

# Size structure and feeding dynamics in estuarine clupeoid fish schools: field evidence for the school trap hypothesis

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## Abstract

An analysis of 273 samples taken at the filter screens of an estuarine power plant cooling water intake showed that herring and sprat were strongly associated with each other and formed mixed species schools. Herring-dominated schools were typically larger, more frequent and contained larger-sized individuals than schools dominated by sprat. The mean body length of both herring and sprat was biased as a function of their relative importance in the school suggesting that the fish schools were assorted by size. However, switching to a fish school dominated by the other species increased the individual body length variation relative to the group average. Diets of both species overlapped strongly but the feeding rate of sprat was significantly lower than that of herring. Our results suggest that during estuarine residency young sprat suffer the consequences of the school trap, possibly to profit from reduced predation risks in herring schools. © 2002 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

## Résumé

**Organisation et dynamique alimentaire des bancs de poissons clupéidés dans un estuaire : évidence de l'hypothèse du banc-piège ou "school trap".** Une analyse de 273 échantillons des poissons, capturés au niveau des filtres d'une prise d'eau d'une centrale électrique, située dans un estuaire de Belgique, a montré que le hareng et le sprat sont fortement associés et forment ensemble des bancs. Les bancs des poissons, dominés par le hareng, sont typiquement plus grands, plus fréquents et comprennent des individus de plus grande taille que ceux dominés par le sprat. La taille moyenne des deux espèces est fonction de leur importance relative dans le banc, ce qui suggère que les bancs des poissons sont organisés suivant leur taille. Cependant, le changement vers un banc de poissons dominé par l'autre espèce augmente la variation individuelle de la taille par rapport à la moyenne du groupe. La composition alimentaire des deux espèces se ressemble fortement mais le taux d'alimentation du sprat est plus faible que celui du hareng. Nos résultats suggèrent que, durant leur séjour dans l'estuaire, les sprats perdent davantage leur possibilité d'alimentation dans les bancs de hareng que dans ceux de sprat, probablement pour échapper à la prédation en supportant l'hypothèse du banc-piège ou "school trap". © 2002 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS. Tous droits réservés.

*Keywords:* Schooling behaviour; School trap hypothesis; Diet composition; Niche overlap; Size-assortativeness; *Clupea harengus*; *Sprattus sprattus*

## 1. Introduction

Models of schooling behaviour in multi-species schools predict that fish schools are strongly assorted by species and body length (Hoare et al., 2000). Anti-predator behaviour is often evoked as a mechanism promoting the tendency of fish to form schools of similar-sized individuals. Thus individuals whose size differs from other group members

experience high fitness costs in terms of reduced foraging efficiency and increased predation risk (Krause et al., 1998). Pelagic species often form mixed schools containing two or more species of similar size. The tendency for small pelagic fish of similar body form to school together has been defined as the school trap, which is the urge to become and remain a member of a fish school, even when it causes ancillary disadvantages such as higher metabolic costs (Bakun and Cury, 1999).

Herring and sprat are small pelagic fish that co-occur in the coastal waters of the North Sea and the Baltic Sea where

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they form mixed schools (De Silva, 1973; Arrhenius and Hansson, 1993). In winter, they often migrate to estuaries and become the dominant members of the estuarine fish assemblage, both by number and by biomass (Maes et al., 1998; Power et al., 2000). These winter migrations have been related to better abiotic conditions and to the reduced predation pressure in turbid brackish water areas. Their presence in large numbers is thought to have concomitant effects on the dynamics of estuaries, which serve as critical over-wintering and nursery areas for many species (Power et al., 2000).

This study investigates the size and length structure of pelagic fish schools composed of juvenile herring and sprat during their estuarine residency. Our second objective was to examine the partitioning of food resources between schools of herring and sprat in the estuarine environment.

## 2. Material and methods

### 2.1. Sampling of the fish

Herring and sprat were collected from the intake screens of the nuclear power plant Doel (Belgium), located on the west bank of the upper Schelde estuary. The station withdraws  $25.1 \text{ m}^3 \text{ s}^{-1}$  of water for cooling purposes. Fish entered the cooling water intake and were removed from vertical travelling screens (4 mm mesh size) by water jets. Here, fish samples of 1 h were collected in nets (mesh size 1 mm). A complete description of the sampling site and the sampling methods is given in Maes et al. (1998). All fish were counted and stored in formaldehyde 7%. Length data were available for the period July 1994–June 1997.

