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Growth, feeding, production, and consumption in 0-group bib (*Trisopterus luscus* L.) and whiting (*Merlangius merlangus* L.) in a shallow coastal area of the south-west Netherlands

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In 1988 juvenile bib (*Trisopterus luscus*) and whiting (*Merlangius merlangus*) were studied in a shallow coastal area by monthly sampling with fine-meshed nets. 0-group fish of both species are first caught in May. By the end of the first growth season bib reached about 150 mm SL (standard length), whiting about 170 mm SL. Maximal densities were recorded in June and by the end of the year most fish had left the area. The instantaneous mortality is estimated at 0.008 day^{-1} (0.77% day^{-1} for bib and 0.76% day^{-1} for whiting) for both species. In May both species depended almost exclusively on calanoid copepods. In June and July mysids and amphipods were the most important invertebrate prey, but small fishes such as gobies provided a substantial proportion of the energy requirements, especially in whiting. From August onwards shrimp and fish dominated the diet in both species. Using Jones' (1974) model, food consumption as per cent body weight day^{-1} varied between 4 and 6% during summer and declined to 2 to 3% in autumn. Total consumption per unit area of subtidal seafloor, by the 0-group fish of both species taken together, was estimated at 0.47 g ash-free dry weight (ADW) m^{-2} year^{-1} using Jones' (1974) model and at 0.57 g ADW m^{-2} year^{-1} using a conversion efficiency (P:C ratio) of 0.34.

Key words: North Sea, trophodynamics, daily ration, production, consumption, 0-group gadoids, *Trisopterus luscus*, *Merlangius merlangus*, conversion efficiency.

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Introduction

0-group bib *Trisopterus luscus* and whiting *Merlangius merlangus* are an important ecological component of estuaries (Claridge and Potter, 1984), marine bays (Hostens and Hamerlynck, in press), and shallow coastal areas (Redant, 1977). Bib are not landed in great quantities in the North Sea but are commercially important in France (Desmarchelier, 1985b), Portugal (Sobral and Rebordão, 1982), and Spain (Benvegnú, 1971). Whiting are of considerable commercial importance (Hislop and MacKenzie, 1976) and rank second in weight terms in groundfish surveys in the central, southern, and eastern North Sea (Daan *et al.*, 1990).

Data on the food of larval bib and whiting, to a size of 11 mm, in the southern North Sea are given in Last (1978). Information on the food of bib of less than 130 mm is needed, but cannot be obtained from commercial catches (Santos, 1989). Some data exist on the food of 0-group bib in the Irish Sea (Nagabhushanam, 1965; Armstrong, 1982), the Loire estuary (Robin and Marchand, 1986), the Medway (van den Broek, 1978), and the Elbe (Kühl, 1973). There is also some "grey" literature on the subject (e.g. Gherbi-Barre, 1983; Puente, 1986). For 0-group whiting there are data from Icelandic waters (Pálsson, 1980), the Scottish west coast (Gordon, 1977b), the Irish Sea (Nagabhushanam, 1965), the northern North Sea (Robb and Hislop, 1980; Robb, 1981), and the Medway estuary (van den Broek, 1978). A very extensive report on the food of whiting in the North Sea is given in Hislop *et al.* (1991), but the smallest size class covered in that study is 100 to 149 mm total length. This size class corresponds to 0-group only for the last quarter of the year.

In order to fill the gap in the knowledge on food consumption by bib and whiting, 0-group fish were collected using fine-meshed nets in a shallow coastal nursery area during 1988.

