J. Mar. Biol. Ass. U.K. (2003), **83**, 603–612
Printed in the United Kingdom

The diet and consumption of dominant fish species in the upper Scheldt estuary, Belgium

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Seasonal changes in the diet composition and trophic niche overlap were examined for the dominant members of the fish assemblage of the turbid low-salinity zone of the Scheldt estuary (Belgium). Samples of fish were taken in the cooling water of a power plant. Juveniles of eight species dominated the fish assemblage: two goby species, herring, sprat, bass, flounder, eel and pikeperch. Together, they had preyed upon 31 different prey taxa. Calanoid copepods and hyperbenthic mysids were the most important prey items with macrobenthic invertebrates being largely ignored. Pair-wise comparisons of trophic niche overlap showed that, in general, niche overlap between individuals of the same species was significantly higher than overlap between individuals from different species, suggesting that the available food resources were partitioned. The total annual prey consumption by the dominant fish species was estimated at 610 mg ash-free dry weight m^{-3}.

INTRODUCTION

Wetlands are nursery areas to many fish species. They supply abundant food resources and offer protection from predators (Day et al., 1989). Especially salt marshes, intertidal mudflats and mangroves, low-salinity areas at the head of estuaries and sea grass beds have proved their role as nurseries (Haedrich, 1983; Day et al., 1989). Accordingly, these areas often support high numbers of larval and juveniles stages of marine and freshwater fish species. The turbid low-salinity zone of the Scheldt estuary (Belgium) may be such a crucial refuge to young fish. Analysis of the temporal patterns of species occurrence has revealed that about 60 species share this area (Maes et al., 1998a). These species have different seasonal patterns of occurrence, so on average, 20 species are present at any one time. Eight fish species dominate the assemblage, including two pelagic, two demersal and four benthic species, representing over 90% of the numbers caught on cooling-water intake screens of a power plant (Maes et al., 1998a). They contribute particularly to the overall energy and nutrient fluxes through the trophic level of secondary consumers. Although the diets of most of these species have been analysed, little attempt has been made to assess seasonal variation in the partitioning of resources by fish communities which occur in low-salinity zones (Henderson et al., 1992; Thiel et al., 1996). Besides, quantitative assessment of the predation impact of estuarine fish on their principal prey is relatively scarce (Evans, 1983; Benneth & Branch, 1990).

The purpose of this paper was to analyse the trophic structure of the fish assemblage of the turbid brackish water zone of the Scheldt estuary and to estimate its impact on lower trophic levels by considering its dominant components. Estuaries and coastal areas are believed to provide non-limiting resources to the level of consumers (Barnes, 1974). As a result, estuarine fish often feed opportunistically on copepods, mysids and caridean shrimps (Hostens & Mees, 1999). The high productivity and standing stock of invertebrate prey may cause high niche overlap between species (Pianka, 1982) and it has been postulated that the impact of fish on these prey populations is rather low (Hostens & Mees, 1999). We have considered these assumptions by using seasonal data from stomach contents analyses on the dominant fish species sampled in the cooling water of an estuarine power plant. Based on literature and field-derived parameters on the daily ration of fish on the one hand and the density of fish in cooling water samples on the other hand, an annual budget of fish consumption was assessed.

MATERIALS AND METHODS

Study area

The Scheldt estuary (Figure 1) is a macrotidal, coastal plain estuary with an average water depth of 11 m. Strong currents in the estuary keep large quantities of silt in suspension. Salt water intrudes for about 100 km inland (Soetaert & Herman, 1995). Although seasonal and annual fluctuations in salinity may be large, salinity zones are relatively stable (Soetaert & Herman, 1995). The lowest oxygen levels are measured in the upper estuary where the heavy load of organic matter catalyses an intense heterotrophic bacterial activity (Heip, 1988). The lower estuary has a much better oxygenated water column, with oxygen saturation increasing from 50% at the Belgian–Dutch border to >90% at the mouth of the estuary.

Collection of the fish and laboratory procedures

Fish were collected on 11 July, 7 October and 4 December 1994 and on 21 March 1995 by sampling the cooling-water