### 2.2. Stomach contents analysis

Diel changes in feeding rhythm of herring and sprat were assessed by changes in gut fullness (Piet et al., 1999). Each month between September 1994 and March 1995, we collected at least 20 individuals per species every 3 h over a 24 h interval. Stomach contents were removed and dried at  $70^\circ\text{C}$  to constant weight. The stomach fullness index was assessed according to Hyslop (1980) by dividing the stomach dry weight by the ash-free dry weight of the fish. From schools sampled at high tides, food organisms in the stomachs were identified to the lowest possible taxon and all prey organisms were counted before drying. Diet composition was presented as a percentage by numbers being the ratio between total abundance ratings of a food organism and the grand sum derived from dietary constituents in all stomachs.

### 2.3. Statistical methods

The hypothesis that herring and sprat formed mixed species schools during their estuarine residency was tested

using a Yates-corrected  $\chi^2$ -test to determine the strength of the association between both species. A *t*-test for independent samples was used to test the null hypothesis that there was no difference in the average body size of herring and sprat between fish schools dominated by herring and sprat, respectively. A third test examined the hypothesis of no difference between the sizes of herring- and sprat-dominated fish schools.

A *t*-test for dependent samples was used to examine if stomach fullness of herring was significantly different from stomach fullness of sprat from the same fish school. The relationship between stomach fullness in herring and sprat was expressed by a Pearson correlation coefficient.

The relation between the average body length and the 10-based logarithm of the average stomach fullness index of herring and sprat and the composition of the schools was investigated using linear regression models. The composition of the fish schools was expressed by an index between  $-1$  for schools consisting entirely of sprat and  $1$  for schools consisting entirely of herring. The index was calculated as  $[\text{herring sample size} - \text{sprat sample size}] / [\text{herring sample size} + \text{sprat sample size}]$ .

Trophic niche overlap was assessed with Renkonen's index of similarity (Marshall and Elliott, 1997). A Mantel test was used to investigate the null hypothesis that there was no difference in the diet overlap of individuals within each species and between herring and sprat (Manly, 1989). This test determines the significance of a correlation between a matrix with all possible pairwise combinations of niche overlap and a binary matrix containing 1s in the positions of the diet overlap measured between individuals of the same species and 0s otherwise. The significance of the correlation coefficient *r* between these two matrices was evaluated through the use of a Monte Carlo procedure where the 1s and 0s of the binary matrix were permuted 1000 times. A significant positive correlation indicates that two individuals from the same group have a higher niche overlap than two individuals from different groups (Manly, 1989).

## 3. Results

The occurrence of herring and sprat in the Schelde estuary is highly seasonal (Fig. 1). Larval stages of herring enter the estuary in spring and peak in June. Both larval and juvenile sprat arrive 2 months later. However, it should be noted that the larval stages of both species were not properly quantified since a substantial part escaped through the meshes of the filter screens. In the inner estuary, numbers of juvenile herring and sprat reached a maximum in November. After this month, herring and sprat moved seaward to join adult marine stocks. At Doel, the pattern of estuarine occupancy was stable and predictable over the different years.

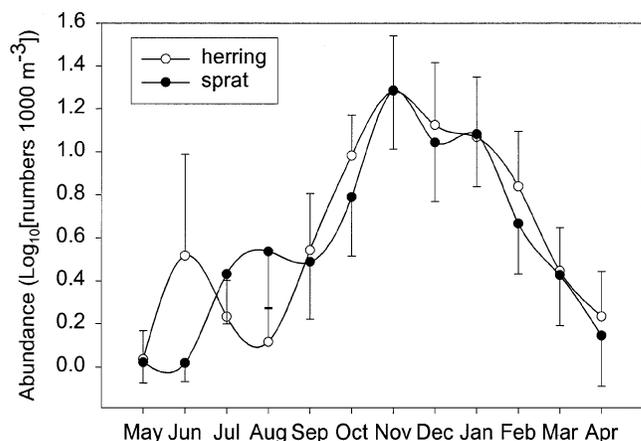


Fig. 1. Average monthly changes in the abundance of herring and sprat > 3 cm in the inner Schelde estuary (Doel, Belgium) between September 1991 and December 1998. Error bars represent standard deviations.