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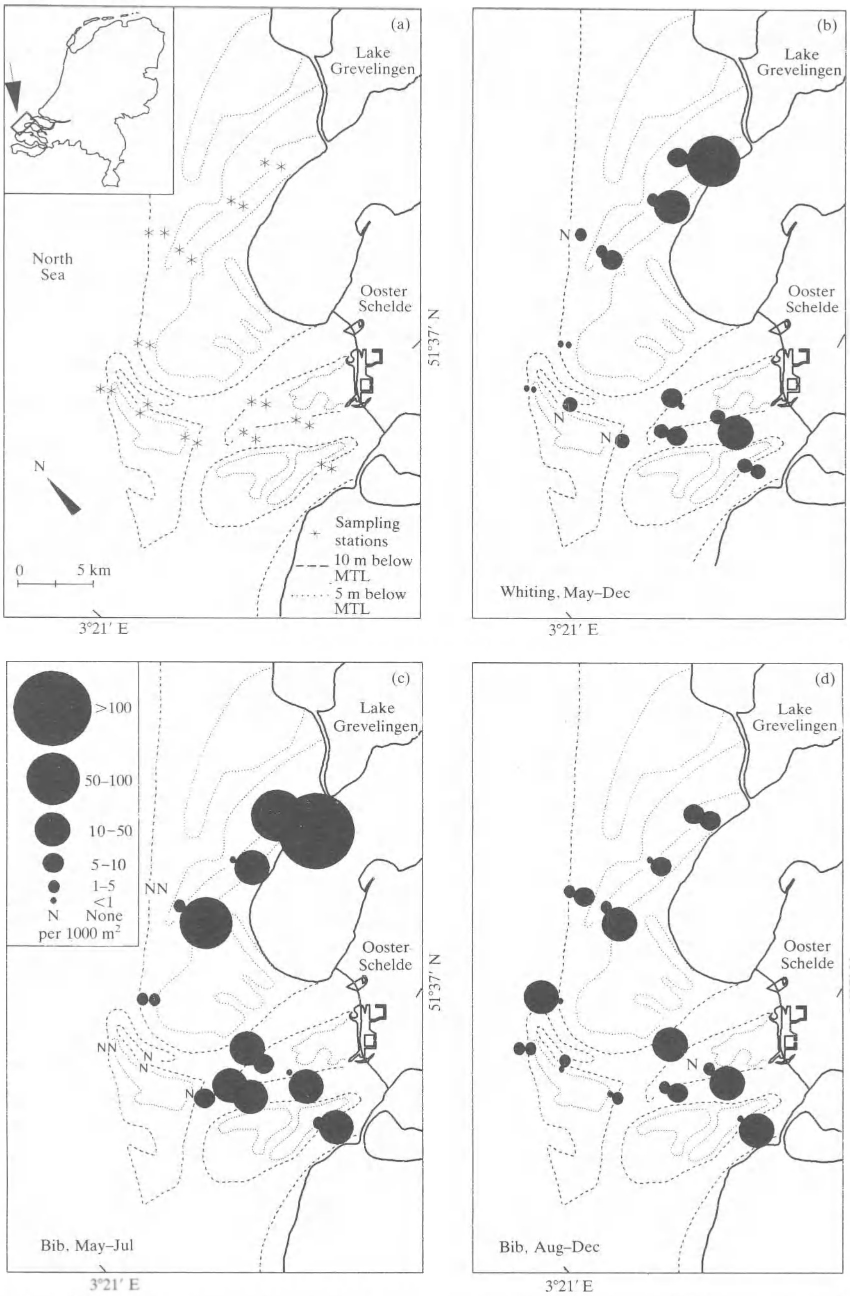

Figure 1. Map of the study area: (a) sampling stations, (b) distribution of whiting mean densities, (c) distribution of bib mean densities from May through July, (d) distribution of bib mean densities from August through December. MTL is the mean tidal level as defined for Amsterdam.

Material and methods

Study area

The study area proper covers the central part of the Voordelta (Fig. 1a) which is the shallow coastal area formed by the interlinked ebb tidal deltas of the (former) estuaries of the Dutch Delta where three main European rivers, the Rhine, the Meuse, and the Schelde, enter the North Sea. The Voordelta stretches from the Belgian–Dutch border in the south to the Hoek van Holland in the north. Its marine boundary is arbitrarily defined by the depth contour of 10 m below mean tidal level (MTL), as defined for Amsterdam, which is at 10 to 15 km seaward from the coastline. A detailed description of the hydrodynamics and geomorphology of the Voordelta is given in Louters *et al.* (1991).

The area was greatly affected by the engineering works which were undertaken to protect Zeeland from disastrous storm surges (Louters *et al.*, 1991). In relation to these engineering works the benthic ecology of the area has been quite extensively studied: meiofauna (Heip *et al.*, 1990; Vanreusel, 1990, 1991), macrofauna (Craeymeersch *et al.*, 1990), and hyperbenthos (Hamerlynck and Mees, 1991; Mees and Hamerlynck, 1992).

The spatial structure of the fish and mobile epifaunal assemblages in the area is discussed in Hamerlynck *et al.* (in press). The area is a nursery for flatfish, especially dab, sole, and plaice (Hamerlynck *et al.*, 1992). Data on the parasites of juvenile gadoids in the area will be published elsewhere (Van Damme *et al.*, in prep.).