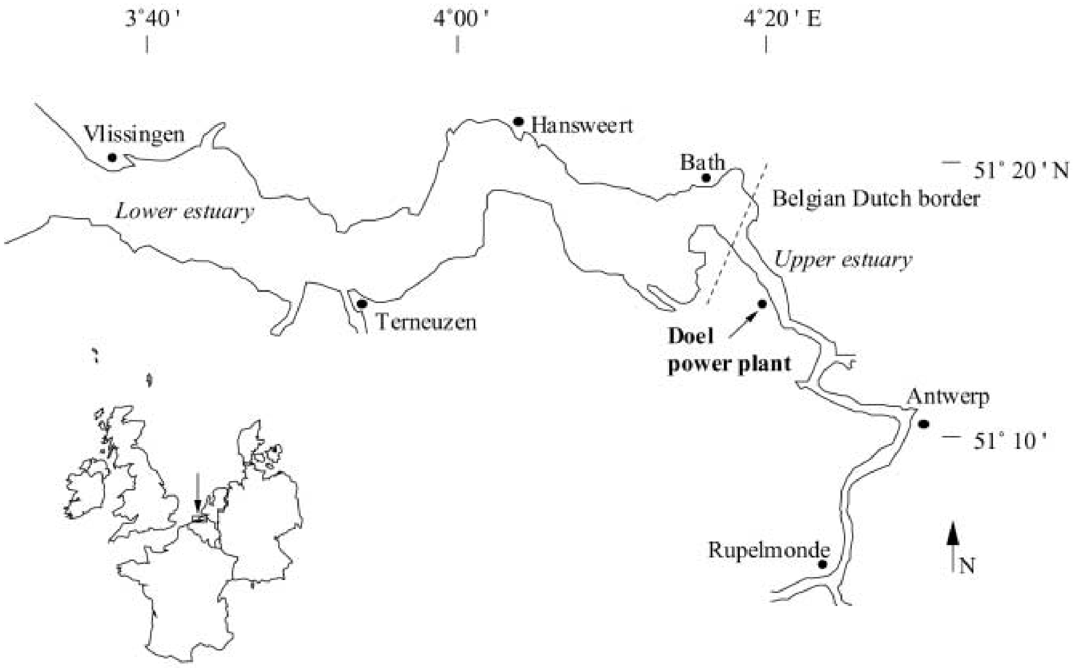

Figure 1. Map of the of the study area and position of the sampling site.

intake screens of the power station Doel (Figure 1). Salinity at the sampling site averaged 8 g l^{-1} and 75% of the annual turbidity measurements were in the range of 38 to 77 mg suspensoids l^{-1}. The cooling-water intake is situated in the subtidal channel about 75 m in an offshore direction of the low water mark. The position of the intake resulted in very high catches of fish and shrimps, mostly exceeding 10^3 individuals captured per hour.

Cooling water (25.1 m^3 s^{-1}) is withdrawn two metres above the bottom. Vertical travelling water screens with a mesh size of 4 mm remove the fish from the cooling water and afterwards, fish are flushed into a container, the sampling point. The time that fish spent between the intake point in the river and the sampling point was 20 min. During each sampling day (24 h), eight sub samples (50×10^3 m^3 cooling water) covering two tidal cycles were taken. Per sample, fish were counted, measured, anaesthetized with benzocaine and fixed in 7% formaldehyde. In July 1994, stomachs of herring *Clupea harengus* L., European eel *Anguilla anguilla* (L.), sand goby *Pomatoschistus minutus* (Pallas) and pikeperch *Stizostedion lucioperca* (L.) were analysed. In 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. In 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 others are benthic (Elliott & Dewaily, 1995).

Per sub sample and per species, the contents of 20 stomachs were removed and the total prey biomass in mg ash-free dry weight (mg ADW) that was present in the stomach was estimated after incineration at 550°C. To standardize the diet analysis, only samples taken at high tide were used to describe the diet composition of fish. Before incineration, the food organisms were identified to the lowest possible taxon and all prey organisms were counted. Prey in early stages of digestion were measured. If needed, telson–standard length and standard length–total length regressions were used (Henderson & Holmes, 1987; Hamerlynck et al., 1990; Mees et al., 1994). Ash-free dry weight 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.

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 analysed. Percentage abundance or weight is the ratio between total abundance or weight ratings of a single food organism and the total derived from all dietary constituents.

Assessment of the trophic structure and niche overlap

The trophic structure of the fish assemblage was investigated by two-way indicator species analysis (Marshall & Elliott, 1997). The analysis 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 the percentage by occurrence of 25 prey types. Prey occurring in less than 0.5% of the stomachs analysed were excluded from the analysis.

The degree of interspecific diet overlap was assessed using Renkonen's index of similarity P (Marshall & Elliott, 1997) (eqn 1):

$$P_{jk} = \sum_i \min(p_{ij}, p_{ik}) \quad (1)$$

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 zero for entirely dissimilar diets to one 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 (Mantel, 1969). This test determines the significance of a correlation between a matrix with all possible pair-wise combinations of niche overlap and a binary matrix containing ones in the positions of the diet overlap measured between individuals of the same species and zeros otherwise. The significance of the correlation coefficient r between these two matrices was evaluated through the use of a Monte Carlo procedure where the ones and zeros of the binary matrix were permuted one thousand times. A significant positive correlation indicates that two individuals from the same group have a higher (intraspecific) niche overlap than two individuals from different groups (interspecific niche overlap) (Manly, 1989).

Estimation of the daily ration and annual consumption

The consumption of prey by seven fish species was assessed using the daily food ration. We adopted the model of Eggers (1977) to calculate the individual daily ration. A literature review showed that the Eggers (1977) model is the most appropriate to compute daily rations based on stomach content data obtained from field studies (Héroux & Magnan, 1996). The estimation of the daily ration C_{24} is given by eqn 2:

$$C_{24} = W_{24} \times R \times 24 \qquad (2)$$

where W_{24} is the mean weight of the food content over 24 h (mg ADW) and R is the instantaneous evacuation rate (h^{-1}). Evacuation rates were derived from literature or from the field observations. Following Boisclair & Marchand (1993), Boudewijns (2000) estimated the evacuation rate of herring and sprat sampled in Doel as the maximum rate for each three hour time interval assuming an exponential evacuation of food. The evacuation rate of sand goby and common goby was calculated according to Andersen (1984): $R = 7.385 \times L^{-0.832} \times \exp[0.0639(t-20)]$ where L is the total length of the goby in mm and t the ambient water temperature (°C). This model was developed for the common goby only but we assume it to be valid for the sand goby. Koed (2001) described the gastric evacuation of pikeperch as $R = 0.000173 \times \exp(0.15t) \times L^{1.15} \times W_{24}^{0.5}$ where L is the total length in cm and t the water temperature in °C. The daily ration of flounder sampled in March 1995 was computed using an evacuation rate measured in plaice, *Pleuronectes platessa* L., that were kept in water of 10°C (Jobling, 1980). Santulli et al. (1993) determined the gastric evacuation of 0-group bass resulting in a rate of 0.028% wet body weight h^{-1} at 15°C. We reanalysed the data of Santulli et al. (1993) using an exponential model instead of a linear model. This procedure yielded an evacuation rate of 0.0552 h^{-1} and we will use this value for the analysis. Data on the daily variation on the stomach content of eel were unavailable due to small sample sizes (<20 individuals per subsample) and therefore, eel was excluded from the consumption budget.

The daily population consumption was estimated by multiplying the daily rations per fish by the population numbers (numbers 10^{-3} m^{-3}) as derived from the cooling water samples. The annual consumption was calculated by multiplying the average daily population consumption with 365.

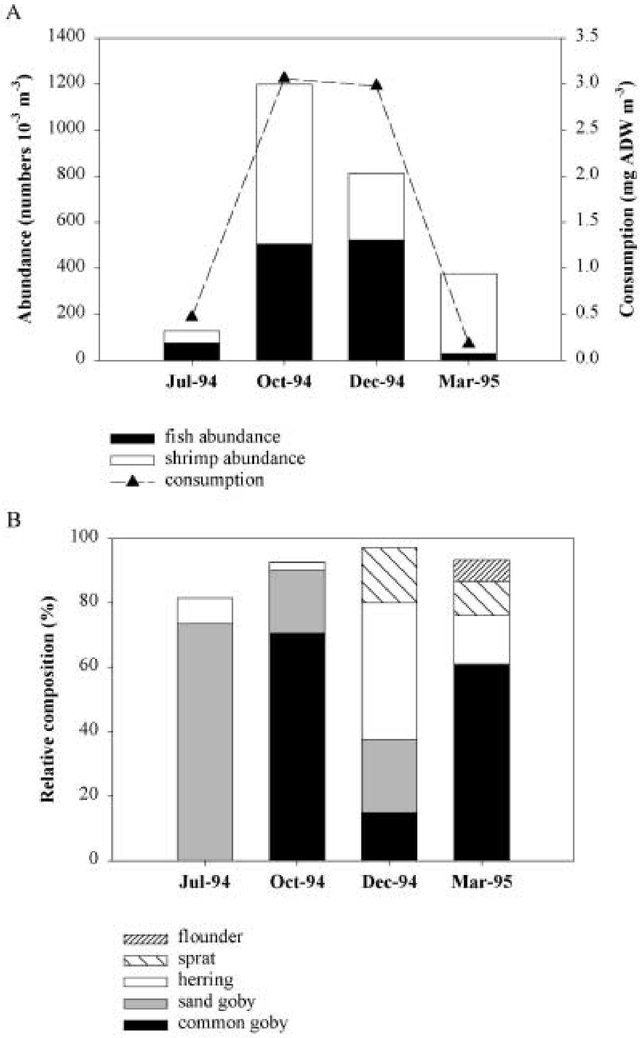

Figure 2. (A) Seasonal changes in the abundance of fish and shrimps in cooling water samples taken at the power plant Doel and variation in the total daily consumption of the dominating fish species. (B) Relative contribution of five fish species to the total abundance of fish in the cooling water samples.

RESULTS

During the study period, the fish catch consisted mainly of gobies and clupeids. Together with bass, eel, flounder and pikeperch, they contributed to >90% of the total yearly catch by the cooling-water intake. Besides fish, also shrimps and crabs were retained by the filter screens. Shrimps contributed to 53% of the total annual catch (Figure 2A). Two species were recorded: the common shrimp *Crangon crangon* (L.) and the prawn *Palaemonetes varians* (Leach). The species composition as well as the abundance of fish varied seasonally (Figure 2A,B). The total fish density in the cooling water ranged between 0.031 m^{-3} and 0.53 m^{-3}. Apart from eel, the majority of the fish were in their first year of growth (0-group) (Table 1, length ranges). Details of the seasonal occurrence of fish populations nearby the sampling station are presented in Maes et al. (1998a).