### 3.1. Structure of the fish schools

When present in the estuary, herring and sprat showed a positive association to each other (Yates-corrected  $\chi^2 = 6.41$ ,  $P = 0.001$ ). Of 273 samples taken at Doel, 82% contained sprat and herring while both species were absent in only seven of the samples. Schools dominated by herring were significantly larger (*t*-test for independent samples,  $t = 3.6$ ;  $P < 0.001$ ;  $n = 266$ ) and more frequent than schools dominated by sprat. Herring schools contained on average 2574 individuals against an average of 689 individuals in sprat schools. Sprat dominated in 100 schools while herring was the dominant species in 166 schools.

Total lengths of 12 260 herring and 7253 sprat were measured to the nearest mm (Fig. 2). Average body length of both species differed significantly between fish schools (Table 1). Herring in herring schools averaged 79.7 mm compared to 65.6 mm for sprat in the same school. Sprat in sprat schools averaged 56 mm compared to 73.8 mm for herring in the same school. Size-assortativeness of the fish schools was further evidenced by a significant linear increase in the average body length of both species with increasing importance of herring in the fish schools (Table 2). A second linear regression model showed that there was a predictable deviation from the average school length as the relative abundance of herring and sprat in the fish school changed (Table 2, Fig. 3). As the dominance ratio of herring increased, the difference in size between the average length of sprat in the fish school and the group average increased. A similar pattern was observed for herring.

### 3.2. Diet composition

Stomachs of 137 herring and 162 sprat were analysed for their dietary constituents (Table 3). Calanoid copepods were the principal prey group for both species. In September, copepods were replaced by mysids in the diet. Diet overlap was high (> 0.87) and in most cases, the overlap between

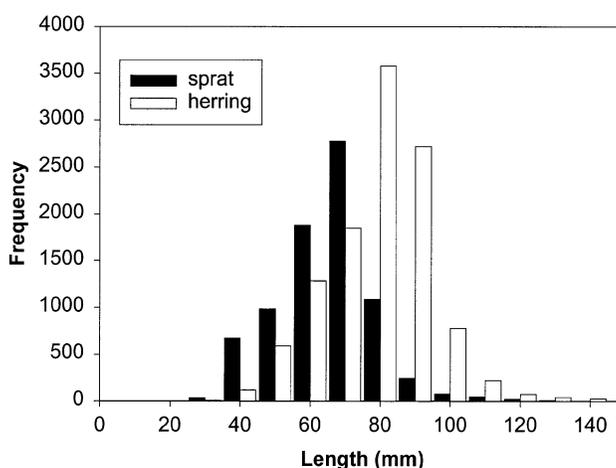


Fig. 2. Length–frequency distribution of 12 260 herring and 7253 sprat sampled at the cooling water intake of the power plant Doel (Belgium) between July 1994 and June 1997.

individuals from the same species was not different than the overlap between individuals from both species ( $P > 0.05$ , Table 3). Only in October was intraspecific diet overlap between herring and sprat significantly higher than interspecific diet overlap ( $r = 0.27$ ,  $P < 0.05$ , Table 3). This difference was likely due to an absence of harpactoid copepods in the diet of sprat. No test was performed on the data of December as sprat apparently ceased to feed in this month.

### 3.3. Feeding intensity

Stomach contents of 1389 herring (523 empty stomachs) and 734 sprat (387 empty stomachs) were used to assess daily changes in feeding intensity. There was a significant correlation between the average stomach fullness index of herring and the average stomach fullness index of sprat (Pearson correlation test:  $r^2 = 0.52$ ;  $t = 6.3$ ;  $P < 0.001$ ;  $n = 38$ ; data  $\log_{10}$  transformed) indicating that both species had been feeding at the same time. Herring was feeding more intensively than sprat: stomach fullness of herring relative to its body size scored significantly higher than the stomach fullness index of sprat (*t*-test for dependent samples:  $t = 2.9$ ;  $P = 0.006$ ;  $n = 38$ ; data  $\log_{10}$  transformed). Feeding intensity of sprat decreased significantly if herring became more important in the schools (Table 2). This relation was, however, not observed in herring.