Sampling

During 1988 monthly samples were taken at 24 stations in the Voordelta (Fig. 1a). These stations cover two depth strata (5 m below MTL and 10 m below MTL) at 12 localities. Samples were taken from the RV "Luctor" (34 m, 500 Hp) using a 3 m beam trawl, equipped with a 6 m long shrimp net with a 5 × 5 mm mesh in the cod end, a tickler chain, and a chain in the groundrope. Hauls were 1 km in length, starting from a buoy or other fixed marker, the distance covered being read from the radar screen. Ship speed relative to the bottom when trawling was about 4.5 knots. All bib and whiting were anaesthetized in a benzocaine solution in sea water to avoid unnecessary suffering and to prevent regurgitation of the stomach content, and were preserved in 7% neutralized formalin. For gadoids of over 70 mm the abdominal cavity was opened to allow rapid fixation of stomach contents. Standard length (SL), which is a more accurate measure than total length (TL), e.g. in case of fin lesions, was recorded for all fish specimens. As in fisheries research, TL is the most commonly used measure, linear regressions were calculated between SL and TL for a size range of both species. When comparing the results from the present study with studies using TL, the TL measurements were first converted to SL. Biomass was calculated from length–ash-free dry weight (ADW) regressions. Ash-free dry weight (ADW) was measured as the difference between dried (60°C for 5 days) and ashed (550°C for 2 h) weights of a size range of both species. Net efficiency, the number of 0-group gadoids caught in comparison to the number actually present per fished unit area of subtidal seabed, was assumed to be 20% for all size classes of fish. This point is taken up in the Discussion. Densities were calculated as N 10^{-3} m^{-2}, biomass as g ADW 10^{-3} m^{-2}. For conversion to numbers caught 10^{-3} m^{-2}, densities have to be divided by five. For conversion to numbers caught h^{-1} of trawling no exact factor can be given. Although the hauls were 1 km in length, haul duration depended on current velocity, wind speed and direction, and wave action but, by multiplying the reported densities by 4.4, the number of fish caught h^{-1} can be approximated.

A Wilcoxon signed rank test on pairs of variables was performed, comparing the densities of the individual 5 m and 10 m depth hauls for each locality, to test for depth preference of bib and whiting.

Stomach analysis

For each month 15 to 20 individuals of each species were selected at random for stomach analysis. Because of the low number of stomachs examined for November and December data were pooled for these months. In total 97 bib and 101 whiting stomachs were analysed. All items in the stomach were identified, if possible to species level, and measured. The original ADW of the prey, prior to ingestion was calculated from length–ADW regressions obtained for prey from the same area (K. Hostens, unpubl. data). Prey importance is expressed both numerically and gravimetrically. Dry weight of the stomach content (110°C for 2 to 4 h) was measured for the calculation of the fullness index (FI) (Berg, 1979). For statistical purposes, FI was arcsin-transformed (Sokal and Rohlf, 1981). About 80% of the fish found in the stomachs could be identified, at least to genus level, by comparing skeletal elements to a reference collection. Unidentified fish were apportioned in accordance to the numerical or gravimetric percentages of the identified ones (Hislop *et al.*, 1991). The diversity of the diets of both species, a measure of niche breadth, was calculated as Shannon–Wiener H′ (Washington, 1984):

$$H' = -\sum_i p_i \log p_i,$$

where p_i is the proportion of the number prey of the ith species in the diet over the total number of items in the diet.

Growth, mortality, production, and consumption

Growth is measured as the increase of mean length of 0-group fish per month. The instantaneous mortality rate Z is defined as the decrease in density of 0-group fish in the study area and is calculated from the linear regression equation fitted through the ln transformed densities (bib: June through December; whiting: June through October).

Total production P of the cohort over the time period considered is:

$$P = \sum \tau P,$$

where the monthly production τP can be estimated as:

$$\tau P = \frac{N_t + N_{t+\tau t}}{2} \tau \bar{w},$$

where N_t is the density at time t and $\tau \bar{w}$ is the mean growth increment for this month (Crisp, 1984).

Food consumption was estimated directly from the stomach content data using Jones' (1974) model. This model estimates the stomach evacuation rate r (in g h^{-1}) from

$$r = S^{0.46} \times (L/40)^{1.4} \times Q \times 10^{0.035(T_0 - T_c)},$$

with S the average weight of the stomach content (g wet weight), L the total length of fish in cm, Q the rate of evacuation for a 1 g meal of a stated food type of a 40 cm fish at temperature T_c and T_0 the temperature of the sea water when sampling. Patterson (1985) gives an erroneous formulation of the same model with 40/L instead of L/40. It seems probable that Patterson's calculations have been done with the correct formula, though this cannot be verified from the paper. For use in the model, ADW measurements were multiplied by five in order to convert to wet weight. After the calculations they were converted back to ADW. Judging from stomach fullness data in Robin and Marchand (1986) bib feed at about the same rate throughout a 24 h cycle. Similarly, Gordon (1977b) finds little variation in whiting stomach fullness over 24 h. Patterson (1985) reports an early morning peak and an evening dip in stomach fullness of whiting. Around noon stomach fullness is average. Robb (1981) finds a two-peaked feeding periodicity in whiting. One of the peaks is around midnight, the other around midday. As both peaks are of the same magnitude stomach content weights of fish collected during daylight hours can be assumed to be representative for the entire 24 h. For the fish part of the stomach content, a Q-value of 0.26 was used and for the crustacean part a Q-value of 0.19 (Jones, 1974). The latter value was also used for the rarely consumed non-crustacean invertebrates. Assuming equilibrium between intake and consumption, the daily food intake C could be calculated:

$$C = r \times 24,$$

where r is the stomach evacuation rate as estimated from Jones' model. Daily food intake C is then expressed as φ, the daily feeding coefficient or the percentage of its body weight the average 0-group fish consumed on that sampling date. For bib φ was also calculated according to Pennington (1985), i.e. applying Jones' model to the individual fish and averaging afterwards.

