowland rivers (Rozas & Odum, 1987; Schuchardt *et al.*, 1993; Araújo *et al.*, 1999).

Anadromous and catadromous species rely on estuaries as a route for their migrations to and from marine environments. Catadromous migrants spawn at sea but use freshwater catchment areas for the juvenile and subadult life stages. Either obligate and facultative catadromous fishes occur in European estuaries. Flounder *Pleuronectes flesus* is a facultative catadromous species while European eel *Anguilla anguilla* is an obligate catadromous species. Anadromous species mature at sea and spawn in the freshwater reaches. Anadromous species are absent from most tropical and subtropical estuaries around the world. They are however, common in the northern hemisphere and thus Petromyzontidae, Acipenseridae, Salmonidae and some members of the Clupeidae should regularly occur in European estuaries. The majority of European anadromous species is threatened though, as impassable barriers, destruction of spawning areas and water pollution seriously inhibit upstream migration (Assis, 1990).

Factors structuring estuarine fish communities

Although many fish species can be found in estuaries, ichthyofaunal diversity is low due to the high abundance of individual taxa, most of which exhibit wide tolerance limits to the fluctuating conditions within these systems (Whitfield, 1999). Abiotic factors affecting estuarine fish assemblages include salinity (Henderson, 1989), temperature (Thorman, 1983; Thiel *et al.*, 1995), water flow, turbidity (Blaber and Blaber, 1980; Cyrus and Blaber, 1987), dissolved oxygen (Möller and Scholz, 1991), habitat diversity and the complexity of aquatic vegetation (Morgan *et al.*, 1988; Thiel *et al.*, 1995). Biotic factors influencing the fish assemblage are food availability and predation (Evans, 1983; Ross, 1986; Day *et al.*, 1989). It is however, generally accepted that physicochemical factors govern the spatial distributions within estuaries while species interactions seem to fine tune these distributions (Day *et al.*, 1989).

Fishes in almost all estuaries are subject to changes in salinity (Blaber, 1997). The most essential adaptation by fish that enter estuarine systems should thus be the ability to adjust to changes in salinity (Whitfield, 1999). Almost all fishes living in estuaries must be euryhaline and routinely able to cope with salinities from almost fresh water (<1‰) to at least water of 35‰ (Blaber, 1997). Positive relationships between salinity and species richness, species diversity and evenness of fish communities were detected in the Elbe (Thiel *et al.*, 1995), in Swedish estuaries (Thorman and Wiederholm, 1986) and in UK inshore waters (Henderson, 1989).

While salinity correlates with the spatial distribution of estuarine fish communities, temperature may be the best predictor of temporal changes in fish abundance and species composition. Temperature directly affects metabolic rate, swimming speed and activity patterns (Wootton, 1984) and induces fish migrations (Fonds, 1975; Claridge and Potter, 1983). A number of marine fish species visiting estuaries avoid winter temperatures and move seaward once temperature has fallen below a critical level (Claridge and Potter, 1983, 1984; Henderson, 1989).

The most detailed studies on fish distribution and turbidity are those done in Australian and South African estuaries (Blaber and Blaber, 1980, Cyrus and Blaber, 1987*a*, 1987*b*, 1987*c*). These studies suggest that turbidity highly influences fishes with juveniles of most estuary-associated species being attracted to turbid waters. Turbid waters indeed provide small fishes with cover against predatory teleosts and birds, increase feeding success, and eventually reduce intraspecific predation as turbidity preferences often differ between adults and juveniles of the same species (Cyrus and Blaber, 1987*a*; Whitfield, 1999). Finally, turbidity can affect fish recruitment into estuarine systems by the export of estuarine suspensoids to the sea (Grimes and Kingsford, 1996). Turbidity gradients usually exist not only within estuaries but also from the mouth region into the sea. Therefore, it has been suggested that by following an increasing turbidity gradient, postlarval fishes in the marine environment ultimately reach estuarine areas (Blaber, 1997).

Oxygen depletion within the water column has the potential to restrict the distribution and movement of fishes within estuaries (Whitfield, 1999). In subtropical or tropical regions, this may be more pronounced because of the generally higher water temperatures. In temperate regions of the northern hemisphere however, the presence of additional oxygen demanding substances in the form of domestic, industrial or agricultural pollution may strongly limit the distribution of fishes in estuaries or even result in fish mortalities (Wharfe *et al.*, 1984). Available evidence suggests that dissolved oxygen levels below 1 $mg \cdot l^{-1}$ are lethal to many estuary-associated species (Burton *et al*, 1980; Whitfield, 1999). Periodic dissolved oxygen depletion can also occur during episodic river floods which, together with excessive silt loads, may cause massive fish mortalities in estuaries (Whitfield, 1995).

Mobile macro-crustaceans in estuaries

Estuarine macro-crustacean populations have received less attention than the demersal and pelagic fish populations. Nevertheless, young shrimps and crabs co-occur with fish and exploit similar resources (Del Norte-Campos and Temming, 1994).

Temperate estuaries in the northern hemisphere hold large populations of crabs (mainly *Carcinus* in Europe and *Callinectes* in North America), and shrimps and prawns (*Crangon*, *Palaemonetes*, *Paelomon*, *Penaeus*) (Gleason, 1986; Kneib, 1987; Hines *et al.*, 1990; Robin, 1992; Cattrijsse *et al.*, 1994) These genera share their preference for areas of brackish water with muddy or sandy substrates and tidal currents (Tiews, 1970, Adema, 1991). As a result, this group of macro-invertebrates forms the most abundant component of the estuarine macrofauna and hence, has a major impact on the local food web (Henderson and Holmes, 1987).

Physiologically, morphologically, and behaviourally, shrimps and crabs are adapted to exploit intertidal areas (Henderson and Holmes, 1987). They are able to withstand a wide range of environmental conditions, with crabs even surviving in open air. Their morphology allows them to walk and swim in vary shallow waters and rapidly hide by burrowing in soft sediments. Related to the exploitation of the intertidal zone, these invertebrate species posses endogenous rhythms liked with tidal amplitude (Adhub and Naylor, 1975; Adema, 1991).

Given their similar ecological preferences as estuarine fishes, the macro-crustaceans will be integrated into this study.

The function of estuaries on a global scale

Estuaries not only support large populations of commercial fish and invertebrates but also sustain internationally important populations of waterfowl. Estuaries are highly productive ecosystems ranking together with coral reefs and mangrove swamps (Constanza *et al.*, 1997). The elevated productivity is maintained because of high nutrient levels in both sediment and water column. Estuaries are regarded as nutrient traps with the essential elements being recycled over and over within the system (Knox, 1986; Houde and Rutherford, 1993). Especially the role of detritus in the estuarine ecosystems seems of high importance. Whereas phytoplankton biomass can vary considerably both spatially and temporally, an abundance of detritus is available to estuarine consumers throughout the year. It would appear therefore, that detritus confers stability to estuarine ecosystems by extending the availability of seasonally fixed energy (Mann, 1988).

Even of greater importance are the ecosystem services that estuaries perform such as nutrient cycling, food production, storm protection and flood control. This role on a global scale has been appreciated by Constanza *et al.* (1997), who calculated the value of the world's ecosystem services and natural capital. Estuaries provide US$ 23 000 $ha^{-1} \cdot y^{-1}$ to human welfare. None of the other ecosystems recorded in this study scored better.

Description of the Schelde estuary and the study site

The Schelde (E: Scheldt; F: Escaut) originates in Saint-Quentin (France) and meets the North Sea nearby Vlissingen (The Netherlands). The Schelde river has a true estuary. An estuary is defined as a coastal body of water with a free connection to the sea (lagoons have a restricted connection to the sea) where fresh water is mixed with sea water (Pritchard, 1967). The estuary, which reaches as far as Gent, is a macrotidal coastal plain estuary with a tidal range of 4-5 m and an average water depth of 11 m (Zwolsman and Van Eck, 1993). The upper estuary (the Zeeschelde) is a narrow channel situated between Ghent and the Belgian-Dutch border (Fig. 1). It consists of fresh water between Ghent and Antwerp and brackish water between Antwerp and the Dutch-Belgian border. This part of the estuary is heavily polluted by domestic, industrial and agricultural waste loads (Zwolsman and Van Eck, 1993). The lower estuary (the Westerschelde) is situated between the Belgian-Dutch border and the North Sea and has a complex morphology of gullies, intertidal marshes, sandflats and channels (Claessens, 1988). The rivers drains 21 500 km^2 at a mean net flow rate of 105 m$^3 \cdot$s^{-1}. Residence time of the water varied from 50 days in winter to about 70 days in summer (Soetaert and Herman, 1995).

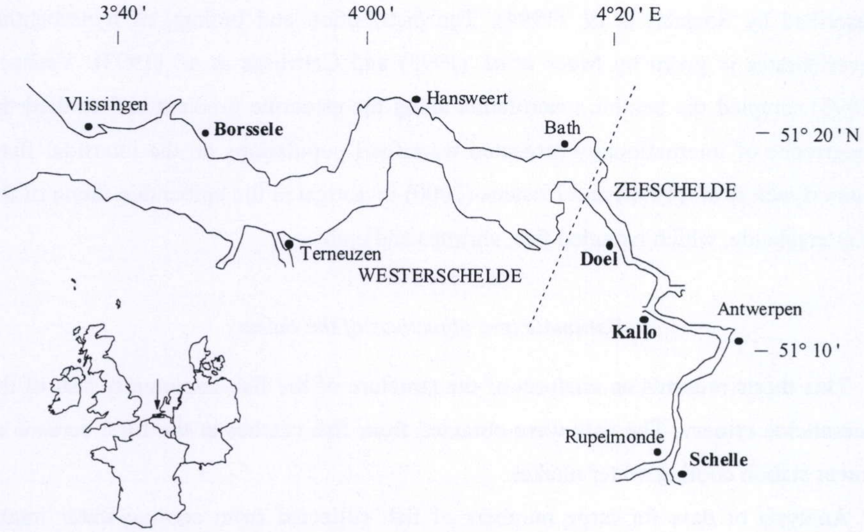

Fig. 1.1. Map of the study area and position of the sampling sites.

The main estuarine water quality parameters are salinity, turbidity, dissolved oxygen and temperature. Salt water intrudes for about 100 km inland (Soetaert and Herman, 1995) resulting in a salinity gradient. Although seasonal and annual fluctuations in salinity may be large, salinity zones are relatively stable (Soetaert and Herman, 1995). The lowest oxygen levels are measured in the Zeeschelde where the heavy load of organic matter catalyses an intense heterotrophic bacterial activity which rapidly exhausts the oxygen in the river, especially in summer (Heip, 1988). The Westerschelde has a much better oxygenated water column, with oxygen saturation increasing from 50% at the border to >90% at the mouth of the estuary. Fine sedimentary deposits are a highly characteristic feature of estuaries and they are derived both from the sea and from land (Heip, 1988). Their deposition is controlled by current velocity. At the oligohaline zone nearby Antwerpen however, settlement rate is increased by flocculation resulting in a turbidity maximum.

General reviews of the ecology of the Schelde estuary are given by Heip (1989) and Meire *et al.* (1992, 1998). Phytoplankton studies have been presented by Van Spaendonk *et al.* (1993) and Muylaert *et al.* (1997); zooplankton dynamics by Soetaert and Van Rijswijk (1993). An important number of studies deal with benthic organisms living in or just above the bottom. The meiobenthic fauna has been described by Soetaert *et al.* (1994). The distribution and biology of hyperbenthic invertebrates is given by Mees *et al.* (1993) and Cattrijsse *et al.* (1993). Ysebaert (1993) sampled the benthic macrofauna along the estuarine gradient and studied the occurrence of internationally protected waterfowl populations on the intertidal flats. Hamerlynck *et al.* (1993) and Hostens (2000) investigated the epibenthic fauna of the Westerschelde, which included fish, shrimps and crabs.

Rationale and objectives of the thesis

This thesis presents an analysis of the structure of the fish community fish of the Zeeschelde estuary. The data were obtained from fish catches at the filter screens of power station cooling-water intakes.

Analysis of data for large numbers of fish collected from cooling-water intake screens has yielded much useful information on annual variation in abundance, seasonal movements, growth, age composition and reproductive status of several species of lamprey and teleosts (Claridge *et al.*, 1986). Although this alternative sampling technique has been employed by a number of authors, little information is available on the efficiency of cooling-water intakes, probably due to substantial differences in the location of intakes relative to the riverbed. A first objective of the present study is thus to evaluate a power station cooling-water inlet as a sampling point for fish. This was done by comparing the abundance as recorded on the filter screens with stow net samples (Chapter 2) and by examining the effect of tidal and diel variations on the intake catches (Chapter 3).

A second objective was to describe spatial and temporal changes in the structure of the fish community in the Zeeschelde. Despite the importance of spatial and temporal patterns of fish assemblages in estuarine water quality assessment, only few attempts have been made to construct multivariate models linking the spatial patterns of species occurrence to environmental parameters (Hamerlynck *et al.*, 1993; Thiel *et al.*, 1995; Marshall and Elliott, 1998; Hostens, 2000; Power *et al.*, in press). This part of the thesis analyzes the influence of environmental parameters on the spatial structure of the fish community in the upper reaches of the Schelde estuary (Chapter 4) and describes seasonal fluctuations in fish abundance and species composition (Chapter 5). Both spatial and temporal patterns in the community structure were investigated using descriptive multivariate ordination techniques. An additional objective of this study is to provide a biological baseline against which further changes in the estuarine fish populations may be evaluated. This study presents for the first time ever quantitatively sampled data of fish occurrence in the Beneden-Zeeschelde. Previous studies (De Selys-Longchamps, 1847; Poll, 1945; Van Damme *et al.*, 1994) only provided qualitative species lists. Chapter 6 concludes this part with data on the vertical distribution of fishes in the study area.

In a review of resource partitioning in fish assemblages, Ross (1986) determined that a high level of separation among coexisting species occurred along at least three resource dimensions, which are time, food and habitat. A third objective of this thesis is to study resource partitioning amongst the dominant fish. More specific, an analysis is presented of the seasonal changes in trophic niche width and overlap between the dominant species of the fish assemblage (Chapter 7).

A fourth objective of our study is to estimate the contribution of the study site to the export of biomass and to recruitment of juvenile marine migrants. Such estimates are few because the complex migration patterns make it difficult to use the standard methods (Day *et al.*, 1989). Yet, we propose a model that describes fish abundance in an estuary as a result of migration and mortality (Chapter 8). This model is used to approximate the amount of biomass that is imported in the Zeeschelde estuary and exported to the sea by a migrating population of Atlantic herring *Clupea harengus*.

Finally, the nursery role of the Zeeschelde estuary is discussed by examining which factors contribute most to stabilize the structure of the fish assemblage in the Zeeschelde and similar estuarine sites. The extensive use of the Zeeschelde estuary by many marine species suggests that some means of partitioning of one of the major niche axes might exist.

It is clear that scientific research stands not on its own. This study has been made possible by a research project sponsored by the Nuclear Power Plant Doel (Electrabel). Increased fish captures by the cooling-water intake in the early 1990s initiated an excellent, professional and still-continuing co-operation between the Laboratory of Aquatic Ecology (KULeuven) and Electrabel Doel. The objective of this co-operation was to reduce the impact of the cooling-water intake on the fish populations present in its influence zone of entrapment. At the start of the project, over 100 tons of fishes and crustaceans were captured every year. The project ended successfully with an overall effect reduction of about 90% (Maes *et al.*, 1999). This reduction was achieved by both deflecting fish away from the intake and transporting fish to the river after impingement.

Chapter 2

Sampling Efficiency and Selectivity of the Cooling-Water Intake at Doel: a Comparison with Stow Net Fishery

In November 1995, fish and crustaceans were simultaneously sampled in the cooling-water of the nuclear power plant Doel (Zeeschelde Estuary, Belgium) and by stow nets. We hypothesized that there were no differences in species abundance, in mean species length, and in the length-frequency distributions drawn by each method. In total, 39 species were caught, 32 by stow net and 33 in the cooling-water, with 26 species common to both methods. Overall, the abundance in the cooling water was three times higher than in the nets but the difference depended on the size of the species. Although average length was for most species significantly higher in stow net samples, almost all length classes present within each population were sampled by the cooling-water intake. The analysis suggests that the cooling-water intake is an effective and representative source for collecting fish and crustaceans reflecting the species abundance in the surrounding waters.

Introduction

Power plants need large amounts of water for cooling their condensers (Hadderingh *et al.* 1983). Cooling-water is withdrawn from canals, rivers, lakes and coasts and may result in considerable fish mortality. It is not uncommon for millions of fish and crustaceans to become impinged on power plant intake screens each year (Kennish, 1992). All over the world, sampling programs have been developed to estimate the magnitude of the problem, and different methods to avoid fish impingement have been introduced with variable success (Hadderingh *et al.*, 1983; Wharfe *et al.*, 1984; Davies, 1988; Turnpenny, 1988; Henderson, 1989; Aprahamian and Jones, 1997; Potter *et al.*, 1997; Van Anholt *et al.*, 1998).

Since the late 1980s, the Doel nuclear power plant situated at the Zeeschelde estuary (Belgium) dealt with increasing numbers of impinged fish, shrimps and crabs due to slightly increasing water quality. Between July 1994 and June 1995, more than 130 ton fish and larger crustaceans were collected on the filter screens. To assess this problem, a sampling program was developed resulting in the installation of sound projectors to repel fish away from the intake openings (Maes *et al.*, 1999).

The aim of this study is to evaluate a power station cooling-water inlet as a sampling point for fish and macro-crustaceans. Confidence in power station cooling-water samples has been provided by their capacity to catch nearly all known species present in surrounding waters (Henderson, 1989; Henderson *et al.*, 1992). It is, however, unclear if the species abundance as recorded in cooling-water samples represents correctly the actual species population density.

The present paper compares sampling in cooling-water with stow net fishery. We used stow nets since both methods yield results with the same dimensions (numbers·m^{-3}). In addition, stow netting is considered to be an ideal fishing technique in estuaries (Breckling and Neudecker, 1994) as it uses tidal currents to catch fish.

To compare cooling-water samples with stow net samples, we tested the null hypothesis that both methods collected fish and crustaceans with the same efficiency and selectivity.

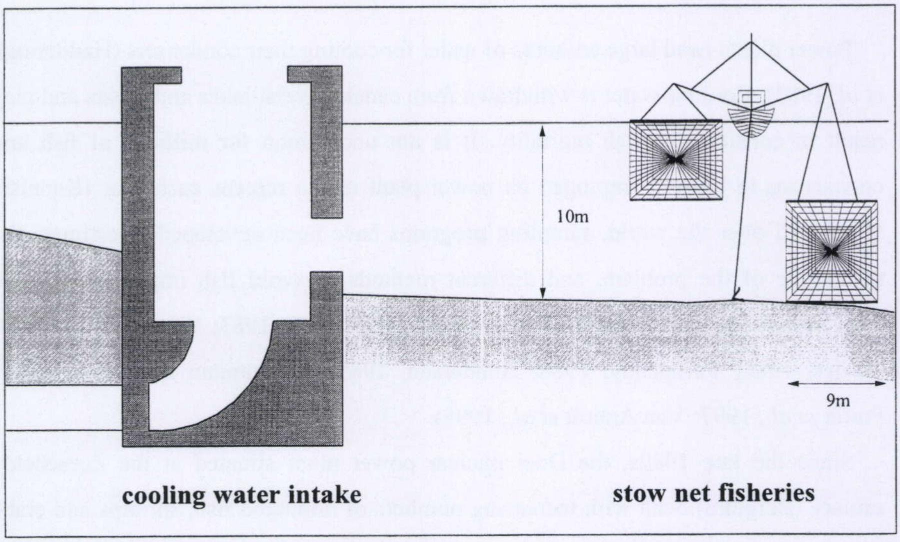

Fig. 2.1. Position of the cooling-water intake of the Nuclear Power Plant Doel and the stow nets relative to the water column.

Materials and methods

During five days in November 1995, fish and crustaceans were simultaneously sampled on the cooling-water filter screens of the nuclear power plant Doel and by stow nets. During sampling, basic water quality variables were measured using a multiprobe data logger (Hydrolab 3.0). Temperature averaged 10.8 °C; oxygen concentration was 6.27 $mg \cdot l^{-1}$. Mean salinity and turbidity were 12.25 ‰ and 42 FTU, respectively.

Sampling with stow nets

Stow netting is a passive fishing technique, which is most suitable in tidal environments. While the ship was anchored at 50 m off the intake, two nets on both sides were exposed for approximately one hour in the tidal currents (Fig. 2.1). Both nets were 70 m in length with decreasing mesh size. The stretched mesh size in the cod end was 1.2 cm. Samples were taken between the water surface and the bottom (-10 m) as presented in Fig. 2.1. In total, 10 samples were selected. After each haul, fish and shrimps were identified, counted and measured. When needed, subsamples were taken by dividing the catch in equal parts. The water volume filtered by the net mouth was calculated using the total cross-sectional area of the two net mouths, current velocity and exact duration of each haul. The total cross-sectional area of both net mouths was variable with the tidal height and was close to 90 m^2. A flow meter was placed in the opening of each net. Current velocity was measured every 15 min and averaged 0.7 $m \cdot s^{-1}$. Numbers of fish and crustaceans of both nets were summed and afterwards transformed to 'net abundance' ($numbers \cdot 10^{-3}\ m^{-3}$) by dividing the total catch by the water volume sampled. On average, approximately $2 \cdot 10^5\ m^3$ water was sampled during each haul.

Sampling at the nuclear power station Doel

The cooling-water intake of the nuclear power plant Doel is situated 2 m above the bottom and withdraws 25.1 $m^3 \cdot s^{-1}$ (0.35% of the Zeeschelde debit at Doel) water through five intake apertures measuring each 9.6 m^2. Water is transported through a 540 m long pipeline to a communicating reservoir at the site. Here, fish, crustaceans, vascular material and debris are removed from the cooling-water by vertical travelling water screens with a mesh size of 4 mm and afterwards flushed into a container, the sampling point. The residence time of fish within the system, which is the time animals spend between the intake point in the river and the sampling point, is approximately 20 min (Chapter 3.). Thus sampling at Doel started 20 min later than stow netting did and lasted for one hour, corresponding to 90 400 m^3 water sampled. Fish and crustaceans were separated from the debris, identified to species level, counted and measured. Subsamples were taken in case of large catches of fish or crustaceans by dividing the total catch in equal parts. For each species, numbers per sample were transformed to numbers$\cdot 10^{-3}$ m^{-3} cooling-water sampled and are further referred as 'intake abundance'.

Non-parametric tests

Since the abundance data and the length-frequency distributions were not normally distributed (Shapiro Wilk's W test; $p < 0.05$) we preferred non-parametrics to test for significant differences between variables. The intake abundance data were compared with the net abundance data using a Wilcoxon matched pair test pairing data over 10 sample periods. A Man Whitney U test was used to examine differences in mean species length as recorded by each fishing method. All correlations made were Spearman rank correlations.

Regression analysis

Linear regression. The relationship between the $\log_{10}$-transformed mean fish length and the ratio between intake abundance and net abundance was investigated with linear regression analysis in Statistica 4.5 (Statsoft, 1994).

Non-linear regression. The intake and net abundance of eight fish species were distributed over 5 mm length classes. Afterwards, these data were fitted in Statistica 4.5 (Statsoft, 1994) by a single Gauss function in case of a population consisting of a single cohort (Equation 2.1). The sum of two Gauss functions was used in case of a population consisting of two cohorts.

$$(2.1) \qquad A = a \times \frac{1}{\sqrt{2\pi\sigma}} e^{-0.5\times\left(\frac{L-\overline{L}}{\sigma}\right)^{2}}$$

All symbols used are explained in Table 2.1. The parameters $\overline{L}$ and σ were estimated using a quasi-Newton non-linear estimation procedure. The parameter a equals five times the fish abundance since length classes of 5 mm were used to distribute the total abundance. The explained variance of the fitting is given by R^2.

Table 2.1. *Symbols used in the equations and in the text*

Symbol	**Explanation**	**Unit**
A	fish abundance per length class	numbers·10^{-3} m^{-3}
a	total fish abundance	numbers·10^{-3} m^{-3}
L	fish length	mm
$\overline{L}$	average fish length	mm
σ	standard deviation of the length distribution	mm

Results

Comparison of the species caught by each method

Thirty-nine species were caught, 32 by stow nets and 33 in the cooling-water, with 26 species common to both methods (Table 2.2). All crab species as well as crucian carp *Carassius carassius*, ten-spined stickleback *Pungitius pungitius*, butterfish *Phonis gunellis* and eelpout *Zoarces viviparus* were present in the cooling-water samples but were absents in the nets. Twaite shad *Alosa fallax*, silver bream *Abramis bjoerkna*, ruffe *Gymnocephalus cernuus*, red gunnard *Trigla lucerna*, sandeel *Ammodytes tobianus* and mackerel *Scomber scombrus* were only found in the nets.

Comparison of the species abundance as recorded by each method

The fishing efficiency of both methods differed as they caught different proportions of demersal and pelagic species. Clupeidae were most abundant in the stow nets. Sprat *Sprattus sprattus* (42%) and herring *Clupea harengus* (35%) outnumbered all other species. In cooling-water samples though, sprat and herring together represented 43% of the total catch while shrimps and Gobiidae consisted of 36% and 20%, respectively.

Table 2.2. *Results of a Wilcoxon matched pair test examining differences in mean net abundance and intake abundance (numbers*$\cdot 10^{-3}$ m^{-3}*) of fish and crustaceans as inferred from stow net samples and cooling-water filter screen catches. The ratio between net abundance and intake abundance is given only for species occurring in both samples with an abundance* $>0.001 \cdot 10^{-3}$ m^{-3}. *The ratio is interpreted as the stow net fishing efficiency assuming that cooling-water fishing efficiency is 100% (see text).*

Species		**Mean net abundance**	**Mean intake abundance**	**Ratio**	**Test statistic**	***p* level**
Crustaceans						
Eriocheir sinensis	Chinese mitten crab		0.009			
Carcinus maenas	Shore crab		0.070			
Rhitropanopeus harrissii	Dwarf crab		0.131			
Crangon crangon	Common shrimp	8.640	54.724	0.16	2.24	0.025
Palaemonetes varians	Prawn	3.230	56.159	0.06	2.28	0.017
Diadromous fish						
Lampetra fluviatilis	Rivern lamprey	0.007	0.016	0.44	0.84	0.400
Alosa fallax	Twaite shad	0.001				
Anguilla anguilla	European eel	0.011	0.113	0.10	2.36	0.017
Freshwater fish						
Abramis bjoerkna	Silver bream	<0.001				
Carassius carassius	Crusian carp		0.002			
Gasterosteus aculeatus	Three-spined stickleback	<0.001	0.022		2.02	0.043
Pungitius pungitius	Ten-spined stickleback		0.010			
Gymnocephalus cernuus	Ruffe	<0.001				
Perca fluviatilis	Perch	0.103	0.296	0.35	2.02	0.043
Stizostedion lucioperca	Pikeperch	0.016	0.022	0.73	0.40	0.686
Marine fish						
Clupea harengus	Herring	37.263	61.335	0.61	2.10	0.035
Sprattus sprattus	Sprat	44.637	72.349	0.62	1.26	0.207
Engraulis encrasicolus	Anchovy	0.056	0.010	5.60	1.15	0.248
Osmerus eperlanus	Smelt	0.061	0.056	1.09	0.42	0.674
Merlangius merlangus	Whiting	0.031	0.045	0.69	0.70	0.484
Trisopterus luscus	Bib	0.005	0.022	0.23	0.67	0.499
Atherina presbyter	Sand-smelt	0.001	0.011	0.09	1.99	0.046
Syngnathus acus	Greater pipefish	0.001	0.003	0.33	-	-
Syngnathus rostellatus	Nillson's pipefish	0.011	0.056	0.20	2.36	0.017
Trigla lucerna	Red gunnard	0.001				
Myoxocephalus scorpius	Bull-rout	<0.001	0.003		-	-
Dicentrarchus labrax	Bass	0.097	0.270	0.40	2.10	0.035
Liza ramada	Thin-lipped grey mullet	0.056	0.103	0.54	1.54	0.123
Phonis gunellus	Butterfish		0.006			
Zoarces viviparus	Eelpout		0.004			
Ammodytes tobianus	Sandeel	<0.001				
Pomatoschistus lozanoi	Lozano's goby	0.488	1.043	0.46	0.84	0.400
Pomatoschistus microps	Common goby	5.718	31.352	0.18	1.96	0.049
Pomatoschistus minutus	Sand goby	5.408	28.580	0.19	2.38	0.017
Scomber scombrus	Mackerel	<0.001				
Limanda limanda	Dab	0.180	1.628	0.11	2.38	0.017
Pleuronectes flesus	Flounder	0.032	0.039	0.82	1.12	0.263
Pleuronectes platessa	Plaice	0.003	0.006	0.50	0.40	0.686
Solea solea	Sole	0.005	0.029	0.17	1.12	0.263

All other species represented <0.5% of the total catch. Table 2.2 summarizes the results of a Wilcoxon matched pair test comparing the intake abundance with the net abundance. Although both fishing techniques sampled the same populations, the intake abundance of most species exceeded the net abundance. This difference was significant for 13 species (Table 2.2). The cooling-water intake sampled shrimps, Gobiidae, eel *Anguilla anguilla*, dab *Limanda limanda* and sole *Solea solea* more efficiently than stow netting did. It is noteworthy that the catch of herring was significantly higher in the cooling-water intake samples even though stow nets are traditionally used to catch this species. Stow nets caught more smelt *Osmerus eperlanus* and anchovy *Engraulis encrasicolus*, but these differences were not significant (Table 2.2). Overall, the intake abundance was three times higher than the net abundance. The ratio between net abundance and intake abundance was higher for small-sized species than it was for large-sized species (Fig. 2.2).

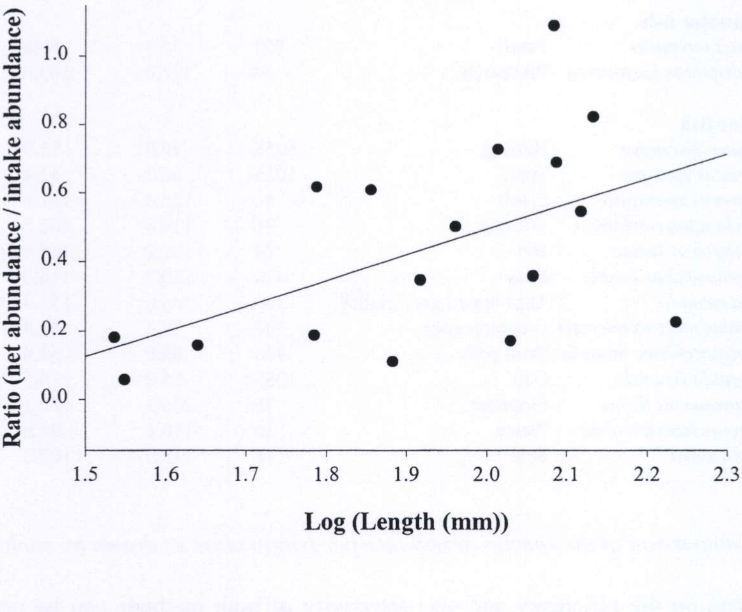

Fig. 2.2. A significant linear regression between the $\log_{10}$ transformed mean species length and the ratio between net abundance and intake abundance. ratio = -0.97 + 0.73 × $\log_{10}$ (length). ($\beta = 0.51$; standard error of $\beta = 0.22$; $R^2 = 0.267$; $F = 5.47$; $p = 0.033$). In the analysis, all species listed in Table 2.3 were used except eel and river lamprey because they are not fusiform.

