

Biomass transport to and from an upper estuarine area by migration of juvenile Atlantic herring *Clupea harengus*

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Abstract: A model describing fish abundance resulting from fish migration and mortality in an upper estuary is presented. This model can be used to estimate biomass transports by fish migrations between estuary and sea and to assess production assimilated in the estuary. It was applied to herring *Clupea harengus* L., a marine species with 0+ juveniles that 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.

Résumé : Nous présentons un modèle qui décrit l'abondance des poissons dans un estuaire en considérant la migration et la mortalité. Ce modèle peut être utilisé pour, d'une part, estimer le transport de biomasse entre les estuaires et la mer, et d'autre part estimer la production assimilée par l'estuaire lors de la migration des différentes populations. Le modèle a été, au cours de nos travaux, appliqué sur le hareng *Clupea harengus* L., une espèce marine dont les juvéniles 0+ migrent vers les estuaires Européens pendant l'hiver. Nos résultats montrent que les différents régimes de mortalité au sein de l'estuaire, influencent grandement le nombre de poissons qui émigrent et la biomasse exportée vers la mer. L'exportation de biomasse a été estimée sous différentes conditions de croissance dépendantes du taux de mortalité. La différence entre la biomasse exportée et la biomasse produite in situ nous permet de montrer que la production de poissons n'est pas toujours exportée lors de l'émigration. Nous avons donc provisoirement conclu que l'exportation de biomasse n'a lieu que lorsque les populations migrent vers la mer avant l'hiver.

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). However, few researchers have focussed on the transport 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 into an estuary or exported

seaward by a migrating population. The model is applied to Atlantic herring, *Clupea harengus* L., a marine species with young-of-the-year that commonly inhabit the brackish-water area of North Sea estuaries.

Materials and methods

Model of fish abundance, biomass transfers, and fish production

The change in fish abundance (N) over time (t) in the estuary as the result of migration and mortality can be expressed as

$$(1) \quad \frac{dN}{dt} = \text{immigration} - \text{emigration} - \text{mortality}$$

Equation 1 is a conceptual model describing fish abundance over time. 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, eq. 1 can be rewritten in a mathematical form:

$$(2) \quad \frac{dN}{dt} = a \cdot \exp(it) - e \cdot N - z \cdot N$$

where a , i , e , and z are the parameters of the model. All symbols used in equations and text are explained in Table 1. Equation 2 is a differential equation with dependent variable N and independent variable t . As immigration and emigration were assumed to be discontinuous with time, eq. 2 has to be split into two parts to find a proper solution. Between t_0 and t_{\max} , eq. 2 can be shortened (eq. 3)

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Table 1. Symbols used in the equations and in the text.

Symbol	Explanation	Unit
$N(t)$	Fish abundance at time t	Number/10 ³ m ³
$N_i(t)$	Fish abundance during immigration	Number/10 ³ m ³
$N_e(t)$	Fish abundance during emigration	Number/10 ³ m ³
t	Time	Day
t_0	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	Number/10 ³ m ³ /day
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
$L_{infinite}$	Asymptotic length	mm
$W_{infinite}$	Asymptotic weight	g
K	Growth coefficient	day ⁻¹
I	Number of fish immigrated	Number/10 ³ m ³
E	Number of fish emigrated	Number/10 ³ m ³
B_i	Imported biomass	g/10 ³ m ³
B_e	Exported biomass	g/10 ³ m ³
P	Production	g/10 ³ m ³ /year

and solved for N_i with t as independent variable and $N_i(0) = 0$ (or at t_0 , no fish are present yet) as initial condition (eq. 4).

$$(3) \quad \frac{dN_i}{dt} = a \cdot \exp(it) - z \cdot N_i$$

$$(4) \quad N_i = \frac{a}{i + z} [\exp(it) - \exp(-zt)]$$

Between t_{max} and t_{end} , eq. 2 can be shortened (eq. 5). Solving eq. 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 eqs. 6 and 7. In eq. 7, the first factor is replaced by $N_i(t_{max})$.