## 4. Discussion

During estuarine residency, young herring and sprat aggregated in large fish schools. Fish schools dominated by herring were typically larger, more frequent and contained larger-sized individuals than schools dominated by sprat. Schools dominated by sprat consisted of small-sized herring and sprat of which the average body size was considerably smaller than the respective population mean. The mean body length of herring and sprat was biased in function of

Table 1

Mean body size in cm (limits of 95% confidence intervals) of herring and sprat between and within fish schools and the mean school body length in cm (limits of 95% confidence intervals) in herring and sprat schools. A *t*-test was used to examine the difference in body length of herring and sprat between fish schools. In total, 144 fish schools were captured between July 1994 and June 1997 at a cooling water inlet of the power plant Doel (Schelde estuary, Belgium)

	Number of samples	Mean body length	Lower limit	Upper limit
<i>Herring</i> ( $t = 3.6$ ; $P < 0.001$ )				
In herring-dominated schools	93	8.0	7.8	8.1
In sprat-dominated schools	51	7.4	7.0	7.7
Population mean	144	7.8	7.6	7.9
<i>Sprat</i> ( $t = 6.2$ ; $P < 0.001$ )				
In herring-dominated schools	93	6.6	6.4	6.7
In sprat-dominated schools	51	5.6	5.3	5.9
Population mean	144	6.2	6.0	6.4
Herring-dominated school mean	93	7.8	7.6	7.9
Sprat-dominated school mean	51	6.0	5.6	6.4

their relative importance in the school suggesting that the fish schools were assorted by size. Size assortiveness in fish schools has been demonstrated for a number of schooling species (Krause et al., 1996; Peuhkuri, 1997; Bakun and Cury, 1999) and can be explained in terms of increased fitness for the school members. Differences in phenotype lead to increased predation risk and decreased foraging efficiency (Krause et al., 1998). As a result, sprat would benefit from being larger in herring-dominated fish schools, in order to maintain group homogeneity. Herring, on the other hand, would benefit from being smaller in sprat-dominated fish schools. This pattern probably explains the linear increase in the length of both herring and sprat as the dominance of herring in the fish schools increases since herring is the larger species. Yet, the difference in body length between herring and sprat on the one hand and the school mean on the other hand became larger as their relative importance in the schools decreased. Average-sized sprat switching from a sprat school to a herring school yield a 24% size disadvantage relative to the herring-dominated school mean to a 2% size advantage relative to the sprat-dominated school mean. On the other hand, average-sized herring yield a 22% size advantage if they switch from a herring school to a sprat school. Switching to a school dominated by the other species apparently increased the phenotypic differences of group membership. The question

thus remains why larger sprat would congregate with herring schools and smaller herring aggregate with sprat schools as by doing so the individual phenotypic difference with the school is increased.

A possible answer may be obtained from the results based on the diet analysis. The strong association between both species was reflected in a high diet overlap. A comparison with reported data on prey distribution suggests that both species were feeding opportunistically on the available prey as the peak abundance of the principal prey species in the estuary coincided with their presence in the fish stomachs. The diets of herring and sprat consisted mainly of calanoid copepods, except for 2 months in the fall when mysids were taken. In the study area, calanoid copepods, predominantly *Eurytemora affinis*, peak in abundance between January and March with densities reaching 250 individuals per l (Soetaert and Van Rijswijk, 1993). During the fall, their densities reach a minimum (12 individuals per l). The most abundant hyperbenthic mysids are *Mesopodopsis slaberry* and *Neomysis integer* (Mees, 1994). The former species peaks in August while the latter species has three distinct abundance maxima: one in spring (March and April), one in summer (July and August) and one in autumn (October and November). Probably, herring and sprat prefer copepods but they may switch between prey during peak densities of mysids. Opportunistic feeding

Table 2

Summary statistics of the linear regression models with school composition as independent variable  $x$ . Regressions with mean body length and the deviation from the mean school length as dependent variables were based on an analysis of 144 fish schools sampled between July 1994 and June 1997. Regressions with the stomach fullness index of herring and sprat, respectively, as dependent variable were based on an analysis of 41 fish schools (1389 herring stomachs, 734 sprat stomachs) sampled between September 1994 and March 1995.  $\beta$ : standardised regression coefficient;  $n$ : number of observations;  $r^2$ : explained variance;  $F$ -statistic and significance level  $P$  for the null hypothesis of  $\beta = 0$