Comparison of the average species size as recorded by each method

The size-selectivity changed in function of the fishing technique (Table 2.3). Stow nets caught larger individuals while the cooling-water intake entrapped smaller specimens of the same population. This difference increased with size (Spearman R = 0.83, N = 17, $p < 0.001$) and varied from a few mm for Gobiidae, shrimps and smaller fish to 11 cm for eel (Table 2.3).

Table 2.3. *Results of a Man Whitney U test examining differences in mean species length (mm) as recorded by each fishing method.*

Species		**Number measured**	**Mean length stow net**	**Mean length cooling-water**	***p*-level**
Crusteceans					
Crangon crangon	Common shrimp	1058	50.2	43.6	< 0.001
Palaemonetes varians	Prawn	1026	36.0	35.4	0.178
Diadromous fish					
Lampetra fluviatilis	River lamprey	58	369.9	362.8	0.307
Anguilla anguilla	European eel	116	440.3	330.4	< 0.001
Freshwater fish					
Perca fluviatilis	Perch	704	82.3	82.8	0.523
Stizostedion lucioperca	Pikeperch	24	172.0	103.4	0.063
Marine fish					
Clupea harengus	Herring	1056	79.0	71.9	< 0.001
Sprattus sprattus	Sprat	1036	66.2	61.4	< 0.001
Osmerus eperlanus	Smelt	58	125.8	121.6	0.416
Merlangius merlangus	Whiting	96	139.8	122.5	0.039
Trisopterus luscus	Bib	74	181.1	172.6	0.079
Dicentrarchus labrax	Bass	498	129.7	114.6	0.001
Liza ramada	Thin-lipped grey mullet	200	166.6	131.4	< 0.001
Pomatoschistus microps	Common goby	302	32.3	34.4	< 0.001
Pomatoschistus minutus	Sand goby	406	63.0	61.0	0.017
Limanda limanda	Dab	1088	85.0	76.5	< 0.001
Pleuronectes flesus	Flounder	78	206.3	136.1	< 0.001
Pleuronectes platessa	Plaice	20	126.1	91.6	0.021
Solea solea	Sole	78	118.9	107.3	0.033

Comparison of the species abundance per length class as drawn by each method

Data on the efficiency and size-selectivity of both methods can be combined in length-abundance distributions. Both the intake and net abundance of eight fish species were separately distributed over different length-classes and fitted by a non-linear regression (Fig. 2.3). Table 2.4 summarizes the estimated average length ($\bar{L}$) and standard deviation (σ) of the fitting procedure. Fig. 2.3 indicates that the entire length-spectra of perch *Perca fluviatilis*, common goby *Pomatoschistus microps*, sand goby *Pomatoschistus minutus*, dab and sprat were more efficiently sampled by cooling-water than they were by stow nets. Two cohorts were recognized within the populations of bass *Dicentrarchus labrax* and thin-lipped grey mullet *Liza ramada* (Fig. 2.3). Again, the intake abundance for almost all length classes was higher than net abundance. Only for herring both fishing methods were complementary. Stow netting as well as cooling-water sampling caught 83 mm sized herring with the same efficiency. Individuals <83 mm were more efficiently sampled in cooling-water, individuals >83 mm were more efficiently caught with stow nets.

If we presume that herring <70 mm cannot resist to the velocity caused by the intake current and that herring >90 mm cannot escape from the stow nets due to the net selectivity, collating these data yielded a third Gauss curve almost overlapping the two others (Table 2.4, Fig. 2.3). The surface between this curve and the X-axis was interpreted as a measure for the real population density as present in the surrounding water (100%). Consequently, the studied cooling-water inlet caught herring with an estimated efficiency of 71.8 %. Almost 30% of the present population is thus able to withstand the intake currents. The mean stow net efficiency for herring was estimated at 41.6%.

Discussion

The number of studies comparing samples of fish and macro-crustaceans taken at cooling-water filter screens with other fishing techniques is rather limited. Van den Broek (1979) compared screen samples with trawl samples and observed that all species but two were common to both sampling methods. The overall number taken in trawls was always less than in cooling-water. This might be due to small fish avoiding capture by passing through the mesh (Van den Broek, 1979). Love *et al.* (1998) concluded that the catch rates of rockfishes by power plats reflected the abundance of these fishes surrounding the plants based on two fishing surveys (impingement versus scuba diving).

Our comparison between simultaneously taken stow net samples and cooling-water samples in the Zeeschelde Estuary suggests that the cooling-water intake is an effective source for collecting fish and crustaceans. Our analysis revealed three major conclusions.

1. Except for rare marine visitors, all species present in the stow nets were also sampled by the cooling-water intake.

2. Depending on the size of the species, the intake abundance was several times higher than the net abundance.

3. Almost all length classes present within each population were sampled by the cooling-water intake.

The number of species cooling-water samples

The effectiveness of using power station intake screens for obtaining representative samples of fish in an area is emphasized by the fact that 118 of the 122 fish species known to occur in the inshore waters of England and Wales have been recorded from the screens of 12 power plants situated in those waters (Henderson, 1989). Since regular sampling commenced at Doel in 1992, 63 fish species and 6 crustacean species have been recorded on the filter screens. Year round fyke netting on an neighbouring intertidal mud flat between 1994 and 1998 yielded only 47 fish species (Maes *et al.*, 1997; Maes, unpublished) while monthly beam trawling for one year in an adjacent part of the estuary resulted in only 28 fish species (Hamerlynck *et al.*, 1993). With comparison to the intake samples, crabs were not observed in the stow nets, as they probably escape under the net. Our results strongly suggest that power stations sample almost all fish present in the area and that they sample pelagic, demersal and benthic species. They act as a suction trap for swimmers and organisms walking over the substrate (Henderson *et al.*, 1992).

Sampling efficiency and selectivity of the cooling-water intake

Although sampling the same populations, the cooling-water intake abundance was, on average, five times higher than the net abundance. The ratio net abundance to intake abundance was relative to fish size. This significant linear relationship gives confidence that abundance data as observed in cooling-water samples were not biased. Statistics on the sampling efficiency of stow nets were not found in literature. Let us thus assume that the cooling-water abundance data were 100% effective. Under this assumption, we can reinterpret Fig. 2.2 as a species size-selection curve for stow nets. In general, stow nets caught small species such as common shrimp, sand goby and common goby at low efficiencies (5-20%) (Table 2.2). Larger species such as Clupeidae, whiting, pikeperch and flatfish were caught at high efficiencies (50-80%) (Table 2.2).

Table 2.4. *Results of a non-linear estimation procedure fitting Equation 2.1 through length-abundance data. Estimated parameters were total fish abundance (a), mean length (L) and its standard deviation (σ). R^2 is the explained variance. For herring the combined plot used intake abundance of herring <70 mm and net abundance of herring >90 mm.*

Species	**Sampling method**	***a***	L	σ	R^2	***p*-level**
Perca fluviatilis	cooling-water	1.5	84.9	8.39	0.95	<0.05
	stow nets	0.5	82.9	6.58	0.98	<0.05
Limanda limanda	cooling-water	7.1	67.2	11.58	0.91	<0.05
	stow nets	0.7	68.42	10.63	0.88	<0.05
Pomatoschistus microps	cooling-water	145.8	35.5	3.59	0.98	<0.05
	stow nets	27.7	32.9	4.87	0.97	<0.05
Sprattus sprattus	cooling-water	347.0	62.7	3.92	0.99	<0.05
	stow nets	188.6	62.7	4.16	0.98	<0.05
Pomatoschistus minutus	cooling-water	145.1	63.4	8.67	0.96	<0.05
	stow nets	27.8	64.8	8.15	0.98	<0.05
Liza ramada	cooling-water cohort I	0.3	43.6	8.56		
	cooling-water cohort II	0.6	174.1	15.4	0.96	<0.05
	stow net cohort I	0.02	50.0	10.6		
	stow net cohort II	0.5	171.4	15.34	0.97	<0.05
Clupea harengus	cooling-water	300.1	68.8	10.51	0.83	<0.05
	stow nets	174.4	79.0	10.21	0.96	<0.05
	combined	418.9	73.5	13.52	0.99	<0.05
Dicentrarchus labrax	cooling-water cohort I	1.9	100.9	14.4		<0.05
	cooling-water cohort II	0.8	167.0	56.4	0.95	<0.05
	stow net cohort I	0.8	111.2	19.6		<0.05
	stow net cohort II	0.2	209.1	40.2	0.96	<0.05

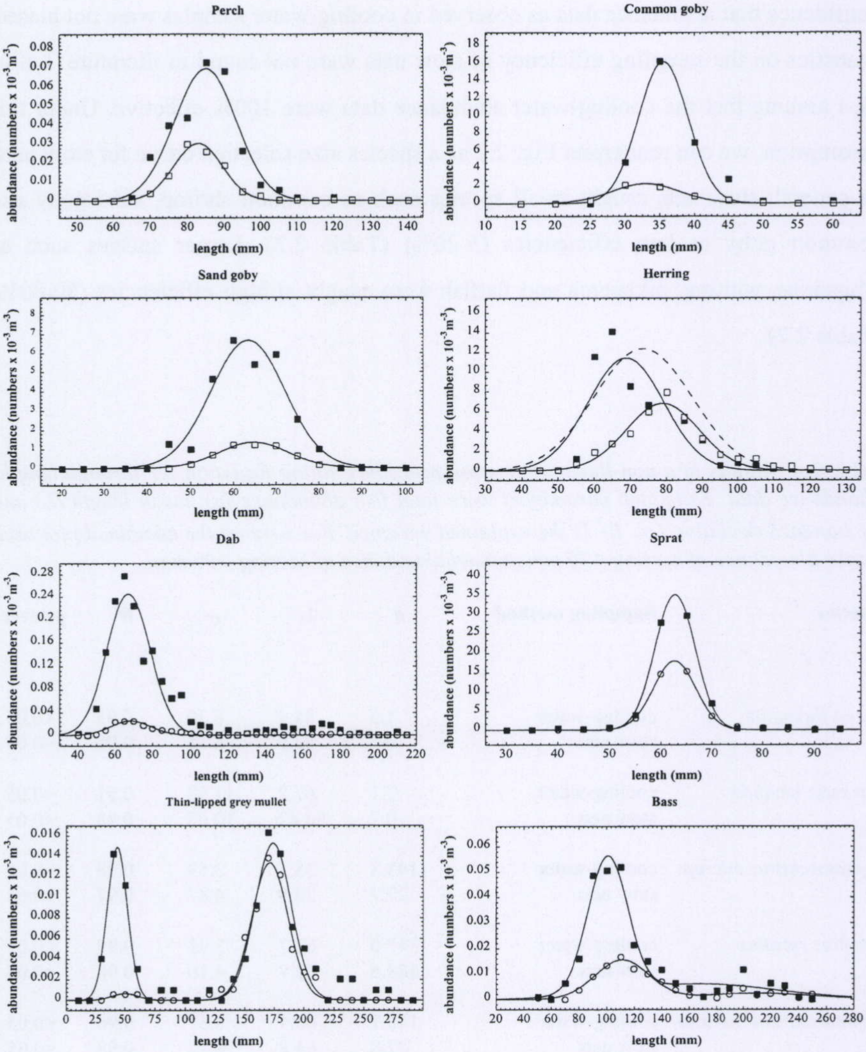

Fig. 2.3. Distribution of the mean net abundance (○) and intake abundance (■) of eight fish species plotted over length-classes. For herring, a third gaussian estimates the real population abundance using data of intake abundance and net abundance. See Table 2.4 for statistical details.

It is obvious, however, that the power station cooling-water inlet does not sample fish and crustaceans at 100% efficiency. This was made clear by the differences in recorded length for herring depending on the fishing method used (Fig. 2.3). Herring >83mm were more efficiently sampled by stow nets. It appears that a cooling-water intake withdraws young fish and small individuals at a higher efficiency than stow nets whereas large-sized fish may resist to the water currents towards the intake.

Turnpenny (1988) observed that the majority of impinged fish at a coastal power plant in England were <20 cm and argued that this reflects the pre-eminence of juvenile fish in inshore and estuarine areas and the selective capture of smaller individuals by their weakened swimming performance. Fish >20 cm represented, however, an insignificant fraction of the total fish abundance in the present study area as shown by stow net fisheries.

The size of the fish captured on screens also depends on escape swimming speeds and the mesh size of the screens. The critical swimming speeds that can be reached by juvenile sprat and herring to escape from a cooling-water intake average 10-12 body lenghts·s^{-1} at water temperatures of 16-19 °C (Turnpenny, 1983). These data suggest that a majority of herring and sprat can easily escape from the intake currents at Doel. However, high turbidities and strong tidal currents probably prevent fish seeing the intake or sensing the water flow towards it (Henderson *et al.*, 1992). At Doel, the entrance speed was 45.8 cm·s^{-1} and decreased rapidly to 6.3 cm·s^{-1} at 10 m off the intake (International Marine and Dredging Consultants, unpublished data), suggesting that only fish which are almost upon the intake will be accelerated into the aperture (Henderson *et al.*, 1992).

We conclude that the studied cooling-water intake sampled fish and crustaceans with a relatively high efficiency, covering almost the complete length spectrum of a population present in the surrounding water. Hence, intake data can be used to estimate real fish population densities, at least for small species. One should be more careful in case of large-sized fish. When studying larger species or individuals, the use of additional fishing techniques may be required.

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Chapter 3
Tidal and Diel Periodicity in the Cooling-Water Intake Catches of Fish and Crustaceans at the Nuclear Power Plant Doel

Daily intake records of fish and crustacean captures on the filter screens of the nuclear power plant Doel, situated in the Zeeschelde estuary (Belgium), were analyzed over a number of tidal and diel periods. Two-way analysis of variance was used to detect significant short-term changes in the intake data. Non-linear estimation was used to measure the variance that can be attributed to cyclic phenomena. The number of species was not related with any tidal stage nor with diel effects. Both statistical methods showed the presence of a significant tidal effect in the abundance data. Mainly benthic and demersal fish species experienced significant higher intake risks at high tide and ebb tide. For pelagic species, the chance on entrapment by the cooling-water system was random. A significant diel effect was only observed for two gobiid species and the prawn. At least part of the variance within the field observations could be attributed to cyclic events. The exploitation of intertidal habitats by bottom-orientated species would explain higher intake catches during high tide. Slightly higher catches overnight may be caused by vertical movements.

Introduction

Long-term changes in the abundance of estuarine fish caused by year-to-year variation and seasonal distribution are clearly recognized in monthly cooling-water samples and have been presented in detail (Claridge *et al.*, 1986; Potter *et al.*, 1997; Chapter 5). Short-term-changes in fish abundance related to tidal stage and the dark-light cycle, however, are sometimes masked by the large variance in the intake catches. Daily patterns in the intake catches are likely to be caused by a combination of both natural and artificial factors. Natural causes include changes in activity and behaviour of the species with respect to tidal and diel cycles as well as instantaneous responses to the intake currents. The many aspects of behaviour during the different cycles are complex and changes in swimming activity may be associated to feeding, vertical migration and shoal dispersion (Woodhead, 1966). Such marked changes would be expected to affect their vulnerability of being captured by the intake. Unnatural causes for messy patterns in the abundance data include the residence time of species inside the cooling-water circuit, and local environmental and geophysical conditions.

This chapter analyzes fish and crustacean samples taken on the filter screens of the Doel nuclear power station, which withdraws cooling-water from the Zeeschelde estuary (Belgium). The data presented were collected during several 24-h intervals and show a large variance in species abundance. In particular, we here examine whether tidal and diel periodicity play a significant role in the abundance data series and explore how much of the variance these cyclic events explain.

Materials and methods

Samples of fish, crabs and shrimps were taken at the Doel nuclear power cooling-water inlet, located in the brackish water part of the Zeeschelde estuary (Belgium). A detailed description of the sampling site, including water quality data is presented in Chapter 5. The cooling-water intake is situated 2 m above the bottom and withdraws 25.1 $m^3 \cdot s^{-1}$ water through five intake apertures measuring 4 × 2.4 m^2. Water is transported through a 540 m long pipeline to a communicating reservoir located on the site. In this reservoir, fish, crustaceans, vascular material and debris are removed from the cooling-water by vertical travelling water screens with a mesh size of 4 mm and afterwards flushed into a container, the sampling point. The residence time of fish within the system e.g. the time animals spend between the intake point in the river and the sampling point is at least 20 min. Goldfish *Carassius auratus* (L.) measuring between 7 and 23 cm were used to estimate more exactly the residence time. After releasing 246 living fish in the cooling-water inlet, 69% of the fish were recaptured after 20 min, and 80% after one hour.

Between July 1994 and June 1995, fish and crustaceans were monthly sampled on the day of the first spring tide. Samples of approximately $67.5 \cdot 10^3$ m^3 cooling-water were taken at low tide, flood tide, high tide and ebb tide during day as well as overnight. Fish and crustaceans were separated from debris, identified to species level, counted, measured and preserved in 7% formol. Subsamples were taken in case of large catches of fish or crustaceans by dividing the total catch in equal parts. Numbers were transformed to abundance (numbers$\cdot 10^{-3}$ m^{-3} cooling-water sampled) and arranged into a data matrix.

Transformation and normalization of the species abundance data

Only commonly occurring species were used for further analysis. For each species a data series was set up containing at least 32 samples (four days × eight samples) and at the most 88 samples (11 days × eight samples). To exclude any seasonal pattern, the abundance data were transformed to percentages by dividing each sample by the total daily catch for the given species. The transformed data were subsequently normalized by Equation 3.1 to meet ANOVA assumptions.

$$y = \arcsin\left(\sqrt{\frac{d_i}{100}}\right) \tag{3.1}$$

Since the tidal cycle does not match with a diel cycle, samples had to be sorted as proposed in Table 3.1, prior to statistical analysis.

Table 3.1. *Sorting the species abundance data matrix. Except for January 1995, fish and crustaceans were sampled each month on the day of the first spring tide. All samples have been numbered and are corresponding to a particular tidal and diel stage (LT, Low Tide, FT, Flood Tide (rising tide) , HT, High Tide, ET, Ebb Tide (falling tide)).*

sample month	**sample number**							
July 1994	1	2	3	4	5	6	7	8
August 1994	9	10	11	12	13	14	15	16
September 1994	17	18	19	20	21	22	23	24
October 1994	25	26	27	28	29	30	31	32
November 1994	33	34	35	36	37	38	39	40
December 1994	41	42	43	44	45	46	47	48
February 1995	49	50	51	52	53	54	55	56
March 1994	57	58	59	60	61	62	63	64
April 1995	65	66	67	68	69	70	71	72
May 1995	73	74	75	76	77	78	79	80
June 1995	81	82	83	84	85	86	87	88
tidal phase	LT	FT	HT	ET	LT	FT	HT	ET
day/night	DAY	DAY	DAY	DAY	NIGHT	NIGHT	NIGHT	NIGHT

Table 3.2. *Results of the two-way analyses of variance examining the main effects and the interaction effect of photoperiod (day, night) or/and tidal stage (low tide, flood tide, high tide, ebb tide) on species abundance. N indicates the number of samples included in the statistics, df: degrees of freedom.*

Species	**Effect**	**N**	**df**	**F**	***p*-level**
Carcinas maenas	tide	5×8	3	4.92	0.006
Shore crab	photoperiod		1	0.51	0.479
	tide × photoperiod		3	0.98	0.413
Rhitrhopanopeus harrissi	tide	6×8	3	5.20	0.004
Dwarf crab	photoperiod		1	1.40	0.243
	tide × photoperiod		3	0.47	0.703
Crangon crangon	tide	8×8	3	6.38	< 0.001
Common shrimp	photoperiod		1	< 0.01	0.925
	tide × photoperiod		3	1.43	0.245
Palaemonetes varians	tide	11×8	3	7.67	< 0.001
Prawn	photoperiod		1	5.93	0.017
	tide × photoperiod		3	0.41	0.244
Pomatoschistus microps	tide	10×8	3	2.89	0.041
Common goby	photoperiod		1	5.62	0.020
	tide × photoperiod		3	1.77	0.159
Pleuronectes flesus	tide	11×8	3	18.07	< 0.001
Flounder	photoperiod		1	1.46	0.231
	tide × photoperiod		3	1.14	0.339
Pomatoschistus minutus	tide	6×8	3	5.70	0.002
Sand goby	photoperiod		1	< 0.01	0.936
	tide × photoperiod		3	7.35	< 0.001
Clupea harengus	tide	6×8	3	2.67	0.060
Herring	photoperiod		1	1.58	0.215
	tide × photoperiod		3	0.99	0.406
Anguilla anguilla	tide	11×8	3	6.00	< 0.001
Eel	photoperiod		1	2.46	0.120
	tide × photoperiod		3	0.03	0.994
Stizostedion lucioperca	tide	4×8	3	15.19	< 0.001
Pikeperch	photoperiod		1	0.87	0.361
	tide × photoperiod		3	0.58	0.632
Sprattus sprattus	tide	8×8	3	1.05	0.375
Sprat	photoperiod		1	< 0.01	0.921
	tide × photoperiod		3	1.19	0.321
Dicentrarchus labrax	tide	11×8	3	1.32	0.271
Bass	photoperiod		1	2.14	0.147
	tide × photoperiod		3	0.18	0.908

Equation 3.2 was used to examine the relationship between the sorted, transformed and normalized abundance data and the tidal and diel cycle. The regression equation is the sum of a diel and tidal wave function (Equation 3.2). An oscillating wave function is determined by its amplitude and its frequency. As we took eight samples over 24 hour, the function which denotes the daily cycle, had a frequency 1/8 (amplitude *A*). Accordingly, the function that represented the tidal cycle had a frequency ¼ (amplitude *B*). The amplitudes *A* and *B* are the parameters of the model that had to be estimated.

The estimation procedure was the Quasi-Newton method available in the software package Statistica 4.5 (Statsoft, 1994). The constant *C* in Equation 3.2 excluded negative values.

$$y - C = A \times \sin(2\Pi \frac{1}{8}) + B \times \sin(2\Pi \frac{1}{4} x) \tag{3.2}$$

Start values for the parameter estimation were obtained from an initial Fourier analysis. The proportion of variance accounted for by the regression was given by R^2. Correlations between observed field data and expected model values were tested with a Spearman Rank Correlation test.

Results

We caught 48 fish species, four crab species and two shrimp species in 88 samples. Only the most abundant species (> 0.05% of the annual catch) were studied in detail. These were shore crab *Carcinas maenas*, dwarf crab *Rhitrhopanopeus harrissi*, common shrimp *Crangon crangon*, prawn *Palaemonetes varians*, common goby *Pomatoschistus microps*, flounder *Pleuronectes flesus*, sand goby *Pomatoschistus minutus*, herring *Clupea harengus*, eel *Anguilla anguilla*, pikeperch *Stizostedion lucioperca*, sprat *Sprattus sprattus* and bass *Dicentrarchus labrax*.

The average number of species did not change neither with the dark-light cycle (F = 0.32; df = 1; $p = 0.57$), nor with the tidal stage (F = 2.00; df = 3; $p = 0.20$), nor with the interaction between both cycles (F = 1.18; df = 3; $p = 0.32$).

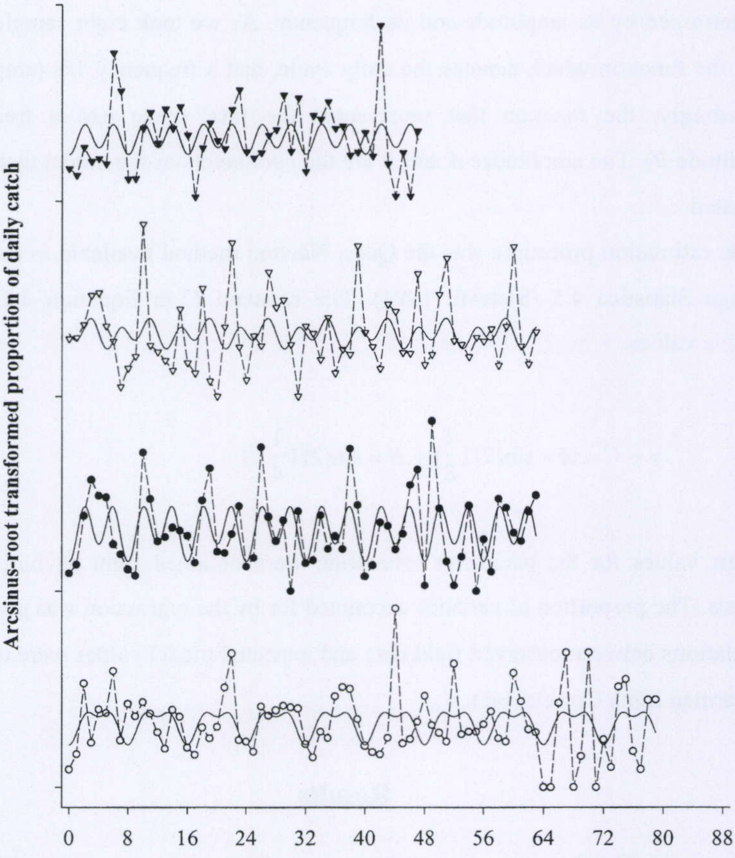

Fig. 3.1. Fitting the species abundance data as inferred from cooling-water catches (dotted line) for common goby *Pomatoschistus microps* (○), common shrimp *Crangon crangon* (●), sprat *Sprattus sprattus* (▽) and herring *Clupea harengus* (▼). The equation used for the regression model is given by Equation 3.2. The parameters estimated by the model are presented in Table 3.3. Sample numbers were assigned to a tidal and diel stage in Table 3.1.

Table 3.2 summarizes the results of the two-way ANOVAs performed on the species abundance data for two grouping variables (photoperiod, tide) and the interaction effect. Based on the analysis three groups of species were recognized:

1. Six species had an exclusive tidal effect present in their daily intake pattern. These species were shore crab, flounder, eel, pikeperch, common shrimp and dwarf crab. The average abundance of the latter was significantly higher at low tides than at any other tidal stage. Filter screen catches of the other species were significantly higher at high tides and ebb tides.

2. Three species had a significant tidal effect combined with a significant diel effect present in the their daily intake pattern. These species were common goby, sand goby and the prawn. Highest numbers occurred at high tide. Night catches of prawns and common goby were significantly higher than day catches. Only for sand goby, the interaction effect was significant. More individuals were captured at high tides during night than at any other tide.

3. Three species, including herring, sprat and bass, showed no patterns in the daily intake catches.

Accordingly, non-linear estimation resulted in significant correlations between observed field data and predicted values for all species but herring, sprat and bass (Table 3.3). These results suggest the presence of either a circadian or circatidal component in the data series. The total explained variance was, however, moderate and was situated between 11.9 % for common goby and 34.3% for pikeperch. In Figs. 3.1, 3.2, 3.3 the results of the parameter estimation were printed upon the field observations. If the respective amplitudes *A* and *B* are interpreted as the relative contribution of each period in the total explained variance of each regression, it is apparent that tidal variation was far more important than diel variation. The tidal intake pattern of flounder, pikeperch and of all crustacean species that was detected by the parameter estimation procedure fitted relatively well with the field observations. This outcome was not surprising, given with respect to the ANOVA results.

Furthermore, the model showed that night catches were, in general, higher than day catches, although this effect was not significant for most of the species. As a result, the diel component of the regression model was slightly superposed on the tidal component. Both statistical methods did not detect any significant effect nor any underlying trend in the series of abundance of herring, sprat and bass.

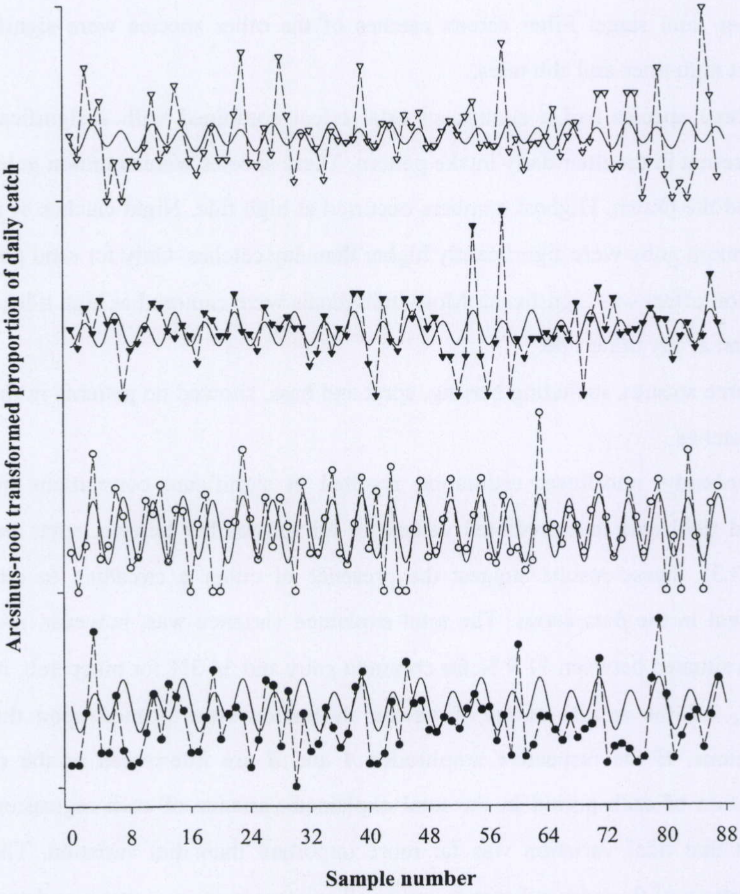

Fig. 3.2. Fitting the species abundance data as inferred from cooling-water catches (dotted line) for flounder *Pleuronectes flesus* (○), prawn *Palaemontes varians* (●), bass *Dicentrarchus labrax* (▽) and eel *Anguilla anguilla* (▼).The equation used for the regression model is given by Equation 3.2. The parameters estimated by the model are presented in Table 3.3. Sample numbers were assigned to a tidal and diel stage in Table 3.1.

Discussion

Sampling fish and crustaceans in the Doel nuclear power plant cooling-water during monthly 24-hours intervals yielded two main conclusions. Firstly, the number of species was not associated with any tidal stage nor with diel effects. Secondly, both

ANOVA and non-linear regression analysis showed that, if any effect was present in a series of cooling-water intake catches, it was predominantly tidal. Mainly benthic and demersal fish species experienced significant higher intake risks at high tide. For pelagic species, the chance on entrapment by the cooling-water system was random. An additional significant diel effect was only observed for two gobiid species and for prawns. At least part of the variance present within the field observations could be attributed to cyclic events.

