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Daily ration of juvenile *Pomatoschistus lozanoi* de Buen (Pisces: Gobiidae)

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In order to estimate daily ration of juvenile *Pomatoschistus lozanoi* and to evaluate the effect of tide and daylight on its feeding activity, two 24-h samplings were performed, one (in 1985) with high water around midnight, the other (in 1986) with low water around midnight. Incidently, the sampling in 1985 was around neap tide and in 1986 it was around spring tide. The fish were observed to feed more intensively during the night. Daily ration in 1985 was estimated to be about 1% of body ash-free dry weight (ADW). For 1986, the estimate is about 5% of body ADW in spite of similar water temperatures at both sampling dates. It is suggested that a semilunar rhythm, either in the fish or in the invertebrate prey, is the basis of the observed difference. This phenomenon may also explain the prominent 14-ring bands observed in the otoliths. Because of the influence of the various rhythms on feeding activity in fishes living in a strongly tidal environment, an accurate estimate of daily ration from production estimates and a P:C ratio established in the laboratory may be logistically less demanding than an estimate from stomach-content data.

Key words: feeding rhythm, spring–neap cycle, otoliths, zooplankton.

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Introduction

Daily ration, the amount of food consumed by an animal over 24 h, is a basic parameter in the study of the trophodynamics of ecosystems. With the development of multispecies models of fisheries management, this parameter has taken on increased importance also in the field of applied ecology (Sissenwine and Daan, 1991).

In field studies of fish, daily ration can be determined by assessing stomach content at regular intervals over a 24-h period and then, with the knowledge of rate of gastric evacuation, calculating total consumption over the period considered. A wide variety of models exists, both for the determination of the rate of gastric evacuation and for the calculation of consumption. The literature on gastric evacuation models is full of heated debate (e.g. Olson and Mullen, 1986; Jobling, 1986) on the respective merits and shortcomings of the various models, but in most circumstances the results of the different models are virtually indistinguishable (Persson, 1986). The exponential model of gastric evacuation is both adequate and convenient because of its simplicity (Persson, 1986). The most widely-used consumption models, namely the Eggers (1977) model and the first model of Elliott and Persson (1978), assume an exponential rate of gastric evacuation (see also Cochran, 1979; Eggers, 1979; Elliott, 1979). Until recently it was assumed that the Eggers model, which is much simpler, required stomach contents to be equal at the beginning and the end of the 24-h period. However, Boisclair and Leggett (1988) have shown the Eggers model to be quite robust: even when the assumptions are violated the estimate of daily ration is accurate. Some models do not require an independent estimate of the rate of gastric evacuation (Sainsbury, 1986; Jarre *et al.*, 1991). However, an abrupt transition between the feeding periods and the non-feeding periods is needed for an estimate of this rate from field data.

In most fish, activity is clearly synchronized with the light–dark cycle, but in the sea there is an additional tidal stimulus (Gibson, 1993). Most often there is a correlation between activity and feeding, although the physiological basis of these rhythms is still poorly understood (Boujard and Leatherland, 1992). The documentation and understanding of these rhythms is also important for aquaculture (Parker, 1984); for example, feeding the fish at the "wrong" time will result in poor growth performance.

Sand gobies of the genus *Pomatoschistus* are the most abundant fish in shallow coastal areas and estuaries of