Dependent variables	Regression equation	$\beta$	$n$	$r^2$	$F$	$P$ -level
<i>Herring</i>						
Mean body length (mm)	$y = 75.9 + 6.07x$	0.39	144	0.15	25.1	< 0.001
Deviation from the mean school length (mm)	$y = 8.65 - 9.33x$	-0.87	144	0.77	454.4	< 0.001
Log <sub>10</sub> stomach fullness index	$y = 0.11 + 0.06x$	0.20	41	0.01	1.6	0.21
<i>Sprat</i>						
Mean body length (mm)	$y = 9.9 + 9.01x$	0.56	144	0.32	65.7	< 0.001
Deviation from the mean school length (mm)	$y = -7.37 - 6.39x$	-0.64	144	0.41	95.2	< 0.001
Log <sub>10</sub> stomach fullness index	$y = 0.28 - 0.09x$	-0.41	41	0.17	7.2	0.01

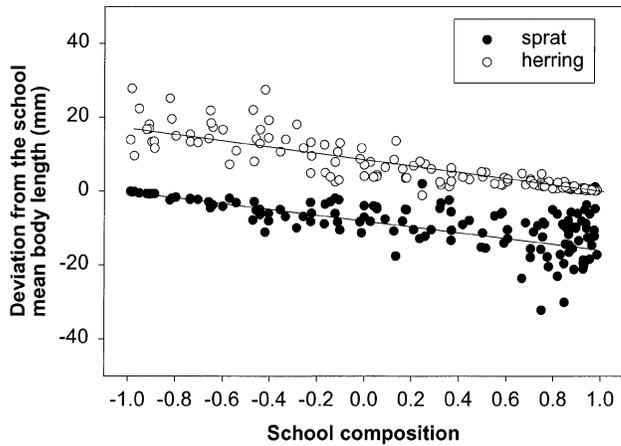


Fig. 3. Deviation from the average school body length in herring and sprat (mm) as a function of the relative school composition, based on an analysis of 144 fish schools sampled between July 1994 and June 1997. The school composition is expressed as a ratio between -1 for 100% sprat schools and 1 for 100% herring schools. The equations for the linear regression models are given in Table 2.

habits have been observed in other estuaries as well and may be attributed to turbidity (Hecht and van der Lingen, 1992). Turbidity reduces the efficiency of visual feeding while it promotes encounter rate feeding (Grecay and Targett, 1996). In the sampling area, turbidities were in the quartile range of 38–77 mg l<sup>-1</sup>, corresponding to an average Secchi disc depth of 18 cm. Herring and sprat can adapt to high turbidity levels by switching from particulate feeding to filter feeding (Gibson and Ezzi, 1992). Such a behavioural change in feeding strategy is only efficient if food is present in high abundance. In the estuary, prey concentrations compare with threshold concentrations at which her-

ring switches from biting to filtering (Gibson and Ezzi, 1992). These authors report that over 50% of herring switched from biting to filtering at concentrations of between 30 and 80 individuals per l of larger-sized *Artemia* and *Calanus*. The lower threshold for filtering ranged from three to 64 individuals per l. Given the above zooplankton concentrations in the estuary (Soetaert and Van Rijswijk, 1993), herring, and probably also sprat, gain more benefit from filter feeding than from particle feeding since the total daily time necessary to meet the metabolic costs and growth is shorter when filtering. Filtering rates of fish vary as a function of fish size (mouth area), swimming speed and prey concentration. Swimming speed and size of the food particles are almost equal amongst the members of the same fish school. The mouth area may vary in favour of the larger-sized individuals. Therefore, we hypothesise that, due to gape-limited filter-efficiency, larger individuals are more competitive.