Table 3.3. *Results of the parameter estimation by a non-linear regression (Equation 3.2) using the Quasi-Newton estimation procedure. A is the amplitude of the diel component, B of the tidal component. N stands for the number of samples used in each of the data series. R is the Spearman Rank correlation between observed field data and expected values. Correlations that were significantly different from zero ($P < 0.05$) are marked with a (*). R^2 represents the explained variance. c., cosinus; s., sinus.*

Species	**N**	***A***	***B***	**constant**	**R**	**R^2**
Carcinus maenas	5×8	-0.026 (c)	-0.133 (c)	0.321	0.504 (*)	25.4 %
Rhitrhopanopeus harrissi	6×8	-0.053 (s)	0.159 (s)	0.307	0.510 (*)	26.5 %
Crangon crangon	8×8	-0.045 (c)	-0.117 (c)	0.318	0.463 (*)	21.5 %
Palaemonetes varians	11×8	-0.048 (s)	-0.098 (s)	0.330	0.425 (*)	18.1 %
Pomatoschistus microps	10×8	-0.073 (c)	-0.039 (c)	0.328	0.340 (*)	11.9 %
Pleuronectes flesus	11×8	0.016 (c)	-0.158 (s)	0.315	0.562 (*)	31.7 %
Pomatoschistus minutus	6×8	-0.053 (c)	-0.101 (c)	0.327	0.446 (*)	19.9 %
Clupea harengus	6×8	-0.017 (c)	-0.068 (c)	0.327	0.285	8.2 %
Anguilla anguilla	11×8	-0.027 (s)	-0.076 (c)	0.336	0.365 (*)	13.3 %
Stizostedion lucioperca	4×8	-0.013 (c)	-0.139 (c)	0.329	0.598 (*)	34.3 %
Sprattus sprattus	8×8	0.033 (s)	-0.056 (s)	0.319	0.236	5.6 %
Dicentrarchus labrax	11×8	-0.023 (c)	-0.055 (s)	0.327	0.227	5.2 %

Some of the results agree with previous observations on the ecology and behaviour of species occurring in tidal environments. It has been noted before that behaviour, activity patterns and vertical movements of the species occurring in estuaries and along coasts are often influenced by tides and the dark-light cycle. Many fish and crustacean species exploit intertidal areas at high tide, mainly for feeding purposes (Gibson, 1992; Gibson *et al.*, 1996). This has been observed for flounder (Wirjoetmodjo and Pitcher, 1984; Stevens, 2000), shore crab and common goby (Cattrijsse *et al.*, 1994), common shrimp (Al-Adhub and Naylor, 1975; Henderson and Holmes, 1987) and sand goby (Gibson and Hesthagen, 1981). These results are in agreement with catches in fyke nets at a nearby intertidal mud flat (Maes *et al.*, 1997).

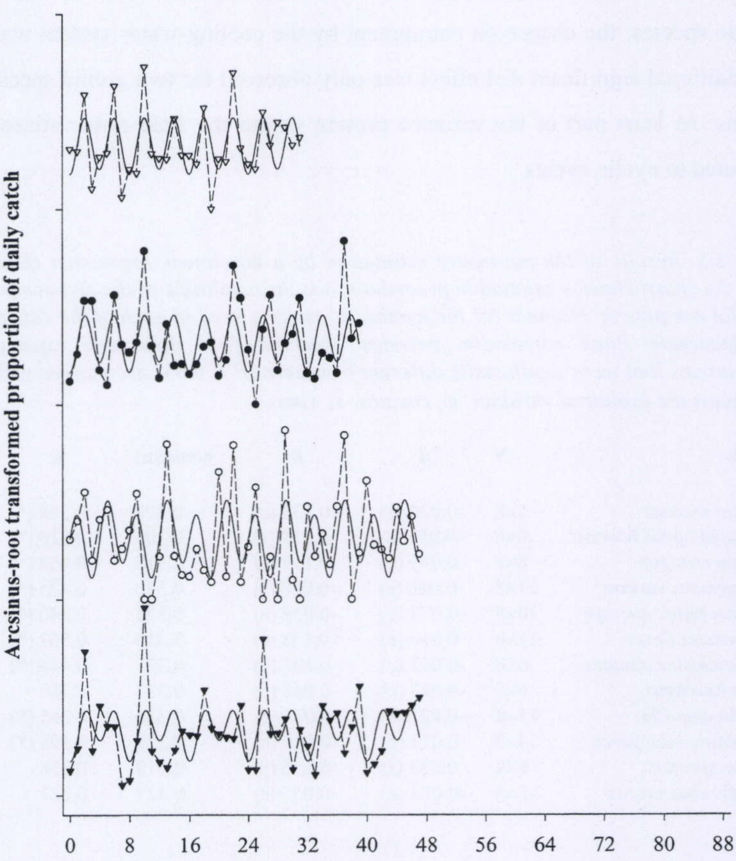

Fig. 3.3. Fitting the species abundance data as inferred from cooling-water catches (dotted line) for dwarf crab *Rhithropanopeus harissii* (○), shore crab *Carcinus maenas* (●), pikeperch *Stizostedion lucioperca* (▽) and sand goby *Pomatoschistus minutus* (▼).The equation used for the regression model is given by Equation 3.2. The parameters estimated by the model are presented in Table 3.3. Sample numbers were assigned to a tidal and diel stage in Table 3.1.

Those catches consisted mainly of eel, flounder, common shrimp and shore crab, as these species utilize the intertidals at high tide (Maes *et al.*, 1997). Migrating onto these mud flats seems to increase the risk of impingement as the cooling-water intake area is situated between the main river channel and an intertidal marsh. Thus increased swimming activity at high tides possibly explains the higher intake rates of demersal and benthic fish and crustacean species. Pelagic species such as herring and sprat avoid intertidal areas (Maes *et al.*, 1997). This can explain their random intake patterns observed at Doel.

Besides the marked periodicity caused by tides, also the photoperiod affects the behaviour of littoral fish and crustaceans (Woodhead, 1966). The effects on the present data were, however, not of equal importance as the tidal effects. Nightly intake catches were slightly higher than intake catches during day. Stow netting revealed that a number of fish species moved towards the upper water layers between sunset and sunrise and thus risk impingement when they move off the bottom (Chapter 6.). This particular behaviour has been studied in detail and has been reviewed by Woodhead (1966) and Neilson and Perry (1990). However, we argue that the effect of vertical movements cannot be observed in cooling-water samples. This is due to the position of the intake apertures relative to the water column. The intake samples pelagic, demersal and benthic species as it acts as a suction trap for both swimmers and organisms walking over the substrate (Henderson *et al.*, 1992). Hence, nocturnal swimming activities displayed by bottom-orientated fish were thus not observed in cooling-water samples.

Higher catches of pikeperch, a freshwater species, during high tide were probably caused by local conditions. At high tide, an increased activity of nearby sluices connecting the Zeeschelde estuary to the adjacent docks possibly produced increased intake catches. The Antwerp harbour docks indeed support a dense population of this species (Maes *et al.*, 1996; Peeters *et al.*, 1999*b*).

Although we observed significant correlations between field observations and the regression model including both circatidal and circadiel components, there still remains a lot of noise present in the data set. We may think of three reasons for unexplained sampling variance. The residence time of fish and crustaceans in the cooling-water system may interfere with the data which is obviously a disadvantage of the method used in comparison with other fishing techniques. While 70% of the fish were expected to reach the sampling point 20 min after impingement, another 30 % remained in the system and thus possibly died or joined subsequent samples. An additional source of sample variance observed in Clupeidae can be attributed to schooling behaviour, sometimes leading to a mass influx of individuals. Finally, unpredictable and turbulent currents may guide fish away from or upon the intake.

Sampling variance is not only common to power station cooling-water samples (Turnpenny and Utting, 1981). Most fishing techniques suffer similar problems. The present detailed analysis should give us, however, sufficient information for a optimal sampling strategy yielding unbiased results. With respect to the observed differences in the catches, we may conclude that averaging samples, taken over one tidal cycle, should represent well the actual abundance of fish in the proximity of the sampling site.

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Chapter 4
Spatial Structure of the Fish Community of the Zeeschelde Estuary

Fish living in the tidal fresh and brackishwater reaches of the Zeeschelde estuary were studied in samples collected from the cooling-water inlets of three power stations. Between July 1994 and June 1995, 42 different species were recorded including 26 marine migrants, 14 freshwater species and two diadromous species. Species number as well as fish abundance were correlated significantly with salinity and oxygen concentration. The community structure was analyzed with a correlation biplot based on principal component analysis of the root-root transformed fish abundance. Four separated assemblages could be distinguished since the first principal component expressed a salinity gradient and the second a temperature gradient. During summer and fall, *Pomatoschistus microps*, *P. minutus*, *P. lozanoi* and *Syngnathus rostellatus* were most abundant in the brackishwater reach. At this time, freshwater species seemed to avoid the freshwater area. During winter, *Sprattus sprattus*, *Clupea harengus* and *Dicentrarchus labrax* were the dominant species of the brackishwater zone while the freshwater reaches were dominated by *Gasterosteus aculeatus*. Migrating fish such as *Pleuronectes flesus*, *Lampetra fluviatilis*, *Anguilla anguilla* and *Osmerus eperlanus* were restricted to the brackish environment.

Maes, J., Van Damme, P.A., Taillieu, A. and Ollevier, F. 1998. Fish communities along an oxygen-poor salinity gradient (Zeeschelde Estuary, Belgium). *Journal of Fish Biology* **52**, 534-546.

Introduction

European estuarine fish communities have been studied relatively well (Wheeler, 1988; Elliott and Dewailly, 1995). They are highly organized and largely structured by temperature, salinity and substratum (Henderson, 1989; Hamerlynck *et al.*, 1993). Fish migrations are related mainly to temperature and result in clear seasonal trends within the fish community. Salinity and substratum determine primarily the spatial distribution of estuarine fish communities. However, most studies have focused on the marine and brackish parts of the estuary. Research on fish occurring in the tidal freshwater reaches of estuaries is relatively scarce (Schuchhardt *et al.*, 1993; Thiel *et al.*, 1995; Araújo *et al.*, 1999), probably due to sampling difficulties and the presumed low biodiversity.

Typically for many European estuaries, human activities have a profound impact on the Zeeschelde Estuary (Belgium). Domestic and industrial wastewater discharges affect the water and sediment quality and lead to hypoxic or even anoxic conditions in the freshwater part (Van Eck *et al.*, 1991). Therefore, oxygen concentration is expected to be an important variable structuring the Zeeschelde fish community. Furthermore, extensive dredging to maintain navigation, and the reduction of habitat diversity for industrial or agricultural purposes, have reduced the area of possible spawning and nursery grounds for fish. Therefore, the loss of these important habitats could limit the distribution of fish even if the water quality improves.

This chapter presents data from fish catches at three power station cooling-water intakes, all situated in the fresh and brackish reaches of the Zeeschelde estuary. Reliable quantitative data on the distribution of fish occurring in the Zeeschelde have never been published before and therefore may provide a baseline for future monitoring.

Materials and methods

During the study, environmental data were measured once a month over one tidal cycle using a water quality multiprobe logger (Hydrolab, Datasonde 3). Water temperature at the sampling sites ranged between 5.1 °C and 24.0 °C (Table 4.1). Salinity as well as oxygen concentration increased downstream. Mean salinities at Schelle, Kallo and Doel were 0.6 ‰, 4.5 ‰ and 8.0 ‰, respectively. At Schelle, oxygen was almost completely absent during the major part of the year. Only in winter, when the solubility of oxygen in water increased, a maximum of 4 $mg \cdot l^{-1}$ was registered. At Kallo, the oxygen concentration was on average 2 $mg \cdot l^{-1}$ whereas at Doel at least 3.1 $mg \cdot l^{-1}$ was recorded. Secchi depths never exceeded 63 cm at any of the sampling stations (Table 4.1).

Sampling

Fish samples were collected from the cooling-water intake screens of the power stations of Doel, Kallo and Schelle (Fig 1.1). The cooling-water intakes are large openings directed towards the main river channel. The intakes are positioned at least 1.2

m below the historical minimum water level and 2 m above the bottom. Water is withdrawn from the Zeeschelde and filtered by a set of screens before entering the condensers. Fish, crustaceans and debris are washed off and discharged. The cooling-water entrance speed at the intakes was 48 $cm\cdot s^{-1}$ at Doel, 75 $cm\cdot s^{-1}$ at Kallo, and 51 $cm\cdot s^{-1}$ at Schelle. The types and mesh-size of the screens, the total amount of cooling-water sampled and the sampling period differ slightly among the stations (Table 4.2). Between July 1994 and June 1995 about 6.1×10^6 m^3 cooling-water was sampled at the three power stations together.

Table 4.1. *Ranges of environmental variables measured at the sampling stations between July 1994 and June 1995 (m stands for minimum, M for maximum).*

	Temperature (°C)			**Oxygen ($mg\cdot l^{-1}$)**			**Salinity (‰)**			**Secchi depth (cm)**		
	m	**mean**	**M**	**m**	**mean**	**M**	**m**	**mean**	**M**	**m**	**mean**	**M**
Schelle	6.8	14.3	22.8	0.0	0.8	2.8	0.1	0.6	1.2	18.7	31.5	35.7
Kallo	6.4	14.0	24.0	0.3	2.0	5.4	0.6	4.5	9.5	19.8	36.9	62.3
Doel	5.1	13.6	23.8	3.1	4.6	6.5	3.4	8.0	13.4	13.7	21.4	31.5

At each station, approximately 200 000 m^3 cooling-water was sampled once a month during a single day. Since tidal periodicity affected intake catches (Chapter 3), samples were taken at low, rising, high and falling tides. Afterwards, the average of these four subsamples (one day sample) was used for further analysis. In total, 31 day samples were taken (12 at Doel, 11 at Kallo and eight at Schelle). At Kallo, sampling ended in May 1995 due to a power station shut-down in June 1995. Sampling in Schelle was hindered by large amounts of leaves and debris. Therefore, sampling was restricted from July 1994 until March 1995. Equipment damage prevented sampling in November 1994.

After sampling, fish were identified to species level according to Wheeler (1992), counted and preserved in 7% formol. Frequency of occurrence (% of total annual catch per station) and abundance (numbers$\cdot 10^{-3}$ m^{-3} cooling-water sampled) were calculated for all species. Only fish >20 mm are included in the analysis. Although smaller individuals as well as larvae were present in the samples, their abundance was not quantified considering the mesh size of the screens (Table 4.2).

Table 4.2. *Sampling details at the three power stations*

Power station	Screens	Mesh-size (mm)	Amount of cooling-water sampled (m^3)	sampling period
Doel	Vertical travelling screens	4	2 800 000	July 1994 to June 1995
Kallo	Rotating drum screens	4	2 400 000	July 1994 to May 1995
Schelle	Rotating drum screens	6	900 000	July 1994 to March 1995

Data analysis

The fish community structure was investigated using correlation biplot based on principal component analysis (PCA) on the root-root transformed abundance data (Field *et al.*, 1982). Relationships between the first two principal components, total fish abundance and species number (dependent variables) and environmental variables were analyzed using Spearman rank correlations. Correlations were significant at $p < 0.05$.

Results

Species number, species composition and fish densities

A total of 42 different fish species was recorded in the cooling-water of the power stations of Doel, Kallo and Schelle (Table 4.3). Of all the fish species, 26 were marine migrants while 14 species occurred typically in fresh water. Both groups included species that spend part of their life in estuaries as well as species occasionally entering estuaries. None of them were strictly estuarine-dependent, i.e. they could spawn and mature in either fully marine or freshwater environments. Two diadromous species were recorded: the catadromous European eel *Anguilla anguilla* (L.) and the anadromous river lamprey *Lampetra fluviatilis* (L.).

Table 4.3. *Species list and relative frequency (%) of the total annual catch per station (set on 100%) of fish sampled in three cooling-water intakes over the period July 1994 to June 1995.*

Scientific name	**Common name**	**Doel**	**Kallo**	**Schelle**
Anadromous species				
Lampetra fluviatilis (L.)	River lamprey	0.032	0.003	-
Catadromous species				
Anguilla anguilla (L.)	European eel	0.081	0.976	3.895
Fresh water species				
Alburnus alburnus (L.)	Bleak	-	-	2.893
Blicca bjoerkna (L.)	Silver bream	< 0.001	0.033	18.207
Carassius carassius (L.)	Crucean carp	< 0.001	-	1.929
Leucaspius delineatus (Heckel, 1843)	Moderliesschen	-	0.006	-
Rhoedeus sericeus (Pallas, 1776)	Bitterling	0.012	0.012	8.062
Rutilus rutilus (L.)	Roach	0.017	0.008	11.572
Tinca tinca (L.)	Tench	-	-	2.717
Gasterosteus aculeatus L.	Three-spined stickleback	0.118	0.666	26.038
Pungitius pungitius (L.)	Ten-spined stickleback	0.002	0.040	16.587
Cottus gobio L.	Bullhead	< 0.001	-	-
Lepomis gibbosus (L.)	Pumpkinseed		-	0.964
Gymnocephalus cernuus (L.)	Ruffe	0.002	-	-
Perca fluviatilis L.	Perch	0.039	0.207	5.979
Stizostedion lucioperca (L.)	Zander	0.070	0.290	-
Marine species				
Clupea harengus L.	Herring	18.632	5.001	-
Sprattus sprattus (L.)	Sprat	3.399	1.449	-
Engraulis encrasicolus (L.)	Anchovy	0.004	0.011	-
Osmerus eperlanus (L.)	Smelt	0.035	0.171	1.157
Gadus morhua L.	Cod	< 0.001	0.002	-
Merlangius merlangus (L.)	Whiting	< 0.001	0.002	-
Trisopterus luscus (L.)	Bib	< 0.001	-	-
Atherina presbyter Cuvier, 1829	Sand-smelt	0.002	0.002	-
Syngnathus acus L.	Greater pipefish	< 0.001	-	-
Syngnathus rostellatus Nilsson, 1855	Nilsson's pipefish	8.943	1.451	-
Trigla lucerna L.	Tub gurnard	< 0.001	-	-
Myoxocephalus scorpius (L.)	Bull-rout	< 0.001	0.003	-
Cyclopterus lumpus L.	Lumpsucker	< 0.001	-	-
Dicentrarchus labrax (L.)	Bass	0.805	0.597	-
Trachurus trachurus (L.)	Horse mackerel	0.008	0.005	-
Liza ramada (Risso, 1826)	Thin-lipped grey mullet	0.030	0.025	-
Zoarces viviparus (L.)	Eelpout	< 0.001	-	-
Ammodytes tobianus L.	Sandeel	0.005	-	-
Pomatoschistus lozanoi (de Buen, 1923)	Lozano's goby	5.210	0.094	-
Pomatoschistus microps (Krøyer, 1838)	common goby	31.099	85.155	-
Pomatoschistus minutus (Pallas, 1770)	Sand goby	31.269	3.217	-
Scophthalmus rhombus (L.)	Brill	< 0.001	0.004	-
Limanda limanda (L.)	Dab	0.003	-	-
Pleuronectes flesus L.	Flounder	0.156	0.132	-
Pleuronectes platessa L.	Plaice	0.002	0.003	-
Solea solea (L.)	Sole	0.019	0.453	-

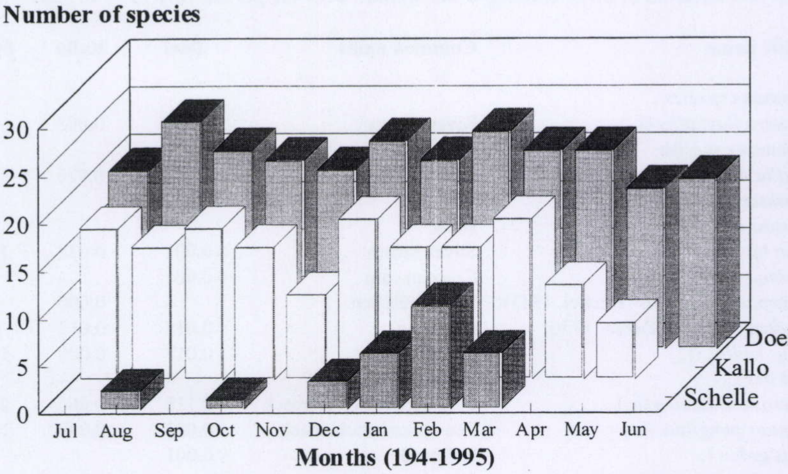

Fig. 4.1. Monthly variation in total species number as recorded at Schelle, Kallo and Doel between July 1994 and June 1995.

There were great differences in species number, species composition and fish abundance amongst the three sampling sites. Sampling at Doel yielded 38 species. Most abundant were Gobiidae, including the common goby *Pomatoschistus microps*, sand goby *P. minutus* and Lozano's goby *P. lozanoi*, Clupeidae, including herring *Clupea harengus* and sprat *Sprattus sprattus*, and Nillson's pipefish *Syngnathus rostellatus*. These species accounted for 98 % of the total numbers caught at Doel. On average, 20 species were present at any one time (Fig. 4.1). The mean fish abundance was 152.1 (± 154.2)$\times 10^{-3}$ m^{-3}. In contrast to species number, the fish abundance varied seasonally. Fish densities were highest in fall, reached a maximum in November 1994 and declined during winter and spring (Fig. 4.2).

Twenty-nine species were caught at Kallo. Except for Lozano's goby the same species as at Doel dominated the samples and represented >96 % of the total numbers caught. However, common goby represented 85 % of all fish impinged in the Kallo power station cooling-water intake (Table 4.3). The mean species number in Kallo was 13. Mean abundance was 21.7 (± 38.3) $\times 10^{-3}$ m^{-3}. Maximum abundance was noted in September (Fig. 4.2) when >95 % of the catch were common Gobiidae.

In Schelle, only 12 fish species were present. Most abundant were sticklebacks (both *Gasterosteus aculeatus* and *Pungitius pungitius*), silver bream *Blicca bjoerkna* and perch *Perca fluviatilis*. Because of the complete absence of oxygen throughout a major part of the year, a permanent fish community was absent in this part of the river. Only in winter were fish caught when their mean abundance approached 0.11 (± 0.15) $\times 10^{-3}$ m^{-3} which differed by three orders of magnitude from that recorded at Doel (Fig. 4.2).

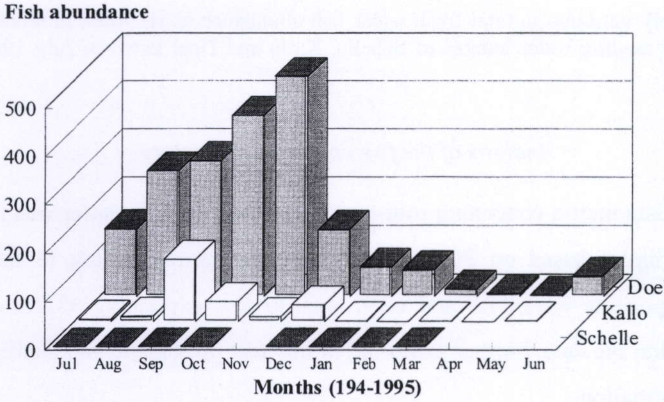

Fig. 4.2. Monthly variation in total fish abundance as recorded in monthly samples collected at the cooling-water intakes of Schelle, Kallo and Doel between July 1994 and June 1995.

Throughout the year, freshwater species were always more abundant in the brackish than the freshwater reaches of the Zeeschelde (Fig. 4.3). High densities of juvenile pikeperch *Stizostedion lucioperca* caused a first maximum in July at Kallo and Doel, while three-spined stickleback was responsible for a second abundance maximum in January at Doel.

Both the species number and fish abundance showed significant positive correlations to oxygen concentration and salinity (Table 4.4).

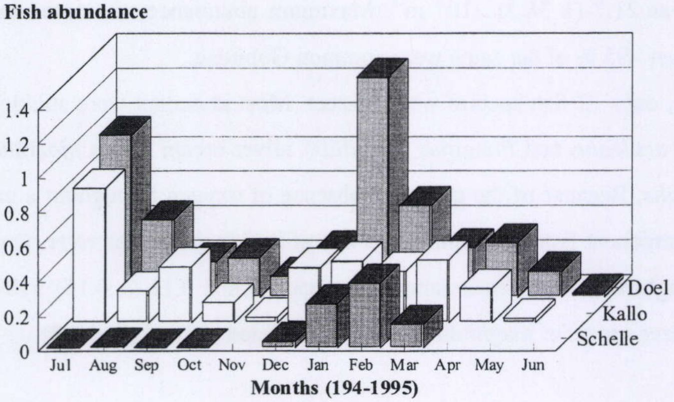

Fig. 4.3. Monthly variation in total fresh water fish abundance as recorded in monthly samples collected at the cooling-water intakes of Schelle, Kallo and Doel between July 1994 and June 1995.

Analysis of the fish community structure

A 31 × 42 data matrix containing root-root transformed fish densities was subjected to a correlation biplot based on PCA. The eigenvalues corresponding to the first two principal components were 11.9 and 6.09, respectively, explaining 38.3% of the total variability within the data. Further exploring of the next principal components yielded no additional information.

The first principal component (PC I) separated samples taken at one site (Fig. 4.4). Samples taken at Doel scored negative values, at Schelle scored positive values and at Kallo scored in between. The second principal component (PC II) separated winter and spring samples more or less from summer and fall samples.

The correlations between both principal components and four environmental variables (Table 4.4) showed that PC I represented a salinity and PC II a temperature gradient (Fig. 4.4). Both principal components were significantly correlated to oxygen concentration. Turbidity showed a negative correlation with PC II. Each of the four quadrants thus corresponded to a well-defined environmental description containing different fish species.

The first quadrant contained four freshwater species restricted to fresh and oligohaline conditions at salinities ≤ 3.5 ‰. These species occurred in small densities, reflecting the poor water quality.

The second quadrant comprised 16 species which seem to prefer euryhaline habitats during summer and fall. Four species were correlated strongly with PC I: common goby, sand goby, Lozano's goby and Nilsson's pipefish.

The third quadrant included 16 species occurring mainly in winter and spring samples. Sprat herring and bass *Dicentrarchus labrax* showed strong correlations with PC I. River lamprey and ruffe *Gymnocephalus cernuus* were correlated with PC II.

The fourth quadrant contained the remaining six species associated to low salinity winter conditions. All these species occurred in freshwater, although three-spined stickleback is known to be euryhaline.

Table 4.4. *Spearman Rank correlations between a set of dependent variables (PC I, PC II, number of species and total abundance for 31 samples) and a set of independent environmental data with indication of the significance level.*

Dependent variables	**Independent variables**	**Spearman Rank correlation**	**p-level**
PC I	temperature	-0.19	0.30
	oxygen concentration	-0.60	< 0.01
	salinity	-0.89	< 0.01
	turbidity	-0.31	0.08
PC II	temperature	0.83	<0.01
	oxygen concentration	-0.57	<0.01
	salinity	0.29	0.10
	turbidity	-0.48	<0.01
Number of species	temperature	-0.13	0.46
	oxygen concentration	0.82	<0.01
	salinity	0.65	<0.01
	turbidity	0.31	0.09
Abundance	temperature	0.10	0.60
	oxygen concentration	0.61	<0.01
	salinity	0.82	<0.01
	turbidity	0.28	0.13

Discussion

At the three power stations, 42 fish species were caught during one year. Elliot and Dewailly (1995) compared data coming from 17 European estuaries and reported a minimum of 22 species the Solway (England) and a maximum of 94 in the Dutch Wadden Sea. However, as the number of species is in part determined by the catch effort (Allen *et al.*, 1992), a relevant comparison to other studies is often difficult. Claridge *et al.* (1986) sampled the intake screens of the Oldbury power station (Severn Estuary, U.K.) extensively and observed that the cumulative number of species increased from 12 in the first month to 78 after 5 years. Therefore, we can expect the species number of the Zeeschelde to increase when continuing the monitoring program.

Species number as well as fish abundance declined in parallel with both declining salinities and oxygen concentrations. At Doel, on average 20 species were present at any one time, while in Schelle a maximum of 11 species occurred in February 1995. During summer, the freshwater zone of the Zeeschelde was almost completely devoid of fish due to insufficient oxygen concentrations. These results were confirmed by the principal component analysis. As PC I was correlated with salinity identifying a spatial axis, PC II was correlated with temperature and may be regarded as a temporal axis. Both principal components thus combine space and time into two dimensions revealing four communities: a summer and winter community in the tidal brackish reach and a summer and winter community in the tidal freshwater reach.

In the brackish water, the fish community occurring in summer and fall was composed mainly of Gobiidae of the genus *Pomatoschistus*. The relative abundance of common goby was striking. Whereas common goby accounted for 30 % of the total catch at Doel, it represented 85 % at Kallo. Young-of-the-year were recruited in summer and maximum densities reached in fall. Our results were opposite to those of Claridge *et al.* (1985), who found sand goby dominating over common goby in numbers and biomass in the upper subtidal reaches of the Severn Estuary (U.K.). These results agree with those of Jones and Miller (1966), Iglesias (1981) and Doornbos and Twisk (1987) that sand goby and common goby segregate in depth, with common goby occurring mainly in the littoral or

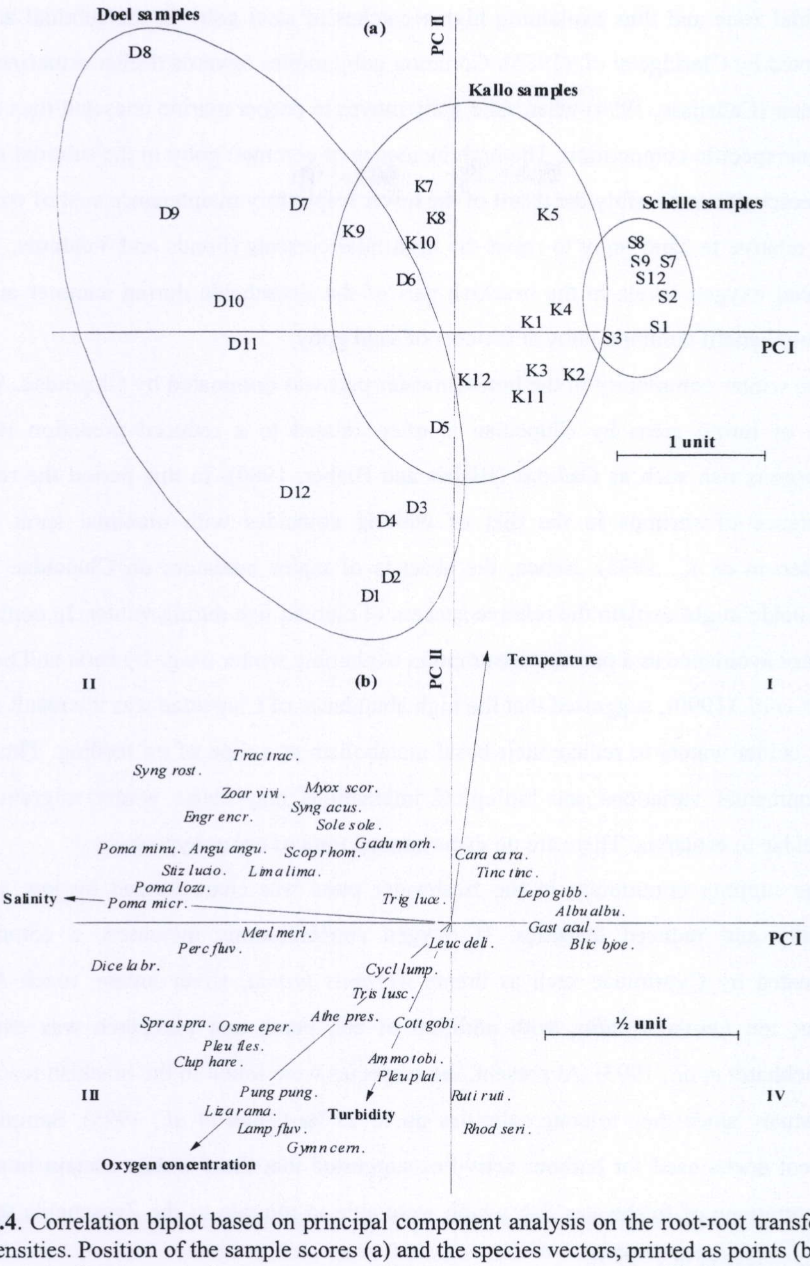

Fig. 4.4. Correlation biplot based on principal component analysis on the root-root transformed fish densities. Position of the sample scores (a) and the species vectors, printed as points (b) with respect to the first two principal components. The sample scores are grouped by location. Species are abbreviated by the first four letters of their genus name and species name, respectively. The correlations between environmental variables and principal components are presented in Table 4.4.

intertidal zone and thus explaining higher catches of sand goby in the subtidal zone as presented by Claridge *et al.* (1985). Common goby moves towards deeper estuarine areas in winter (Cattrijsse, 1994) when sand goby moves to deeper marine ones and thus avoids any interspecific competition. The high incidence of common goby in the subtidal area of the Zeeschelde is possibly the result of the lower respiratory maintenance cost of common goby relative to sand goby to resist the high tidal currents (Fonds and Veldhuis, 1973). Reduced oxygen levels in the brackish part of the Zeeschelde during summer and fall possibly benefit common goby at the cost of sand goby.