$$(5) \quad \frac{dN_e}{dt} = -e \cdot N_e - z \cdot N_e$$

$$(6) \quad N_e = \frac{a}{i + z} [\exp(it_{max}) - \exp(-zt_{max})] \times \exp(-(z + e)(t - t_{max}))$$

$$(7) \quad N_e = N_i(t_{max}) \cdot \exp(-(z + e)(t - t_{max}))$$

Equations 4 and 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 (eq. 8) or for biomass (eq. 9):

$$(8) \quad L(t) = L_{infinite}[1 - \exp(-K(t - t_0))]$$

$$(9) \quad W(t) = W_{infinite}[1 - \exp(-K(t - t_0))]^3$$

We now can 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 eq. 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 (eq. 10). Equation 10 combined with eq. 9 gives the imported biomass B_i (eq. 11).

$$(10) \quad I = \int_0^{t_{max}} a \cdot \exp(it) dt = \frac{a}{i} \exp(it_{max}) - \frac{a}{i}$$

$$(11) \quad B_i = \int_0^{t_{max}} a \cdot \exp(it) \cdot W(t) dt$$

Accordingly, the number of fish E that have emigrated is given by eq. 12. Combining eq. 12 with eq. 9 gives the exported biomass B_e (eq. 13).

$$(12) \quad E = \int_{t_{max}}^{t_{end}} e \cdot N_e dt = \frac{e}{e + z} N_i(t_{max}) \times [1 - \exp((e + z)(t_{max} - t_{end}))]$$

$$(13) \quad B_e = \int_{t_{max}}^{t_{end}} e \cdot N_e \cdot W(t) dt$$

We calculated fish production P or the biomass assimilated between t_0 and t_{end} according to eq. 3 of Mertz and Myers (1998) as the product of fish abundance and growth rate (Allen method).

$$(14) \quad P = \int_{t_0}^{t_{end}} N_i(t) \frac{dW(t)}{dt} dt + \int_{t_{max}}^{t_{end}} N_e(t) \frac{dW(t)}{dt} dt$$

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.

Field sampling

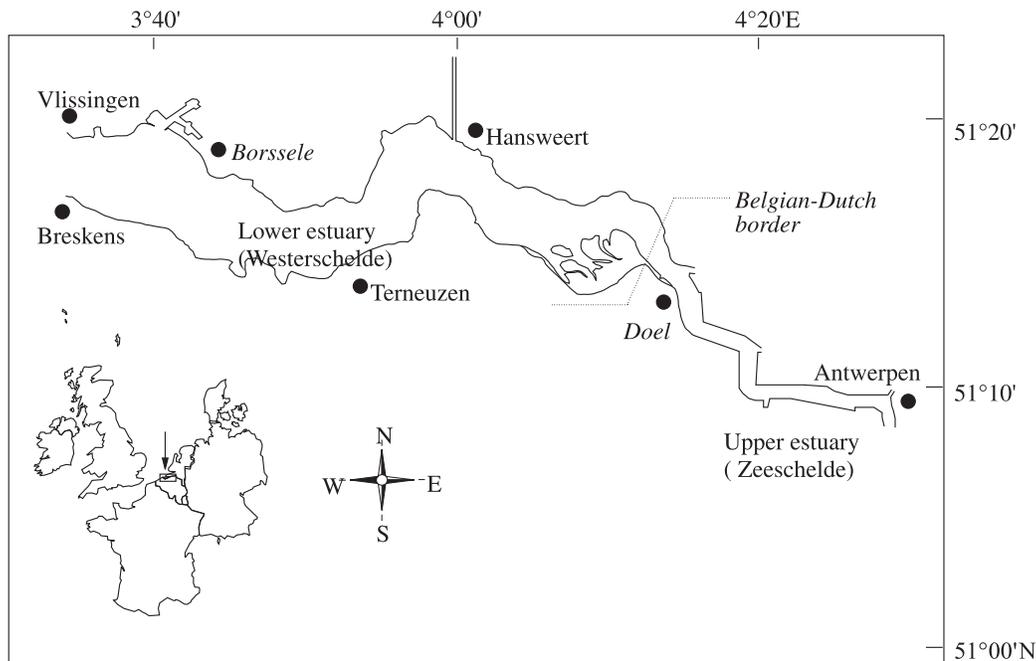
Between July 1994 and June 1995, herring were collected every 2 weeks on the cooling-water filter screens of the nuclear power plant Doel, situated in the Schelde Estuary (Belgium). Approximately 8×10^6 m³ of cooling water was monitored in 135 samples. Mean salinity at the sampling site was 8‰. A full description of the sampling site and sampling method is given in Maes et al. (1998). Number per sample were transformed to number per 10³ m³ 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) = $\exp[-10.529 + 2.6889 \ln(\text{total length (mm)})]$.