The assumption of herring and sprat filter feeding is useful to explain some of the observed patterns in our data. If gape size is the determining factor, herring in sprat-dominated fish schools are probably unaffected by the presence of sprat because they are larger and hence, better able to compete for food. By switching from herring schools to sprat schools, smaller herring avoid intraspecific competition and increase their feeding opportunity. Sprat, on the other hand, do not exceed the herring population mean, even in the sprat-dominated fish schools. From the presumed relation between body length and filtering rate of individuals foraging in the same fish school, it can be expected that the feeding rate of sprat is lower than the feeding rate of herring. This assumption agrees with our data of stomach

Table 3  
Monthly variation in diet composition of 137 herring and 162 sprat by percentage numbers. Diet overlap between both species was assessed using the Renkonen index of similarity for the period September 1994–March 1995. Significance of overlap was tested using a Mantel test (correlation coefficient *r* and significance level *P*). H: herring, S: sprat

Diet descriptor	September		October		November		December		January		February		March	
	H	S	H	S	H	S	H	S	H	S	H	S	H	S
Number of fish analysed	41	12	20	20	6	46	20	20	20	16	10	28	20	20
Number of empty stomachs	15	6	9	10	1	20	7	20	0	1	1	8	3	0
Average number of prey	24	14	23	17	16	1	6	0	250	194	254	125	538	425
Ostracoda	–	–	–	–	–	–	–	–	–	–	–	–	–	< 0.01
<i>Daphnia</i> sp.	–	–	–	–	–	–	–	–	–	0.01	–	–	–	0.03
<i>Ceriodaphnia</i> sp.	–	–	–	–	–	–	–	–	–	< 0.01	–	–	–	0.01
Copepoda	–	–	–	–	–	–	–	–	0.99	0.99	1.00	0.99	–	–
Calanoidea	–	–	0.78	0.85	–	–	0.98	–	–	–	–	–	0.89	0.96
Harpacticoida	–	–	0.05	–	–	–	0.02	–	–	–	–	–	0.07	–
<i>Neomysis integer</i>	0.12	0.18	0.08	0.01	0.63	0.80	–	–	0.01	–	< 0.01	0.01	< 0.01	–
<i>Mesopodopsis slabberi</i>	0.88	0.81	0.08	0.12	0.38	0.20	–	–	< 0.01	–	< 0.01	< 0.01	–	–
<i>Gammarus salinus</i>	–	–	< 0.01	–	–	–	–	–	< 0.01	–	–	–	–	–
<i>Corophium volutator</i>	–	–	–	–	–	–	0.01	–	–	–	–	–	–	–
<i>Orchestia</i> sp.	–	–	–	–	–	–	–	–	–	< 0.01	–	–	–	–
<i>Crangon crangon</i>	0.01	–	< 0.01	–	–	–	–	–	–	–	–	–	–	–
Decapoda	–	–	–	< 0.01	–	–	–	–	–	–	–	–	–	–
Chironomids	–	–	–	–	–	–	–	–	–	–	–	–	< 0.01	–
Teleost scales	–	0.01	–	0.01	–	–	–	1.00	–	–	–	–	–	–
Diet overlap	0.93		0.88		0.83		0		0.99		0.99		0.90	
Correlation coefficient <i>r</i>	0.03		0.27		-0.18		–		-0.07		-0.03		-0.03	
<i>P</i> -level	0.26		< 0.01		0.86		–		0.42		0.62		0.61	

fullness. Stomach fullness of sprat was consistently lower than stomach fullness of herring. As the dominance ratio of herring increased, sprat increasingly became confined to the tail of the school length frequency distribution and also became increasingly less competitive. The decline in relative numbers was directly reflected in the reduced foraging efficiency and a decline in stomach fullness. It is thus likely that sprat switching to herring schools have less to eat. In turn, they are probably better protected from predation due to the larger school size. Herring schools were, on average, four times larger than sprat schools. Because of their larger size relative to sprat schools, the per capita predation risk in herring schools is reduced (Krause and Godin, 1995). This conclusion does not reject previous results reporting that phenotypic differences lead to increased predation risk (Landeau and Terborgh, 1986; Krause et al., 1998) as long as the size of schools is taken into account in the assessment of predation risk. School size may interact with group homogeneity to change the relative predation risk. In addition, herring and sprat show high overlap in other phenotypic characteristics such as colour and body shape, which possibly compensate for body length variation in mixed species schools (Krause et al., 1998).

To summarise, we hypothesise that smaller herring trade-off between the increased relative risk of predation in small sprat schools due to increased phenotypic difference on the one hand and an increased ration necessary to increase size-related fitness on the other hand. Larger sprat may prefer the decreased relative predation risk in larger herring schools but face a lower foraging efficiency. Either way, herring exploits sprat while sprat cannot exploit herring due to the species-specific differences in body length. Accordingly, our data suggest that during estuarine residency, young sprat suffer the consequences of the school trap.

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