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Diel changes in the vertical distribution of juvenile fish in the Zeeschelde Estuary

J. Maes*, J. Pas, A. Taillieu, P. A. Van Damme and F. Ollevier
Katholieke Universiteit Leuven, Zoological Institute, Laboratory of Aquatic Ecology, Naamsestraat 59, B-3000 Leuven, Belgium

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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 present exploited surface water during the night. Pelagic fish maintained their position underneath the water surface throughout the day.

Key words: vertical movement; estuary; Zeeschelde.

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 advances and predator avoidance have also been evoked as controls in mediating vertical distribution (Neilson & Perry, 1990). This paper 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 as the sampling programme was designed to analyse the spatial species distribution.

Fish were sampled using two commercial stow nets, a passive fishing technique, which is the most convenient for sampling in tidal environments (Breckling & Neudecker, 1994). While the ship was anchored, two nets on both sides were exposed to the tidal currents. 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 2 weeks in November 1995, samples were taken between the water surface and -4 m, and between -4 m and the bottom (-10 m), respectively. Samples taken between sunrise and sunset were categorized as day samples, other samples were night samples. In total, 20 samples were collected for this study (Table I). During the first week, high water was around midday and midnight; in the second week, high waters occurred at 0400 and 1600 hours. A description of the sampling area can be found in Maes *et al.* (1998).

After each haul, fish were identified and counted. If necessary, sub-samples 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.

More than 7×10^5 individuals comprising 34 fish species were captured during the sampling period (Table II). Sprat *Sprattus sprattus* (L.) (67%) and herring *Clupea harengus* L. (29%) dominated the fish catches. Together with gobies *Pomatoschistus* spp.,

*Author to whom correspondence should be addressed. Tel.: +32 16 32 37 09; fax: +32 16 32 45 75; email: joachim.maes@bio.kuleuven.ac.be

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TABLE I. Sampling details of the fishing survey

Date	Tide	Photoperiod	Depth	Duration (min)	Sampled water volume (m^3)
20 Nov. 1995	Rising	Day	Bottom	95	228 421
20 Nov. 1995	Rising	Day	Top	89	98 388
20 Nov. 1995	Falling	Day	Top	60	104 509
20 Nov. 1995	Falling	Day	Bottom	60	287 401
21 Nov. 1995	Falling	Night	Top	65	117 711
21 Nov. 1995	Falling	Night	Bottom	65	294 278
22 Nov. 1995	Falling	Night	Top	60	114 890
22 Nov. 1995	Falling	Night	Bottom	60	229 781
22 Nov. 1995	Rising	Day	Top	60	171 798
22 Nov. 1995	Rising	Day	Bottom	60	257 697
23 Nov. 1995	Falling	Night	Top	60	184 667
23 Nov. 1995	Falling	Night	Bottom	60	277 001
29 Nov. 1995	Rising	Night	Top	45	91 465
29 Nov. 1995	Rising	Night	Bottom	45	182 930
29 Nov. 1995	Falling	Day	Top	60	143 960
29 Nov. 1995	Falling	Day	Bottom	60	323 909
30 Nov. 1995	Rising	Night	Top	60	174 286
30 Nov. 1995	Rising	Night	Bottom	60	261 429
30 Nov. 1995	Falling	Day	Top	60	106 998
30 Nov. 1995	Falling	Day	Bottom	60	187 246

these species represented >99% of the fish captures. The majority of species were demersal. However, only bib *Trisopterus luscus* (L.), sand goby *P. minutus* (Pallas), Lozano's goby *P. lozanoi* (de Buen) and dab *Limanda limanda* (L.) showed a significant preference for the bottom. Anchovy *Engraulis encrasicolus* (L.), herring and sprat were predominantly present near the surface. After sunset, the vertical distribution of smelt *Osmerus eperlanus* (L.), common goby *P. microps* (Krøyer), sand goby and dab changed significantly suggesting that they were spreading out over the water column (Fig. 1). This behaviour was not observed for clupeids. The pikeperch *Stizostedion lucioperca* (L.) population was more abundant near the surface during the day but numbers were significantly higher at the bottom during the night (Fig. 1).

No tidal effects in the catch or in the vertical distribution were noticed. Only three species, eel *Anguilla anguilla* (L.), dab and flounder *Pleuronectes flesus* L., were caught in significantly higher numbers during the night (Table II).

It seems that in the Zeeschelde Estuary, demersal 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 & 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 & Masson (1988) and Del Norte-Campos & 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, *Crangon crangon* and *Palaemonetes varians* and of the calanoid copepod *Eurytemora affinis* also changed overnight as these species moved up from the bottom (Soetaert & Herman, 1994). These species are the principal prey items for almost all fish recorded in the Zeeschelde Estuary (Maes, unpubl.) and other European estuaries (Doornbos & Twisk, 1987; Henderson

TABLE II. 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 (NS, not significant)