During the same period, KEMA Power Generation & Sustainable collected fish on the filter screens of the nuclear power plant Borssele, situated downstream of Doel near 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 with ours, only 1×10^6 m³ cooling water was monitored in 48 samples taken every month. Fish density at Borssele was generally lower than at Doel because of 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.

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 the field data. Back-extrapolation of the length-frequency modes of herring yielded t_0 (Titmus et al. 1978). Time of hatching was 6

Fig. 1. Map showing the Schelde Estuary and the sampling sites Borssele and Doel.



May 1994. We used two growth models to calculate production and transported biomass. The first model used growth parameters K and W_{∞} , estimated by fitting eq. 9 through our own biomass-at-age data (Fig. 2, Table 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_{∞} because 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) ($W_{\infty} = 200$ g; $K = 0.0011 \cdot \text{day}^{-1}$).

Statistical analysis and mathematical calculations

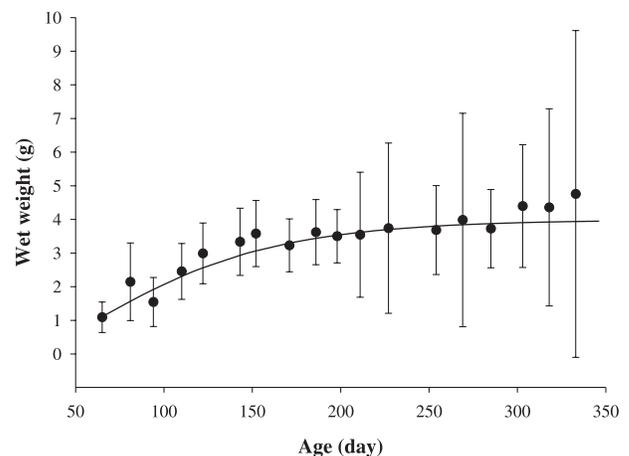
Non-linear estimation procedures were used to fit eqs. 4 and 7 through the observed abundance data. We used the quasi-Newton method as algorithm for estimating the different model parameters. The loss function used was the least squares estimation method. Explained variance by the fitting was expressed by R^2 . All integrals were solved in Mathematica 3.0.

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). The proportion of the annual catch caught in each month at Doel and Borssele is shown in Fig. 3. Abundance of herring peaked first at Borssele in November, after which numbers declined because of 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.

Herring abundance at Doel (Table 2) was modelled using eqs. 4 and 7 (Fig. 4). Using nine different values for mortality (z), the model parameters a , i , and e were estimated (Table 3). Increasing mortality rates caused decreasing emigra-

Fig. 2. Mean weight-at-age for herring (●) caught on the cooling-water intake screens at Doel. Error bars represent standard deviations. A non-linear regression (eq. 9) was used compute growth parameters. $W(t) = 3.99(1 - \exp(-0.0163t))^3$ ($R^2 = 0.84$, $p < 0.01$).



tion rates and increased the value for the intercept a . The rate of immigration remained constant at $0.05 \cdot \text{day}^{-1}$.

The model was used to estimate the number of fish that immigrated (eq. 10) and emigrated (eq. 12) as well as their biomass transported during migration (eqs. 11 and 13, respectively) (Table 3). As mortality increased, the number of fish that immigrated into the brackish water 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. 5. The growth model that used growth parameters of the North Sea herring stock resulted in

Table 2. Field observations on the presence of Atlantic herring in the upper Schelde Estuary including sampling date (day/month/year), age (days), mean fish abundance (N), and average length-at-age ($L(t)$).

Sampling date	Age	N	$L(t)$
11/07/1994	65	0.007	50.88
27/07/1994	81	0.409	64.4
09/08/1994	94	0.169	57.6
25/08/1994	110	0.085	69.17
06/09/1994	122	2.222	75.04
27/09/1994	143	5.627	77.72
06/10/1994	152	7.912	78.79
25/10/1994	171	13.262	75.58
09/11/1994	186	19.705	78.79
21/11/1994	198	138.709	78.23
04/12/1994	211	174.285	77.93
20/12/1994	227	55.811	78.38
16/01/1995	254	49.407	79.84
30/01/1995	268	5.725	81.79
16/02/1995	285	38.37	80.17
06/03/1995	301	2.431	84.45
22/03/1995	319	9.407	83.94
05/04/1995	333	1.054	84.88
18/04/1995	346	1.038	90.84

a lower biomass import and export under different mortality regimes than the growth model that used growth parameters estimated from field data (Fig. 5). Likewise, recruitment, which was interpreted as the percentage of (living) individuals emigrating seaward relative to the number of fish immigrating, decreased as mortality rates increased. Without mortality, recruitment was 100%; maximal mortality yielded zero recruitment as all fish that immigrated eventually died (Table 3).