Analysis of the diet

During the study, 420 stomachs were analysed for their contents. A total of 31 prey taxa was distinguished. Copepods in terms of numbers and mysids in terms of weight were the most important prey items as revealed by stomach analysis. Table 1 presents the composition of the stomach contents expressed as the annual average of the percentage occurrence, percentage abundance and percentage weight. The main components in the diet of herring and sprat throughout the study were calanoid copepods. The mysids *Neomysis integer* (Leach) and *Mesopodopsis slabberi* (Van Beneden) were important food supplements, especially in the fall. Also the common goby fed almost exclusively on calanoid copepods. Additional prey items were annelids and *Daphnia* sp. in March, the mysids *N. integer* and *M. slabberi* in October and cirripeds and the amphipod *Corophium volutator* (Pallas) in December. The diet of sand goby consisted of calanoid and harpacticoid copepods in March and *C. volutator* and *N. integer* in other

Table 1. *The composition of the stomach contents of eight fish species. Stomach analyses contents are expressed as an annual average of percentage occurrence (%O), percentage abundance (%N) and percentage biomass or weight (%W).*

	Clupea harengus			*Sprattus sprattus*			*Dicentrarchus labrax*			*Pleuronectes flesus*		
Dietary categories and items	%O	%N	%W	%O	%N	%W	%O	%N	%W	%O	%N	%W
Annelida												
Nereis sp.	–	–	–	–	–	–	14.7	1.3	3.7	57.0	3.0	53.0
Oligochaeta	–	–	–	–	–	–	3.7	1.0	0.2	14.0	0.5	1.0
unidentified annelids	–	–	–	–	–	–	2.3	0.2	0.2	–	–	–
Mollusca												
Gastropoda												
unidentified gastropods	–	–	–	–	–	–	3.0	1.0	0.2	–	–	–
Arthropoda (Crustacea)												
Ostracoda	–	–	–	2.5	0.3	0.3	–	–	–	–	–	–
Anomopoda												
Daphnia sp.	14.5	0.8	1.8	47.5	1.0	1.0	4.3	3.7	0.2	–	–	–
Ceriodapnhia sp.	13.0	0.3	0.8	47.5	1.0	1.0	–	–	–	–	–	–
Bosminidae	–	–	–	2.5	0.3	0.3	–	–	–	–	–	–
Copepoda												
Calanoidea	63.8	89.8	55.3	91.5	84.5	62.5	11.0	19.7	0.3	64.0	86.0	3.0
Harpacticoidea	45.5	4.3	0.5	50.0	6.0	1.0	8.7	5.0	0.2	–	–	–
Cirripeda	–	–	–	–	–	–	–	–	–	–	–	–
Mysidacea												
Neomysis integer	23.5	2.0	24.8	16.5	0.5	2.0	13.7	1.7	13.0	21.0	2.0	38.0
Mesopodopsis slabberi	21.0	2.1	5.3	16.5	6.0	32.5	–	–	–	–	–	–
unidentified mysids	13.0	0.5	5.3	–	–	–	6.7	0.2	3.0	–	–	–
Isopoda												
Lekanesphaera rugicauda	–	–	–	–	–	–	10.3	7.0	0.5	–	–	–
Gnathiidae	3.0	0.1	0.3	2.5	0.3	0.3	16.0	3.5	4.7	–	–	–
unidentified isopods	–	–	–	–	–	–	2.3	0.2	0.2	–	–	–
Amphipoda												
Orchestia sp.	–	–	–	–	–	–	7.3	9.0	2.7	–	–	–
Gammarus salinus	2.8	0.3	3.3	–	–	–	4.3	0.3	1.3	21.0	1.0	3.0
Bathyporeia sp.	–	–	–	–	–	–	6.0	1.2	0.3	–	–	–
Corophium volutator	11.0	0.5	1.6	–	–	–	9.0	1.0	0.3	29.0	6.0	2.0
Pleusymptes sp.	–	–	–	2.5	0.3	0.3	–	–	–	–	–	–
unidentified amphipods	–	–	–	–	–	–	6.7	0.3	0.3	14.0	0.5	0.5
Decapoda												
Palaemonetes varians	–	–	–	–	–	–	38.3	25.2	23.7	–	–	–
Crangon crangon	10.5	0.4	1.0	–	–	–	33.7	14.8	39.7	–	–	–
unidentified carideans	–	–	–	–	–	–	–	–	–	–	–	–
Majidae	–	–	–	–	–	–	–	–	–	–	–	–
unidentified crustaceans	1.5	0.1	0.3	21.5	0.8	1.3	2.3	0.2	0.2	–	–	–
Arthropoda (Insecta)												
Chironomidae	1.5	0.1	0.3	–	–	–	2.3	0.2	0.2	–	–	–
Chelicerata												
Acaridae	–	–	–	–	–	–	–	–	–	–	–	–
Chordata												
Teleostei	1.5	0.1	0.1	–	–	–	–	–	–	–	–	–
Number of fish analysed		80			40			60			20	
Length range (mm)		39–115			52–77			60–132			70–115	
Number of empty stomachs		22			14			14			6	
Average number of prey items		202.3			310.5			11.8			13.0	