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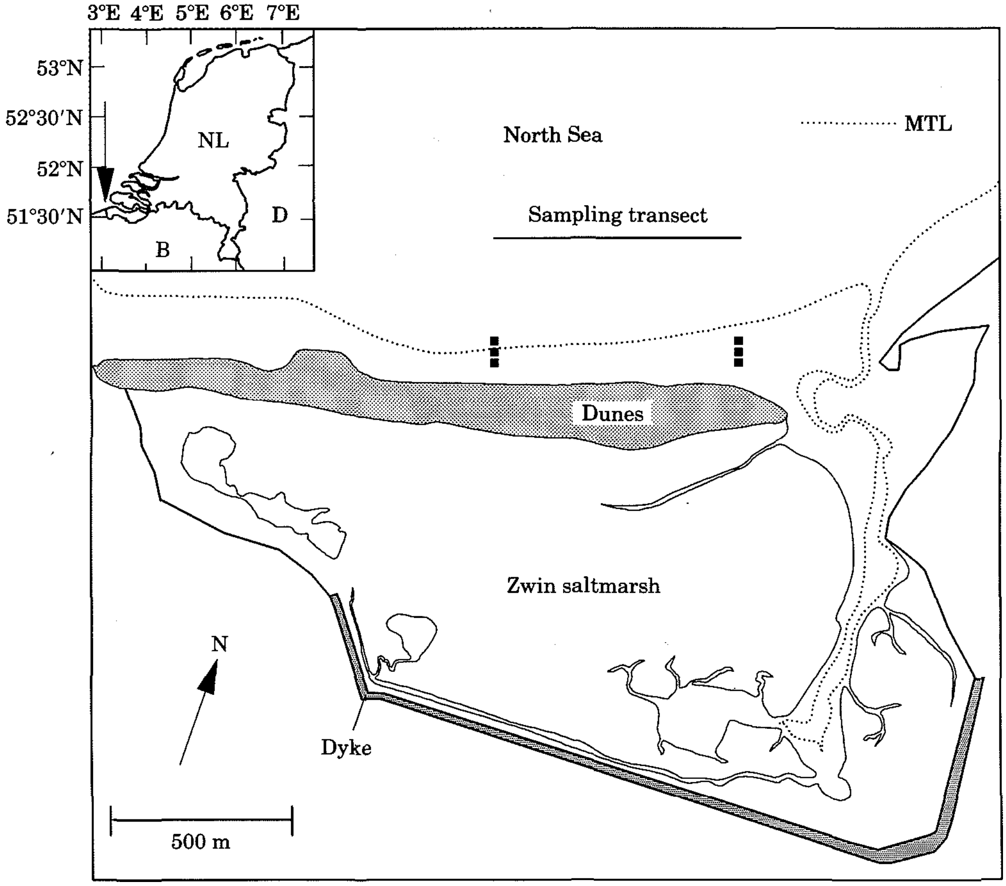

Figure 1. Map of the study area with the sampling transect. MTL is the mean tidal level as defined for Amsterdam. Inset: position of the study area in relation to the Netherlands (NL), Belgium (B), and Germany (D).

the North Sea (Hamerlynck *et al.*, in press) and, like other small gobiids, are important prey for 0-group gadoids (Fosså, 1991; Hamerlynck and Hostens, 1993). *Pomatoschistus lozanoi* is known to feed mainly on hyperbenthic animals, primarily mysids (Hamerlynck *et al.*, 1990). No studies have so far addressed the feeding rhythm of *Pomatoschistus lozanoi.* It is known that the closely-related and sympatrically-occurring *Pomatoschistus minutus* is mostly active during the night (Berge *et al.*, 1983). However, in a tide-less environment Evans (1984) could not detect any diurnal rhythm in feeding activity. According to Gibson and Hesthagen (1981), in constant conditions *P. minutus* has an endogenous circatidal rhythm with peak activity around low tide. In normal light–dark conditions this activity is greatly enhanced at night. In the Ythan estuary Healey (1971) observed peak feeding by *P. minutus* is at high tide.

In the present study the existence of a feeding rhythm in *Pomatoschistus lozanoi* of 25–29 mm standard length is assessed, daily ration is calculated using different models and, the nature of the rhythm found is tentatively defined, on the basis of two 24-h cycles.

Material and methods

Study area

The study site is an exposed sandy beach close to the mouth of a tidal creek which is the entry to a 125-ha saltmarsh: the Zwin nature reserve. This reserve is situated at the mouth of the Westerschelde estuary, the southernmost estuary of the Dutch Delta, near to the Dutch–Belgian border (Fig. 1). The fish and epibenthic invertebrate community of the Delta is described in Hamerlynck *et al.* (in press). A Rijkswaterstaat tidal gauge about 1 km north of the sampling site records tidal height every 10 min. Salinity at the sampling site varies between 27 and 32. Average tidal amplitude is 429 cm at spring tide and 283 cm at neap tide (total average 368 cm) (Fig. 2). Tidal currents are longshore (SW–NE) with maximal velocities of 1.7 m s^{-1} about 1 h before high and low water. Median grain size of the sand fraction at 6 m below mean tidal level (MTL) is 171 μm, mud content is on average 4.7%. Some *Lanice conchilega* beds are found close to the sampling site.