The winter community in the brackishwater part was dominated by Clupeidae. Winter usage of turbid areas by Clupeidae is often related to a reduced predation risk by piscivorous fish such as Gadidae (Blaber and Blaber, 1980). In this period the reduced occurrence of shrimps in the diet of whiting coincides with maximal sprat intake (Henderson *et al.*, 1992). Hence, the absence of major predators on Clupeidae in the Zeeschelde might explain the relative success of clupeid fish during winter. In contrast to predator avoidance as a possible assumption explaining winter usage by sprat and herring, Elliott *et al.* (1990), suggested that the high abundance of Clupeidae was the result of fish using colder waters to reduce their basal metabolism at a time of no feeding. Thus both environmental variations and biological interactions may cause winter migrations of Clupeidae to estuaries. There are no experimental tests of either hypothesis.

The summer community in the freshwater parts was characterized by low species diversity and reduced densities. If oxygen concentrations increased, a community dominated by Cyprinidae such as bream *Abramis brama*, silver bream, roach *Rutilus rutilus*, ide *Leusiscus idus*, with addition of eel, perch and pikeperch was expected (Schuchhardt *et al.*, 1993). At present, these species were found in the brackish reaches of the estuary since they tolerate salinities up to 15 ‰ (Thiel *et al.*, 1995). Sampling in adjacent docks used for harbour activities suggested that these waters sustain important concentrations of freshwater fish which were able to migrate to the Zeeschelde through sluices (Maes *et al.*, 1996).

The winter community in the freshwater part was dominated by three-spined stickleback. Migrant species such as flounder *Pleuronectes flesus* and smelt *Osmerus* *eperlanus* are absent in this region although they frequented the brackish area. Möller and Scholz (1991) found similar results in the Elbe estuary as they observed that both flounder and smelt were concentrated downstream from the low-oxygen zone and thus avoided the freshwater reach. Another notable absentee was the anadromous twaite shad *Alosa fallax* which once spawned on freshwater sandy beaches near Schelle.

So the ongoing recovery of the Zeeschelde ecosystem is restricted as yet to the brackishwater reaches. The freshwater reaches still suffer from severe oxygen depletion forcing fish towards the oligosaline zone. However, the tidal freshwater reaches, including almost unique intertidal fresh marshes, are important areas for fish occurring in lowland rivers (Rozas and Odum, 1987). Therefore, the protection of these habitats as well as the addition of flood plains to the tidal excursion is a matter of major concern since they both contribute significantly to the total biodiversity of the entire ecosystem (Van den Brink *et al.*, 1996; Pas *et al.*, 1998).

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Chapter 5
Seasonal Structure of the Fish and Crustacean Community of the Zeeschelde Estuary

Between July 1994 and June 1995, 55 fish species, two shrimp species and four crab species were recorded in 135 samples taken at the cooling-water filter screens of the nuclear power plant Doel. The fish community was composed of 36 marine species, 16 freshwater species and three diadromous species. Only few species dominated the fish community contributing to >96% of the numbers caught on cooling-water filter screens. These were three Gobiidae *Pomatoschistus minutus*, *P. lozanoi* and *P. microps*, two Clupeidae *Clupea harengus* and *Sprattus sprattus* with addition of *Syngnathus rostellatus*, *Pleuronectes flesus* and *Dicentrarchus labrax*. It was notable that all these dominating fish species had a marine nature and occurred as juveniles. Both freshwater and diadromous species represented only a small fraction of the fish community. The abundance of two shrimp species, the common shrimp *Crangon crangon* and the prawn *Palaemontes varians* equalled total fish abundance. The brackishwater reach was seasonally used by the community resulting in an exceptionally clear pattern of species occupancy. It was argued that young fish and crustaceans use the highly turbid Zeeschelde estuary as a refuge from predators.

Maes, J., Taillieu, A., Van Damme, P.A., Cottenie, K. and Ollevier, F. 1998. Seasonal patterns in the fish and crustacean community of a turbid temperate estuary (Zeeschelde Estuary, Belgium). *Estuarine, Coastal and Shelf Science* **47**, 143-151.

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 residents 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 and Duke, 1990*b*). 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 is resulting 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 and Duke, 1990*a*). 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 and Blaber, 1992; Ruiz *et al.*, 1993)

Seasonal changes in the structure of the fish and crustacean communities in the highly turbid Zeeschelde estuary, Belgium (Fig. 1.1) are the focus of this chapter. Therefore, sampling was conducted for one 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 fish 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 regime

Samples of fish, shrimps and crabs were collected every two weeks from the cooling-water intake screens of the Nuclear Power Plant Doel, located in the brackish part of the Zeeschelde (Fig. 1.1). 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 $m^3 s^{-1}$ 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 Mysidacea could be sampled. Approximately $8 \times 10^6 m^3$ cooling-water was monitored in 135 samples.

Fish and crustaceans were separated from debris, identified to species level, counted, measured and preserved in 7 % formol. 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 (ash-free dry weight) was calculated using length-biomass regressions (Hostens and Hamerlynck, 1993; Maes, unpublished).

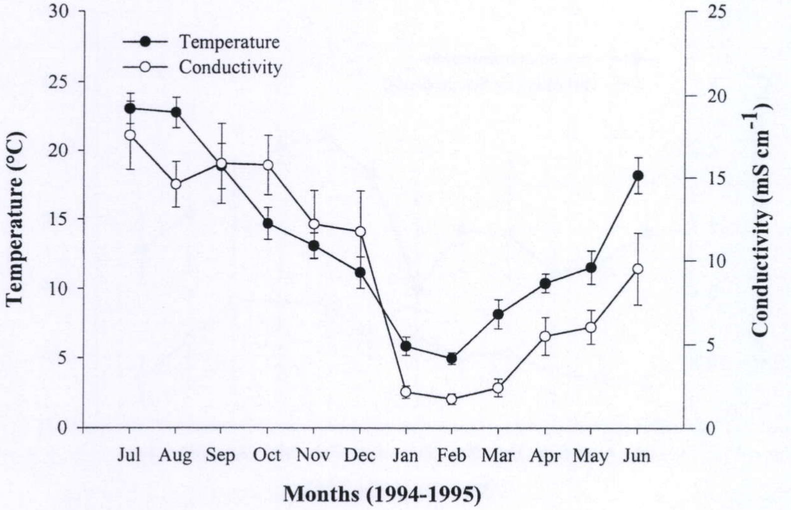

Fig. 5.1. Seasonal changes in water temperature and conductivity at the sampling site.

During sampling the following environmental variables were measured using a water quality multiprobe logger (Hydrolab, Datasonde 3): temperature (°C), conductivity ($mS{\cdot}cm^{-1}$), salinity (‰), dissolved oxygen concentration ($mg{\cdot}l^{-1}$) and turbidity (NTU). Secchi disc depth was measured in cm.

Data analysis

Abundance data ($numbers{\cdot}10^{-3}\ m^{-3}$ cooling-water sampled) and biomass data ($g\ ADW{\cdot}10^{-3}\ m^{-3}$ 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) were 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.

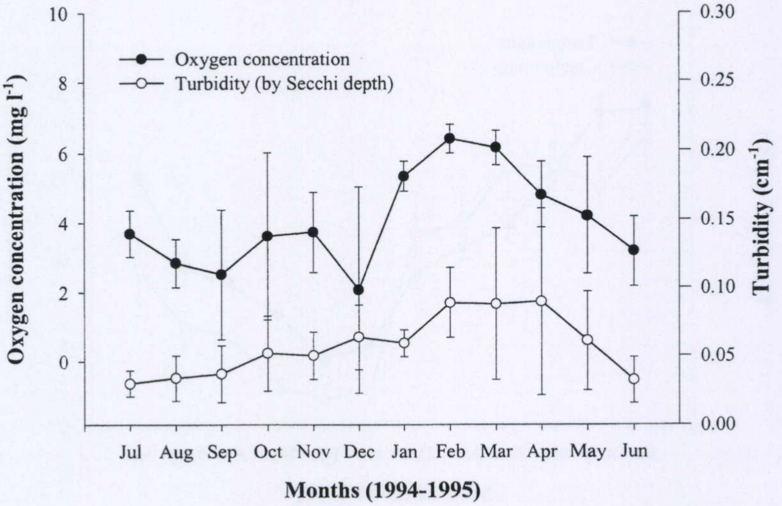

Fig.2. Seasonal changes in oxygen concentration and turbidity at the sampling site.

Results

Environmental data

Minimum and maximum temperatures recorded in the Zeeschelde ranged from 4.9 °C in February to 24.8 °C in August (Fig.5.1). Mean salinity and oxygen concentration were 7.99‰ and 4.59 mg·l^{-1}, respectively (Figs. 5.1, 5.2). 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 (Fig. 5.2). Mean turbidity was 165 NTU.

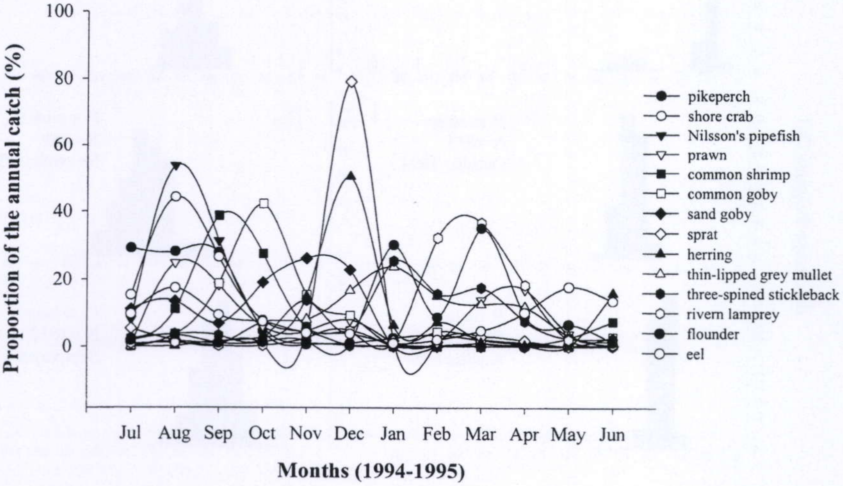

Fig. 5.3. Seasonal use of the estuary by 15 dominant fish species. For each species, the proportion of the annual catch was estimated by dividing the monthly catch by the total annual catch.

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 5.1). Both groups included species that spend part of their life in estuaries as well as species occasionally entering estuaries. None of the species were strictly estuarine dependent i.e. they can either spawn and mature in fully marine or freshwater environments. European eel *Anguilla anguilla* was the only catadromous species, while river lamprey *Lampetra fluviatilis* and twaite shad *Alosa fallax* are anadromous (Table 5.1). Crustaceans caught at Doel included two shrimp species and four crab species (Table 5.2). It was noted that, except for shore crab *Carcinus maenas*, all crab species were exotics. A living specimen of the blue crab *Callinectes sapidus* was recorded for the first time in Belgium.

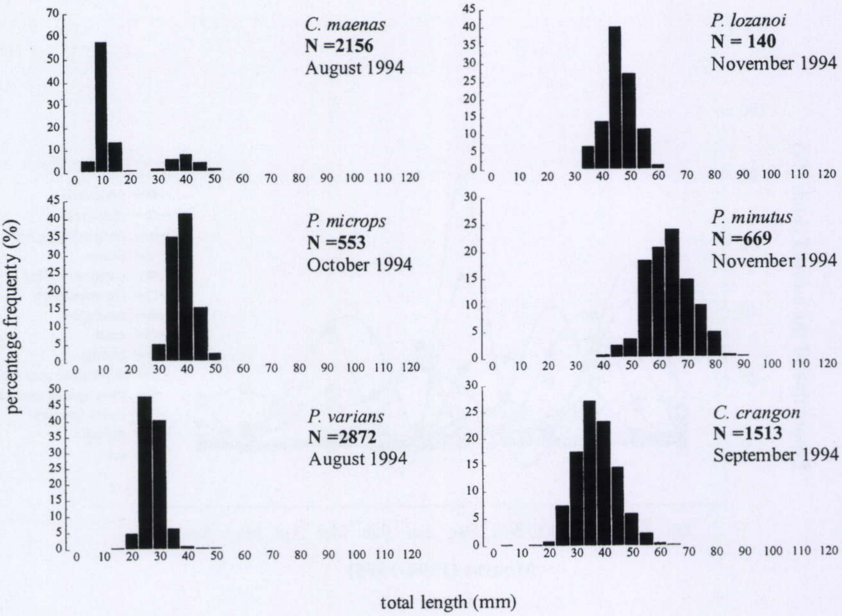

Fig. 5.4. Length-frequency distributions of three crustacean species and three Gobiidae measured in the month when each of them reached peak abundance.

Abundance and biomass data

In terms of numbers, eight species made up >95 % of the total catches. The most abundant species were the prawn *Palaemonetes varians* (37.4 %) and the common shrimp *Crangon crangon* (29.8%). The most numerous fish species were Gobiidae [common goby *Pomatoschistus microps* (12.6 %), sand goby *P. minutus* (7.8 %) and Lozano's goby *P. lozanoi* (1.0 %)], Clupeidae [herring *Clupea harengus* (6.4 %) and sprat *Sprattus sprattus* (1.7 %)] and Nilsson's pipefish *Syngnathus rostellatus* (2.5 %). In terms of biomass, the same species, with addition of bass *Dicentrarchus labrax* and flounder *Pleuronectes flesus*, dominated the community: Herring (29.2 %), prawns (18.0 %), sand goby (17.7 %), common shrimp (10.6 %), sprat (7.5 %) common goby (5.0 %), bass (4.5 %), flounder (1.9 %) and Nilsson's pipefish (1.0 %).

Table 5.1. *Species list, mean abundance (numbers* $\times 10^{-3}$ m^{-3} *cooling-water sampled) and standard deviation of fish sampled in the cooling-water of the nuclear power plant Doel over the period July 1994 to June 1995.*

Scientific name	**common name**	**mean**	**±SD**
Anadromous species			
Lampetra fluviatilis (L.)	River lamprey	0.06	0.14
Alosa fallax (Lacepède, 1803)	Twaite shad	< 0.01	< 0.01
Catadromous species			
Anguilla anguilla (L.)	Eel	0.16	0.15
Freshwater species			
Abramis brama (L.)	Bream	< 0.01	< 0.01
Carassius auratus (L.)	Goldfish	< 0.01	< 0.01
Carassius carassius (L.)	Crucian carp	< 0.01	< 0.01
Cyprinus carpio L.	Carp	< 0.01	< 0.01
Leuciscus leuciscus (L.)	Dace	< 0.01	< 0.01
Leucaspius delineatus (Heckel, 1843)	Moderlieschen	< 0.01	< 0.01
Rhoedeus sericeus (Pallas, 1776)	Bitterling	0.02	0.07
Rutilus rutilus (L.)	Roach	0.02	0.05
Tinca tinca (L.)	Tench	< 0.01	< 0.01
Gasterosteus aculeatus L.	Three-spined stickleback	0.19	0.30
Pungitius pungitius (L.)	Ten-spined stickleback	0.01	0.02
Cottus gobio L.	Bullhead	< 0.01	< 0.01
Lepomis gibbosus (L.)	Pumpkinseed	< 0.01	< 0.01
Gymnocephalus cernuus (L.)	Ruffe	< 0.01	< 0.01
Perca fluviatilis L.	Perch	0.06	0.09
Stizostedion lucioperca (L.)	Pikeperch	0.16	0.37
Marine species			
Clupea harengus L.	Herring	37.48	92.09
Sprattus sprattus (L.)	Sprat	10.00	36.30
Engraulis encrasicolus (L.)	Anchovy	0.05	0.36
Osmerus eperlanus (L.)	Smelt	0.06	0.10
Ciliata mustela (L.)	Five-bearded rockling	< 0.01	< 0.01
Gadus morhua L.	Cod	< 0.01	< 0.01
Merlangius merlangus (L.)	Whiting	< 0.01	< 0.01
Trisopterus luscus (L.)	Bib	< 0.01	< 0.01
Raniceps raninus (L.)	Tadpole-fish	< 0.01	< 0.01
Atherina presbyter Cuvier, 1829	Sand-smelt	< 0.01	< 0.01
Spinachia spinachia (L.)	Fifteen-spined stickleback	< 0.01	< 0.01
Syngnathus acus L.	Greater pipefish	< 0.01	< 0.01
Syngnathus rostellatus Nilsson, 1855	Nilsson's pipefish	14.47	44.25
Eutrigla gurnardus (L.)	Grey gurnard	< 0.01	< 0.01
Trigla lucerna L.	Tub gurnard	< 0.01	< 0.01
Myoxocephalus scorpius (L.)	Bull-rout	< 0.01	< 0.01
Agonus cataphractus (L.)	Hook-nose	< 0.01	< 0.01
Cyclopterus lumpus L.	Lumpsucker	< 0.01	< 0.01
Liparis liparis (L.)	Sea snail	< 0.01	< 0.01
Dicentrarchus labrax (L.)	Bass	2.00	3.36
Trachurus trachurus (L.)	Horse mackerel	0.04	0.43
Liza ramada (Risso, 1826)	Thin-lipped grey mullet	0.03	0.06
Pholis gunnellus (L.)	Butterfish	< 0.01	< 0.01
Zoarces viviparus (L.)	Eelpout	< 0.01	< 0.01
Ammodytes tobianus L.	Sandeel	0.01	0.06

Table 5.1. *Continued.*

Scientific name	**common name**	**mean**	**±SD**
Marine species continued			
Hyperoplus lanceolatus (Le Sauvage, 1824)	Greater sandeel	< 0.01	< 0.01
Callionymus lyra L.	Dragonet	< 0.01	< 0.01
Pomatoschistus lozanoi (de Buen, 1923)	Lozano's goby	6.20	19.01
Pomatoschistus microps (Krøyer, 1838)	Common goby	46.29	85.82
Pomatoschistus minutus (Pallas, 1770)	Sand goby	74.33	164.89
Scomber scombrus L.	Mackerel	< 0.01	< 0.01
Scophthalmus rhombus (L.)	Brill	< 0.01	< 0.01
Limanda limanda (L.)	Dab	0.01	0.05
Pleuronectes flesus L.	Flounder	0.45	1.46
Pleuronectes platessa L.	Plaice	< 0.01	< 0.01
Solea solea (L.)	Sole	0.03	0.07

Seasonal community structure

The seasonal changes in the community of fish and crustaceans were analysed using correlation 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 Fig. 5.6. 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 (Fig. 5.6*a*). Samples taken in the same month were closely located to each other in the biplot and arranged in a clear seasonal succession. (Fig. 5.6*b*). Five groups of species were more or less separated by the analysis:

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

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

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

Group D [*Dicentrarchus labrax, Clupea harengus, Sprattus 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 [thin-lipped grey mullet *Liza ramada,* river lamprey *Lampetra fluviatilis*, three-spined stickleback *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 *Gasterosteus aculeatus*, but *also* bitterling *Rhoedeus sericeus*, ruffe *Gymnocephalus cernuus* and bream *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 European eel, pikeperch *Stizostedion lucioperca* and prawn were badly represented by the analysis and could therefore not be placed in a species set. The proper reconstruction of the penaid shrimp *P. varians* was obstructed by two abundance maxima (April and August). Eel and pikeperch were present throughout the year with no marked abundance maximum.

The dominant species almost exclusively consisted of juveniles (Figs. 5.4, 5.5) and reached maximum abundance in the following chronological order starting from July: (1) Young of shore crab *C. maenas*, (2) young of prawn *P. varians*, (3) Nilsson's pipefish *S. rostellatus*, (4) Young of common shrimp *C. crangon*, (5) Young of common goby *P. microps*, (6) Young of Lozano's goby *P. lozanoi*, (7) Young of sand goby *P. minutus*, (8) Juvenile herring *C. harengus*, (9) Juvenile sprat *S. sprattus* (10) Recently metamorphosed river lamprey *L. fluviatilis*, (11) O+flounder *P. flesus*, (12) Spring stock of prawn *P. varians* (Fig. 5.3).

Table 5.2. *Species list, mean abundance (numbers × 10^{-3} m^{-3} cooling-water sampled) and standard deviation of crustaceans sampled in the cooling-water of the Nuclear Power Plant Doel over the period July 1994 to June 1995.*

Scientific name	**common name**	**mean**	**±SD**
Crangon crangon (L.)	Common shrimp	175.32	383.73
Palaemonetes varians (Leach, 1814)	Prawn	219.88	333.05
Eriocheir sinensis H. Milne Edwards, 1854	Chinese mitten crab	< 0.01	< 0.01
Callinectes sapidus Rathbun, 1896	Blue crab	< 0.01	< 0.01
Rhithropanopeus harrisii (Gould, 1841)	Dwarf crab	0.24	0.60
Carcinus maenus (L.)	Shore crab	0.71	2.04

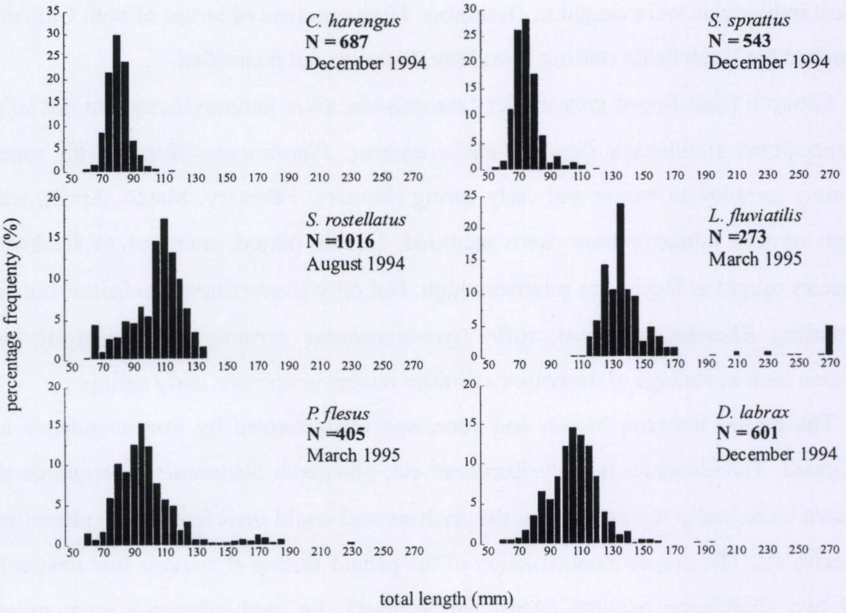

Fig. 5.5. Length-frequency distributions of six fish species measured in the month when each of them reached peak abundance.

Discussion

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 river lamprey, smelt, and twaite shad is noteworthy, since they are indicators of good water quality. 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). We 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 published an extensive literature on temporal fish distribution of northern temperate estuaries (Iglesias, 1981; Evans and 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 brackishwater 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 and Duke, 1990*a*), but there is less evidence they do so in temporal 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 European eel, 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 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 and 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 and 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 and 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 brackishwater 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 and Blaber, 1980; Cyrus and 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 and van der Lingen, 1992).

The observed migration sequence of juvenile crustaceans and fish in our data, match more or less with changes in the diet of Gadidae, their major predators in the adjoining coastal area (Hamerlynck and Hostens, 1993). After feeding on copepods in May and June, the fraction of gobies and shrimps in the diet of most Gadidae increases (Hamerlynck and Hostens, 1993; Salvanes and Jarle, 1993). With increasing length of the Gadidae, the fraction of gobies in the diet decreases and the fraction of larger fish including Clupeidae and juvenile Gadidae increases. (Hyslop *et al.* 1991; Henderson *et al.*, 1992). In the highly turbid Zeeschelde estuary, numbers of whiting *Merlangius merlangus*, cod *Gadus morhua* and bib *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 may be avoided by large numbers of piscivores and may act as a refuge for prey species.

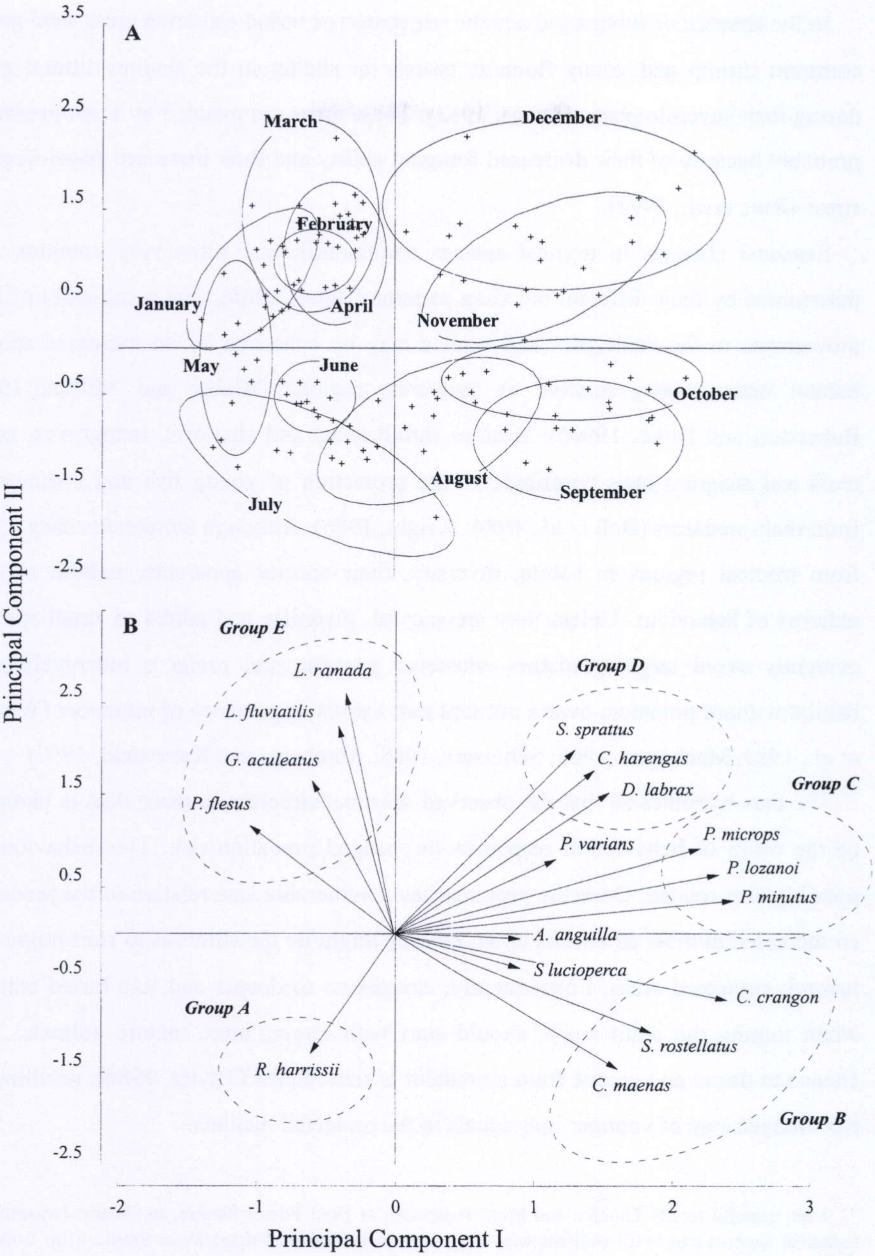

Fig. 5.6. Correlation biplot based on Principal Component Analysis. Position of the sample scores (A) and the species vectors (B) with respect to first two principal components. For a better interpretation of the biplot the sample scores are grouped by month and the species scores are multiplied by three.

In the absence of submerged aquatic vegetation or turbid estuarine areas sand goby, common shrimp and young flounder 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 and Milton, 1990, Robertson and Duke, 1990*b*). 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). Although 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 nutrient rich habitat in presence of predators (Werner *et al.*, 1983, Manhagen, 1988; Schlosser, 1988; Abrahams and Kattenfeld, 1997)

We thus hypothesize 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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Chapter 6
Diel Changes in the Vertical Distribution of Juvenile Fish in the Zeeschelde Estuary

By use of stow netting in the Zeeschelde Estuary, evidence is presented that the vertical distribution of fish changed at night. Demersal fish remained on the bottom during the day while at least a part of the populations exploited surface water during the night. Pelagic fish maintained their position underneath the water surface throughout the day.

Maes, J., Pas, J., Taillieu, A., Van Damme, P.A. and Ollevier, F. 1999. Diel changes in the vertical distribution of juvenile fish in the Zeeschelde Estuary. *Journal of Fish Biology* **54**, 1329-1333.

Introduction

Marine fish alter their position in the water column at regular intervals often controlled by tides and photoperiod (Helfman, 1986; Gibson, 1992). Food requirements, bioenergetic advantages and predator avoidance have also been evoked as controls in mediating vertical distribution (Neilson and Perry, 1990). This chapter reports on the diel vertical distribution of fish in the Zeeschelde (Belgium), a highly turbid tidally dominated estuary. Vertical movements expressed by fish were observed incidentally in a the sampling programme that was designed to analyse the spatial species distribution and to evaluate the cooling-water inlet as a sampling point for fishes and crustaceans (Chapter 2).

Material and methods

Fish were sampled using two commercial stow nets, a passive fishing technique, which is the most convenient for sampling in tidal environments (Breckling and Neudecker, 1994). While the ship was anchored, two nets on both sides were exposed to the tidal currents (Fig. 2.1). The nets were 70 m in length with a stretched mesh size varying from 16 cm at the net mouth to 12 mm at the cod end.

During two weeks in November 1995, samples were taken between the water surface and -a depth of m, and between 4 m depth and the bottom (10 m), respectively. Samples taken between sunrise and sunset were categorized as day samples, other samples were considered night samples. In total, 20 samples were collected for this study. Sampling details, including duration of each haul and sampled volume of water, are presented in Table 6.1. During the first week, high water was around midday and midnight; in the second week, high waters occurred at 0400 and 1600 hours.

Table 6.1. *Sampling details of the fishing survey.*

date	tide	photoperiod	depth	Duration (minutes)	sampled water volume (m^3)
20 November 1995	rising	day	bottom	95	228 421
20 November 1995	rising	day	top	89	98 388
20 November 1995	falling	day	top	60	104 509
20 November 1995	falling	day	bottom	60	287 401
21 November 1995	falling	night	top	65	117 711
21 November 1995	falling	night	bottom	65	294 278
22 November 1995	falling	night	top	60	114 890
22 November 1995	falling	night	bottom	60	229 781
22 November 1995	rising	day	top	60	171 798
22 November 1995	rising	day	bottom	60	257 697
23 November 1995	falling	night	top	60	184 667
23 November 1995	falling	night	bottom	60	277 001
29 November 1995	rising	night	top	45	91 465
29 November 1995	rising	night	bottom	45	182 930
29 November 1995	falling	day	top	60	143 960
29 November 1995	falling	day	bottom	60	323 909
30 November 1995	rising	night	top	60	174 286
30 November 1995	rising	night	bottom	60	261 429
30 November 1995	falling	day	top	60	106 998
30 November 1995	falling	day	bottom	60	187 246

After each haul, fish were identified and counted. If necessary, subsamples were taken by dividing the catch into equal parts. The water volume filtered by the net was calculated using the cross-sectional area of the net mouth, current velocity of the water and exact duration of each haul. Numbers of fish were transformed to numbers·m^{-3} by dividing the total catch by the water volume sampled.

One-way analysis of variance (ANOVA) was used to test the effect of depth, photoperiod and tidal stage on the root-root transformed species abundance. Two-way ANOVA examined the interaction effects, depth × photoperiod and depth × tides.