The estimated fish production computed using eq. 14 differed between the two growth models. When growth parameters were estimated from field measurements, the fish biomass produced by the herring population when present in the upper estuary was 46.3 g wet weight per 10^3 m^3 per year. Using growth parameters from the North Sea herring population stock, total production amounted to 145.7 g wet weight per 10^3 m^3 per year.

Discussion

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

The first hypothesis cannot be confirmed or rejected by our observations. However, the pattern of estuarine movements as revealed by Fig. 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 this assumption is legitimate. These results are not available yet.

Fig. 3. The annual intake pattern of Atlantic herring in the upper Schelde Estuary at Doel (○) and the lower Schelde Estuary at Borssele (●).

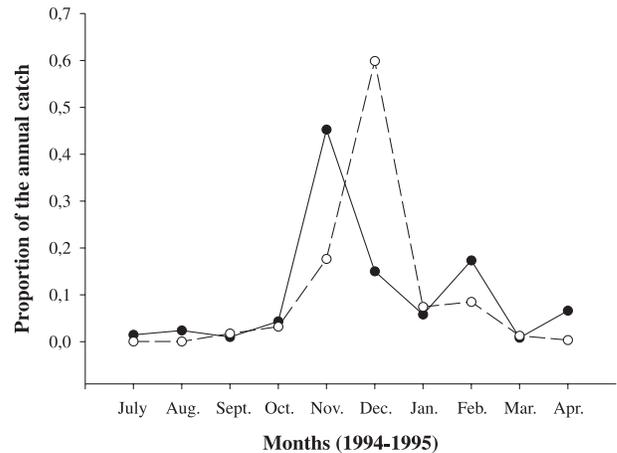
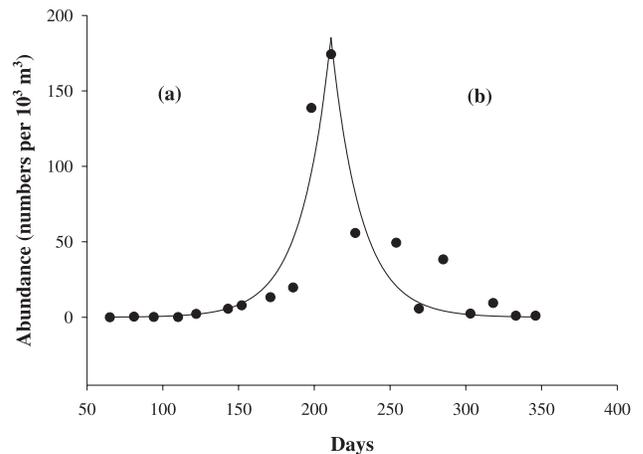


Fig. 4. Abundance of Atlantic herring (●) in the upper Schelde Estuary during immigration (a) and emigration (b) as determined from cooling-water screen catches at Doel. Fish abundance was fitted (a) during immigration by eq. 4 and (b) during emigration by eq. 7. Maximum abundance was reached at t_{max} = day 211; emigration was completed at t_{end} = day 346. Explained variance by the fitting (R^2) was 0.918 for immigration and 0.881 for emigration ($p < 0.01$).



The second hypothesis assumed that the mortality rate was constant. With increasing fish size, however, this rate may change (King 1995; De Barros and Toresen 1998). However, major changes in the natural mortality rate of herring visiting the upper estuary at Doel were not expected for three reasons. Firstly, juvenile herring all survived their first summer at sea and were about to recruit to the age-1 group. Secondly, the majority of herring recorded at Doel were only present for a relatively short period of time. Thirdly, piscivorous fish (gadoids) avoided the upper estuary because turbidity levels were unsuitable for visual predation on herring (Maes et al. 1998).