Total (or annual) consumption A over the time period considered is then estimated as:

$$A = \sum_{d=164}^{d=335} \varphi_m \bar{B}_d,$$

with φ_m the daily feeding coefficient for the month (or intersampling interval) considered and $\bar{B}_d$ the average population biomass linearly interpolated between two sampling dates. A P:C ratio or "ecological efficiency" or "conversion efficiency" is calculated from production (P) and consumption (A) values. Gross conversion efficiency is the ratio of the growth increment and the reproductive output over food intake. As 0-group gadoids are juvenile, reproductive output can be assumed to be zero and the P:C ratio is equivalent to the net conversion efficiency.

With the partitioning of the food (in weight terms) over the various prey types for each month, the annual consumption of the different prey types is estimated.

Food consumption was also calculated using a P:C ratio of 0.34, as established for 1-group cod by Pihl (1982). According to the data in Jones and Hislop (1978) net conversion efficiencies do not seem to differ substantially between different gadoid species. For whiting Jones and Hislop (1978) report an average P:C of 0.3 but there is a tendency for it to be higher in smaller fish. The 0.34 of Pihl (1982) therefore seems acceptable.

Results

Growth, density, and spatial distribution

The observed relationship between total length (TL) and standard length (SL) was $TL = 1.157 + 1.084\ SL$ ($n = 111$, $r^2 = 0.999$) for whiting and $TL = 2.35 + 1.102\ SL$ for bib ($n = 78$, $r^2 = 0.97$). The observed length–weight relationship was $ADW = 7.25\ 10^{-7}\ SL^{3.293}$ ($n = 45$, $F = 7490$, $p < 0.001$) for bib, and $ADW = 1.59\ 10^{-6}\ SL^{3.066}$ ($n = 47$, $F = 6124$, $p < 0.001$) for whiting.

The first 0-group bib ($n = 5$) and whiting ($n = 52$) were caught in the study area in May, though smaller postlarvae had already been caught with the finer-meshed nets of the hyperbenthic sampler (Hamerlynck and Mees, 1991) in April (J. Mees, unpubl. data). Growth was quite fast with mean lengths of the cohorts increasing from less than 50 mm in May to 154 mm for bib and 173 mm for whiting in November (Fig. 2). In December there was a slight decrease in mean length for bib. No mean length was calculated for the two 0-group whiting caught in December.

From June onwards bib densities were about double those of whiting (Table 1). By November 0-group fish of both species had mostly left the area or had died.

Both species had a strong preference for the 10 m below MTL depth stratum. The Wilcoxon test was highly significant ($p < 0.001$) for both species (bib: $Z = -4.8$; whiting: $Z = -3.6$). There was a clear maximum of abundance in the inner part of the ebb tidal delta of the Grevelingen (Fig. 1b, c). For whiting this remained so throughout the year, for bib the centre of gravity of the distribution shifted

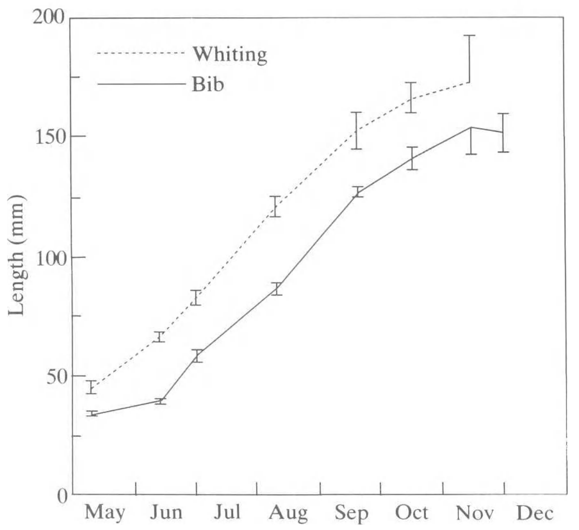

Figure 2. Growth of 0-group bib and whiting: mean standard length per month with standard errors.

towards the ebb tidal delta of the Oosterschelde from August onwards (Fig. 1d).