Results

More than 7 × 10^5 individuals comprising 34 fish species were captured during the sampling period (Table 6.2). Sprat *Sprattus sprattus* (42%) and herring *Clupea harengus* (35%) dominated the fish catches. Together with Gobiidae *Pomatoschistus spp.*, these species represented >99% of the fish captures.

The majority of species was demersal or benthic (Table 6.2). However, only bib *Trisopterus luscus*, sand goby *P. minutus*, Lozano's goby *P. lozanoi* and dab *Limanda limanda* showed a significant preference for the bottom (Table 6.2). Anchovy *Engraulis encrasicolus*, herring and sprat were predominantly present near the surface (Table 6.2). After sunset, the vertical distribution of smelt *Osmerus eperlanus*, common goby *P. microps*, sand goby and dab changed significantly suggesting that they were spreading out over the water column (Table 6.2, Fig. 6.1). This behaviour was not observed for Clupeidae. The pikeperch *Stizostedion lucioperca* population was more abundant near the surface during the day but numbers were significantly higher at the bottom during the night (Fig. 6.1).

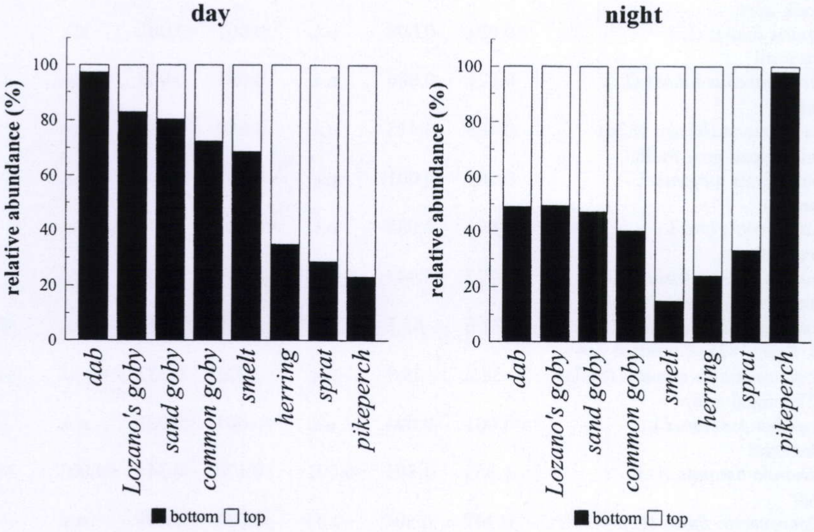

Fig. 6.1. *Vertical distribution of eight fish species in the Zeeschelde estuary with respect to depth and photoperiod.*

Table 6.2. *Species list and mean fish abundance (numbers·10^{-4} m^{-3} water sampled) during day and night and for the top and bottom. ANOVA results indicating the effect of photoperiod (day, night), depth (bottom, top) and the interaction effect of depth × photoperiod on species abundance (n.s. = not significant).*

	Day	**Night**	***p*-level**	**Top**	**Bottom**	***p*-level**	***p*-level**
Marine species							
Clupea harengus L. Herring	495.3	455.1	n.s.	62.2	26.7	<0.05	n.s.
Sprattus sprattus (L.) Sprat	1 067.5	1 045.0	n.s.	136.9	60.3	<0.05	n.s.
Engraulis encrasicolus (L.) Anchovy	0.495	0.213	n.s.	0.061	0.003	<0.05	n.s.
Osmerus eperlanus (L.) Smelt	0.643	0.708	n.s.	0.072	0.060	n.s.	<0.05
Gadus morhua L. Cod	0.005	<0.001	n.s.	<0.001	0.001	n.s.	n.s.
Merlangius merlangus (L.) Whiting	0.435	0.292	n.s.	0.033	0.043	n.s.	n.s.
Trisopterus luscus (L.) Bib	0.085	0.043	n.s.	0.001	0.015	<0.001	n.s.
Atherina presbyter Cuvier, 1829 Sand-smelt	0.013	0.008	n.s.	0.002	<0.001	n.s.	n.s.
Syngnathus acus L. Greater pipefish	<0.001	0.008	n.s.	0.001	<0.001	n.s.	n.s.
Syngnathus rostellatus Nilsson, 1855 Nilsson's pipefish	0.187	0.017	n.s.	0.014	0.008	n.s.	n.s.
Trigla lucerna L. Tub gurnard	<0.001	0.003	n.s.	<0.001	<0.001	n.s.	n.s.
Myoxocephalus scorpius (L.) Bull-rout	0.007	0.003	n.s.	<0.001	0.001	n.s.	n.s.
Agonus cataphractus (L.) Hook-nose	0.003	<0.001	n.s.	<0.001	<0.001	n.s.	n.s.
Liparis liparis (L.) Sea snail	<0.001	0.008	n.s.	0.001	<0.001	n.s.	n.s.
Dicentrarchus labrax (L.) Bass	0.821	0.806	n.s.	0.091	0.068	n.s.	n.s.
Liza ramada (Risso, 1826) Thin-lipped grey mullet	0.405	0.413	n.s.	0.059	0.014	n.s.	n.s.
Ammodytes tobianus L. Sandeel	0.003	<0.001	n.s.	<0.001	<0.001	n.s.	n.s.
Callionymus lyra L. Dragonet	<0.001	0.058	n.s.	<0.001	0.006	n.s.	n.s.
Pomatoschistus lozanoi (de Buen, 1923) Lozano's goby	3.227	5.943	n.s.	0.336	0.600	<0.05	n.s.
Pomatoschistus microps (KrØyer, 1838) Common goby	71.6	63.3	n.s.	5.679	8.420	n.s.	<0.05
Pomatoschistus minutus (Pallas, 1770) Sand goby	38.2	59.9	n.s.	3.722	6.337	<0.05	<0.05
Scomber scombrus L. Mackerel	<0.001	0.004	n.s.	<0.001	<0.001	n.s.	n.s.
Limanda limanda (L.) Dab	1.353	3.805	<0.001	0.176	0.344	<0.001	<0.05
Pleuronectes flesus (L.) Flounder	0.247	0.504	<0.05	0.033	0.041	n.s.	n.s.
Pleuronectes platessa (L.) Plaice	0.035	0.045	n.s.	0.003	0.005	n.s.	n.s.
Solea solea (L.) Sole	0.033	0.093	n.s.	0.006	0.005	n.s.	n.s.

Table 6.2. *Continued*

	Day	Night	*p*-level	Top	Bottom	*p*-level	*p*-level
Anadromous species							
Lampetra fluviatilis (L.) River lamprey	0.078	0.110	n.s.	0.088	0.010	n.s.	n.s.
Alosa fallax (Lacepède, 1803) Twaite shad	0.007	<0.001	n.s.	0.001	<0.001	n.s.	n.s.
Catadromous species							
Anguilla anguilla (L.) Eel	0.051	0.268	<0.001	0.017	0.012	n.s.	n.s.
Freshwater species							
Abramis brama (L.) Bream	0.006	<0.001	n.s.	0.001	<0.001	n.s.	n.s.
Gasterosteus aculeatus L. Three-spined stickleback	<0.001	0.267	n.s.	0.020	<0.001	n.s.	n.s.
Gymnocephalus cernuus (L.) Ruffe	<0.001	0.003	n.s.	<0.001	<0.001	n.s.	n.s.
Perca fluviatilis L. Perch	0.274	1.379	<0.05	0.059	0.102	n.s.	n.s.
Stizostedion lucioperca (L.) Pikeperch	0.020	0.168	n.s.	0.002	0.018	n.s.	<0.05

No tidal effects in the catch or in the vertical distribution were noticed. Four species, eel *Anguilla anguilla*, perch *Perca fluviatilis*, dab and flounder *Pleuronectes flesus*, were caught in significantly higher numbers during the night (Table 6.2).

Discussion

It seems that in the Zeeschelde Estuary, demersal and benthic fish remained on the bottom during the day while at least a part of the populations exploited surface waters at night. Pelagic fish, by contrast, utilized the surface layers throughout light and dark periods. Woodhead (1966) and Neilson and Perry (1990) reviewed fish behaviour in relation to light and presented considerable evidence that many demersal species regularly move up in the water column at the onset of night, and down with the onset of day. For the species recorded here, increased activity or vertical movements at dusk and dawn have been reported by, for example, Nash (1982), Marchand and Masson (1988) and Del Norte-Campos and Temming (1994). The vertical distribution of these species thus exhibits a pronounced relation to photoperiod. However, turbidity in the Zeeschelde estuary is exceptionally high, for example, measuring at least 30 FTU during the sampling period. It is noteworthy therefore, that the distribution of two shrimp species, common shrimp *Crangon crangon* and prawn *Palaemonetes varians* and of the calanoid copepod *Eurytemora affinis* also changed overnight as these species moved up from the bottom (Soetaert and Herman, 1994). These species are major prey items for almost all fish recorded in the Zeeschelde Estuary (Chapter 7) and other European estuaries (Doornbos and Twisk, 1987; Henderson *et al.*, 1992). Pikeperch, on the other hand, is the major fish predator in the Zeeschelde Estuary. Stomach contents analysis suggested that pikeperch preyed on Gobiidae. Pikeperch is well-adapted to turbid waters and feeds just above the bottom (Craig, 1987). Our data suggest that this happens at night. Nocturnal off-bottom activity may thus represent a behavioural pattern which enables demersal fish to both follow the prey distribution and avoid predation (Gibson and Hesthagen, 1981).

Stow netting further showed that the diel distribution of herring and sprat did not change, possibly due to the high turbidity. In clearer waters, herring have traditionally been caught near the surface at night. In the turbid waters of the southern North Sea, herring have been reported as swimming rapidly up into the surface layers either by day or night (Woodhead, 1966).

The majority of species was caught in equal proportions during day and night indicating the absence of diel variation in catchability. Any tidal effects in the vertical species distribution were presumably obscured by the fishing method. Stow netting is not effective at the calm waters of high and low tides. It is clear that fish use tidal currents for migration purposes to move upstream (Day *et al.*, 1992) or to exploit intertidal areas (Cattrijsse *et al.*, 1994). However, some disagreement still remains in the literature on the exact role of tides and photoperiod in mediating species behaviour (Neilson and Perry, 1990). Different sampling techniques and differences in local conditions, such as tidal height, turbidity, water depth, the presence of neighbouring sandy beaches and salt marshes, bottom structure, prey spectrum and the occurrence of predators influence both the perception of observed phenomena as well as the particular behaviour of individual species. It seems that there is no comprehensive theory claiming to include all aspects of vertical fish migrations (Woodhead, 1966) as local conditions probably play a crucial role in determining the extent of vertical distribution patterns displayed by fish.

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Chapter 7
Diet Composition and Predation Impact of the Fish Community of the Zeeschelde Estuary

Seasonal changes in diet composition, niche width, niche overlap and predation pressure of eight members of the fish community of the Zeeschelde estuary were assessed with a number of descriptive multivariate techniques and randomization procedures. Copepods in terms of numbers and mysids in terms of biomass were the most important prey items. Macrobenthic prey were poorly presented in the diet of most species. Niche width of all fish species as measured by the Shannon-Wiener index changed over the different months but no consistent pattern of variation was found. Although dietary overlap between species was rather high, most of the interspecific pair-wise comparisons of niche overlap differed significantly from one, suggesting that intra-specific niche overlap was higher than interspecific niche overlap. Our results show that the Mantel test, which was used to assess the value of niche overlap, was able to detect small differences in the diet composition of specialist species preying upon a few taxa, whereas it only recognized strong differences in the diet composition of generalist species consuming a wide range of prey. The analysis of niche overlap as well as the use of principal components and two way indicator species analysis (TWINSPAN) suggested that there was at least some degree of niche segregation within the estuarine fish community. This was, however, unexpected because in estuaries, only few prey species dominate the invertebrate community. The fish community consumed about 13 % of the annual prey production suggesting that food was not in short supply. If the consumption of copepods and mysids by shrimps is included, the total annual consumption of the fish and crustacean community amounted to almost 42% of the production of mysids and copepods.

Introduction

Estuaries are nursery areas to many fish species as they provide a physiologically suitable habitat with respect to temperature and salinity. They not only supply an abundance of suitable food resources but also offer a degree of protection from predators (Day *et al.*, 1989). Especially wetlands, including salt marshes, mudflats, and mangroves, the low salinity area at the head of the estuary, and sea grass beds have proved their role as nurseries (Haedrich, 1983; Day *et al.*, 1989). As a result, these areas support high numbers of larvae and juveniles.

The Zeeschelde forms the turbid low-salinity zone of the Schelde estuary, and hence may be a crucial refuge to young fish. Analysis of the temporal patterns of species occurrence has revealed that about 60 species share this area (Chapter 5). These have different seasonal patterns of occupancy, so on average, 20 species are present at any one time. Of these species, only few dominate the community, including two pelagic, two demersal and four benthic species. As these species represent over 90% of the numbers caught on cooling-water intake screens, we felt it was desirable to focus in greater detail on the seasonal changes in diet composition. More specific, we have investigated three hypotheses. First, we tested the idea assumed that diet composition as revealed by stomach analysis were related to food availability in the water column. Unlike other studies, we expected no major differences between pelagic, demersal or benthic fish species as they use the entire water column (Chapter 6). Since data of food availability were obtained from literature, this was discussed rather than tested.

Secondly, we hypothesized that there were no significant differences in the diet between the species under study. Although species that simultaneously occupy the same habitat are likely to compete for food resources (Evans, 1983; Allen *et al.* 1995), an abundance of food resources may cause a high trophic niche overlap without affecting species co-occurrence (Pianka, 1982; Schoener, 1982; González-Solís *et al.*, 1997). Since estuaries can be viewed as sources of high food abundance, it may be expected that fish shared the common pool of prey. This hypothesis was tested using a randomization technique.

A third objective was to present information on diets and feeding behavior of estuarine fishes and to estimate the foraging impact of the fish community on their major prey. Hereto, we compared available data on the production of prey with the consumption rates of the fish assemblage.

Material and methods

Collection of the fish and laboratory procedures

Fish were collected at spring tides in July 1994, October 1994, December 1994 and March 1995 by sampling the cooling-water intake screens of the nuclear power station

Doel. All fish were counted, measured, anaesthetized with benzocaine, fixed in 7% formol and preserved in ethanol 70%. Only stomachs of fish species of which at least 20 individuals were caught were included in this study. For July 1994, twenty stomachs of herring *Clupea harengus* L., European eel *Anguilla anguilla* (L.), sand goby *Pomatoschistus minutus* (Pallas) and pikeperch *Stizostedion lucioperca* (L.) were randomly chosen and analyzed. For October and December 1994, stomachs of herring, sprat *Sprattus sprattus* (L.), sand goby, common goby *Pomatoschistus microps* (Krøyer) and bass *Dicentrarchus labrax* (L.) were selected. For March 1995 guts of the latter species together with eel and flounder *Pleuronectes flesus* L. were examined. Of these species, herring and sprat are pelagic, bass and pikeperch are demersal and the other species are benthic (Elliott and Dewaily, 1995).

In the laboratory, stomach contents, if present, were removed. Food organisms were identified to the lowest possible taxon and all prey organisms were counted. Some of the prey items were too strongly fractionated or digested, so that only particular body parts resistant to digestion could be counted. If the stomachs contained too many copepods, only a subsample (1/4 or 1/8) was counted. Only prey in early stages of digestion were measured. If needed, telson-standard length and standard length-total length regressions were used (Henderson and Holmes, 1987, Hamerlynck *et al.*, 1990, Mees *et al.*, 1994). Ash-free dry weight (ADW) of all prey items was estimated by total length-ADW regressions (Hamerlynck *et al.*, 1990, Mees *et al.*, 1994) or by incineration at 550°C in a muffle furnace. All stomachs were dried at 70°C to constant weight.

The frequency of occurrence of all prey items in non-empty stomachs was recorded and the composition of the stomach contents was described as a percentage by numbers and a percentage by weight. Percentage occurrence of a dietary component refers to its occurrence in non-empty guts analyzed. Percentage abundance or weight is the ratio between total abundance or weight ratings of a food organism and the grand sum derived from dietary constituents in all stomachs.

Measurement of niche width and overlap

The width of the trophic niche was measured with the Shannon-Wiener diversity index, and a jackknife procedure was used to estimate its value and associated 95%

confidence intervals. Comparisons of diversity values were performed using the test proposed by Hutcheson (1970).

The degree of interspecific diet overlap was assessed using Renkonen's index of similarity P (Marshall and Elliott, 1997) (Equation 7.1).

$$(7.1) \quad P_{jk} = \sum_i \min\left(p_{ij}, p_{ik}\right)$$

where p_{ij} and p_{ik} are the estimated proportions by numbers of prey i in the diet of predators j and k. The index ranges from 0 for entirely dissimilar diets to 1 when the compositions of the diets of the predators are identical. Afterwards, a Mantel test was performed to test the null hypothesis that there was no difference in the diet overlap of individuals within and between populations. The Mantel Test (Mantel, 1967; Sokal, 1979) is a commonly used statistical tool that can be used to determine the significance of a correlation between two matrices. The first matrix was a half-matrix of all pairwise combinations of individuals containing information about their diet overlap. The second matrix, a binary matrix, was formed containing 1's in the positions of the diet overlap measured between individuals of the same population and 0's in the positions of the diet overlap measured between individuals of the different populations. The significance of the correlation between these two matrices was evaluated through the use of a Monte Carlo procedure where the 1's and 0's of the binary matrix were a thousand times randomly redistributed.

Descriptive multivariate statistics

The trophic community structure of the fish assemblage was investigated by TWINSPAN and principal component analysis. TWINSPAN orders samples with great affinity together, giving the main divisions of each group and an indication of the main attributes responsible for each division. Twinspan was performed on a 20×25-matrix containing prey percentage by occurrence data. Principal component analysis was performed on a matrix containing 14 ecological niche variables as columns and eight fish species as rows. Nine of the 14 ecological niche variables were different prey taxa including annelids, anomopods, copepods, mysids, isopods, amphipods, decapods, chironomids and teleosts. For each fish species, seasonal stomach contents were pooled and expressed as percentage by numbers per prey taxon. Four other variables contained data on seasonal fish abundance, again expressed as a percentage of the total yearly catch. The last variable was a habitat variable discriminating whether fish used demersal or pelagic habitats. Each fish species was given a score between 0 and 1 depending on its vertical distribution as revealed by stow net fisheries (Chapter 6). A score of 0 was assigned to pelagic species never occurring below –4 m while completely bottom oriented fish should were given score of 1.

Estimation of the annual consumption

We used the regression model presented by Pauly (1989) to calculate annual food consumption by the fish community. The model (Equation 7.2) expresses annual consumption (*Q*) per unit biomass (*B*) in function of average temperature t (°C), asymptotic weight (g) and meristic charactersists, which reflect metabolic activity levels. To assess the annual consumption of each fish species (*Q*), the ratio Q/B was multiplied by the yearly average biomass (ADW$\cdot 10^{-3}$ m^{-3} cooling water). Q/B is thus the number of times the population under study consumes its own weight, per year (Pauly, 1989).

The merestic characteristics for each single species were taken from the database FishBase 98 (Froese and Pauly, 1998).

$$\log_{10} Q/B = -0.102 + 0.444 \cdot \log_{10} t - 0.115 \cdot \log_{10} W_{infinity} + 0.427 \cdot \log_{10} A + 0.577 \cdot \log_{10} D - 0.464 \cdot \log_{10} P \qquad (7.2)$$

where

Q: Annual consumption (g prey per area or volume water)

B: Average biomass (g per area of volume water)

t: temperature (°C)

A: Aspect ratio (height of the caudal fin squared / surface area of the caudal fin)

D: Depth ratio (standard length / maximum body depth)

P: Relative depth of the caudal peduncle (depth of the caudal peduncle / maximum body depth)

The annual consumption of shrimps was assessed using the daily food ration. Average shrimp daily ration is equivalent to 16% of the body weight (Del Norte-Campos and Temming, 1994). The daily consumption of shrimps was computed by multiplying the daily ration (16%) with the average biomass of shrimps (g ADW$\cdot 10^{-3}$ m^{-3}) in the Schelde estuary. The annual consumption of shrimps was calculated by multiplying the daily consumption with 365.

Results

Between July 1994 and June 1995, the fish assemblage of the Zeeschelde estuary was dominated by Gobiidae and Clupeidae. Together with bass, eel, flounder and pikeperch, they contributed to >90% of the total yearly catch of the cooling-water intake. Apart from eel, the majority of the fish caught were in their first year of growth. Details of the seasonal occurrence of fish populations in the Zeeschelde estuary are presented in Chapter 5. During the study, 420 stomachs were analyzed, of which 231 were empty. A total of 34 prey taxa were distinguished. Copepods in terms of numbers and mysids in terms of weight were the most important prey items as revealed by stomach analysis. Prey of the fish species analyzed are presented in Appendix 1.

Single species analysis of the diet

The main components in the diet of herring and sprat throughout the year were calanoid copepods with the mysids *Neomysis integer* (Leach) and *Mesopodopsis slabberi* (Van Beneden) as an important food supplement, especially in fall (Appendix 1). Feeding intensity of herring increased towards summer and decreased during winter. In contrast with sprat, however, herring never ceased to feed.

The two goby species differed in their food items (Appendix 1). The common goby fed almost exclusively on calanoid copepods. Additional prey items were annelids and *Daphnia sp.* in March, the mysids *Neomysis integer* and *Mesopodopsis slabberi* in October and cirripeds and the amphipod *Corophium volutator* (Pallas) in December (Table 7.4). The dietary composition of sand goby showed some variation. Calanoid and harpacticoid copepods occurred more often and in greater abundance in the stomachs in March than in any other month. In July, calanoids stayed an important prey item, but

Corophium volutator in terms of numbers and *Neomysis integer* in terms of weight were consumed more often. In October and December, larger prey items such as *Neomysis integer* and shrimps predominated in the diet of sand goby. One specimen had preyed upon a relative, explaining the rather large fraction of Teleostei in the diet of October.

In March as well as in July, stomach contents of eel were dominated by *Neomysis integer*. In both months, *Corophium volutator*, the decapods *Palaemonetes varians* (Leach) and *Crangon crangon* (L.) and teleost fish were also included in the diet of eel.

In October and December bass fed mainly on *Crangon crangon* and *Palaemonetes varians*. Other crustaceans present in the diet of bass were *Neomysis integer*, the amphipods *Orchestia sp.* and *Bathyporeia sp.* and the isopod *Lekanesphaera rugicauda* (Leach). In March, copepods became more important in the diet of bass, but the prawn shrimp *Palaemontes varians* and *Neomysis integer* were dominant in terms of biomass.

Flounder fed on large prey as well as on smaller crustaceans. Large prey such as *Neomysis integer*, *Gammarus salinus* Spooner and *Corophium volutator* only contributed to 10% of the total number of prey items counted in the stomachs, while smaller prey such as calanoid copepods represented 86% of the stomach contents. The polychaet *Nereis sp* and unidentified species of oligochaetes occurred frequently in the diet, and formed a large proportion of the biomass present in the stomachs.

Pikeperch consumed mainly *Neomysis integer*, while teleosts, annelids and caridean shrimps were important supplementary food items.

Niche width of all fish species as measured by the Shannon-Wiener index changed monthly but no consistent seasonal pattern of variation was found (Fig. 7.1). Only in spring, the niche width of copepod consuming fish narrowed. Sand goby, bass, eel and pikeperch had the highest niche width while herring, sprat, common goby and flounder had lower niche widths. Significant seasonal differences between niche widths measured within species are given in Appendix 1.

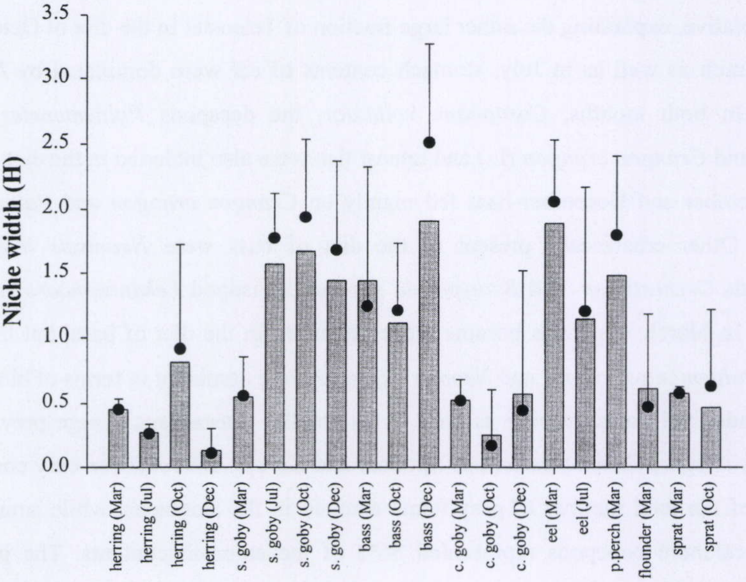

Fig. 7.1. Trophic niche width *H* of eight fish species assessed by the Shannon-Wiener diversity index (bars). Error bars and black dots are 95% confidence intervals and the jackknife estimator, respectively, after a jackknife procedure. Differences within species are presented in Appendix 1. s. goby: sand goby; c.goby: common goby; p.perch: pikeperch.

Multispecies analysis of the trophic structure

Niche overlap was measured using the Renkonen index. Dietary overlap between species was rather high but not uniform across months. In March, herring, common goby and sand goby had almost identical niches, all feeding almost exclusively on copepods. Although diet overlap between sprat and the latter species was >90%, the analysis showed that overlap between individuals within the sprat population was significantly higher than diet overlap between sprat and other species. The same holds for flounder and the other members of the fish assemblage. On the other hand, bass and eel showed a rather low diet overlap, but the analysis did not recognize individuals drawn from each population and thus the diets of both species were not significantly different (Table 7.1).

Table 7.1. *Interspecific diet overlap measured in March 1995. Renkonen's index is given in the right upper part. Below the diagonal the species pair-wise correlation coefficients yielded by the Mantel test and significance levels are displayed. The combined correlation of two matrices containing the data of all species was r = 0.1687 (p=0.001). Ns, not significant; *, p<0.05; **, p<0.01; ***, p=0.001.*

	Bass	Sprat	Eel	Herring	Sand goby	Common goby	Flounder
Bass		0.738	0.119	0.694	0.699	0.718	0.670
Sprat	0.515 ***		0.044	0.938	0.927	0.954	0.835
Eel	0.036 ns	0.735***		0.044	0.067	0.049	0.150
Herring	0.365 ***	0.115***	0.562***		0.944	0.948	0.965
Sand goby	0.220 **	0.226***	0.454***	0.047 ns		0.962	0.876
Common goby	0.350 ***	0.113***	0.583***	0.012 ns	0.001 ns		0.869
Flounder	0.121 *	0.383***	0.259**	0.187***	0.065 *	0.169 **	

In July, pair-wise diet overlaps between the fish species were not as high as in March (Table 7.2). The trophic niche of herring was significantly different from that of the other species. Diet of eel was similar to the diets of pikeperch and sand goby, but the two latter species had significantly different diets.

In October, herring, sprat, common goby and sand goby shared food resources, mainly mysids and copepods (Table 7.3). However, the diet composition of both goby species differed significantly. Diet overlap between bass and the other members of the fish assemblage was always <0.13.

Table 7.2. *Interspecific diet overlap measured in July 1994. Renkonen's index is given in the right upper part. Below the diagonal the species pair-wise correlation coefficients yielded by the Mantel test and significance levels are displayed. The combined correlation of two matrices containing the data of all species was r = 0.2067 (p=0.0010). Ns, not significant; *,p<0.05; **, p<0.01; ***, p=0.001.*

	Sand goby	Eel	Pikeperch	Herring
Sand goby		0.367	0.332	0.226
Eel	-0.044 ns		0.404	0.011
Pikeperch	0.144 *	0.142 ns		0.011
Herring	0.173 *	0.362 ***	0.429 ***	

In December, interspecific niche overlap was low. Only the niche of herring and common goby overlapped, both eating mainly copepods and the amphipod *Corophium volutator* (Table 7.4).

Table 7.3. *Interspecific diet overlap measured in October 1994. Rekonen's index is given in the right upper part. Below the diagonal the species pair-wise correlation coefficients yielded by the Mantel test and significance levels are displayed. The combined correlation of two matrices containing the data of all species was r = 0.1569 (p = 0.0010). Ns, not significant; *, p<0.05; **, p<0.01; ***, p=0.001.*

	Herring	Sprat	Common goby	Sand goby	Bass
Herring		0.875	0.794	0.319	0.037
Sprat	0.065 ns		0.877	0.252	0.017
Common goby	0.176 *	- 0.056 ns		0.156	0.035
Sand goby	0.007 ns	0.060 ns	0.138 *		0.125
Bass	0.456 ***	0.370 **	0.280 **	0.322 ***	

TWINSPAN separated the species into seven different groups, each sharing particular prey items (Fig. 7.2). The first division separated zooplanktivorous fish species caught in spring together with herring captured in winter from mysid feeding fish. In the first group, further divisions were made based upon the presence or absence of annelids in the diet (Fig. 7.2). In the latter group, four different clusters were recognized: a group comprising winter samples of bass and sand goby and a spring sample of bass feeding on caridean shrimps, a group comprising eel, flounder and pikeperch with *Nereis sp* as a typical food supplement, a group comprising the summer and fall samples of herring and the fall samples of sprat and sand goby separated due to the occurrence of harpactoid copepods in their stomachs, and finally, a group containing samples of the two gobiid species (Fig. 7.2).

Table 7.4. *Interspecific diet overlap measured in December 1994. Renkonen's index is given in the right upper part. Below the diagonal the species pair-wise correlation coefficients yielded by the Mantel test and significance levels are displayed. The combined correlation of two matrices containing the data of all species was r = 0.314 (p=0.0010). Ns: not significant, *:p<0.05, **: p<0.01, ***:p=0.001*

	Common goby	Sand goby	Herring	Bass
Common goby		0.111	0.860	0.034
Sand goby	0.402 ***		0	0.159
Herring	-0.052 ns	0.452 ***		0
Bass	0.478 **	0.320 **	0.481 ***	

Principal components were used to display the seasonal changes in the trophic structure of the fish assemblage of the Zeeschelde estuary (Figs. 7.3-7.4). Factor loadings, factor scores and eigenvalues of the four first principal components extracted by the analysis are presented in Appendix 2. The first principal component separated the pelagic species from demersal and benthic species occurring in winter (Fig. 7.3). Food items, if present, were chiefly amonopods and copepods. The second principal component separated the bottom-orientated species in three clearly defined groups. One group comprised pikeperch, a piscivorous species occurring only in summer. The second group comprised flounder, a species showing maximal intake rates in spring feeding on benthic prey. The third group comprised bass, eel and Gobiidae reaching highest abundance during fall. Gobiidae were separated from bass by the two following principal components (Fig. 7.4). Bass showed a clear preference for decapods and isopods, while the gobiid species mainly fed on mysids and copepods.

Predation impact of fish and shrimps on copepods and mysids

Table 7.5 summarizes all data used to calculate the annual prey consumption by the fish community. The ratio *Q*/*B* varied from 2.2 for pikeperch to 8.7 for sprat. Multiplying this ratio with the average annual biomass yielded the annual consumption for each species. To summarize, the whole fish community consumed during one year 259 g ADW prey per 10^3 m^3 water, corresponding to 6.5 times its own average biomass. The both shrimp species consumed, on average, 3.1 g $ADW \cdot 10^{-3}$ $m^{-3} \cdot day^{-1}$. This corresponds to 1 135.56 g $ADW \cdot 10^{-3}$ $m^{-3} \cdot year^{-1}$.

Discussion

Before discussing our results, it is useful to consider the statistical techniques used to evaluate trophic niche overlap between two species and to assess the value of niche width.