Table 1. *Continued.*

	Pomatoschistus microps			*Pomatoschistus minutus*			*Stizostedion lucioperca*			*Anguilla anguilla*		
Dietary categories and items	%O	%N	%W	%O	%N	%W	%O	%N	%W	%O	%N	%W
Annelida												
Nereis sp.	–	–	–	3.8	0.1	0.1	–	–	–	15.0	2.0	4.3
Oligochaeta	3.3	0.3	1.3	1.8	0.1	0.1	–	–	–	6.5	0.5	1.0
unidentified annelids	5.3	0.2	0.2	7.8	0.5	0.1	10.0	7.0	0.5	4.0	0.5	0.3
Mollusca												
Gastropoda												
unidentified gastropods	–	–	–	–	–	–	–	–	–	–	–	–
Arthropoda (Crustacea)												
Ostracoda	–	–	–	–	–	–	–	–	–	–	–	–
Anomopoda												
Daphnia sp.	7.3	0.7	1.7	3.8	0.1	0.5	–	–	–	–	–	–
Ceriodapnhia sp.	–	–	–	–	–	–	–	–	–	–	–	–
Bosminidae	2.0	0.2	0.2	–	–	–	–	–	–	–	–	–
Copepoda												
Calanoidea	66.3	88.7	55.7	30.3	30.0	9.3	–	–	–	4.0	2.0	0.3
Harpacticoidea	20.3	3.3	0.2	13.3	3.8	0.3	–	–	–	–	–	–
Cirripeda	6.7	1.5	0.3	6.8	4.8	0.1	–	–	–	4.0	0.5	0.3
Mysidacea												
Neomysis integer	2.7	0.2	7.0	33.0	27.8	37.8	40.0	29.0	63.0	56.5	52.5	67.5
Mesopodopsis slabberi	5.7	0.3	5.0	8.3	6.5	0.6	10.0	7.0	0.5	25.0	9.0	2.0
unidentified mysids	–	–	–	2.3	1.5	1.8	–	–	–	–	–	–
Isopoda												
Lekanesphaera rugicauda	–	–	–	–	–	–	–	–	–	–	–	–
Gnathiidae	–	–	–	13.8	7.9	24.5	–	–	–	–	–	–
unidentified isopods	2.7	0.2	0.7	1.8	1.0	2.8	–	–	–	–	–	–
Amphipoda												
Orchestia sp.	–	–	–	–	–	–	–	–	–	–	–	–
Gammarus salinus	–	–	–	–	–	–	–	–	–	–	–	–
Bathyporeia sp.	–	–	–	–	–	–	–	–	–	–	–	–
Corophium volutator	4.7	1.3	5.0	5.8	8.8	0.5	–	–	–	29.0	12.0	0.5
Pleusymptes sp.	–	–	–	–	–	–	–	–	–	–	–	–
unidentified amphipods	2.7	0.2	0.2	–	–	–	–	–	–	–	–	–
Decapoda												
Palaemonetes varians	–	–	–	–	–	–	–	–	–	21.0	4.5	9.5
Crangon crangon	–	–	–	2.3	1.5	2.5	10.0	7.0	0.5	15.0	4.0	2.3
unidentified carideans	–	–	–	1.8	0.1	0.1	–	–	–	15.0	2.5	3.3
Majidae	–	–	–	–	–	–	–	–	–	4.0	0.5	0.3
unidentified crustaceans	26.3	3.3	22.7	1.8	0.1	1.5	10.0	7.0	13.0	16.5	1.5	1.5
Arthropoda (Insecta)												
Chironomidae	2.0	0.2	0.3	1.8	0.1	1.5	–	–	–	–	–	–
Chelicerata												
Acaridae	–	–	–	1.8	0.1	0.1	–	–	–	–	–	–
Chordata												
Teleostei	–	–	–	1.8	1.3	5.0	60.0	42.0	22.0	19.0	7.0	9.0
Number of fish analysed		80			80			20			40	
Length range (mm)		25–44			31–79			45–73			118–342	
Number of empty stomachs		23			28			5			11	
Average number of prey items		12.3			4.9			0.7			4.2	

months. The stomach contents of eel were dominated by *N. integer* and *C. volutator*. The shrimp species *P. varians* and *Crangon crangon* and teleost fish were also included in its diet. Bass fed mainly on caridean shrimps. Other crustaceans present in the diet of bass were *N. integer*, the amphipods *Orchestia* sp. and *Bathyporeia* sp. and the isopod *Lekanesphaera rugicauda* (Leach). In stomachs of flounder, calanoid copepods represented 86% of the contents. *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 *N. integer*, while teleosts, annelids and caridean shrimps were important supplementary food items.

Two-way indicator species analysis separated the species into seven different groups, each sharing particular prey items (Figure 3). 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. In the latter group, four different clusters were recognized: a group comprising winter samples of bass and sand goby and a spring sample