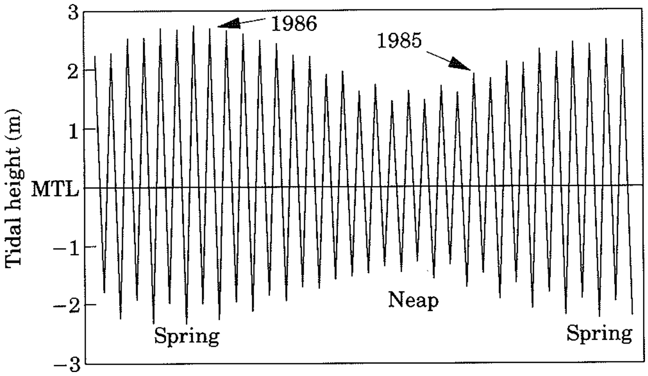

Figure 2. Typical spring–neap tidal cycle at the sampling site with the position of the 1985 and 1986 samplings in relation to the spring–neap cycle.

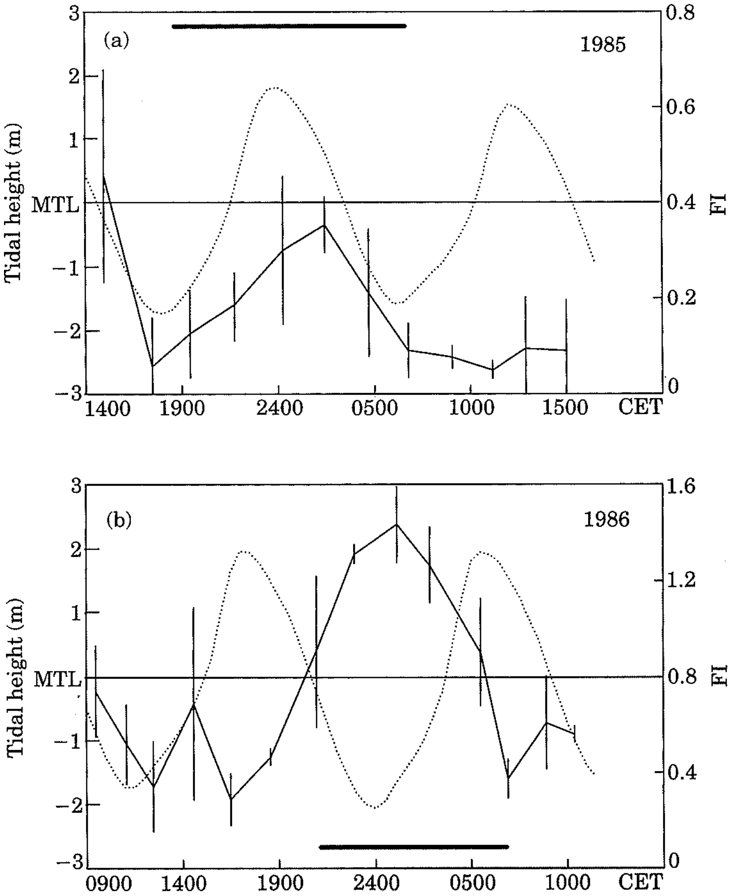

Figure 3. Time trajectories of mean stomach fullness (FI, backtransformed arcsin transformed) with standard deviation (full line, right scale), and tidal height (dotted line, left scale) for 1985 (a) and 1986 (b). The dark bar represents darkness.

Sampling

Samples were taken from a small vessel in the shallow subtidal of a sandy beach using a two-beam trawl (Kuipers, 1975) equipped with a 5 × 5-mm mesh net. Hauls were taken parallel to the beach at 6 m below MTL. Haul length, between two sets of radar beacons set on the beach, was approximately 700 m. Haul duration varied depending on current velocities, but was 13 min on average (minimum 7, maximum 26 min). Depending on the number of fish caught, two to four hauls were taken for each time interval. All fishes caught were anaesthetized in

Table 1. Pairwise multiple comparison of two consecutive minima and the intermediate maximum (arcsin transformed) fullness indices (k = number of pairs, v = degrees of freedom).

1985 GT2 method ($k = 3$; $v = 50$)		
Critical value for $p < 0.01 = 3.087$		
Hauls	H2	H10
H6	4.297	5.073
1986 T′ method ($k = 3$; $v = 56$)		
Critical value for $p < 0.01 = 4.301$		
Hauls	H5	H12
H9	8.466	7.682

Table 2. Daily ration for 1985 and 1986, expressed as per cent of body ADW, as estimated from the different models.