Mortality

The linear regressions fitted through the (ln transformed) densities versus time are highly significant ($r^2_{bib} = 0.94$, $r^2_{whiting} = 0.81$, $p < 0.01$ in both cases) (Fig. 3). From these regressions the instantaneous total mortality rate was estimated at 0.0077 day^{-1} (0.77% day^{-1}) for bib and 0.0076 day^{-1} (0.76% day^{-1}) for whiting. This corresponds to approximately 21% $month^{-1}$ in both species.

Production

Total production per unit area of subtidal seabed for the 0-group (June through December 1988) amounted to 0.13 g ADW $m^{-2} year^{-1}$ for bib and to 0.06 g ADW $m^{-2} year^{-1}$ for whiting. The P:B ratio for the time period considered was 4.5 for bib and 3.8 for whiting.

Feeding and food consumption

Average fullness index (FI) (backtransformed) over the study period was 1.75 (S.E. 0.004) for bib and 1.39 (S.E. 0.004) for whiting. Empty stomachs were rare, only three being found in bib and only one in whiting. There was no clear seasonal pattern in the FI (Table 2).

Numerical and gravimetric percentages of the main food categories are shown in Figure 4. After feeding exclusively on calanoid copepods both species shifted to fish, mysids, and amphipods at about 50 mm SL. From about 100 mm SL both species fed nearly exclusively on shrimp and small fish.

According to Jones' model, bib consumed 0.29 g ADW $m^{-2} year^{-1}$, whiting 0.18 g ADW $m^{-2} year^{-1}$. Daily feeding coefficient φ was between 4 and 6% of body weight in summer and declined to 2 to 3% in autumn. For bib there is little difference between φ as estimated through Pennington's procedure and the more classical approach using the average stomach content (Table 2).

The P:C ratio was 0.45 for bib and 0.36 for whiting. Using the P:C ratio of 0.34 (Pihl, 1982) total consumption amounted to 0.38 g ADW $m^{-2} year^{-1}$ for bib and to 0.19 g ADW $m^{-2} year^{-1}$ for whiting. A major part of this consumption consisted of a restricted number of species (Fig. 5), mainly the brown shrimp *Crangon crangon*, two species of goby (*Pomatoschistus minutus* and *P. lozanoi*) and larval and early postlarval herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). In bib, which has a more diverse diet (Shannon–Wiener $H' = 1.05$) than whiting ($H' = 0.61$), other fishes such as young sandeel *Ammodytes tobianus*, dragonet *Callionymus lyra*, early postlarval flatfish, and gadoids occurred on a par with juvenile clupeids. The only other important prey were three mysids *Gastrosaccus spinifer*, *Schistomysis kervillei*, and *S. spiritus* and two amphipods *Gammarus crinicornis* and *Atylus swammerdami*.

Discussion

The estimates of all the variables in this paper are subject to various sources of bias. Most of these have been discussed by Patterson (1985) but in the present study the estimate of net efficiency, defined as the percentage of 0-group gadoids, feeding on or above the sampled surface area, caught in the net, is an added major source of uncertainty. The assumption that net efficiency is only 20% is something of a wild guess. Following Kuipers (1975) there are four possible ways for fish in the trawl path to escape from an approaching beam trawl: through the meshes, underneath the ground rope, over the beam, and sideways. Escapement through the meshes can be assumed to be low once the fish have reached a certain size, i.e. from July onwards. Creutzberg *et al.* (1987), though they state that pelagic fish such as whiting are not supposed to be influenced by the number of tickler chains on a beam trawl, found that the slope relating numbers caught on sandy bottoms to the number of tickler chains used was actually significantly different from zero in whiting. Variability in whiting catches was high but using three tickler chains Creutzberg *et al.* (1987) caught 1.5 times more whiting than with one tickler chain. Catches reached a plateau at three tickler chains. Therefore there seems to be some escapement under the gear when using only one tickler chain on sandy bottoms. Engås and Godø (1989) also report on substantial numbers of small gadoids

Table 1. Month and day number of sample counting from 1 January (d_s), density (N 10^{-3} m^{-2}), and biomass (g ADW 10^{-3} m^{-2}) with standard errors for 0-group bib and whiting.