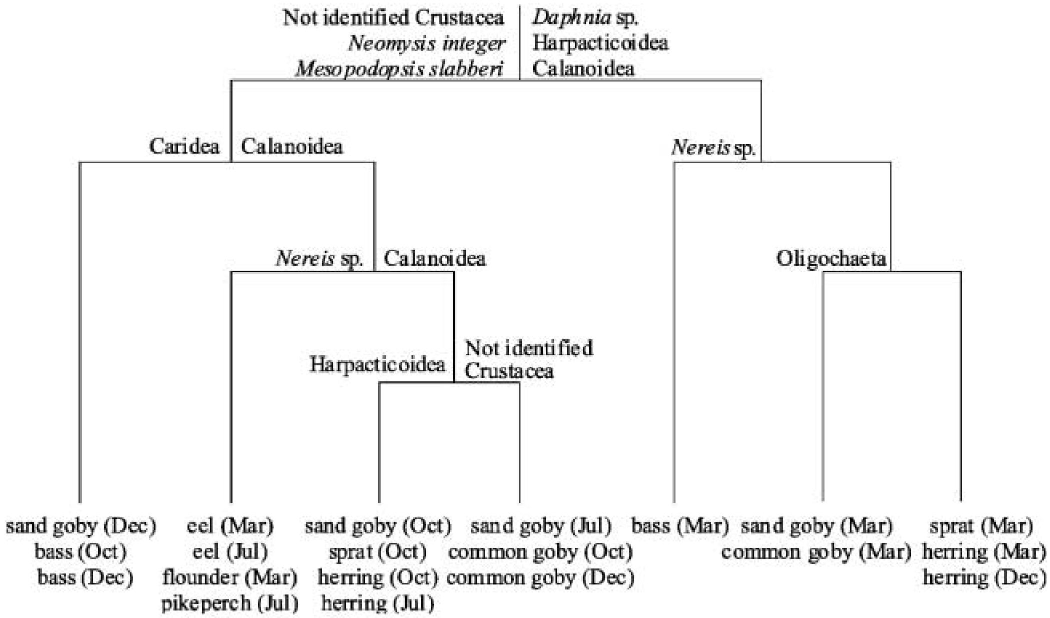

Figure 3. Dendrogram showing dietary similarities within the fish community of the brackish part of the Scheldt throughout a seasonal gradient as revealed by two-way indicator species analysis.

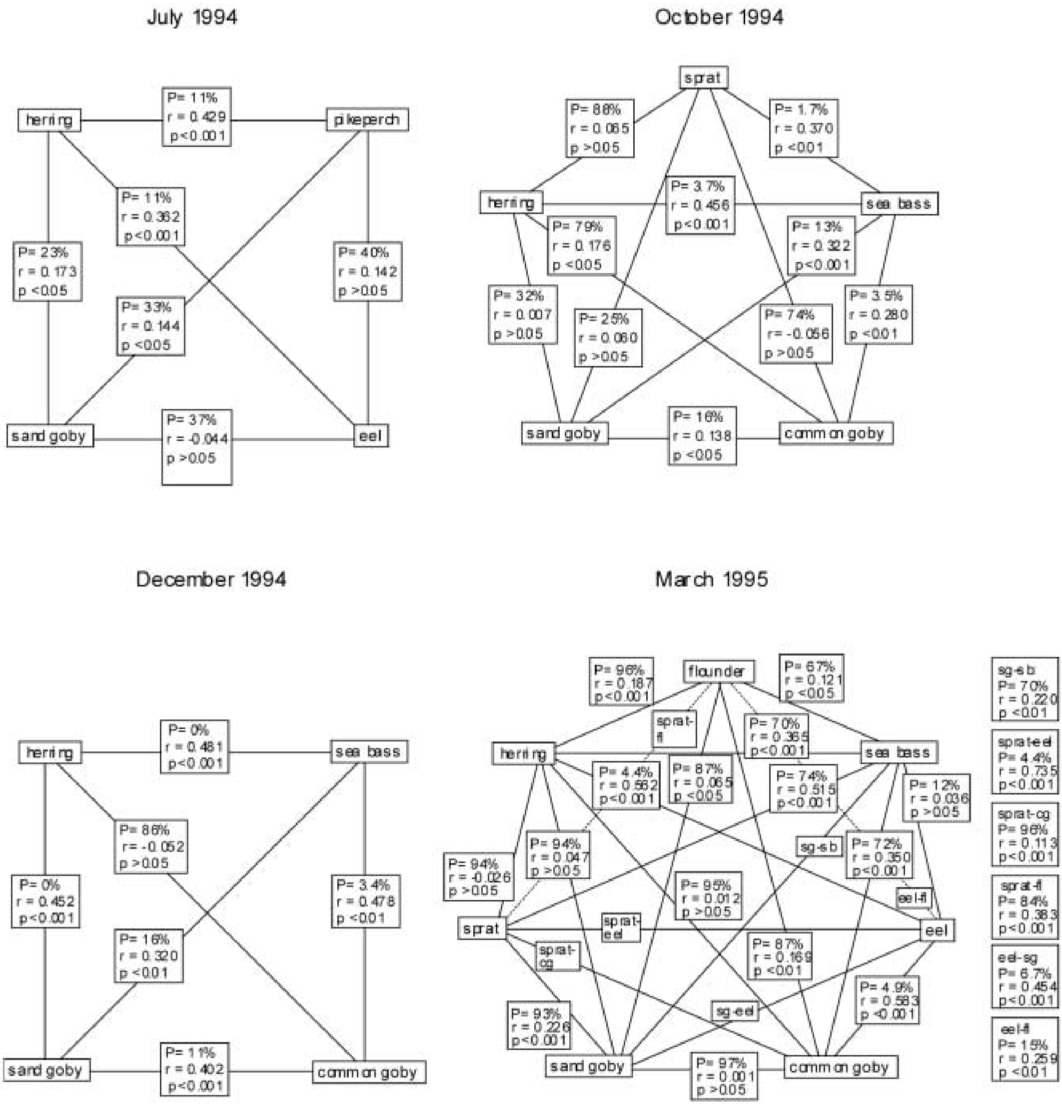

Figure 4. Interspecific diet overlap measured in four different months. Boxes between the species display the Renkonen's index of diet overlap P (%), the species pair-wise correlation coefficient r yielded by a Mantel test and significance level p. A significant positive correlation indicates that two individuals of the same species have a significantly higher overlap than two individuals from different species.