The third hypothesis assumed an exponential increase and decrease in fish abundance as the result of fish migration. Basically, this assumption questions why fish use estuaries and what factors control migration behaviour. Both environmental variations and biological interactions may cause

Table 3. Model parameters estimated by a non-linear estimation procedure.

z	a	i	N_{\max}	e	I	E	B_i (1)	B_e (1)	B_i (2)	B_e (2)
0	0.000202	0.050964	185.45	0.050864	185.4	185.3	640.8	686.5	225.2	367.7
0.000686	0.000207	0.050916	185.80	0.050177	188.3	183.1	650.7	669.3	228.6	363.4
0.001373	0.000209	0.050927	185.52	0.049490	190.5	180.3	658.4	650.4	231.3	357.9
0.002746	0.000216	0.050888	185.43	0.048117	195.4	175.2	675.3	615.7	237.2	347.8
0.005493	0.000225	0.050938	185.53	0.045370	205.5	165.3	710.3	552.2	249.6	328.1
0.010987	0.000247	0.050932	185.39	0.039876	225.4	145.2	778.8	441.3	273.6	288.2
0.021975	0.000290	0.050954	185.66	0.028888	265.7	105.3	918.3	271.2	322.7	209.1
0.043950	0.000379	0.05094	185.93	0.006913	346.4	25.2	1196.9	49.8	420.5	50.1
0.050864	0.000408	0.050913	185.56	0.000000	370.9	0.0	1281.9	0.0	450.3	0.0

Note: Equation 4 was used to estimate the intercept a and the immigration coefficient i under different mortality regimes. Equation 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).

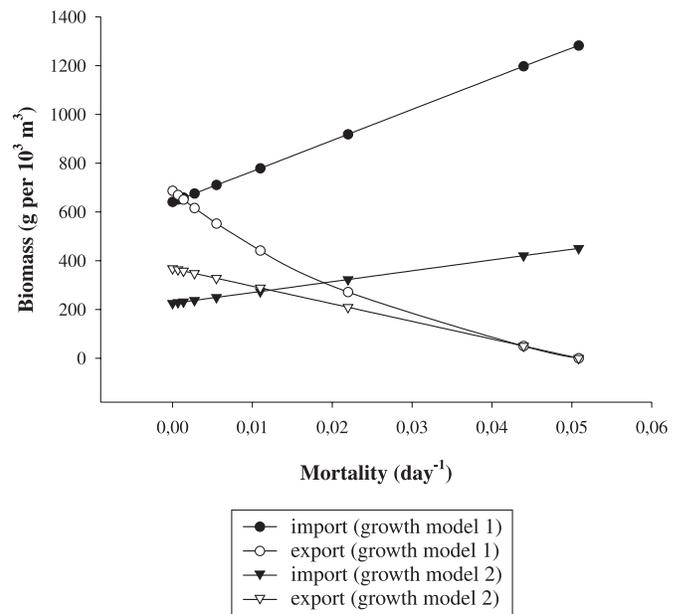
migrations of fish upstream or downstream. Large-scale experiments discriminating between factors controlling the movement of marine fish to an estuary are difficult to deploy. Ecological cost-benefit models, however, may predict seasonal usage of an estuary by fish. For example, the downstream movement 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 et al. 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 because of the entrapment of smaller individuals (Henderson et al. 1992), which could cause the marked slow down of growth in November and December. In addition, no reliable estimate of the maximum weight W_{∞} could be obtained as the samples consisted almost exclusively of age-0 juveniles.

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 $z = 0.012 \cdot \text{day}^{-1}$. Using growth parameters estimated from field observations, import balanced export at a mortality rate $z = 0.0012 \cdot \text{day}^{-1}$.

A weakness of this study was 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 was caused only by mortality and not by sampling bias, the mortality rate for the herring population was estimated at $0.011 \cdot \text{day}^{-1}$. At this rate of mortality, approximately 65% of the fish that immigrated

Fig 5. The relationship between mortality rate and transport of biomass by the Atlantic herring population. Two different growth models were used. Growth model 1 was as presented in Fig 2. Growth model 2 used growth constants from the North Sea herring population (Pauly 1982) ($W_{\infty} = 200$ g; $K = 0.0011 \cdot \text{day}^{-1}$).



were able to move out of the upper estuarine region while 35% died in the estuary (Table 3).

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 the findings of Deegan (1993), who estimated that average net biomass exported by *Brevoortia patronus* from a Louisiana estuary to the Gulf of Mexico was $38 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$, 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. It is thus tentatively concluded that export significantly exceeds import if populations move seaward before winter.

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