Model	1985	1986
Eggers	1.183	5.384
Elliott and Persson	1.044	5.886
Sainsbury	0.906	4.585

a benzocaine solution in sea water to avoid unnecessary suffering and to prevent regurgitation of stomach contents and then preserved in neutralized formaldehyde in sea water (10% final concentration). Data on the variation in catch rates of gobies and other fish will be reported elsewhere.

In the laboratory between 13 and 20 *Pomatoschistus lozanoi* of between 25 and 29 mm standard length (SL) were selected at random, preferably from a single haul, for stomach analysis. The midpoint between the start and the end of that haul (or occasionally of a set of hauls) was taken as the time of the sample. All prey items encountered were identified, if possible to species level. In the present study only the numerically dominant prey types (occurring on average with over one item per stomach): two groups of Copepoda, namely harpacticoids and calanoids, and two larval stages of Cirripedia, namely nauplii and cypris larvae, are discussed. The original ash-free dry weight (ADW) of the prey items prior to digestion was calculated from regressions established for the same general area (Hostens, unpublished). Stomach contents were weighed on a Mettler M3 microbalance (accuracy 1 µg) after drying for 2 h at 110°C and expressed as fullness index (FI):

$$FI = \frac{S_i}{W_i} \times 100,$$

with S_i the dry weight of the stomach content in mg and W_i the ash-free dry weight (ADW) of the fish in mg. Fish ADW were taken from a length–ADW regression (Hamerlynck *et al.*, 1986). Prior to use of FI data in consumption models or statistical tests these were arcsin transformed for normalization and backtransformed when mean FIs were needed (Sokal and Rohlf, 1981).

In 1985 sampling was started at 1458 Central European Time (CET) on 25 September (tidal amplitude about 360 cm, high tide at midnight). Twelve approximately 2-hourly samples, H1 to H12 (average interval 172 min), were taken and sampling was concluded at 1502 CET the next day. Seawater temperature was 17.5°C. Because of low catches during the day most stomach content data are a mixture of two consecutive hauls. H2 and H9 are mixtures of four consecutive hauls.

In 1986 sampling was begun at 930 CET on 11 August (tidal amplitude just over 4 m, low tide at midnight). Fourteen samples, H1 to H14 (average interval 106 min), were taken and sampling was concluded at 1025 CET the next day. Seawater temperature was 18°C. Because of the high number of gobies caught all stomach content data refer to single hauls.

As, for a specific locality, the time of day of a certain semilunar tidal phase, e.g. spring tide high water, is constant, the deliberate choice of comparing a high-water midnight with a low-water midnight sampling resulted in the 1985 and 1986 samplings to be at roughly contrasting periods of the spring–neap cycle (Fig. 2).

To assess if a feeding rhythm was present two consecutive minima and the intermediate maximum within each 24-h cycle were tested using a pairwise multiple comparison among means (Sokal and Rohlf, 1981). Because of the range of sample sizes (13 to 20 stomachs analysed per time interval) in 1985 the GT2 method was used. For the 1986 data (19 or 20 stomachs analysed per time interval) the more powerful T′ method could be used. In view of the small size interval of the fishes examined it was unnecessary and impracticable to use ANCOVA (Jenkins and Green, 1977; Fernandez *et al.*, in press) to adjust for size differences among the fishes.

Calculation of daily ration

Several approaches were followed in order to estimate the daily ration from the 24-h sampling. In the different models the terminology of Jarre *et al.* (1991) is followed throughout.

For use in the Eggers (1977) and Elliott and Persson (1978) models the instantaneous rate of gastric evacuation E as determined by Andersen (1984) for *Pomatoschistus microps* was used:

$$E = 7.385 \times TL^{-0.832} \times e^{0.0639(T-20)},$$

where TL is the total length of the fish, which equals $1.089 + 1.157 \times$ standard length (SL) (Hamerlynck *et al.*, 1986) and T is the ambient temperature.