		Trisopterus luscus		*Merlangius merlangus*	
Month	d_s	Density	Biomass	Density	Biomass
May	130	0.4±0.3	0.04±0.03	4.6±2.3	0.9±0.4
Jun	164	72.6±52.3	13.3±9.6	28.1±14.7	21.2±11.9
Jul	182	18.1±7.3	11.3±3.8	11.0±4.1	15.2±5.7
Aug	222	11.3±5.8	23.5±14.8	5.8±2.8	23.5±12.4
Sep	263	12.7±4.6	85.8±32.1	3.5±1.1	29.6±10.6
Oct	290	7.0±2.3	68.0±22.5	3.7±1.9	40.0±19.4
Nov	319	1.3±0.5	16.7±7.0	0.2±0.2	2.7±1.9
Dec	335	1.1±0.6	12.6±6.4	0.2±0.1	1.9±1.3

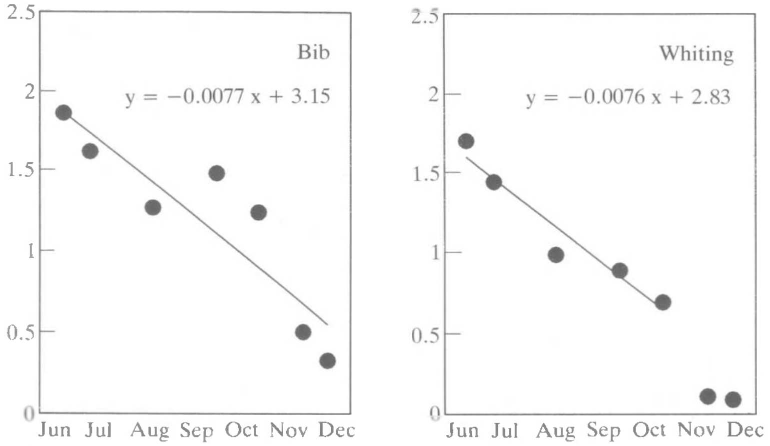

Figure 3. Density of 0-group bib and whiting (ln transformed): means per month with the regression lines for mortality.

Table 2. Number of fish caught (N_c), number of stomachs analysed (N_s), mean fullness index with standard error (F.I.±S.E.), total number of prey items (N_p), daily feeding coefficient according to Jones (φ_j), according to Pennington (φ_p) for 0-group bib and whiting.

	Trisopterus luscus						*Merlangius merlangus*				
	N_c	N_s	F.I.±S.E.	N_p	φ_j	φ_p	N_c	N_s	F.I.±S.E.	N_p	φ_j
May	5	4	0.9±0.09	184	–	–	57	17	1.6±0.02	1388	–
Jun	902	21	1.8±0.01	856	4.7	5.1	349	19	1.1±0.03	328	4.2
Jul	234	14	3.3±0.01	247	5.9	6.4	143	17	1.4±0.03	241	4.4
Aug	147	12	1.9±0.05	149	5.8	5.5	75	15	1.4±0.05	137	6.0
Sep	165	16	1.0±0.02	237	3.2	3.3	45	14	1.7±0.02	55	4.8
Oct	90	20	1.8±0.02	344	3.1	3.1	48	15	1.4±0.03	67	2.8
Nov–Dec	31	10	1.4±0.05	93	2.5	2.1	5	4	0.8±0.03	12	1.8

escaping under an, admittedly quite different, trawled gear. The observations of Creutzberg *et al.* (1987) put maximum efficiency at 68%. Bib and whiting are fast swimmers, so an unknown proportion, especially of the larger fish, can be expected to be able to avoid the gear by moving up or sideways. Moreover, as bib and whiting are pelagic at first and, even when becoming demersal, do not spend all of their time in close proximity to the bottom, some proportion of the population is also out of reach of the gear, the headrope of which is at 0.55 m from the bottom. Net efficiency is therefore unlikely to be over 50% and in this study it was assumed to be a lot less. This means