Table 2. *Estimation of the individual daily ration and daily population consumption of seven fish species. Daily rations were computed per month. The relative contribution of the species that were included in the consumption assesment to the total catch in numbers is given as a percentage.*

Month	N	W_{24}	R	C_{24}	C
July 1994	82%				
herring	6.6	2.76	0.16	10.6	0.070
pikeperch	0.5	1.76	0.09	3.8	0.002
sand goby	57.8	0.64	0.45	6.9	0.396
October 1994	93%				
bass	1.9	14.48	0.06	19.2	0.036
common goby	358.7	0.40	0.31	2.9	1.050
herring	11.9	3.33	0.61	48.8	0.578
sand goby	99.2	3.21	0.18	13.9	1.383
sprat	0.9	1.61	0.36	13.9	0.012
December 1994	97%				
bass	1.6	6.93	0.06	9.2	0.015
sand goby	119.2	1.96	0.15	6.9	0.824
common goby	78.3	0.23	0.22	1.2	0.096
herring	222.6	1.17	0.30	8.4	1.875
sprat	90.0	0.26	0.30	1.9	0.168
March 1995	95%				
bass	0.5	4.93	0.06	6.5	0.003
common goby	18.8	0.59	0.17	2.5	0.046
flounder	2.1	2.07	0.04	2.2	0.005
herring	4.7	7.53	0.12	21.7	0.101
sand goby	0.1	0.58	0.15	2.1	<0.001
sprat	3.3	3.52	0.08	6.8	0.022

N, fish abundance (numbers 10^{-3} m^{-3}); W_{24}, average stomach content over 24 h (mg ADW); R, instantaneous evacuation rate (h^{-1}); C_{24}, average individual daily ration (mg ADW d^{-1}); C, daily consumption of the population (mg ADW m^{-3} d^{-1}).

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.

Analysis of the niche overlap

Dietary overlap between species was rather high but not uniform across months (Figure 4). In July, 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. However, the diet composition of both goby species differed significantly. Diet overlap between bass and the other members of the fish assemblage was always $<13\%$. 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*. In March, herring, sprat, common goby and sand goby had almost identical niches, all feeding almost exclusively on copepods. Although diet overlap between sprat and gobies 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.

Annual consumption of fish

Table 2 summarizes all the data that were used to estimate the daily consumption of fish in the study area. Monthly variation in daily ration was evident and caused both by changes in the average stomach content and temperature-dependence of the instantaneous evacuation rates. The relative contribution of the fish species that were included in the consumption assessment to the total numbers sampled varied between 82% and 97% (Table 2). Hence, these species contribute principally to the overall consumption of the fish assemblage nearby the sampling station. The seasonal pattern in total daily consumption resembled the seasonal changes in fish density (Figure 2A) and ranged between 0.18 mg ADW d^{-1} in March 1995 and 3.06 mg ADW d^{-1} in October 1994. The total annual consumption of prey was estimated at 609.9 mg ADW m^{-3}.

DISCUSSION

Before discussing our results, we consider first the possible advantages and disadvantages of the sampling technique for analysing dietary habits of fish. Sampling in estuarine power station cooling-water inlets has been successfully used to analyse the species composition of fish faunas (Van Damme et al., 1994), spatial and temporal assemblage patterns (Claridge et al., 1986; Henderson, 1989; Potter et al., 1997), dietary habits of fish populations (Van den Broek, 1978) and trophic structure of fish communities (Henderson et al., 1992). A comparison with stow net fishery in the close vicinity of the cooling-water inlet suggested that the intake was an effective source for collecting pelagic, demersal and benthic fish (Maes et al., 2001). This sampling technique provided a good estimate of the species abundance of the surrounding waters but the method was selective towards smaller species and juveniles (Maes et al., 2001). At Doel, fish took 20 min to reach the sampling point after capture by the intake. As a result, no substantial digestion occurred and most food organisms could be identified. For the diet analysis, we selected the stomachs from high tide samples. At this time, teleosts feeding on the intertidal mudflats were outside the influence area of the cooling-water intake and hence, not available for capture. Accordingly, the conclusions of this study are applicable to the fish assemblage feeding in the subtidal area of the brackish water part of the estuary.

Prey availability and diet composition

Our analysis of the stomach contents of two pelagic, two demersal and four benthic fish species inhabiting the upper estuary indicated that this feeding guild mainly foraged on hyperbenthic mysids and pelagic copepods.

Thiel (2001) found similar results for the upper Elbe estuary (Germany) and Costa & Elliott (1991) stress the importance of these prey for estuarine fish in the Tagus (Portugal) and the Forth (Scotland). In the brackish water area of the Scheldt estuary, calanoid copepods and in particular *Eurytemora affinis* (Poppe), form the most important component of the pelagic zooplankton assemblage (Soetaert & Van Rijswijk, 1993). High numbers of calanoid copepods found in fish stomachs in March coincided with traditional seasonal peak abundances in the brackish water zone (Tackx, 1995). The benthic fauna in this part of the estuary consisted largely of the mysids *Neomysis integer* and *Mesopodopsis slaberri* (Mees et al., 1994). In winter, the latter species is virtually absent from the estuary and it occurred only in fish stomachs during summer and fall. *Neomysis integer* occurs throughout the year and was consumed at all times. Mees et al. (1994) reported distinct abundance peaks of *N. integer* in spring and summer which may explain its increased incidence in stomachs of eel and young-of-the-year pikeperch. Macrobenthic invertebrates such as polychaetes and amphipods occurred less in the diets. As argued above, infauna from intertidal mud flats present in the fish stomachs could be underestimated due to the sampling scheme. In addition, the diversity of these organisms is much higher at the mouth of the estuary than in the brackish water part, because of natural physical and human-induced disturbance (Ysebaert et al., 2000).