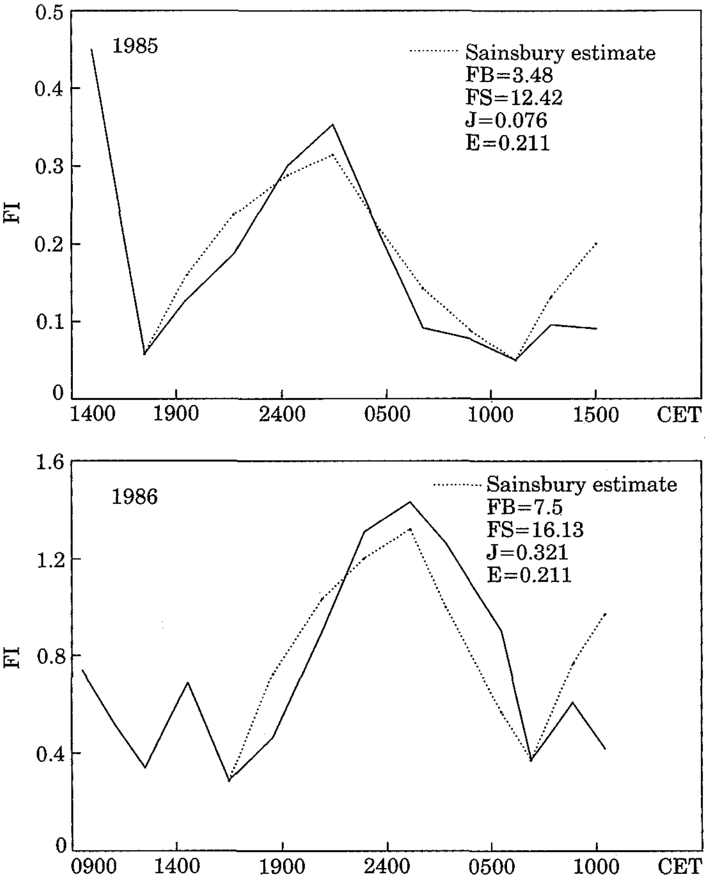

Figure 4. Time trajectories of measured stomach fullness (FI, full line) and as estimated from the Sainsbury (1986) model (dotted line) for 1985 (a) and 1986 (b). FB is the moment at which the fish begin to feed (relative to origin, i.e. 1400 h Central European Time (CET) for 1985), FS is the moment at which the fish stop feeding, J is ingestion rate, and E is the gastric evacuation rate.

According to the Eggers (1977) model daily ration R_d is determined as:

$$R_d = \overline{FI} \times E \times 24,$$

where $\overline{FI}$ is the average fullness index of all fish collected.

The Elliott and Persson (1978) model states that:

$$R_d = \sum_{\Delta t=1}^{p} \overline{J_{\Delta t}},$$

where $\overline{J_{\Delta t}}$ is the quantity of food consumed during an interval Δt between two successive sampling periods t and $t+1$, and p is the number of such intervals per day. $\overline{J_{\Delta t}}$ is defined as:

$$\overline{J_{\Delta t}} = \frac{(\overline{FI_{t+1}} - \overline{FI_t} e^{-ET}) E T}{(1 - e^{-ET})},$$

where $\overline{FI_t}$ and $\overline{FI_{t+1}}$ are the mean fullness indices at two successive sampling periods and T is the time between two successive samplings.

The first model of Sainsbury (1986) was slightly adapted and applied to the data using the Nonlin option in Systat for parameter estimation. According to this model R_{cd}, the food consumed during time interval cd is:

$$R_{cd} = \int_{t=F_b}^{t=F_s} J\,dt = J(F_s - F_b),$$

where cd is the duration of a complete feeding cycle, F_b is the moment at which the fish begin to feed, and F_s is the moment at which the fish stop feeding. In Sainsbury's original model cd was set equal to 24 h, but in the present study feeding cycles were clearly shorter than 24 h. We have therefore preferred to define cd as the time between two successive minima in the stomach fullness trajectory, i.e. 17 h 42 min for the 1985 data and 14 h 25 min for the 1986 data. Assuming the cycles before and after the modelled time interval are of similar duration and intensity, consumption over 24 h can be calculated as:

$$R_d = \frac{R_{cd}}{cd} \times 24.$$

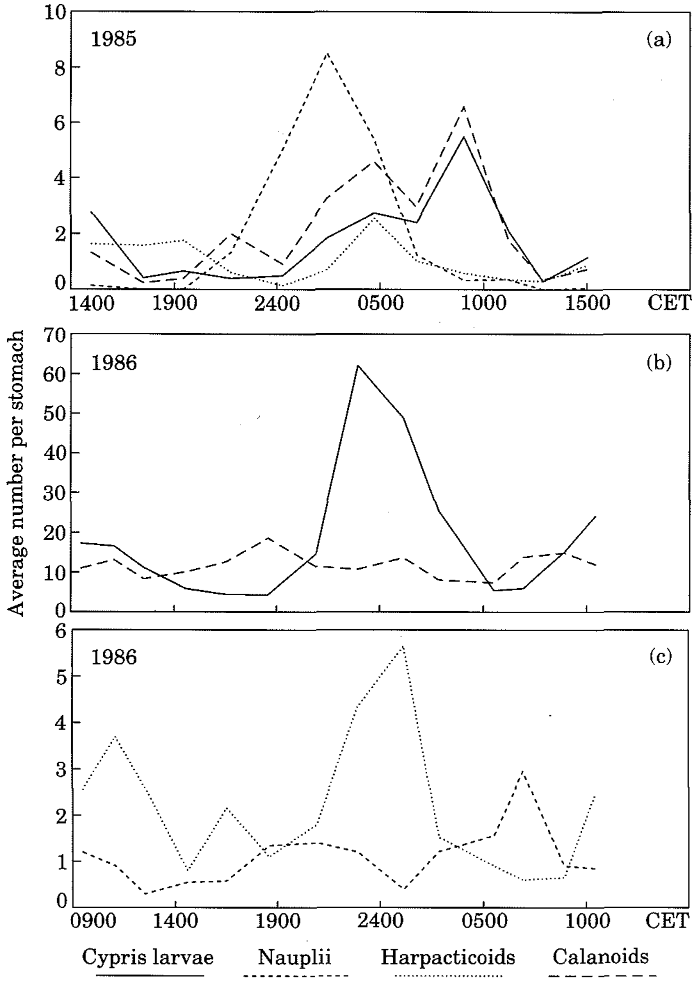

Figure 5. Time trajectories for the average number of items per stomach of the numerically dominant food categories (a, 1985; b, and c, 1986).

The time trajectory of stomach fullness in the model has two different forms:
when feeding

$$FI_t = \frac{J}{E} + \left(FI_{F_b} - \frac{J}{E} \right) e^{-E(t-F_b)}$$

and when not feeding

$$FI_t = FI_{F_s} e^{-E(t-F_s)}.$$

F_b, F_s, J, and E are the four parameters estimated by the model. The two remaining quantities, namely FI_{Fb} and FI_{Fs}, are defined in terms of the parameters as follows:

$$FI_{F_b} = \frac{J}{E} = \frac{(e^{-E \times (cd-(F_s-F_b))} - e^{-cd \times E})}{(1 - e^{-cd \times E})}$$

and

$$FI_s = \frac{J}{E} + \left(FI_{F_b} - \frac{J}{E} \right).$$

For the 1986 data the fit between the model and the data in the time trajectory between the supposed end of feeding activity and the start of the next feeding cycle was poor. Therefore, the gastric evacuation rate E, as estimated by the model from the 1985 data, was used as a constraining variable in the model for the 1986 data, and only three parameters were estimated.

As there are indications that daily ration may be correlated to fish and otolith growth (Campana and Neilson, 1985), thin slices of goby otoliths were prepared according to the methodology described in Karakiri *et al.* (1989). Fishes for otolith examination were collected in the central Voordelta, a comparable shallow coastal area 50 km north of the study site (Hamerlynck and Hostens, 1993; Arellano, unpublished).