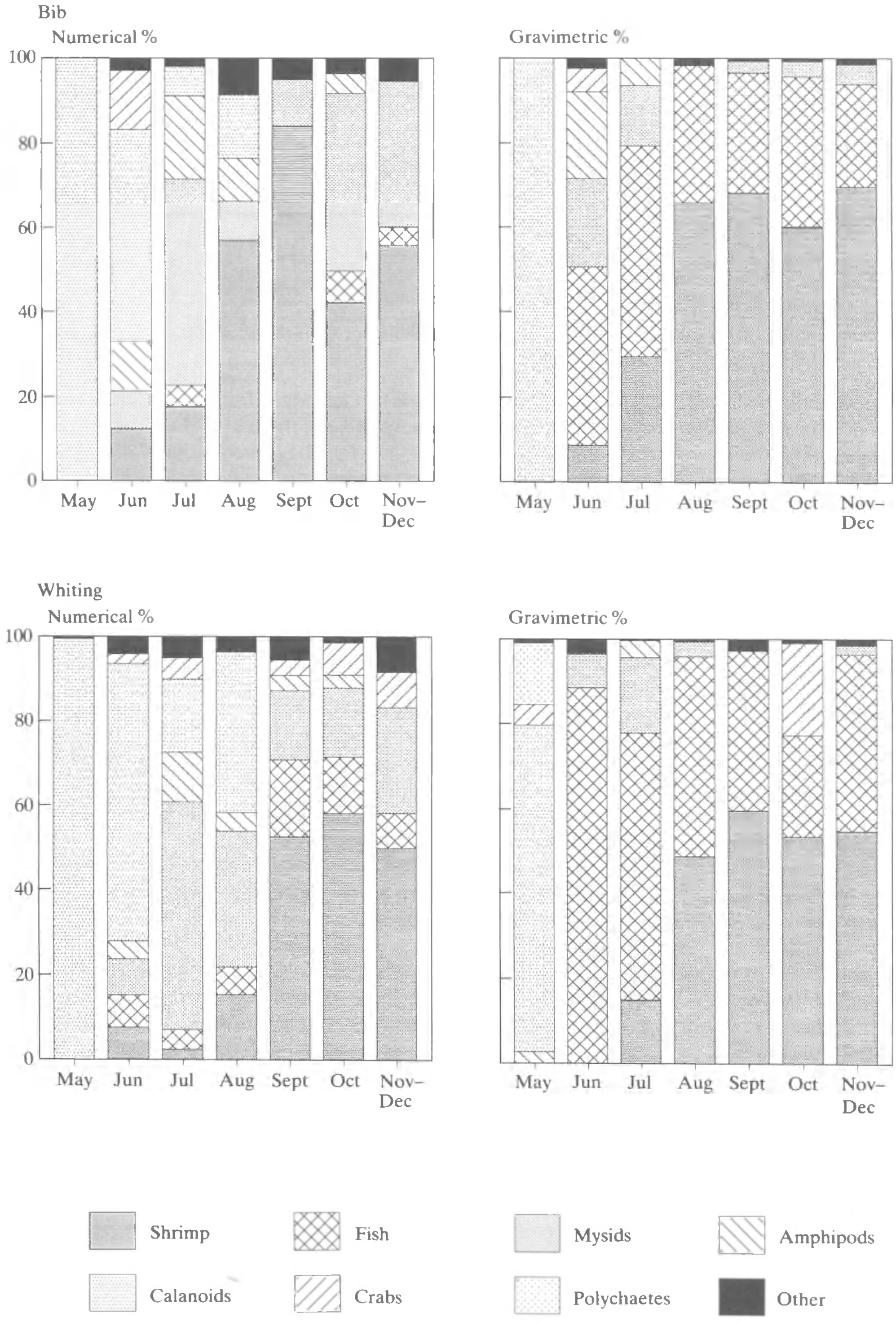

Figure 4. Numerical and gravimetric food composition for bib and whiting.

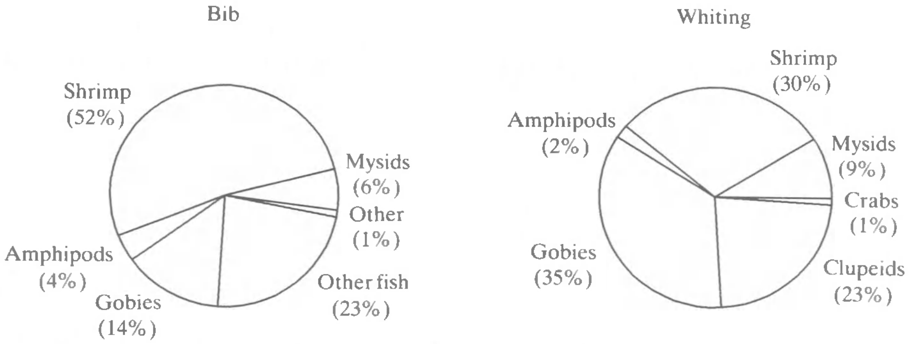

Figure 5. Partitioning of food consumption by 0-group bib and whiting (June through December) for the main prey categories.

there are considerable margins of uncertainty to the estimates based on this assumption. If efficiency were 40% density, biomass and production would only be half of the estimates given. More detailed studies on net efficiency, along the lines proposed by Kuipers *et al.* (1992), are clearly warranted. Only then can studies of fish trophodynamics be expected to match the accuracy of macrobenthic studies.

Growth as recorded in this study closely matches the results from other studies: in Moroccan waters (Coupé and Maurin, 1955) and on the Atlantic coast of Spain (Oliver, 1949) 0-group bib averaged between 125 and 130 mm SL by the end of the first growth season. By February of the next year the model class reaches 150 mm SL in the southern North Sea (Desmarchelier, 1985a). Fish collected from the intake screens of power stations have a seemingly slower growth: model length class of bib in the Severn estuary increased from 40–49 mm SL in August to 70–79 mm in November–December (Claridge and Potter, 1984). Similarly, 0-group whiting in the Severn estuary grew from 60–70 mm SL in June–July to only 100 mm SL in December (Henderson and Holmes, 1989). This slow "growth" is probably an artefact of the collection method. Perhaps the larger 0-group gadoids have sufficiently high swimming speeds to avoid being sucked into the power station. On the Scottish west coast whiting grew from about 100 mm SL in July to about 160 mm SL in November (recalculated from Gordon, 1977a). This is very similar to growth in Kiel Bight (Arntz and Weber, 1972) and closely resembles the results of the present study.