Prey abundance and niche dynamics

A comparison between the annual consumption of the dominant fish species in the study area and the annual production of estuarine copepods and mysids suggest that food is not in short supply. Escaravage & Soetaert (1995) estimated the total annual production of the most abundant copepod species in the brackish water area at 1600 mg ADW m^{-3} y^{-1}. The annual production of the standing stock of *Neomysis integer* was about 300 mg ADW m^{-2} y^{-1} (Mees et al., 1994). High prey densities may cause a high diet overlap between species since there is no need to partition the available resources (Pianka, 1982). However, random redistribution of all pair-wise combinations of niche overlap between individuals of two different species showed that in most cases, the diet overlap between individuals of the same species was significantly higher than the diet overlap between individuals of different species. The remaining species pairs had statistically similar diet compositions, but eight of these pairs involved species that were vertically separated into a pelagic, demersal or benthic component. Thus, although the foraging resources apparently meet the annual food demands of the dominant fish species, the pair-wise comparisons suggest some degree of trophic segregation amongst the dominant members of the estuarine fish assemblage. Seasonality in both the estuarine prey and predator populations possibly contributes to the observed segregation of trophic niches. The fish assemblage sampled nearby the sampling station undergoes continuous changes due to rapid movements of young-of-the-year fish and crustaceans which stay for a relatively short period of time (Maes et al., 1998a). These migrations are held between spawning grounds at sea and the estuary and typically result in high fish densities, mostly during the second part of the year (July–December) and, in particular, during the last trimester (Maes et al., 1998b). The total amount of food consumed by the different fish populations inhabiting the upper parts of the estuary depends primarily on the population size and is further modified by the species-specific daily food ration. Consequently, the consumption by fish in the study area was greatest in October 1994 and December 1994. This contrasts with seasonal data on the production and standing stock of the major prey species. Copepod production in the brackish water part of the estuary peaks in May and August but the biomass of calanoid copepods as well as its associated production rate are relatively low between October and January (Escaravage & Soetaert, 1995). The production and biomass of hyperbenthic mysid species reaches a minimum in winter, increases towards summer and decreases again in autumn (Mees, 1994). It is thus remarkable that five of the most common fish species in the upper Scheldt estuary i.e. common goby, sand goby, bass, herring and sprat peak in their abundance at a time when the production and standing stock of food are at their annual minimum. It is therefore acceptable that migrations sometimes lead to the rapid depletion of resources, for instance in years of high fish recruitment (Henderson et al., 1992). Only in March 1995, the trophic niches of flounder, sand goby, common goby, herring and sprat overlapped considerably due to a high incidence of calanoid copepods in the stomachs. At this time, the density of marine juvenile fish dropped due to seaward movements to join adult stocks (Maes et al., 1998a) while the density of copepods increased (Escaravage & Soaetaert, 1995). Flounder was the only species of which the timing of arrival of young-of-the-year fish in the estuary matches with the first bloom of copepods.

Fish were probably not the only predators upon the estuarine mysid and copepod populations. In the cooling water samples, the numbers of the common shrimp and the prawn *Palaemonetes varians* equaled those of fish (Figure 2A). Caridean shrimp were important prey items only for sea bass but these fish restricted themselves to the smaller individuals. Shrimps are highly mobile and exhibit a unique escape reaction under turbid conditions which may prevent them from heavy fish predation (Moore & Moore, 1976). Hostens & Mees (1999) suggest that *Crangon crangon* is probably the most important predator on mysids. In the study area, the common shrimp reaches an annual abundance peak in October while the prawn has two distinct peaks: one in September and one in March. As a consequence, they possibly compete with 0-group fish for the same resources, further enhancing trophic niche segregation within the level of secondary consumers.

This study has shown that pelagic copepods and hyperbenthic mysids form an important resource the dominant fish species of the low-salinity zone of the Scheldt estuary. From previous reports, it was clear that the great majority of these fish species are marine juveniles which reside for short periods in the estuary (Maes et al., 1998a,b). The abundance of these species in the estuary varies from year to year and depends largely on recruitment success at marine spawning grounds (Potter et al., 1997). In contrast, the estuarine copepod and mysid populations are confined to brackish water areas and hence, limited by estuarine conditions. The impact of yearly changing quantities of juvenile fish on the long-term stability of estuarine prey populations has not been investigated and warrants further study.

Joachim Maes is a postdoctoral fellow at the Fund for Scientific Research-Flanders, Belgium. Electrabel Doel permitted and financed sampling in the cooling water intake. Arne Taillieu helped sampling; Jan Sys and André Cattrijsse assisted with the prey identifications. This study was funded by project no. G.0104.99 of the Fund for Scientific Research-Flanders, Belgium.

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Submitted 12 February 2002. Accepted 30 September 2002.