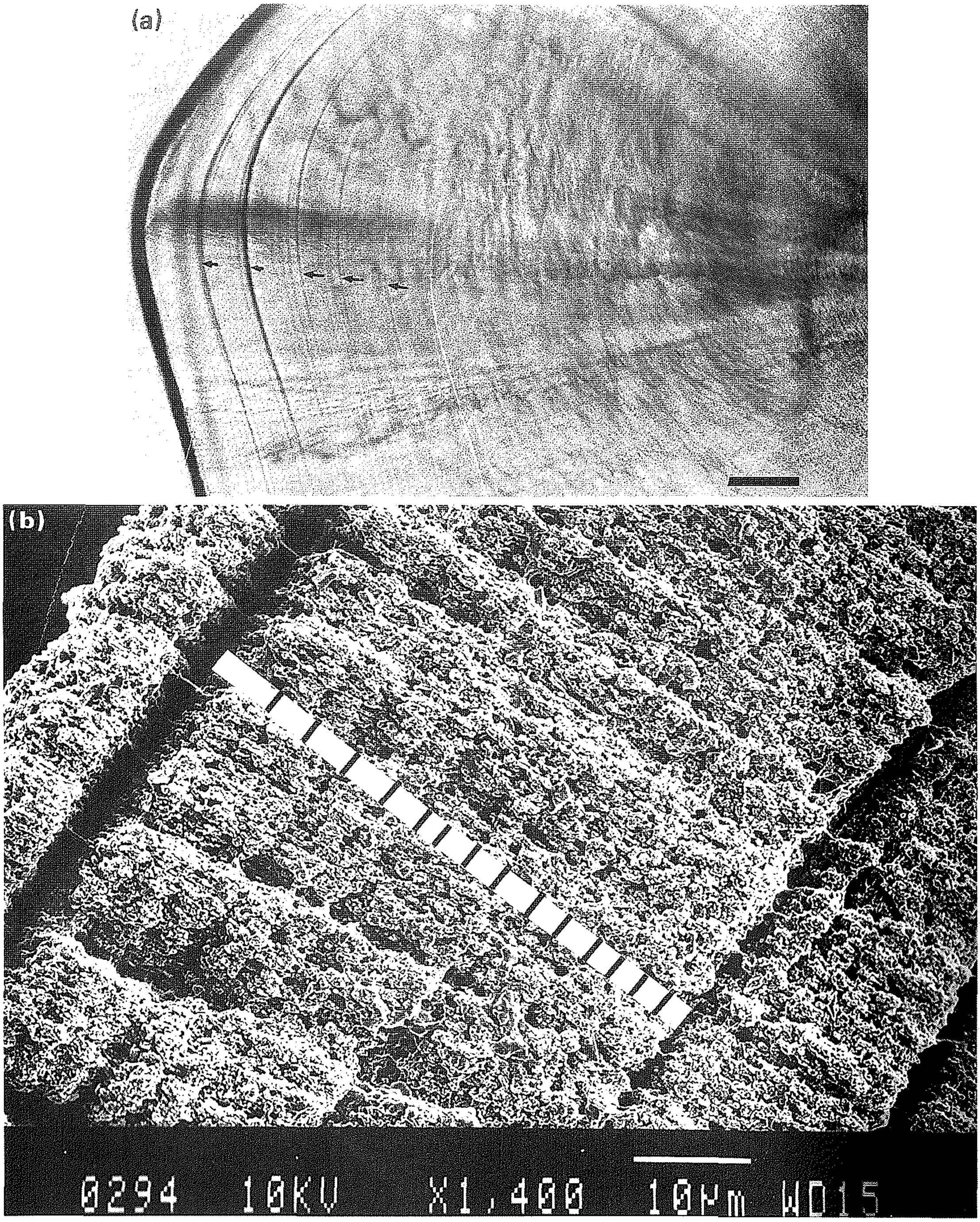

Figure 6. *Pomatoschistus lozanoi* otolith transverse sections (a) light microscope, arrows highlight the banding pattern, the bar is 50 µm; (b) scanning electron microscope detail of one such band with a 14-ring structure.

Results

In both years the fish exhibited strongly fluctuating stomach fullness with high individual variability (Fig. 3). In 1985 (Fig. 3a) highest FI was found in the first haul. Next, mean FI followed tidal height of a first tidal cycle quite closely with a peak a few hours after midnight. During the next (daytime) tidal cycle feeding activity was low, with a slight increase in variability of stomach content at the end of the investigated time period. In 1986

(Fig. 3b) mean FI was decreasing during the first three hauls, then there was a small peak with high variability in H4. Next, mean FI increased steadily until about midnight corresponding to the low tide. Then stomach fullness decreased again until dawn, with possibly a new feeding cycle starting towards the end of the investigated time period.