As in other studies fish "growth" as defined here is a combination of true growth of individuals, predation (possibly size-selective), migration (probably also dependent on size), and mesh selection in an unknown mixture. Mean lengths in November and December are less reliable because of the low numbers of 0-group caught. The apparent length decrease of bib in December may be caused by differential migration, the largest fish leaving the area first. The same phenomenon was observed in other gadoids (Cooper, 1980).

As can be judged from the standard errors of the densities (Table 1) the spatial distribution of both species is very patchy. The concentration in the ebb tidal delta of the Grevelingen, which is especially strong in the early part of the year and is most pronounced in bib, may be partly caused by passive transport into the area. The current patterns in the ebb tidal delta of the Grevelingen create a sink for mud and detritus. Other neutrally buoyant particles e.g. macrobenthos larvae, larval decapods, and fish eggs and larvae may also be trapped in the area (Hamerlynck *et al.*, 1992). According to Cooper (1980) 0-group gadoids in Scottish waters reach their nurseries mostly through active migration. Just like postlarval flatfish (Rijnsdorp *et al.*, 1985), juvenile gadoids are probably rather versatile. They can make use of the residual current for passive drift but, through vertical migration, they may also be able to make use of the tidal currents to move in the opposite direction.

The observed shift in bib distribution from the ebb tidal delta of the Grevelingen to the ebb tidal delta of the Oosterschelde may be partly due to migration, but there may be an add-on effect of 0-group bib leaving the Oosterschelde proper. This second effect may also form the basis of the slight increase in density of bib in September and of whiting in October (Table 1).

The estimates of the instantaneous mortality rate are a combination of natural mortality, (indirect) fishing mortality and migration. Indirect fishing mortality of 0-group gadoids in the area is thought to be low since few shrimp trawlers operate in this part of the Voordelta. Migration can be an important contributing factor as it is well known that 0-group bib and whiting migrate to deeper areas by the end of their first growth season. Migration is thought to be the main cause for the sudden decrease in whiting densities after October. Therefore, the last 2 months were not used for the calculation of Z in this species.

The production:biomass (P:B) ratio calculated is higher than the often used P:B = 2.75 (Elliott and Taylor, 1989) or 2.5 (Hostens and Hamerlynck, in press). These last two figures may be valid for mixed age groups of fishes but less so for the 0-group.

For whiting there is close similarity between consumption estimated directly from the stomach contents and indirectly from production using a production:consumption (P:C) ratio of 0.34. For bib the estimate using Jones' model is about 25% lower than using the P:C ratio. Possibly Jones' model has limited applicability for the deeper bodied and shorter lived *Trisopterus* species. The feeding coefficient φ is in close agreement to the findings of Daan (1973) who gives 5.3% for North Sea cod of 100 mm (probably total length, measurement procedure not mentioned in Daan, 1973) and 2.5% for cod of 200 mm.

Food preference at different sizes closely resembles the pattern observed by other authors (see references in the introduction): first calanoids, then mysids and amphipods and finally shrimp and small fishes.

Our estimate of the P:C ratio, or ecological efficiency, seems high for bib, but for whiting it is closely similar to Pihl's (1982) estimate for 1-group cod and to the estimate of Jones and Hislop (1978) for different gadoid species. All these estimates are much higher than the 0.11 to 0.18 suggested for whiting by Patterson (1985), though his data did not include 0-group fish. Moreover, if consumption was calculated by Patterson (1985) using the stated formula, it may have been seriously overestimated, leading to a very low P:C.

Though Pennington (1985) showed that one should first raise the individual weights in the stomachs to a certain power (0.43 in the case of Jones' model) and then calculate the mean to find an unbiased estimator of food consumption, this procedure was not followed in the present study, nor by Hislop *et al.* (1991). The possible consequences of this are illustrated in a very extreme example given in Ursin *et al.* (1985) where consumption was overestimated by over 40% using our procedure. However, as long as variability in the amount of food in the stomachs of the fish is low, which, in the present study, is the case for both species, the final result of both procedures is rather similar and the calculations are very substantially simplified using the average of stomach content per sample as the input to Jones' model. Thus, in bib, there was on average less than 0.4% difference between per cent body weight consumption using Pennington's procedure and the simpler approach. From the variability in stomach contents in whiting it seems highly likely that, if any, the difference between the two procedures for whiting would have been of the same order of magnitude. However, Pennington's procedure should be used in species taking single meals of large and heavy items with long (e.g. several days) non-feeding intervals between two meals.

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