A Mantel test to evaluate an overlap measure

We used a mantel test to see whether intraspecific diet overlap between individuals of a given species is significantly different from interspecific diet overlap. If so, we can identify these two species by using their stomach contents only. Hence, it is likely that their trophic niches might differ significantly. Hereby, we assumed that there were no dietary shifts present within the population under study. Cluster analysis revealed no meaningful clusters when all individuals of a species were pooled in one matrix.

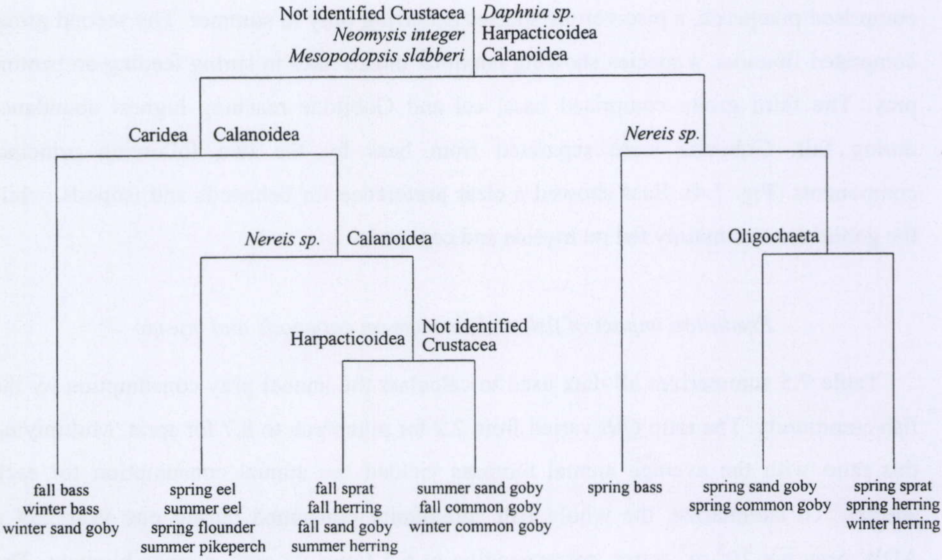

Fig 7.2. Dendrogram showing dietary similarities within the fish community of the Zeeschelde estuary throughout a seasonal gradient as revealed by TWINSPAN

This approach is different from other studies where trophic niche overlap is generally considered to be biologically significant when the value exceeds 0.60 (Macpherson, 1981; Labropoulou and Eleftheriou, 1997). Our results suggest that the Mantel test is able to detect small differences in the diet composition of species preying upon few taxa, while it recognizes broad differences in the diet composition of species consuming a wide range of prey. This is likely due to the addition of all individuals of which stomachs were analyzed in the data matrix. By doing so, the test not only considered the relative composition of the stomach contents by numbers. Implicitly, frequency of occurrence of each prey type was included. This explains that diet overlap between herring and sprat in March was significantly different from 1, while eel and bass apparently shared the same prey. All sprats ate copepods, while at least some herring had consumed other prey. With contrast to herring and sprat sharing four prey items, bass and eel shared 10 prey items with none of the prey exclusively dominating the diet. It is interesting to note that the use of Schoener's index for niche overlap (Krebs, 1989) yielded overlaps that were, on average, 11% closer to 1. Yet, results after a Mantel test were identical to the ones using Renkonen's index. Anyway, it is clear that caution should be given when niche overlap indices are used, certainly when arbitrary levels are chosen to distinguish between significant or insignificant niche overlap between species.

The use of diversity indices as measures for niche width

We used the Shannon-Wiener statistic to detect seasonal changes in niche breath. This index may be biased as it assumes that resources are equally distributed (Petraitis, 1979). Therefore, a measure of niche width should be used if it analyzes whether or not the utilization of resources by a species can be drawn from the environmental resource spectrum. Regretfully, studies on the lower trophic levels ended a few km downstream from Doel. The real food supply is hard to measure, unless very detailed laboratory experiments are carried out on the availability of each prey organism for each fish species. We expected that niche width would be low in spring and summer but would increase towards winter, since the optimal foraging theory predicts that niche width should increase as the availability of foraging resources decreases because the consumption of a wide rage of suboptimal prey types is promoted (Pianka, 1982). This was likely to happen in winter. Yet, no consistent patterns were found (Fig. 7.1), neither relationships between niche width, the number of prey items eaten and the fullness index were found.

Diet composition versus prey availability

Out analysis of the stomach contents of two pelagic, two demersal and four benthic fish species inhabiting the Zeeschelde indicates that this feeding guild mainly forages on the hyperbenthos and zooplankton, thereby largely ignoring the infauna. We can think of two reasons why copepods and mysids were largely preferred over other crustaceans: the availability and the motility of the prey items.

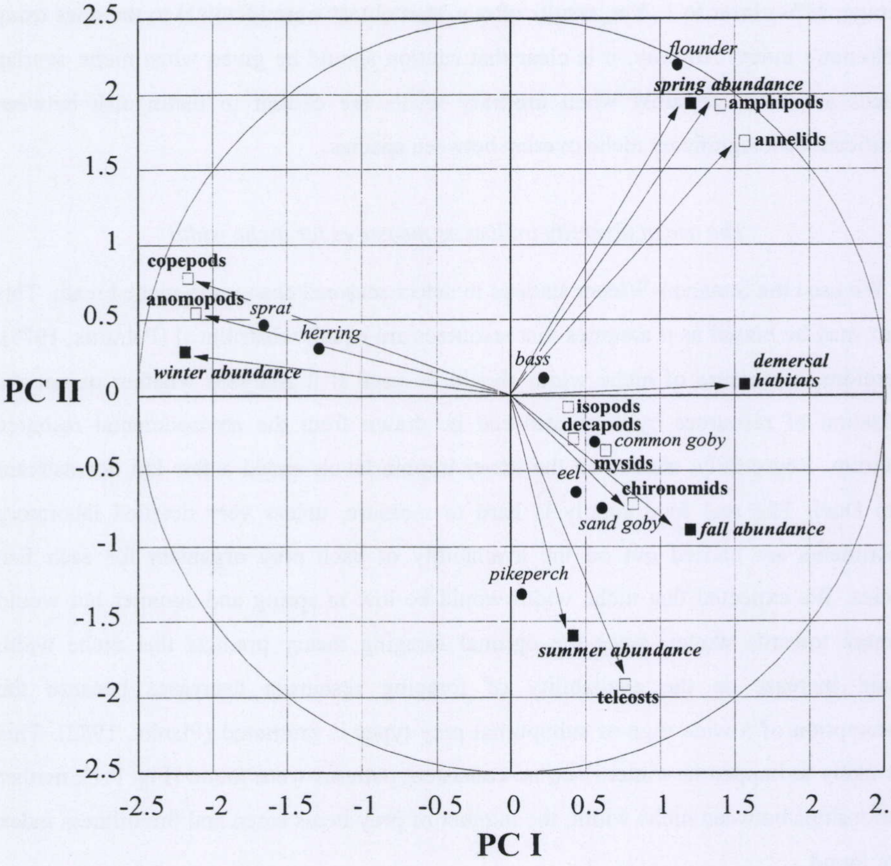

Fig. 7.3. Position of the ecological axes and individual species with respect to the first two principal components.

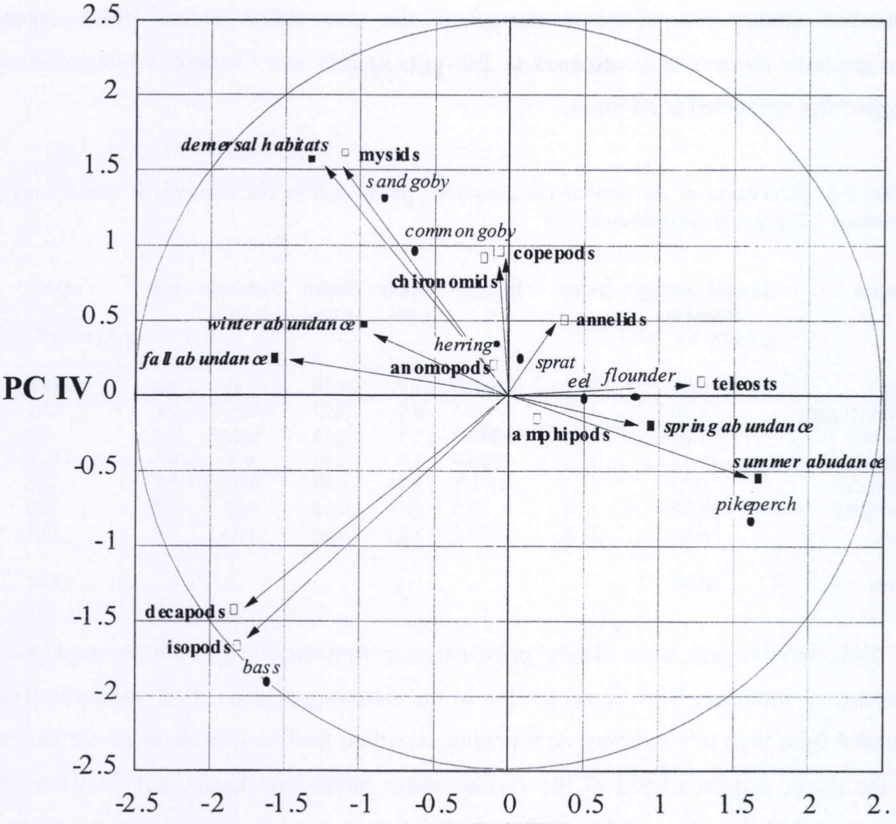

Fig. 7.4. Position of the ecological axes and individual species with respect to the third and fourth principal components.

First, mysidacea and calanoid copepoda were probably exploited in proportion to their availability. Of all pelagic organisms that occurred in the water column between April 1989 and March 1991, >99.5% were calanoid copepods, predominantly *Eurytemora affinis* (Poppe) (Soetaert and Van Rijswijk, 1993). High numbers of copepods in the stomachs found in March 1995 probably coincided with maximum copepod density in the water. In 1990 and 1991, the benthic component that occurred above the bottom a few km downstream of Doel consisted largely of the mysids *Neomysis integer* and *Mesopodopsis slaberri*. The latter species is virtually absent from the estuary in winter, but reaches maximal abundance in the eastern part in August.

Neomysis integer was abundant throughout the year (Mees *et al*, 1994). Again, *Mesopodosis slaberri* only occurred in fish guts in July and October, while *Neomysis integer* was consumed at all times.

Table 7.5. *Estimation of the annual consumption (Q) by fish in the Zeeschelde estuary using Equation 7.2. See text for abbreviations.*

Species	**Annual average biomass** g ADW·10^{-3} m^{-3}	**Temp.** °C	$W_{infinity}$ g	**Aspect ratio**	**Depth ratio**	**Peduncle ratio**	***Q/B***	***Q*** g ADW·10^{-3} m^{-3}
bass	2.63	11.5	6 860.0	1.9	4.26	0.43	3.8	10.0
common goby	2.90	11.5	2.3	0.9	5.93	0.54	7.6	22.0
flounder	1.20	11.5	1 040.0	1.5	2.11	0.24	3.7	4.5
herring	17.13	11.5	200.0	1.9	4.13	0.3	6.6	113.8
pikeperch	0.27	11.5	$15 \cdot 10^3$	2.8	4.68	0.32	2.2	0.6
sand goby	11.15	11.5	4.5	0.7	6.14	0.52	6.5	72.9
sprat	4.09	11.5	20.4	1.8	4.66	0.33	8.7	35.4
totals	**39.40**							**259.2**

Two, mobile prey were clearly preferred over immobile prey such as amphipods, annelids or molluscs. This could be due to the sampling scheme. Fish stomachs were selected from high tide samples. At this time, intertidal feeding teleosts were not present in the direct neighbourhood of the cooling-water intake and hence, not available for capture. Adult flounder caught in gillnets after a foraging trip on an intertidal mudflat nearby the sampling site consumed almost exclusively *Corophium volutator* and *Macoma balthica* L. (Stevens, 2000), both species that rarely occurred in stomachs in the present study. However, it is more likely that the high densities of suitable non-burrowing prey prevent fish from searching for the relatively inaccessible burrowing forms (Moore and Moore, 1976; Van den Broek, 1978). It is thus suggested that the energetic cost of detecting and successfully hunting mobile prey in turbid waters is less than the cost for searching infauna.

Resource partitioning within the fish community

Our second hypothesis stated that trophic niche overlap amongst these species was high. Thirty-two of the 43 pair-wise measured trophic niche overlaps were significantly different from 1. This means that our null hypothesis was rejected in most of the cases. The remaining 11 species pairs had statistically similar diet compositions. Eight of these pairs involved species that were vertically separated into a pelagic, demersal or benthic component. Our pair-wise comparisons thus suggested a reasonable degree of trophic segregation amongst the dominant species of the fish community. The results of the multivariate descriptive analyses also suggest niche segregation within the estuarine fish community. This was, however, unexpected. Comparing production rates of mysids and copepods to consumption rates of fishes showed that about 13% of the annual prey production was consumed (Table 7.6).

Very little quantitative information is available on the predation impact of estuarine fishes on their prey. In the Bot estuary (South Africa), resident fish consumed 30% of the secondary production of prey species (Benneth and Branch, 1990), suggesting that food was not in short supply. Evans (1983) showed that the yearly predation of *Crangon crangon*, plaice *Pleuronectes platessa* L. and sand goby inhabiting a marine shallow Swedish fjord amounted to 12% of the total macrofauna production. Pihl (1985) found a P/C ratio for fishes and shrimps in shallow waters of the Swedish west coast of 0.3 and 0.2, respectively, suggesting that 60% to 98% of the annual macrobenthic production was consumed by predators. However, we largely ignored the role of shrimps and prawns in the food web. *Crangon crangon* and *Palaemonetes varians* both reached numbers often exceeding those of the whole fish community. Carideans were for none of the fish species major prey items. If preyed upon, fish restricted themselves to smaller specimens. This is due to the high mobility and the unique escape reaction of shrimps under turbid conditions. (Moore and Moore, 1976).

If shrimps are included in the Q/P budget, and under the assumption that they preyed upon mysids and copepods (Boddeke *et al.*, 1986), total annual consumption of the fish and crustacean community amounted to almost 50% of the prey production by mysids and copepods (Table .12). These data contradict those of Hostens and Mees (1999). They pointed out that only 1% of the mysid standing stock was removed by the fish assemblage.

Table 7.6. *Comparison of the average standing stock in biomass of copepods (Eurytemora affinis and Acartia tonsa (Dana)), mysids (Neomysis integer), shrimps (Crangon crangon and Palaemonetes varians) and fish, and annual consumption and production rates. Data for copepods were from the brackish part of the Westerschelde (Escaravage and Soetaert, 1995). Data for N. integer are from Mees (1994). Dates of the different studies are shown. Q/P ratios represent the ratio of total consumption of shrimps and fish, respectively, over the total prey production by mysids and copepods. For conversion of dry weight (DW) to ash-free dry weight (ADW), a conversion factor of 0.5 g ADW × (g DW)*$^{-1}$ *was used (Escaravage and Soetaert, 1995).*

Copepods (1989-1990)	
Mean biomass (mg DW·m^{-3})	71.00
Annual production (mg DW·m^{-3}·year^{-1})	3201.00
Neomysis integer (1990-1991)	
Mean biomass (mg ADW·m^{-2})	95.97
Annual production (mg ADW·m^{-2}·year^{-1})	322.69
Shrimps (1994-1995)	
Average biomass (mg ADW·m^{-3})	19.44
Average daily consumption (mg ADW·m^{-3})	3.11
Average annual consumption (mg ADW·m^{-3})	1 135.56
Fish (1994-1995)	
Average biomass (mg ADW·m^{-3})	39.41
Average annual consumption (mg ADW·m^{-3})	259.25
$Q_{shrimps}/P_{prey}$	29.5%
Q_{fish}/P_{prey}	13.4%

Our data suggest that the fish species that simultaneously occupy the Zeeschelde estuary were likely to partition available resources even in the face of a sufficient food supply. This observation is most likely the result of adaptations to minimize competion and maximize resource utilization (Høines and Bergstad, 1999).

Arne Taillieu sampled, identified and counted most of the fish. Loreto De Brabandere analyzed the stomach contents. I thank Jan Mees, Jan Sys and Andre Cattrijsse for helping with some of the prey identifications. This study was funded by the FWO Vlaanderen.

Appendix 1

In this appendix, we present the stomach analysis data used in this chapter. Each table contains the composition of the stomach contents of one or two species by season. Stomach analyses contents are expressed as percentage occurrence (%O), percentage abundance (%N) and percentage biomass or weight (%W) Significant differences between niche widths H are shown by exponents.

Table 1. *Herring Clupea harengus*

Prey item	**Spring**			**Summer**			**Fall**			**Winter**		
	%O	%N	%W	%O	%N	%W	%O	%N	%W	%O	%N	%W
Foraminifera	-	-	-	-	-	-	0.11	<0.01	<0.01	-	-	-
Daphnia sp.	0.58	0.03	0.07	-	-	-	-	-	-	-	-	-
Ceriodapnhia sp.	0.52	0.01	0.03	-	-	-	-	-	-	-	-	-
Calanoidea	0.94	0.89	0.38	0.68	0.94	0.83	0.22	0.78	0.06	0.71	0.98	0.94
Harpacticoidea	0.82	0.07	<0.01	0.50	0.05	<0.01	0.22	0.04	<0.01	0.28	0.01	<0.01
Neomysis integer	0.12	<0.01	0.34	0.38	<0.01	0.13	0.44	0.07	0.52	-	-	-
Mesopodopsis slabberi	-	-	-	0.18	<0.01	0.01	0.66	0.08	0.20	-	-	-
Unidentified Mysidacea	0.06	<0.01	0.15	0.13	<0.01	0.01	0.33	0.01	0.05	-	-	-
Gammarus salinus	-	-	-	-	-	-	0.11	0.01	0.13	-	-	-
Corophium volutator	0.17	<0.01	0.01	0.13	<0.01	<0.01	-	-	-	0.14	0.01	0.05
Crangon crangon	-	-	-	0.31	<0.01	0.01	0.11	0.01	0.03	-	-	-
Gnatidae	-	-	-	-	-	-	0.11	0.01	<0.01	-	-	-
Unidentified Crustacea	0.12	<0.01	0.01	-	-	-	-	-	-	-	-	-
Chironomidae	0.06	<0.01	0.01	-	-	-	-	-	-	-	-	-
Teleostei (eggs)	-	-	-	0.06	<0.01	<0.01	-	-	-	-	-	-
Number of fish analyzed	20			20			20			20		
Length range (mm)	75 – 115			39 - 68			68 - 93			67 – 90		
Number of empty stomachs	3			5			11			13		
Average number of prey	538			242			23			6.2		
Niche width H	0.45^a			0.27^b			0.82^c			0.13^d		

Table 2. *Sand goby Pomatoschistus minutus*

Prey item	**Spring**			**Summer**			**Fall**			**Winter**		
	%O	%N	%W	%O	%N	%W	%O	%N	%W	%O	%N	%W
Nereis sp.	0.15	<0.01	<0.01	-	-	-	-	-	-	-	-	-
Oligochaeta	0.07	<0.01	<0.01	-	-	-	-	-	-	-	-	-
Unidentified Annelida	0.31	0.02	<0.01	-	-	-	-	-	-	-	-	-
Daphnia sp.	0.15	<0.01	0.02	-	-	-	-	-	-	-	-	-
Calanoidea	0.85	0.87	0.36	0.23	0.22	<0.01	0.13	0.11	<0.01	-	-	-
Harpacticoidea	0.46	0.09	<0.01	-	-	-	0.07	0.06	<0.01	-	-	-
Cirripeda	-	-	-	-	-	-	-	-	-	0.27	0.19	<0.01
Neomysis integer	-	-	-	0.38	0.22	0.68	0.40	0.39	0.24	0.54	0.50	0.59
Mesopodopsis slabberi	-	-	-	0.07	0.04	0.02	0.26	0.22	<0.01	-	-	-
Unidentified mysidacea	-	-	-	-	-	-	-	-	-	0.09	0.06	0.07
Unidentified Isopoda	-	-	-	0.07	0.04	0.11	-	-	-	-	-	-
Corophium volutator	-	-	-	0.23	0.35	0.02	-	-	-	-	-	-
Crangon crangon	-	-	-	-	-	-	-	-	-	0.09	0.06	0.10
Unidentified Caridea	-	-	-	-	-	-	0.13	0.11	0.45	0.09	0.06	0.09
Acaridae	-	-	-	-	-	-	0.07	<0.01	<0.01	-	-	-
Unidentified Crustacea	0.07	<0.01	0.55	0.23	0.13	0.17	0.07	0.06	0.11	0.18	0.12	0.15
Chironomidae	0.07	<0.01	0.06	-	-	-	-	-	-	-	-	-
Teleostei	-	-	-	-	-	-	0.07	0.05	0.20	-	-	-
Number of fish analyzed		20			20			20			20	
Length range (mm)		35 – 70			31 – 49			49 – 79			47 – 75	
Number of empty stomachs		7			7			5			9	
Average number of prey		17			1.2			0.9			0.8	
Niche width H		0.55^{a}			1.57^{b}			1.67^{b}			1.44^{b}	

Table 3. *Bass Dicentrarchus labrax and flounder Pleuronectes flesus*

Prey item	**Bass**									**Flounder**		
	Spring			**Fall**			**Winter**			**Spring**		
	%O	%N	%W	%O	%N	%W	%O	%N	%W	%O	%N	%W
Nereis sp.	0.33	0.01	0.09	-	-	-	0.11	0.03	0.02	0.57	0.03	0.53
Oligochaeta	-	-	-	-	-	-	0.11	0.03	<0.01	0.14	<0.01	0.01
Unidentified Annelida	0.07	<0.01	<0.01	-	-	-	-	-	-	-	-	-
Unidentified Gastropoda	-	-	-	-	-	-	0.09	0.03	<0.01	-	-	-
Daphnia sp.	0.13	0.11	<0.01	-	-	-	-	-	-	-	-	-
Calanoidea	0.33	0.59	0.01	-	-	-	-	-	-	0.64	0.86	0.03
Harpacticoidea	0.26	0.15	<0.01	-	-	-	-	-	-	-	-	-
Neomysis integer	0.33	0.02	0.37	0.08	0.03	0.02	-	-	-	0.21	0.02	0.38
Unidentified Mysidacea	0.20	<0.01	0.09	-	-	-	-	-	-	-	-	-
Lekanesphaera rugicauda	0.20	0.04	0.01	-	-	-	0.11	0.17	<0.01	-	-	-
Unidentified Isopoda	0.07	<0.01	<0.01	-	-	-	-	-	-	-	-	-
Orchestia sp.	-	-	-	-	-	-	0.22	0.27	0.08	-	-	-
Gammarus salinus	0.13	0.01	0.04	-	-	-	-	-	-	0.21	0.01	0.03
Bathyporeia sp.	0.07	<0.01	<0.01	-	-	-	0.11	0.03	<0.01	-	-	-
Corophium volutator	0.27	0.03	0.01	-	-	-	-	-	-	0.29	0.06	0.02
Unidentified Amphipoda	0.20	0.01	0.01	-	-	-	-	-	-	0.14	<0.01	<0.01
Palaemonetes varians	0.13	<0.01	0.22	0.58	0.55	0.39	0.44	0.20	0.10	-	-	-
Crangon crangon	0.07	<0.01	0.03	0.50	0.31	0.43	0.44	0.13	0.73	-	-	-
Unidentified Caridea	0.07	<0.01	0.08	0.08	0.03	0.08	0.11	0.07	0.02	-	-	-
Gnatidae	0.07	<0.01	<0.01	-	-	-	-	-	-	0.07	<0.01	<0.01
Unidentified Crustacea	0.20	<0.01	0.03	0.17	0.07	0.07	0.11	0.03	0.04	-	-	-
Chironomidae	0.07	<0.01	<0.01	-	-	-	-	-	-	-	-	-
Number of fish analyzed	20			20			20			20		
Length range (mm)	84-132			60-115			72-120			70-115		
Number of empty stomachs	5			8			11			6		
Average number of prey	32.5			1.5			1.5			13		
Niche width H	1.44[a]			1.11[a]			1.91[b]			0.61		

Table 4. *Common goby Pomatoschistus microps and pikeperch Stizostedion lucioperca*

Prey item	**Common goby**									**Pikeperch**		
	Spring			**Fall**			**Winter**			**Summer**		
	%O	%N	%W	%O	%N	%W	%O	%N	%W	%O	%N	%W
Oligochaeta	0.10	0.01	0.04	-	-	-	-	-	-	-	-	-
Unidentified Annelida	0.16	<0.01	<0.01	-	-	-	-	-	-	0.10	0.07	<0.01
Daphnia sp.	0.22	0.02	0.05	-	-	-	-	-	-	-	-	-
Bosminidae	0.06	<0.01	<0.01	-	-	-	-	-	-	-	-	-
Calanoidea	0.94	0.86	0.88	0.33	0.95	0.24	0.72	0.85	0.55	-	-	-
Harpacticoidea	0.61	0.10	<0.01	-	-	-	-	-	-	-	-	-
Cirripeda	0.06	<0.01	<0.01	-	-	-	0.14	0.04	<0.01	-	-	-
Neomysis integer	-	-	-	0.08	<0.01	0.21	-	-	-	0.40	0.29	0.63
Mesopodopsis slabberi	-	-	-	0.17	0.01	0.15	-	-	-	0.10	0.07	<0.01
Unidentified Isopoda	-	-	-	0.08	<0.01	0.02	-	-	-	-	-	-
Oniscoidea	-	-	-	0.08	<0.01	<0.01	-	-	-	-	-	-
Corophium volutator	-	-	-	-	-	-	0.14	0.04	0.15	-	-	-
Crangon crangon	-	-	-	-	-	-	-	-	-	0.10	0.07	<0.01
Unidentified Crustacea	-	-	-	0.50	0.03	0.38	0.29	0.07	0.30	0.10	0.07	0.13
Chironomidae	0.06	<0.01	0.01	-	-	-	-	-	-	-	-	-
Teleostei	-	-	-	-	-	-	-	-	-	0.60	0.42	0.22
Number of fish analyzed	20			20			20			20		
Length range (mm)	32-44			25-41			30-43			45-73		
Number of empty stomachs	2			8			13			10		
Average number of prey	37			10			1.4			0.7		
Niche width *H*	0.52^{ab}			0.25^{ac}			0.57^{bc}			1.48		

Table 5. *Sprat Sprattus sprattus and European eel Anguilla anguilla*

Prey item	**Sprat**						**European eel**					
	Spring			**Fall**			**Spring**			**Summer**		
	%O	%N	%W	%O	%N	%W	%O	%N	%W	%O	%N	%W
Nereis sp.	-	-	-	-	-	-	0.17	0.03	0.08	0.13	0.01	<0.01
Oligochaeta	-	-	-	-	-	-	-	-	-	0.13	0.01	0.02
Unidentified Annelida	-	-	-	-	-	-	0.08	0.01	<0.01	-	-	-
Ostracoda	0.05	<0.01	<0.01	-	-	-	-	-	-	-	-	-
Daphnia sp.	0.95	0.02	0.02	-	-	-	-	-	-	-	-	-
Ceriodapnhia sp.	0.95	0.02	0.02	-	-	-	-	-	-	-	-	-
Bosminidae	0.05	<0.01	<0.01	-	-	-	-	-	-	-	-	-
Calanoidea	1.00	0.83	0.95	0.83	0.86	0.30	0.08	0.04	<0.01	-	-	-
Harpacticoidea	1.00	0.12	0.02	-	-	-	-	-	-	-	-	-
Cirripeda	-	-	-	-	-	-	0.08	0.01	<0.01	-	-	-
Neomysis integer	-	-	-	0.33	0.01	0.04	0.50	0.39	0.46	0.63	0.66	0.89
Mesopodopsis slabberi	-	-	-	0.33	0.12	0.65	-	-	-	0.50	0.18	0.04
Corophium volutator	-	-	-	-	-	-	0.33	0.16	<0.01	0.25	0.08	<0.01
Pleusymptes sp.	0.05	<0.01	<0.01	-	-	-	-	-	-	-	-	-
Palaemonetes varians	-	-	-	-	-	-	0.42	0.09	0.19	-	-	-
Crangon crangon	-	-	-	-	-	-	0.17	0.07	0.04	0.13	0.01	<0.01
Majidae	-	-	-	-	-	-	0.08	0.01	<0.01	-	-	-
Unidentified Caridea	-	-	-	-	-	-	0.17	0.04	0.06	0.13	0.01	<0.01
Gnatidae	0.05	<0.01	<0.01	-	-	-	-	-	-	-	-	-
Unidentified Crustacea	0.10	<0.01	<0.01	0.33	0.01	0.02	0.08	0.01	0.01	0.25	0.02	0.02
Chironomidae	-	-	-	-	-	-	-	-	-	-	-	-
Teleostei	-	-	-	-	-	-	0.25	0.13	0.16	0.13	0.01	0.02
Number of fish analyzed	20			20			20			20		
Length range (mm)	55-77			52-74			140-342			118-228		
Number of empty stomachs	0			14			8			12		
Average number of prey	594			27			4.15			4.3		
Niche width *H*	0.58[a]			0.47[b]			1.89[a]			1.14[b]		

Appendix 2

In this appendix, we present the results of the principal component analysis. Table 6 gives the position of the ecological variables (factor loadings) and the fish species (factor scores) on the four first principal components. The eigenvalues and the proportion of variance they represent are also included in the table.

Table 6.

Factor loadings	**PC I**	**PC II**	**PC III**	**PC IV**
Summer abundance	0.16	-0.64	0.66	-0.22
Fall abundance	0.45	-0.37	-0.59	0.11
Winter abundance	**-0.86**	0.12	-0.35	0.17
Spring abudance	0.48	**0.78**	0.33	-0.11
Ddemersal habitat	0.61	0.02	-0.47	0.61
Annelids	0.61	0.68	0.11	0.19
Anomopods	**-0.84**	0.22	-0.07	0.08
Copepods	**-0.86**	0.31	-0.05	0.30
Mysids	0.26	-0.15	-0.49	0.61
Isopods	0.15	-0.03	**-0.71**	-0.66
Amphipods	0.55	**0.77**	0.10	-0.15
Decapods	0.17	-0.12	-0.69	-0.61
Chironomids	0.34	-0.30	-0.01	0.34
Teleosts	0.30	**-0.77**	0.49	0.03
Eigenvalues	4.02	3.08	2.73	1.91
Proportion of the variance explained	0.29	0.22	0.20	0.14
Cumulative proportion of the variance	0.29	0.51	0.70	0.84
Factor scores	**PC I**	**PC II**	**PC III**	**PC IV**
Herring	-1.29	0.30	-0.06	0.33
Sprat	-1.83	0.49	0.10	0.23
Common goby	0.57	-0.31	-0.62	0.95
Sand goby	0.65	-0.66	-0.82	1.31
European eel	0.45	-0.64	0.50	-0.04
Bass	0.22	0.06	-1.59	-1.92
Pikeperch	0.11	-1.30	1.63	-0.83
Flounder	1.12	2.07	0.85	-0.02

Chapter 8

Biomass Transport to and from the Zeeschelde Estuary by Migration of Juvenile Atlantic Herring *Clupea harengus* L.

We present a model that describes fish abundance in an upper estuary as the result of fish migration and mortality. The model can be used to estimate biomass transports by fish migrations between estuary and sea and to assess production assimilated in the estuary. The model was applied to herring *Clupea harengus* L., a marine species of which 0+ juveniles migrate during winter to temperate European estuaries. It was shown that different mortality regimes greatly affected the number of fish that eventually emigrated and hence, the biomass that was exported during the seaward migration. The difference between imported and exported biomass was assessed under different growth conditions and varied from positive to negative as mortality rates increased. The discrepancy between export of biomass and *in situ* produced biomass showed that fish production was not necessarily transported to the sea when emigrating. It was tentatively concluded that export of biomass out of the estuary only occurs if populations move seaward before winter.