Species	Photoperiod			Depth			Photoperiod × depth
	Day	Night	*P*	Top	Bottom	*P*	*P*
Marine species							
Clupea harengus L. (herring)	495·3	455·1	NS	62·2	26·7	<0·05	NS
Sprattus sprattus (L.) (sprat)	1067·5	1045·0	NS	136·9	60·3	<0·05	NS
Engraulis encrasicolus (L.) (anchovy)	0·495	0·213	NS	0·061	0·003	<0·05	NS
Osmerus eperlanus (L.) (smelt)	0·643	0·708	NS	0·072	0·060	NS	<0·05
Gadus morhua L. (cod)	0·005	<0·001	NS	<0·001	0·001	NS	NS
Merlangius merlangus (L.) (whiting)	0·435	0·292	NS	0·033	0·043	NS	NS
Trisopterus luscus (L.) (bib)	0·085	0·043	NS	0·001	0·015	<0·001	NS
Atherina presbyter Cuvier (sand-smelt)	0·013	0·008	NS	0·002	<0·001	NS	NS
Syngnathus acus L. (greater pipefish)	<0·001	0·008	NS	0·001	<0·001	NS	NS
Syngnathus rostellatus Nilsson (Nilsson's pipefish)	0·187	0·017	NS	0·014	0·008	NS	NS
Trigla lucerna L. (tub gurnard)	<0·001	0·003	NS	<0·001	<0·001	NS	NS
Myoxocephalus scorpius (L.) (bull-rout)	0·007	0·003	NS	<0·001	0·001	NS	NS
Agonus cataphractus (L.) (hook-nose)	0·003	<0·001	NS	<0·001	<0·001	NS	NS
Liparis liparis (L.) (sea snail)	<0·001	0·008	NS	0·001	<0·001	NS	NS
Dicentrarchus labrax (L.) (bass)	0·821	0·806	NS	0·091	0·068	NS	NS
Liza ramada (Risso) (thin-lipped grey mullet)	0·405	0·413	NS	0·059	0·014	NS	NS
Ammodytes tobianus L. (sandeel)	0·003	<0·001	NS	<0·001	<0·001	NS	NS
Callionymus lyra L. (dragonet)	<0·001	0·058	NS	<0·001	0·006	NS	NS
Pomatoschistus lozanoi (De Buen) (Lozano's goby)	3·227	5·943	NS	0·336	0·600	<0·05	NS
Pomatoschistus microps (Krøyer) (common goby)	71·6	63·3	NS	5·679	8·420	NS	<0·05
Pomatoschistus minutus (Pallas) (sand goby)	38·2	59·9	NS	3·722	6·337	<0·05	<0·05
Scomber scombrus L. (mackerel)	<0·001	0·004	NS	<0·001	<0·001	NS	NS
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	NS	NS
Pleuronectes platessa L. (plaice)	0·035	0·045	NS	0·003	0·005	NS	NS
Solea solea (L.) (sole)	0·033	0·093	NS	0·006	0·005	NS	NS
Anadromous species							
Lampetra fluviatilis (L.) (river lamprey)	0·078	0·110	NS	0·088	0·010	NS	NS
Alosa fallax (Lacepède) (twaite shad)	0·007	<0·001	NS	0·001	<0·001	NS	NS
Catadromous species							
Anguilla anguilla (L.) (eel)	0·051	0·268	<0·001	0·017	0·012	NS	NS
Freshwater species							
Abramis brama (L.) (bream)	0·006	<0·001	NS	0·001	<0·001	NS	NS
Gasterosteus aculeatus L. (three-spined stickleback)	<0·001	0·267	NS	0·020	<0·001	NS	NS
Gymnocephalus cernuus (L.) (ruffe)	<0·001	0·003	NS	<0·001	<0·001	NS	NS
Perca fluviatilis L. (perch)	0·274	1·379	<0·05	0·059	0·102	NS	NS
Stizostedion lucioperca (L.) (pikeperch)	0·020	0·168	NS	0·002	0·018	NS	<0·05

et al., 1992). Pikeperch, on the other hand, is the major fish predator in the Zeeschelde Estuary. Stomach contents analysis suggested that pikeperch preyed mainly on gobies and shrimps. 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 & Hesthagen, 1981).

Stow netting showed further that the diel distribution of herring and sprat did not change, possibly due to the high turbidity. In clearer waters, herring have 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).

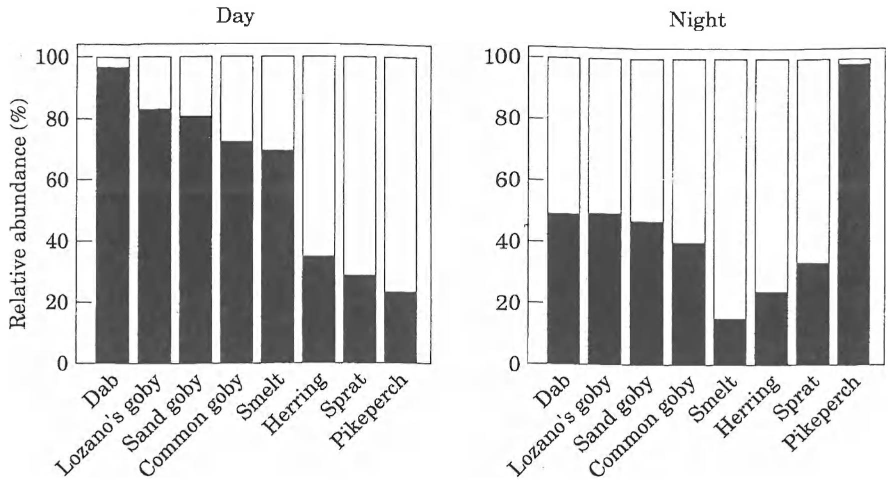

FIG. 1. Relative distribution of eight fish species in the Zeeschelde Estuary with respect to depth and photoperiod. ■, Bottom; □, top.

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 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 & 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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