Maes, J. and Ollevier, F. 2000. Biomass transport to and from an upper estuarine area by migration of juvenile Atlantic herring *Clupea harengus* L. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, in press.

Introduction

Marine fish and crustaceans often migrate to shallow turbid coastal areas and estuaries during the first stages of their life to join highly productive feeding habitats and to profit from enhanced protection from predators (Haedrich, 1983; Day *et al.*, 1989; Blaber, 1997). Yet, few researchers have focussed on the transports of energy and biomass between estuaries and coastal marine ecosystems by fish migrations (Deegan, 1993). This contrasts with the rather well developed export budgets available for nutrients and plankton (Heip and Herman, 1995). The number of studies estimating export of fish biomass and fish production is limited because the complex migration patterns make it difficult to use the standard methods (Day *et al*,. 1989). The purpose of this paper is to present a model that describes fish abundance in an estuary as a result of migration and mortality. The second objective is to use the model to approximate the amount of biomass that is either imported in an estuary or exported seaward by migrating population. The model is applied to a marine species, Atlantic herring, *Clupea harengus* L., of which young-of-the-year commonly inhabit the brackishwater area of North Sea estuaries.

Materials and methods

Model of fish abundance, biomass transfers and fish production

The change in fish abundance over time $\frac{\mathrm{d}N}{\mathrm{d}t}$ in the estuary due to migration and mortality can be expressed as:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \text{immigration - emigration - mortality} \tag{8.1}$$

Equation 8.1 is a conceptual model describing fish abundance over time. Only one biological process, immigration, is responsible for increasing fish abundance (source). Two biological processes, mortality and emigration, are responsible for decreasing fish abundance (sinks). Given that both migration and mortality have an exponential course, equation 8.1 can be rewritten in a mathematical form:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = a \times \exp(it) - e \times N - z \times N \tag{8.2}$$

where a, i, e and z are the parameters of the model. All symbols used in equations and text are explained in Table 8.1. Equation 8.2 is a differential equation with dependent variable N and independent variable t. As immigration and emigration were assumed to be discontinuous with time, equation 8.2 has to be split into two parts to find a proper solution. Between t_o and t_{max} equation 8.2 can be shortened (equation 8.3) and solved for N_i with t as independent variable and with $N_i(0) = 0$ (or at t_o no fish are present yet) as initial condition (equation 8.4).

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = a \times \exp(it) - z \times N_i \tag{8.3}$$

$$N_i = \frac{a}{i+z} \times \left[\exp(it)\text{-}\exp(-zt)\right] \tag{8.4}$$

Table 8.1. *Symbols used in the equations and in the text*

Symbol	**explanation**	**unit**
$N(t)$	fish abundance at time t	numbers$\cdot 10^{-3}$ m^{-3}
$N_i(t)$	fish abundance during immigration	numbers$\cdot 10^{-3}$ m^{-3}
$N_e(t)$	fish abundance during emigration	numbers$\cdot 10^{-3}$ m^{-3}
t	time	day
t_o	time of hatching	day
t_{max}	time of maximum abundance	day
t_{end}	time by which emigration is ended	day
a	intercept with dN/dt	numbers$\cdot 10^{-3}$ m$^{-3}\cdot$day^{-1}
i	immigration coefficient	day^{-1}
e	emigration coefficient	day^{-1}
z	total mortality coefficient	day^{-1}
$L(t)$	length at age t	mm
$W(t)$	weight at age t	g
$L_{infinity}$	asymptotic length	mm
$W_{infinity}$	asymptotic weight	g
K	growth coefficient	day^{-1}
I	number of fish immigrated	numbers$\cdot 10^{-3}$ m^{-3}
E	number of fish emigrated	numbers$\cdot 10^{-3}$ m^{-3}
B_i	imported biomass	g$\cdot 10^{-3}$ m^{-3}
B_e	exported biomass	g$\cdot 10^{-3}$ m^{-3}
P	production	g$\cdot 10^{-3}$ m$^{-3}\cdot$year^{-1}

Between t_{max} and t_{end} equation 8.2 can be shortened (equation 8.5). Solving equation 8.5 for N_e with t as independent variable and with the initial condition that $N_i(t_{max})$ should equal $N_e(t_{max})$ gives equation 8.6 and equation 8.7. In equation 8.7 is the first factor replaced by $N_i(t_{\max})$.

(8.5) $$\frac{\mathrm{d}N_e}{\mathrm{d}t} = -e \times N_e - z \times N_e.$$

(8.6) $$N_e = \frac{a}{i+z}\left[\exp(it_{\max}) - \exp(-zt_{\max})\right] \times \exp\left(-(z+e)(t-t_{\max})\right)$$

(8.7) $$N_e = N_i(t_{\max}) \times \exp\left(-(z+e)(t-t_{\max})\right)$$

Equation 8.4 and equation 8.7 are analytical functions explaining increasing fish abundance during a period of immigration and decreasing fish abundance during a period of emigration, respectively. These equations, combined with growth data, can now be used to calculate biomass transports. Growth may be expressed by a Von

Bertalanffy growth function (Von Bertalanffy, 1938) for length (equation 8.8) or for biomass (equation 8.9):

$$L(t) = L_{infinity} \times \left[1 - exp\left(-K\left(t - t_0\right)\right)\right] \tag{8.8}$$

$$W(t) = W_{infinity} \times \left[1 - \exp\left(-K\left(t - t_0\right)\right)\right]^3 \tag{8.9}$$

We now calculate successively the number of fish that have immigrated, the imported biomass, the number of fish that have emigrated, the exported biomass and the production or the biomass assimilated in the estuary. Integrating equation 8.3 from 0 to t_{max} with the mortality coefficient z set to zero yields the number of fish I that have immigrated to the estuary (equation 8.10). Equation 8.10 combined with equation 8.9 gives the imported biomass B_i (equation 8.11).

$$I = \int_0^{t_{\max}} a \exp(it)dt = \frac{a}{i}\exp(it_{\max}) - \frac{a}{i} \tag{8.10}$$

$$B_i = \int_0^{t_{\max}} a \exp(it) \times W(t)dt \tag{8.11}$$

Accordingly, the number of fish E that have emigrated is given by equation 8.12. Combining equation 8.12 with equation 8.9 gives the exported biomass B_e (equation 8.13).

$$E = \int_{t_{\max}}^{t_{end}} e \times N_e dt = \frac{e}{e+z} \times N_i(t_{\max}) \times \left[1 - \exp\left((e+z)(t_{\max} - t_{end})\right)\right] \tag{8.12}$$

$$B_e = \int_{t_{\max}}^{t_{end}} e \times N_e \times W(t)dt \tag{8.13}$$

We calculated fish production P or the biomass assimilated between t_o and t_{end} according to equation 3 of Merz and Myers (1998) as the product of fish abundance and growth rate (Allen method).

$$(8.14) \qquad P = \int_{t_0}^{t_{end}} N_i(t)\frac{\mathrm{d}W(\mathrm{t})}{\mathrm{d}t}\mathrm{d}t + \int_{t_{\max}}^{t_{end}} N_e(t)\frac{\mathrm{d}W(\mathrm{t})}{\mathrm{d}t}\mathrm{d}t$$

Fish production is thus the amount of tissue elaborated per unit time per unit area, regardless of its fate (Clark, 1946). In contrast, transported biomass is the amount of tissue per unit area that is either imported or exported by living animals.

Table 8.2. *Field observations on the presence of Atlantic herring in the Zeeschelde estuary including sampling date, age in days, mean fish abundance N and average length at age L(t).*

Sampling date	**Age**	**N**	**L(t)**
11/07/94	65	0.007	50.88
27/07/94	81	0.409	64.4
09/08/94	94	0.169	57.6
25/08/94	110	0.085	69.17
06/09/94	122	2.222	75.04
27/09/94	143	5.627	77.72
06/10/94	152	7.912	78.79
25/10/94	171	13.262	75.58
09/11/94	186	19.705	78.79
21/11/94	198	138.709	78.23
04/12/94	211	174.285	77.93
20/12/94	227	55.811	78.38
16/01/95	254	49.407	79.84
30/01/95	268	5.725	81.79
16/02/95	285	38.37	80.17
06/03/95	301	2.431	84.45
22/03/95	319	9.407	83.94
05/04/95	333	1.054	84.88
18/04/95	346	1.038	90.84

Field sampling

Between July 1994 and June 1995 herring were collected every two weeks on the cooling-water filter screens of the nuclear power plant Doel situated in the Schelde estuary (Belgium). Approximately 8×10^6 m^3 cooling-water was monitored in 135 samples. Mean salinity at the sampling site was 8‰. Numbers per sample were transformed to numbers$\cdot10^{-3}$ m^{-3} cooling-water sampled. Afterwards, mean abundance for each sampling day was computed and used for further analysis. Biomass of herring was calculated using a length-weight regression ($N=168$, $R^2=0.97$, $p<0.01$): wet weight (g) = $\exp\left[-10.529 + 2.6889 \times \ln\left(\text{total lenght (mm)}\right)\right]$.

During the same period KEMA Power Generation & Sustainables collected fish on the filter screens of the Nuclear Power plant Borssele situated downstream of Doel nearby the mouth of the estuary (The Netherlands) (De Potter and Van Aerssen, 1995). Salinity at Borssele varied between 18 ‰ and 35‰. Although the sampling method at Borssele was identical to ours, only 1×10^6 m^3 cooling-water was monitored in 48 samples taken every month. Fish density at Borssele was generally lower as at Doel due to the sheltered position of the cooling-water intake after dams. Therefore, data from Borssele were considered to be of indicative value. The sampling sites are presented in Fig. 1.1.

Growth and mortality parameters used in the model

Mortality rates were obtained from Pauly (1982) and ranged from 0 day^{-1} to 0.05086 day^{-1}. Higher mortality rates contradicted with the field data. Back-extrapolation of the length-frequency modes of herring yielded t_o (Titmus *et al.*, 1978). Time of hatching corresponded to the date of 6 May 1994. We used two growth models to calculate production and transported biomass. The first model used growth parameters K and $W_{infinity}$ that were estimated by fitting equation 8.9 through our own biomass-at-age data (Fig. 8.1, Table 8.2). These data suggested rapid growth during summer and fall and slow growth in winter. The maximum biomass reached after the first growing season was taken as start value for $W_{infinity}$ since the herring population consisted only of young-of-the-year. The second growth model used growth parameters taken from a North Sea herring population (Pauly, 1982) ($W_{infinity}$ = 200 g; $K = 0.0011$ day^{-1}).

Statistical analysis and mathematical calculations

Non-linear estimation procedures were used to fit equation 8.4 and equation 8.7 through the observed abundance data. We used the quasi-Newton method as algorithm for estimating the different model parameters. The loss function used was the least squares estimation method. Explained variance by the fitting was expressed by R^2. All integrals were solved in Mathematica 3.0.

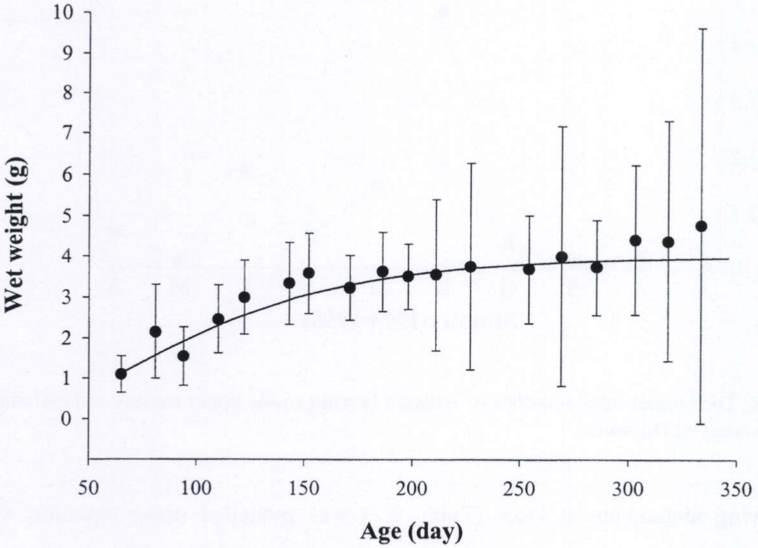

Fig. 8.1. Mean weight at age for herring (●) caught on the cooling-water intake screens at Doel. Error bars represent standard deviations. A non-linear regression (equation 8.9) was used to compute growth parameters.

$W(t) = 3.99 \times \left(1 - \exp(-0.0163t)\right)^3$ (R^2=0.84, $p < 0.01$).

Results

By comparing the annual pattern of capture of herring at Doel, in the upper estuary, with data for Borssele in the lower estuary, the movement of 0-group herring can be inferred (Henderson and Holmes, 1989). Fig. 8.2 shows the proportion of the annual catch caught in each month at Doel and Borssele. Abundance of herring peaked first at Borssele in November, after which numbers declined due to the movement of fishes to the upper estuary. At Doel, maximum abundance was reached in December. By the end of December, the fish retreated seaward yielding another abundance maximum at Borssele in February. By April the fish had almost completed their seaward migration.

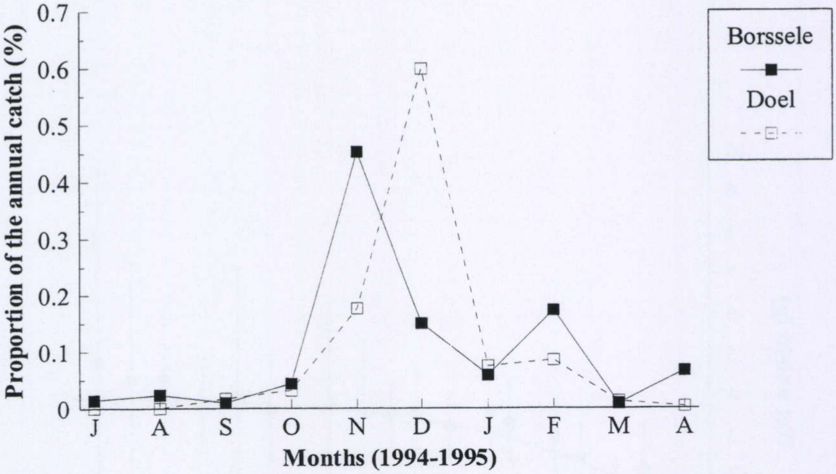

Fig. 8.2. The annual intake pattern of Atlantic herring in the upper estuary at Doel and in the lower estuary at Borssele.

Herring abundance at Doel (Table 8.2) was modelled using equation 8.4 and equation 8.7, respectively (Fig. 8.3). Using nine different values for mortality (*z*), the model parameters *a*, *i* and *e* were estimated (Table 8.3). Increasing mortality rates caused decreasing emigration rates and increased the value for the intercept *a*. The rate of immigration remained constant at 0.05 day^{-1}.

The model was used to estimate the numbers of fish that have immigrated (equation 8.10) and emigrated (equation 8.12) as well as their biomass transported during migration (equation11 and equation 8.13) (Table 8.3). As mortality increased, the number of fish that immigrated into the brackishwater area and the imported biomass had to increase to maintain the maximal fish abundance as observed in the field. Accordingly, the number of fish that moved seaward as well as the exported biomass from the upper estuarine site decreased.

The difference between the imported biomass and exported biomass decreased as mortality rates increased. This relationship is presented in Fig. 8.4. The growth model using growth parameters of the North Sea herring stock resulted in a lower import and export of biomass under different mortality regimes than the growth model using growth parameters estimated from field data (Fig. 8.4). Likewise, recruitment, which was interpreted as the percentage of (living) individuals that have emigrated seaward relative to the number of fish that have immigrated, decreased as mortality rates increased. Without mortality, recruitment was 100%; maximal mortality yielded zero recruitment as all fish that immigrated eventually died (Table 8.3).

The estimated fish production computed using equation 8.14 differed amongst the two growth models. The fish biomass produced by the herring population when present in the upper estuary was 46.3 g wet weight$\cdot 10^{-3}$ m$^{-3}\cdot$year^{-1} if growth parameters were estimated from field measurements. Using growth parameters from the North Sea herring population stock, the total production was 145.7 g wet weight$\cdot 10^{-3}$ m$^{-3}\cdot$year^{-1}.

Discussion

The present formulation of fish abundance at an upper estuarine site as a result of migration and mortality implied three major assumptions: (1) there was no temporal overlap between immigration and emigration; (2) the mortality rate was assumed not to vary with time; and (3) immigration and emigration occur at an exponential rate.

The first assumption can not be confirmed or rejected by our observations. However, the pattern of estuarine movements as revealed by Fig. 8.2 suggests that this assumption appears to be valid. Analysis of the stable isotopes of carbon and nitrogen in herring tissue can distinguish between newly arrived herring and herring that have been present for some time in the estuary (Hobson, 1999). Using this technique would reveal if our assumption is legitimate, but these results are not available yet.

Table 8.3. *Model parameters estimated by a non-linear estimation procedure. Equation 8.4 was used to estimate the intercept a and the immigration coefficient i under different mortality regimes. Equation 8.7 was used to estimate the emigration coefficient e. Import and export of biomass B was calculated using two different growth models. (1) Growth parameters from field observations, (2) growth parameters from Pauly (1982).*

z	a	i	N_{max}	e	I	E	B_i (1)	B_e (1)	B_i (2)	B_e (2)
0	0.00020	0.05096	185.45	0.05086	185.4	185.3	640.8	686.5	225.2	367.7
0.00068	0.00020	0.05091	185.80	0.05017	188.3	183.1	650.7	669.3	228.6	363.4
0.00137	0.00020	0.05092	185.52	0.04949	190.5	180.3	658.4	650.4	231.3	357.9
0.00274	0.00021	0.05088	185.43	0.04811	195.4	175.2	675.3	615.7	237.2	347.8
0.00549	0.00022	0.05093	185.53	0.04537	205.5	165.3	710.3	552.2	249.6	328.1
0.01098	0.00024	0.05093	185.39	0.03987	225.4	145.2	778.8	441.3	273.6	288.2
0.02197	0.00029	0.05095	185.66	0.02888	265.7	105.3	918.3	271.2	322.7	209.1
0.04395	0.00037	0.05094	185.93	0.00691	346.4	25.2	1196.9	49.8	420.5	50.1
0.05086	0.00040	0.05091	185.56	0.00000	370.9	0.0	1281.9	0.0	450.3	0.0

The second assumption is that of a constant mortality rate. With increasing fish size this rate may however, change. (King, 1995; De Barros and Toresen, 1998). Yet, major changes in the natural mortality rate of herring visiting the upper estuary at Doel are not expected for three reasons. First, juvenile herring all survived their first summer at sea and were about to recruit to the 1-group. Second, the majority of herring recorded at Doel were only present for a relatively short period of time. Third, piscivorous fish (gadoids) avoid the upper estuary, as turbidity levels are unsuitable for visual predation on herring (Chapter 5).

The third assumption is that of an exponential increase and decrease in fish abundance due to fish migration. Basically, this assumption involves the question why fish use estuaries and what factors control migration behaviour. Both environmental variations and biological interactions may cause migrations of fish up- or downstream. Large-scale experiments to discriminate between factors controlling the movement of marine fish to an estuary are difficult to deploy. Ecological cost-benefit models however, may predict seasonal usage of an estuary by fish. For example, the downstream movement of young shad in the Hudson river was delayed by the presence of predators in the lower estuary. Decreasing temperatures and food resources forced the fish to move downstream, even in the face of a high predation risk (Limburg, 1996). Increased size-related predation at sea or temperature and salinity tolerance limits may cause exponential increase or decrease in abundance. Further confidence for exponential migration rates was given by the fact that large increases of juvenile herring and sprat during winter months have been observed in other North Sea estuaries as well (Van Den Broek, 1979; Wharfe, 1984; Elliott *et al.*, 1990; Henderson *et al.*, 1992).

The use of a second growth model obtained from the North Sea herring population (Pauly, 1982) was necessary as the average length of herring measured at Doel may be biased due to the entrapment of smaller individuals (Henderson *et al.*, 1992). This could cause the marked slow down of growth in November and December. In addition, no reliable estimate of the maximum weight $W_{infinity}$ could be obtained from our data as the samples consisted almost exclusively of 0-group juveniles.

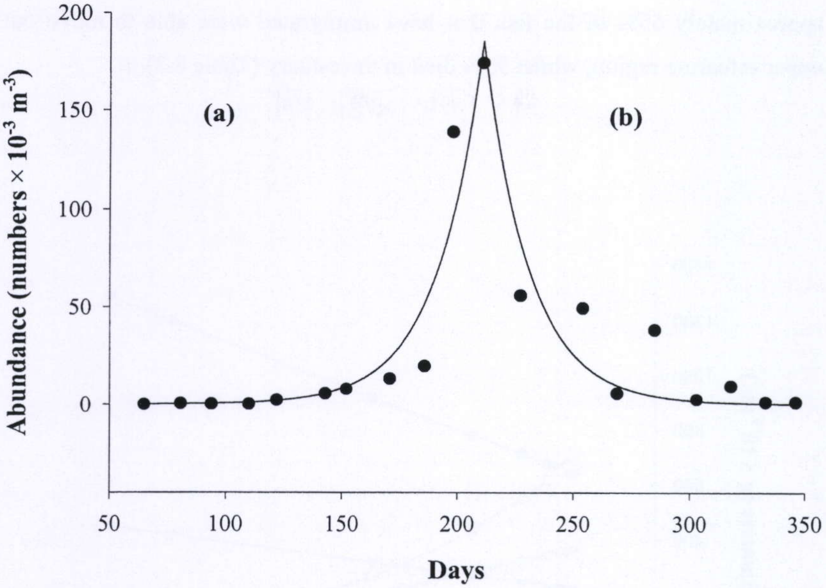

Fig. 8.3. Abundance of Atlantic herring (●) in the upper Schelde estuary during immigration (a) and emigration (b) as inferred from cooling-water screen catches at Doel. Fish abundance during immigration (a) was fitted by equation 8.4; during emigration (b) by equation 8.7. Maximum abundance was reached at t_{max} = day 211; emigration was completed at t_{end} = day 346. Explained variance by the fitting (R^2) was 0.918 in case of immigration and 0.881 in case of emigration ($p<0.01$).

It was shown that different mortality regimes greatly affected the number of fish that eventually emigrated and hence, the biomass that was transported during the seaward migration. The difference between import and export was assessed under different growth conditions and varied from positive to negative as mortality rates increased. If growth parameters from the North Sea herring stock were used, import equalled export at a mortality of $z = 0.012$ day^{-1}. Using growth parameters estimated from field observations, import balanced export at a much lower mortality rate $z = 0.0012$ day^{-1}. A weakness of this study is that mortality rates for the Schelde estuary herring population were not available. As a result, we used nine different mortality rates ranging from zero mortality to complete extinction. Under the assumption that the difference between two abundance peaks recorded at Borssele in November and February were caused only by mortality and not by sampling bias, the mortality rate for the herring population was estimated at 0.011 day^{-1}. At this rate of mortality, approximately 65% of the fish that have immigrated were able to move out of the upper estuarine region, whilst 35% died in the estuary (Table 8.3).

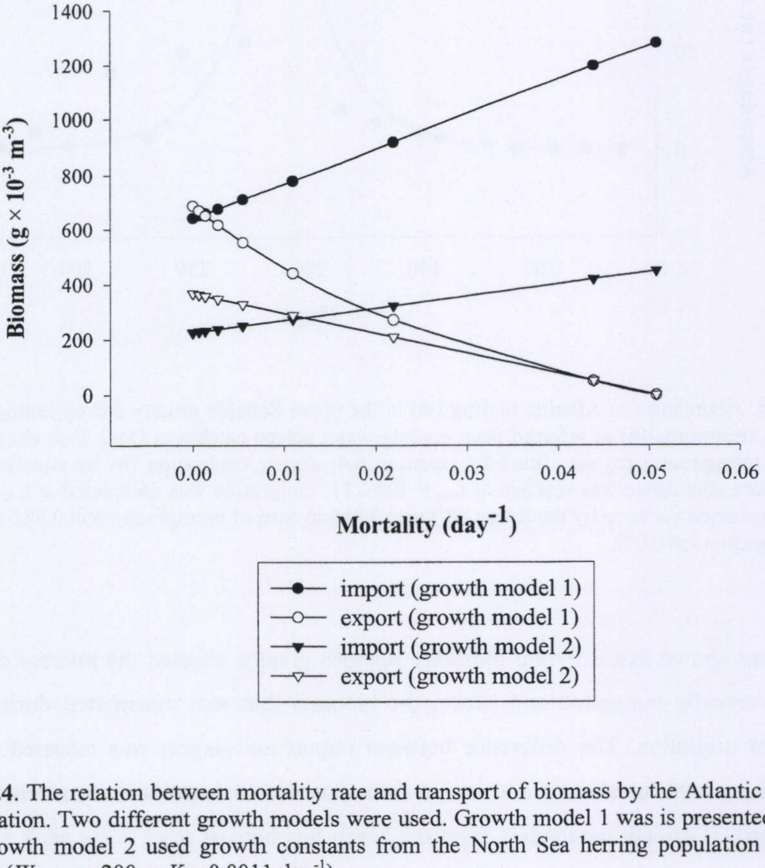

Fig 8.4. The relation between mortality rate and transport of biomass by the Atlantic herring population. Two different growth models were used. Growth model 1 was is presented in Fig 2. Growth model 2 used growth constants from the North Sea herring population (Pauly, 1982) ($W_{infinity}$ = 200 g; K = 0.0011 day^{-1}).

Given the differences between export biomass and *in situ* produced biomass, it is apparent that fish production at an estuarine site is not necessarily transported to the sea when emigrating. This observation contradicts with the findings of Deegan

(1993). She estimated that average net biomass exported by *Brevoortia patronus* from a Louisiana estuary to the Gulf of Mexico was 38 $g \cdot m^{-2} \cdot year^{-1}$, corresponding to 5-10% of the total primary production. Unlike herring, *Brevoortia patronus* occupied the estuary between February and November resulting in net export of biomass. We tentatively conclude that export significantly exceeds import if populations move seaward before winter.

R. Hadderingh kindly gave permission to use data from KEMA. I thank A. Taillieu for sampling support and G. Verbouwe, Dr. F. Volckaert, P. Puelinckx and I. De Saedeleer for mathematical advice. Dr. K. Soetaert substantially improved the paper by assisting with the modelling. Electrabel Doel and the F. W. O. Vlaanderen have funded this study.

Chapter 9
Final Discussion and Conclusions

We formulate five major conclusions of this study with respect to the structure of the fish community in the Zeeschelde estuary. These conclusions are compared to findings made in other European estuaries and give rise to a discussion wherein we question which factors contribute most to the stability of the estuarine fish community structure. Further research topics are suggested and include the development of ecological models to study estuarine ichthyofaunas.

Sampling cooling-water intakes situated in the Zeeschelde estuary has produced a large amount of data on the occurrence, the biology and the ecology of the fish and macrocrustacean fauna. Although data are now available for almost 10 consecutive years, this study largely deals with samples taken between July 1994 and June 1995. Other data have been presented in various reports or are still to be studied. Yet, the present analysis of the spatial, temporal and trophic structure of the fish fauna occurring in the Zeeschelde estuary has yielded five main conclusions with respect to the community structure.

1. About sixty species share the Zeeschelde estuary with, on average, 20 species present at any one time.

2. There is a marked upstream decrease in species diversity and fish abundance, probably due to water pollution. The tidal freshwater reach of the Zeeschelde is almost completely avoided by fish during summer.

3. In the brackishwater area only few species dominate the fish community contributing to >96% of the numbers caught on cooling-water filter screens. These were three Gobiidae sand goby *Pomatoschistus minutus*, Lozano's goby *P. lozanoi* and common goby *P. microps*, two Clupeidae herring *Clupea harengus* and sprat *Sprattus sprattus*, Nilsson's pipefish *Syngnathus rostellatus*, flounder *Pleuronectes flesus* and bass *Dicentrarchus labrax*. It was notable that all these dominant fish species had a marine nature and occurred as juveniles. Both freshwater and diadromous species represented only a small fraction of the fish community.

4. The brackishwater reach is seasonally used by the fish community, resulting in an exceptionally clear pattern of species occupancy. The seasonal structure was caused by sequential fish migrations. Subsequent sampling programs confirmed this

seasonal structure. Species composition at any one time is thus very predictable. The abundance of one of these species, herring, could be explained by a migration-mortality-model.

5. Analysis of the stomach contents of dominating fish species suggest that the community is highly dependent on copepods and mysids for their food. There were no arguments to support that either prey or predators were limiting fish abundance.

Our results strongly suggest that the Zeeschelde estuary functions as an important nursery area for juveniles of marine and freshwater species. This conclusion has been drawn for other European estuaries as well. The similarity between our results and those of studies on other estuaries suggests that there is an overall structure present in European estuarine fish assemblages. Henderson (1989) and Elliott and Dewailly (1995) make a fair attempt to search for this overall community structure. Henderson (1989) collated data on fish abundance at 12 English and Welsh estuarine and inshore sites and presented a comprehensive analysis yielding rules which could be used to generate predictions of the English estuarine and inshore fish fauna. These rules assessed the maximum number of species, the ranking of dominant species in relation to abiotic factors (salinity, degree of shelter, and temperature), the seasonal occupancy of dominant species, and the vertical distribution into a pelagic, demersal and benthic component. Elliott and Dewailly (1995) collected published data obtained from 19 different European estuaries. They failed to produce these generalizations but this may be due to the fact that their guild approach resulted in a data reduction. Elliott and Dewailly (1995) do not take into account temporal and spatial structure present within individual estuaries. In addition, sampling effort by trawling was dissimilar amongst the different studies. Henderson (1989) used data of fish catches in cooling-water intake screens that comprised several years, with a catch effort exceeding at each station many times our sampling effort. Again, we may conclude that sampling cooling-water is an excellent tool to collect large and reliable datasets containing information on the seasonal and spatial distribution of fish.

In the following, we will discuss the factors determining the estuarine fish community structure. More specifically, we focus on the question whether the ichthyofaunal composition at an estuarine site is bottom-up controlled by salinity and temperature or whether its community structure is the result of the partitioning of resources along the heading niches and of predatory pressure.

Abiotic factors structuring the fish community

Fishes come in, locate themselves within estuaries and leave in a seasonal pattern in response to changes in environmental conditions. Community-based studies of estuarine ichthyofaunas have largely linked spatial organization to salinity, turbidity and substrate type and seasonal structure to salinity and temperature (Blaber and Blaber, 1980; Claridge *et al.*, 1986; Potter *et al.*, 1986, 1997; Cyrus and Blaber, 1987*a*; Henderson, 1989; Elliott *et al.*, 1990; Hamerlynck *et al.*, 1993; Thiel *et al.*, 1995; Marchand and Elliott, 1998; Hostens, 2000). When surveying literature, however, it was striking that studies investigating spatial patterns mostly pooled seasonal or monthly data (e.g. Henderson, 1989; Hamerlynck *et al.*, 1993) and that studies analyzing seasonal trends used data from one site (e.g. Claridge *et al.*, 1986; this study). By doing so, most univariate or multivariate techniques used have often produced trivial correlations, because seasonal changes in community structure at one estuarine site are inherently associated to changing temperature and the average spatial species composition on a longitudinal axis must be correlated with salinity. In addition, most individual water quality parameters are intercorrelated. Salinity shows an inverse relationship to turbidity, as high inflow of water in spring increases turbidity and decreases salinity. More generally, seasonal changes in any environmental variable cause strong relationships with temperature. Therefore, we argue that most of the correlations existing between fish distribution and environmental variables are not causal. We support this statement by presenting two examples. At Doel, the seasonal changes in ichthyofaunal compositions were assumed to be caused by sequential immigration and emigration of marine, freshwater and diadromous species. As a result, Nillson's pipefish peaked in abundance in August and September, common goby in October, sand goby in October and November, herring, sprat and bass in December, three-spined stickleback *Gastereosteus aculeatus* and thin-lipped grey mullet *Liza ramada* in January and river lamprey *Lampetra fluviatilis* in February and March. It is thus without any doubt that the community structure of the fish fauna in fall is markedly different from the community structure in spring. Yet, salinity and temperature may be similar during these periods. In addition, these species were each abundant at Doel for a relatively brief period of time. Hence, the maximum abundance of, for example, marine species at Doel should be preceded and followed by maximal numbers at a site downstream of Doel. Put another way, marine species should peak once in abundance at an upper estuarine site but should have two distinct abundance peaks at a lower estuarine site, one during upstream movement and one during seaward movement. Yet, all water quality parameters are most likely dissimilar at these two periods. Hence, if ordination methods were used to analyze seasonal patterns in the lower estuary, the two different abundance peaks may have masked a clear seasonal pattern of species occupancy.

Only by analyzing monthly samples from different stations, the effects of environmental gradients in the fish species composition can be studied. Potter *et al.* (1997) assessed carefully both temporal and spatial variation in the ichthyofauna composition in the Severn estuary. They concluded that the species composition was not related with either salinity or water temperature. Superimposition of salinities on the mean monthly species percentage composition data showed that there was no overall consistent relationship between faunal composition and salinity (Potter *et al.*, 1997). Data from a mesohaline site in a Mississippi estuary support this suggestion, as a variety of euryhaline marine species numerically dominated this area and were found throughout the course of the study even as salinity increased or decreased (Peterson and Ross, 1991).

Although we argued that the impact of salinity in structuring estuarine fish communities may have been overrated, it is clear that salinity can modify the community structure to some degree. For instance, dry winters or wet summers can result in upstream or downstream shifts of communities (Peterson and Ross, 1991; Potter *et al.*, 1997). This contrasts with the situation for sessile organisms and plant communities which have settled along the salinity gradient. Whereas marine fish occur in all areas, most macrobenthic invertebrates are restricted to some part of the estuary with only a few species present on all stations of the estuarine gradient. There is a continual change in species composition rather than a gradual change, mainly controlled by salinity (Beeftink, 1984; Ysebaert, 1993). We suggest that immediate effects of temperature and salinity on fish communities are only displayed if species-specific tolerance limits are exceeded. Yet, it is not excluded that abiotic factors indirectly structure the fish community by affecting prey and predator distribution, or by initiating migration behavior.

Resource partitioning as a structuring mechanism in the fish community

Pianka (1982) has pointed out that dimensions along which species divide resources can be classified under three general headings: food type, habitat and time. Ross (1986) reviewed resource partitioning in fish assemblages. Based on 37 studies which concurrently examined habitat, food and temporal axes, he found that 32% of the studies showed primary separation by habitat, 57% showed the greatest variation by food and 11 % showed temporal variation to be most important. In the Zeeschelde estuary, about 20 species were present at any one time. The total number of fish was, however, close to 60. We argue that the diversity of the fish community is linked to the way species share the space and food niches over the annual cycle. Such temporal subdivisions are only possible because fish are able to move either offshore or inland (Henderson, 1989). We will now examine along which of these niche axes (space, food, time) estuarine fishes share resources.

Spatial partitioning of the estuary. Fish species can separate spatially within the estuary along three axes: a longitudinal axis defined by the salinity gradient, a vertical axis defined by water depth and a horizontal axis defined by the tides. We have already precluded salinity as a major force along which the dominant species separate. The high mobility of fishes, combined with euryhalinity which is a prerequisite for estuarine visitors, are probably much more important in structuring the fish community.

Henderson (1989) concluded that the estuarine fish community held 14% pelagic, 30% demersal and 56% benthic species. The vertical distribution of fishes in the Zeeschelde is discussed in Chapter 6. We have presented evidence that the firm separation of the fish community in a pelagic, demersal and benthic component is not *so* evident as many authors may hold. Most species showed no significant difference in their abundance when caught by stow nets at different depths. And those species with a clear preference for the bottom during day exploited the upper column during night. Therefore, we do not expect that the estuarine fish community was vertically segregated. Furthermore, spatial variation along the vertical axis may be reduced because of the large scale mixing of water and sediments produced by the tidal forces (Henderson et al., 1992).

This means that only one spatial axis remains along which estuarine fish species may segregate, namely the horizontal axis generated by the tides. Daily fluctuations in the water surface level create a gradient with brackish and salt marshes at locations at high tide water levels, intertidal mudflats and sand plates between flood and ebb water levels, and a subtidal area underneath the low tide water level. Superimposed, this gradient changes fortnightly due to alternating springs and neaps, while an annual cycle may further amplify these extremes between high and low tide. The success of benthic species in an estuary is linked to this unique gradient, as shallow areas provide relatively more space. We have investigated an intertidal area nearby the sampling site for several years (Maes *et al.*, 1997; Pas *et al.* 1998; Peeters *et al.* 1999*a*). The fish fauna entering this mudflat during high tide is markedly different from the fauna entrapped by the cooling-water intake. Sole *Solea solea*, flounder, plaice, *Pleuronectes platessa* and eel *Anguilla anguilla* dominated fyke catches. Although this alkso may reflect the selectivity of the fishing gear, we believe that these species show a preference for these areas. Other species such as bass and the common goby may actively search for intertidal salt marsh creeks to exploit the abundant resources (Cattrijsse *et al.*, 1994).

Food partitioning by the estuarine fish community. An abundance of resources may cause a high diet overlap between species. When foraging resources become less abundant, diet overlap is expected to decrease, since interspecific competition becomes more intense (Pianka, 1982; Schoener, 1982, González-Solís *et al.*, 1997). However, if the restrictions in food supply persist, trophic niche overlap may once again increase. A given degree of overlap in use of resources can thus be both cause and consequence of interspecific competition (Holbrook and Schmitt, 1989).

As shallow soft bottoms of estuaries and coastal embayments provide an abundant food supply, neither growth is limited nor severe competition between the epibenthic fish species is observed. As a result, most studies examining trophic niche overlap in estuarine and coastal fish communities have suggested that competition for food is of minor importance (Thorman, 1982, 1983; Evans, 1983, Thorman and Wiederholm, 1984, Thorman and Wiederholm, 1986; Day *et al.*, 1989; Salini *et al.*, 1998). Little experimental work has, however, been done documenting the absence of interspecific competition. Magnhagen and Wiederhom (1982) showed that common goby segregated from sand goby by habitat rather than by feeding strategies, as prey choice and consumption rates were the same but habitat preference differed when the two species were kept together. Our study indicated some degree of trophic niche segregation within the estuarine fish community, as *intra*specific diet compositions between individuals differed significantly less than *inter*specific diet compositions. This result was unexpected, certainly since the total annual foraging impact of the fish community, with addition of two shrimp species was, at maximum, 50% of the annual biomass produced by the dominant prey, the mysid *Neomysis integer* and the copepods *Eurytemora affinis* and *Arcaria tonsa*. This latter observation suggests that food was not limiting and that interspecific competition is unimportant as factor structuring the fish community. It should be stressed, however, that our study assumed little year-to-year difference in production rates. In addition, seasonal data for copepods and mysids could not be obtained. Seasonality may be very important within the estuarine food web. As shown in our study, the fish community undergoes continuous changes due to rapid movements of young fish and crustaceans which stay for a their relatively short period of time. Thus when arrived, fish have to maximize their feeding behaviour and feeding rates. It is possible that migrations sometimes lead to the rapid depletion of resources, even in an estuarine environment.

Muus (1967) examined in detail the times of arrival, growth, and the moment of seaward autumn emigration for the dominant crustacean and fish species in a Danish estuary. The immigration sequence and the trophic sequence formed a pattern that, through the whole summer, seemed to make the exploitation of invertebrate prey in some cases optimal for the consumers, because the migration ensured that there was almost no direct competition. He also found that prey living in the uppermost layer of the substrate, such as harpactoid copepods and amphipods, generally were top-down controlled to a relatively low level, which was maintained through the summer in spite of a high potential of reproduction and growth of these organisms. Whenever there was a reduction in predation pressure, local blooms of these benthic species resulted. This supports our view that at some times, decreased food resources may affect the fish community. Especially in years of high fish recruitment (fish recruitment not being directly linked to estuarine productivity) this may cause differences in niche overlap. Therefore, this topic needs further investigation.

Seasonal partitioning of the estuary. Many fish assemblages, especially coastal ones, are temporally structured, using a habitat for only a given part of the year or period of the life cycle (Ross, 1986). Particularly in estuaries, the complexity of fish movements may produce a regular or occasional presence of over 80 species at one place over the course of the year (Claridge *et al.*, 1986; Henderson, 1989; Potter *et al.*, 1997). Our study is one of the few to show an exceptionally clear pattern of seasonal use of the estuary by fishes. Sampling fish on the cooling-water filter screens at Doel between 1991 and 2000 revealed that the seasonal structure observed is stable. The species composition at any one time of the year is very predictable. The annual cycle in the occurrence and abundance of the fish fauna thus seems important in estuaries, and may provide an important mechanism for resource partitioning (Day *et al.*, 1989). It is tempting to interpret seasonal differences in the abundance of ecologically similar species as evidence for temporal resource partitioning, in which species manage to coexist by using the same limiting resources at different times of the year. The assumption is that competition among species would be more intense than if the same set of species would use the same resource all at the same time. This scenario is most plausible in situations in which resource levels rapidly recover from utilization (Morin, 1999). Estuaries provide such conditions for small invertebrates. The seasonal partitioning of resources in an estuary by fishes and crustaceans could perhaps enhance the long-term stability of these highly dynamic systems (Henderson *et al.*, 1992), time sharing resulting in the nekton carrying capacity of the estuary being fully realized during the year.

Predation as a mechanism controlling fish community structure

Larger fish such as cod *Gadus morhua*, whiting *Merlangius merlangus*, bib *Trisopterus luscus* and pikeperch *Stizeostedion lucioperca* are piscivorous consuming young fish. In addition, waterfowl also forage on fish. Yet, we argued before that predation is not considered a major factor affecting the estuarine fish community. Numbers of predatory fish were low in fyke nets (Maes *et al.*, 1997), cooling-water samples (this study), stow nets (Pas, 1996) and gill nets (Stevens, 2000). Only in December, fishermen tend to capture whiting and cod that are about to recruit into the I-group in their gill nets. Predatory success of piscivores is strongly affected by the high turbidity of the water. Turbid waters increase the escape reaction of prey and decrease the distance at which predators detect their prey (Moore and Moore, 1976; Cyrus and Blaber, 1987*a*, 1987*b*). As a result, fish biomass and density in the turbid

Schelde estuary are higher than in the adjacent less turbid Oosterschelde, but species diversity is lower (Hamerlynk *et al.*, 1993). This suggests that the fish community in the Oosterschelde may be more predator-controlled than that in the Westerschelde and the Zeeschelde.

Effects of abiotic factors, resource partitioning, and predators on the estuarine fish community: finale.

1. The abiotic environment in general and temperature and salinity in particular have often been evoked as important forces structuring estuarine fish communities. Yet, evidence to support their impact is largely circumstantial.

2. Predation is often excluded as a factor contributing to the structure of the estuarine fish community. Our results also suggest that the impact of predation is limited.

3. We have presented arguments that support the idea of a partitioning of resources as a mechanism of structuring the fish community. There is at least some evidence that the habitat gradient, caused by the tidal excursions, is partitioned among species. In this respect, the historical decrease of intertidal wetlands and salt marshes in European estuaries may strongly limit the estuarine fish (and shrimp) populations. Young fish use the estuarine nursery to maximize their feeding rates. Hence, the seasonal partitioning of the estuary possibly contributes to the stability of both the invertebrate prey populations and the predatory fish populations.

Factors controlling the migration behaviour and the abundance of fish in an estuary

Our study has attempted to investigate the ecology of an estuarine fish community by analyzing its distribution pattern. The next step in the study of estuarine fish community structure is to understand what factors explain fish distribution in an estuary. Therefore, two questions need to be addressed. (1) What causes young fish and shrimps to move inland during summer an autumn and to move offshore during autum and winter? (2) What factors determine the year-to-year abundance of fish in the estuary?

Several factors are considered to contribute to the quality of estuaries as areas for temporary colonization by juveniles of marine species:

1. Suitable temperatures promote growth, while low salinities decrease the osmotic differential between the body fluids of the fish and the environment, thereby reducing the energy cost of osmoregulation (Potter *et al.*, 1990). Avoiding unsuitable tempe-ratures and salinities in winter has been related to the seaward movements of fish and shrimps (Claridge and Potter, 1984; Henderson and Holmes; 1987).

2. Intraspecific competition between juveniles and adults can be minimized if juveniles move to shallower waters (Ross, 1986).

3. Gradients in food may attract fish to estuaries. However, the extent to which availability of small invertebrates such as copepods and mysids initiates the movement of fish is difficult to asses (Day *et al.*, 1989). One study by Henderson and Holmes (1989), showed that whiting migrations were directly related to shrimp migrations.

4. The level of predation on juveniles in estuaries is presumably reduced by a lower incidence of piscivores than in their natal marine environment and hence, anti-predator behaviour may cause fish migrations. Turbidity gradients are hypothesized to act as one of the orientation cues for juveniles migrating into estuaries (Blaber, 1997).

Factors controlling the year-to-year abundance of the estuarine fish community are not likely to be linked to the factors controlling fish migration behaviour. Year-to-year abundance probably varies in function of recruitment and mortality. Recruitment itself is determined by reproductive success, distance from the spawning ground, larval survival and the efficiency of larval and juvenile transport (Potter *et al.*, 1997).

Further research: ecological models for species composition and abundance

To determine which of the above mentioned factors control fish migration and variations in year-to-year abundance in the estuary, their role should be investigated in experiments. However, large-scale experiments to discriminate between factors controlling the movement of marine fish to an estuary are difficult to deploy. A solution to this problem may be the use of ecological models. For instance, Werner and Gilliam (1984) presented a model to predict when organisms change between habitats in their life-history. The decision criterion was a size-based cost-benefit ratio, cost being the size specific mortality rate, and benefit being the size-specific growth rate in different habitats. The underlying assumption is that the larger size corresponds to increased fitness (expected lifetime reproduction).

A primary objective of future research should be to quantify the ecological benefits and costs of remaining in the native habitat versus moving into the estuary or out to the sea. Major costs that juvenile fish encounter are habitat- and size-specific predation (Werner and Gilliam, 1984) and the probability of encountering physiologically unfavorable environmental conditions. A major benefit derived from a given habitat is manifested in the size-specific growth rate (Werner and Gilliam, 1984), which is enhanced by the increased productivity of estuaries. Models like the one of Werner and Gilliam (1984) are numerical ones optimize fitness by searching an optimal solution (Limburg, 1996).

A second objective of future research should be the development of models to predict fish abundance in the estuary. In this study, we have presented a model that describes fish abundance in the estuary through the use of migration and mortality parameters. This model may act as the basis for the development of a larger model that includes dispersal rates from the spawning grounds, environmental parameters, a predator submodel, an optimal food source model, real-life mortality rates and hydrodynamics. We strongly believe that more emphasis should be given to the construction of estuarine fish models.

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Summary

This thesis presents an analysis of the structure of the fish community fish of the Zeeschelde estuary (Belgium). The data were obtained from fish catches at the filter screens of power station cooling water intakes. We had four main objectives. (1) the evaluation of the sampling method as a sampling point for fish and crustaceans, (2) a general description of the spatial and temporal changes in the structure of the fish community in the Zeeschelde, (3) an analysis of the seasonal changes in trophic niche width and overlap between the dominant species of the fish assemblage, (4) the estimation of biomass export and recruitment of juvenile marine migrants.

To evaluate a power station cooling water inlet as a sampling point, fish and crustaceans were simultaneously sampled in the cooling water of the nuclear power plant Doel and by stow nets. We hypothesized that there were no differences in species abundance, in mean species length, and in the length-frequency distributions drawn by each method. In total, 39 species were caught, 32 by stow net and 33 in the cooling water, with 26 species common to both methods. Overall, the abundance in the cooling water was three times higher than in the nets but the difference depended on the size of the species. Although average length was for most species significantly higher in stow net samples, almost all length classes present within each population were sampled by the cooling-water intake. The analysis suggests that the cooling-water intake is an effective and representative source for collecting fish and crustaceans reflecting the species abundance in the surrounding waters.

The daily variation in intake catches was studied by examining the effect of tidal and diel periodicity on the intake catches. Two-way analyses of variance was used to detect significant short-term changes in the intake data. Non-linear estimation was used to measure the part of the variance that can be attributed to cyclic phenomena. The number of species was not related with any tidal stage nor with diel effects. Both statistical methods showed the presence of a significant tidal effect in the abundance data. Mainly benthic and demersal fish species experienced significant higher intake risks at high tide and flood tide. For pelagic species the chance on entrapment by the cooling water system was random. A significant diel effect was only observed for two gobiid species and the prawn. At least part of the variance within the field observations could be attributed to cyclic events. The exploitation of intertidal habitats by bottom-orientated species would explain higher intake catches during high tide. Slightly higher catches overnight may be caused by vertical movements.

Spatial and temporal patterns of the fish community were studied in samples collected from the cooling water inlets of three power stations. Between July 1994 and June 1995, 55 different species were recorded including 36 marine migrants, 16 freshwater species and three diadromous species. Only few species dominated the fish community contributing to >96% of the numbers caught on cooling water filter screens. These were three Gobiidae *Pomatoschistus minutus*, *P. lozanoi* and *P. microps*, two Clupeidae *Clupea harengus* and *Sprattus sprattus* with addition of *Syngnathus rostellatus*, *Pleuronectes flesus* and *Dicentrarchus labrax*. It was notable that all these dominating fish species had a marine nature and occurred as juveniles. Both freshwater and diadromous species represented only a

small fraction of the fish community. The abundance of two shrimp species, the common shrimp *Crangon crangon* and the prawn *Palaemontes varians* equalled total fish abundance. Species number as well as fish abundance were correlated significantly with salinity and oxygen concentration. The community structure was analyzed with a correlation biplot based on principal component analysis of the root-root transformed fish abundance. Four separated assemblages could be distinguished since the first principal component expressed a salinity gradient and the second a temperature gradient. During summer and fall *Pomatoschistus microps*, *P. minutus*, *P. lozanoi* and *Syngnathus rostellatus* were most abundant in the brackishwater reach. At this time, freshwater species seemed to avoid the freshwater area. During winter, *Sprattus sprattus*, *Clupea harengus* and *Dicentrarchus labrax* were the dominant species of the brackishwater zone while the freshwater reaches were dominated by *Gasterosteus aculeatus*. Migrating fish such as *Pleuronectes flesus*, *Lampetra fluviatilis*, *Anguilla anguilla* and *Osmerus eperlanus* were restricted to the brackish environment. Seasonal patterns in the fish and crustacean community were studied between July 1994 and June 1995. The brackish-water reach was seasonally used by the community resulting in an exceptionally clear pattern of species occupancy. It is argued that young fish and crustaceans use the highly turbid Zeeschelde estuary as a refuge from predators.

By use of stow netting in the Zeeschelde Estuary, evidence was presented that the vertical distribution of fish changed at night. Demersal fish remained on the bottom during the day while at least a part of the populations exploited surface water during the night. Pelagic fish maintained their position underneath the water surface throughout the day.

Seasonal changes in diet composition, niche width, niche overlap and predation pressure of eight members of the fish community of the Zeeschelde estuary were assessed with a number of descriptive multivariate techniques and randomization procedures. Copepods in terms of numbers and mysids in terms of biomass were the most important prey items. Macrobenthic prey were poorly presented in the diet of most species. Niche width of all fish species as measured by the Shannon-Wiener index changed over the different months but no consistent pattern of variation was found. Although dietary overlap between species was rather high, most of the interspecific pair-wise comparisons of niche overlap differed significantly from one, suggesting that intra-specific niche overlap was higher than interspecific niche overlap. Our results show that the Mantel test, which was used to assess the value of niche overlap, was able to detect small differences in the diet composition of specialist species preying upon a few taxa, whereas it only recognized strong differences in the diet composition of generalist species consuming a wide range of prey. The analysis of niche overlap as well as the use of principal components and two way indicator species analysis (TWINSPAN) suggested that there was at least some degree of niche segregation within the estuarine fish community. This was, however, unexpected because in estuaries, only few prey species dominate the invertebrate community. The fish community consumed about 13 % of the annual prey production suggesting that food was not in short supply. If the consumption of copepods and mysids by shrimps is included, the total annual consumption of the fish and crustacean community amounted to almost 42% of the production of mysids and copepods.

Finally, a model was presented that described fish abundance in an upper estuary as the result of fish migration and mortality. The model was used to estimate biomass transports by migrations between estuary and sea and to assess production assimilated in the estuary. The

model was applied to herring *Clupea harengus*, a marine species of which 0+ juveniles migrate during winter to temperate European estuaries. It was shown that different mortality regimes greatly affected the number of fish that eventually emigrated and hence, the biomass that was exported during the seaward migration. The difference between imported and exported biomass was assessed under different growth conditions and varied from positive to negative as mortality rates increased. The discrepancy between export of biomass and *in situ* produced biomass showed that fish production was not necessarily transported to the sea when emigrating. It was tentatively concluded that export of biomass out of the estuary only occurs if populations move seaward before winter.

These conclusions were compared to findings made in other European estuaries and give rise to a discussion wherein we question which factors contribute most to the stability of the estuarine fish community structure. Further research topics were suggested and included the development of ecological models to study estuarine ichthyofaunas.

Samenvatting

Estuaria vervullen een cruciale rol voor tal van vissoorten. Sommige mariene vissoorten worden er toevallig aangetroffen als dwaalgasten. Van andere mariene vissoorten migreren de juvenielen van onder meer grondels en haringachtigen naar het estuarium om er opgroeien. Estuaria zijn immers gekenmerkt door de hoge voedselconcentratie (landafvloei) en door de afwezigheid van belangrijke predatoren (troebel water). Zoetwatervissen zoals de snoekbaars, de pos en de driedoornige stekelbaars kunnen er gedijen omdat ze goed bestand zijn tegen water met een hoog zoutgehalte. In de winter kunnen karperachtigen er profiteren van de lagere zoutgehaltes. Migrerende vissoorten passeren estuaria op hun doortocht naar de paaigebieden.

In deze thesis wordt de visgemeenschap van het Zeeschelde estuarium (België) nader onderzocht aan de hand van stalen genomen in het koelwater van enkele elektriciteitscentrales. Deze studie heeft vier voorname doelstellingen. De eerste doelstelling is het evalueren van een koelwaterinlaat als staalnamelocatie voor vissen. Meer specifiek willen we nagaan of de bemonstering van vissen in koelwater de werkelijke visdensiteit en de leeftijdsstructuur van de bemonsterde populaties goed benaderd. De tweede doelstelling is de gedetailleerde beschrijving van de temporele en ruimtelijke structuur van de visgemeenschap van het Zeeschelde estuarium. De derde doelstelling is de studie van de voedingsecologie van enkele dominante vissoorten. In het bijzonder wordt nagegaan of er seizoenale veranderingen optreden in de breedte van enkele dominante vissoorten. Ook wordt berekend in welke mate deze niches elkaar overlappen. De vierde en laatste doelstelling is het modelleren van visdensiteit, het transport van biomassa en de productie in het estuarium in functie migratiesnelheid, mortaliteit en groei.

De vangstefficiëntie en de selectiviteit van de koelwaterinlaat van de kerncentrale van Doel werd geëvalueerd door tegelijk stalen van vissen te nemen in het koelwater en met behulp van ankerkuilnetten. Vooraf werd aangenomen dat er geen verschillen waren tussen de vangstefficiëntie en de grootte-selectiviteit van de beide vismethoden. Tijdens dit vergelijkend onderzoek werden, in totaal, 39 verschillende soorten aangetroffen, waarvan 26 soorten zowel in het koelwater als in de netten werden aangetroffen. Alhoewel beide methodes dezelfde populaties bevisten, was de visdensiteit in het koelwater verscheiden keren hoger dan de visdensiteit in de netten. Dit verschil was soortafhankelijk. Bovendien was de koelwaterinlaat minder selectief dan de ankerkuilnetten gezien via het koelwater een breder lengtespectrum perr soort werd bemonsterd. Daarom kunnen we besluiten dat de staalname van vissen en grotere kreeftachtigen via koelwater een geschikte methode is om uitspraken te doen over de werkelijke visdensiteit in de Zeeschelde.

Ondanks de hoge vangstefficiëntie van de bestudeerde koelwaterinlaat is de dagelijkse variatie in de vangsten relatief groot. Om de oorzaak van deze variatie te achterhalen werd in detail nagegaan in welke mate de visdensiteit gemeten in het koelwater varieert in functie van het getijde en de lichtperiode. Met behulp van two-way ANOVA werden significante densiteitsverschillen tussen verschillende getijdenfazen en tussen dag en nacht opgespoord. Met een niet-lineaire regressie werd berekend hoeveel variatie kon worden toegeschreven aan de cyclische fenomenen. Het aantal soorten dat werd aangetroffen veranderde niet in functie van de getijden of de lichtperiode. Wel was er een duidelijk getijdeneffect aanwezig in de inzuigdensiteiten. Vooral benthische en demersale vissen lopen een verhoogd risico om ingezogen te worden bij hoog tij en bij neergaand tij. We vermoeden dat de migratie van het subtidaal naar het intertidaal deels verantwoordelijk is voor de vzerhoogde vangsten. Voor pelagische soorten werd geen trend gevonden. Verschillen tussen dag- en nachtvangsten werden enkel genoteerd voor twee grondelsoorten en voor de steurgarnaal. 's Nachts migreren immers heel wat soorten van de bodem naar hoger gelegen waterlagen. Alleszins is het duidelijk dat een deel van de dagelijkse variatie in de inzuigdensiteiten kan toegeschreven worden aan minstens een van deze cyclische fenomenen.

De seizoenale en ruimtelijke patronen aanwezig in de structuur van de visgemeenschap werden bestudeerd in het koelwater van drie centrales in Doel, Kallo en Schelle. Tussen juli 1994 en juni 1995 werden 55 verschillende vissoorten aangetroffen. Hierbij waren 36 mariene vissoorten, 16 typische zoetwatervissoorten en drie migrerende vissoorten.Slechts enkele van deze vissoorten domineren de levensgemeenschap wat betreft aantallen en biomassa. Het betreft drie grondelsoorten (Gobiidae) *Pomatoschistus minutus*, *P. lozanoi* and *P. microps*, twee haringachtigen (Clupeidae) *Clupea harengus* and *Sprattus sprattus*, en verder *Syngnathus rostellatus*, *Pleuronectes flesus* en *Dicentrarchus labrax*. Al deze soorten zijn mariene vissoorten waarvan enkel de juvenielen de Zeeschelde bezoeken. Zoetwatervissen en trekvissen komen slechts in beperkte aantallen voor. Ongeveer de helft van de totale jaarlijkse vangst in het koelwater bestaat uit de garnalen *Crangon crangon* en *Palaemontes varians*. Het voorkomen van vissen in het Zeeschelde estuarium is significant gecorreleerd aan de veranderingen in saliniteit en zuurstofconcentratie. De ruimtelijke gemeenschapsstructuur werd geanalyseerd met behulp van ordinatiemethoden. De eerste twee ordinatie-assen waren respectievelijk gecorreleerd aan saliniteit en temperatuur. Aldus werden vier deelgemeenschappen onderscheiden. Tijdens de zomer en het najaar domineren *Pomatoschistus minutus*, *P. lozanoi*, *P. microps* en *Syngnathus rostellatus* de visgemeenschap in het brakke deel van de Zeeschelde. Op dat moment wordt het zoetwaterdeel van het estuarium door vissen vermeden. Tijdens de winter komen *Sprattus sprattus*, *Clupea harengus* en *Dicentrarchus labrax* in grote aantallen voor in het brakwaterdeel. Hogerop wordt het zoetwaterdeel bevolkt door voornamelijk *Gasterosteus aculeatus*. De verspreiding van trekvissen zoals *Pleuronectes flesus*, *Lampetra fluviatilis*, *Anguilla anguilla* en *Osmerus eperlanus* blijft beperkt tot het brakwaterdeel van de Zeeschelde. De soortensamenstelling in dit deel van de Schelde verandert seizoenaal. Deze seizoenale veranderingen in soortensamenstelling worden vermoedelijk veroorzaakt opeenvolgende migratie-golven van jonge vissen die er beschutting vinden tegen vispredatoren.

De verticale verdeling van de vispopulaties verandert tijdens de nacht. Dit werd achterhaald door gebruik te maken van ankerkuilnetten. Demersale vissen verblijven overdag op de bodem. 's Nachts verkennen ze de hoger gelegen waterlagen. Pelagische soorten verblijven zowel overdag als 's nachts vlak onder het wateroppervlak.

Seizoenale veranderingen in de trofische structuur van de visgemeenschap werden bestudeerd aan de hand van maaganalyses uitgevoerd op de meest voorkomende vissoorten.De belangrijkste prooi-items waren copepoden en aasgarnalen. Macrobenthische prooien werden nauwelijks geconsumeerd. De nichebreedte van de vissoorten, gemeten aan de hand van de Shannon-Wiener index, varieert over de stalen maar een consistent seizoenaal patroon werd niet terug gevonden. De niche overlap tussen de meeste vissoorten was vrij hoog. Nochtans bleek uit een Mantel test, uitgevoerd op paarsgewijze combinaties van prooispectra, dat de intraspecifieke niche overlap groter is dan de interspecifieke niche overlap wat aantoont dat er een zekere trofische nichesegregatie bestaat tussen de verschillende vissoorten. Ook het gebruik van multivariaat beschrijvende methoden (TWINSPAN en principaal componenten) leidde tot dit besluit. Nochtans werd geschat dat de visgemeenscahp op jaarbasis slechts 13% van de prooiproductie consumeerde. Wordt er rekening gehouden met garnalen, dan stijgt de geschatte predatie-impact op aasgarnalen en copepoden door gemeenschap van vissen kreeftachtigen tot iets meer dan 40%. Dit geeft aan dat voedsel niet limiterend is voor de vis- en kreeftachtigengemeenschap. Wij argumenteren dan ook dat het voorkomen van voldoende habitats in de vorm van slikken en schorren mogelijk limiterend kan zijn voor vissen en garnalen.

In de laatste deelstudie wordt een model gepresenteerd dat de densiteit van jonge haring *Clupea harengus*, beschrijft in functie van migratiesnelheid en mortaliteit. Met dit model kunnen we aantonen dat mortaliteit in sterke mate de rekrutering en de getransporteerde biomassa naar zee beïnvloedt. Het verschil tussen biomassa geïmporteerd tijdens de immigratie in het estuarium en de biomassa geëxporteerd tijdens de emigratie naar zee werd berekend voor verscheidene groeimodellen. Dit netto verschil kan negatief worden als de mortaliteit toeneemt. Dit betekent dat biomassa die geproduceerd wordt tijdens de aanwezigheid in de Zeeschelde niet noodzakelijk wordt geëxporteerd naar zee.

Tot slot worden de algemene besluiten van dit onderzoek vergeleken met de resultaten van visbemonsteringen in andere Europese estuaria. Hierbij gaat de meeste aandacht uit naar de vraag welke factoren bepalend zijn voor een stabiele structuur van de levensgemeenschap. Ook suggereren we topics voor verder onderzoek. Het bouwen van ecologische vismodellen neemt hierbij een centrale plaats in.