There were significant differences between two consecutive minima and the intermediate maximum FI in both years (Table 1), indicating that a rhythm was present ($p < 0.01$ for all comparisons). The daily ration as a percentage of body weight, calculated according to the different models, is tabulated in Table 2. Daily ration in 1986 was at least four times higher than in 1985 for each of the models used. Figure 4 shows the result of the Sainsbury model simulation. The gastric evacuation rate E, as estimated from the 1985 data (0.211), was lower than that estimated from the Andersen (1984) formula (0.35 for 1985 and 0.36 for 1986) used in the Eggers (1977) and the Elliott and Persson (1978) models. Qualitatively, the 1985 feeding peak at high tide corresponded to an increased intake of nauplii (Fig. 5a). Afterwards, cypris larvae and calanoids became more important. In 1986 average numbers of cypris larvae and calanoids found in the stomachs were much higher than in 1985 (Fig. 5b). The time trajectory of the number of cypris larvae and, to a lesser extent, harpacticoids (Fig. 5c) found in the stomachs corresponded to the pattern observed in the fullness indices. It should be noted that in gravimetric terms the numerically dominant prey items were relatively unimportant. Differences in FI were mainly due to rare but large items such as shrimp larvae, mysids, and small fishes, but these were too rare to show any meaningful time trajectory numerically (Cattrijsse, unpublished).

In the goby otoliths, collected in the Voordelta, a clear banding pattern (Fig. 6a) could be observed, and each band consists of 14 rings (Fig. 6b).

Discussion

Juvenile *P. lozanoi* fed more intensively at night than during the day in both years. This result seems to confirm the observations in the closely-related *P. minutus* (Gibson and Hesthagen, 1981; Berge *et al.*, 1983). The obvious reason for feeding under the cover of darkness would be predator avoidance: Magnhagen (1988) observed a decrease in feeding activity of *P. minutus* in the presence of cod. In highly turbid estuarine areas avoidance of visual predators may be less important. In such areas the flood-tide-linked activity observed by Healey (1971) may be primarily related to the exploitation of the food-rich intertidal areas.

Estimates of daily ration in fish can be made, either from the (instantaneous) rate of passage of food through the gut or from growth measurements (Wootton, 1990). In the field the first method requires measurements of stomach fullness made at regular intervals over a 24-h period, as was done in the present study. For the second method field measurements of growth and mortality have to be done over a longer time interval, e.g. 1 month. It is then possible to calculate production over that interval (Crisp, 1984) and, with the use of a production:consumption (P:C) ratio, to estimate the consumption needed to achieve that production (e.g. Hamerlynck and Hostens, 1993). Both methods are logistically demanding and labour intensive and most often some laboratory measurements of essential parameters have to be accomplished.

In the present study the different models used for the estimation of daily ration all gave comparable results. The estimates of the Sainsbury (1986) model were lower than in the Eggers (1977) and Elliott and Persson (1978) models because the gastric evacuation rate derived from the 1985 field data was lower than that established for *P. microps* by Andersen (1984). This may be due to the fact that Andersen (1984) used polychaetes for his experiments. It is well known that polychaetes are evacuated more rapidly than crustaceans (Jones, 1974), the dominant prey type in the present study. As already stated by Sainsbury (1986), his model requires quite an abrupt and synchronized transition from feeding to non-feeding in the whole population for the parameter estimates to be reliable. In 1985 this seems to have been the case, but in 1986 the 'bulge' on the descending arm of the feeding trajectory precluded unconstrained use of the model. However, the fit of the model as constrained by the 1985 gastric evacuation estimate seems acceptable (Fig. 4b). From Figure 4 it can also be seen that the adaptation of the model to a shorter time interval than 24 h has probably biased the result in both years. Jarre *et al.* (1991) developed a model that can accommodate two feeding periods within 24 h and that potentially would use all the data instead of only the time period between two successive minima. However, though Jarre *et al.* (1991) applied it to a 24-h data set for cod (Arntz, 1974) it is our contention that, for an accurate estimate, the data should then extend over at least two complete feeding cycles and that the time interval between samples should even be shorter than in the present study. Otherwise, almost any collection of points can be accommodated by the model.

No confidence intervals have been provided for the different estimates of daily ration. Elaborate techniques for statistical treatment have been proposed by Worobec (1984) but not all sources of variance can be estimated separately. The Sainsbury model as used in Systat gave a measure of fit (r^2 of 0.82 and 0.93 for 1985 and 1986, respectively) but, as only the averages were used, only part of the total variance was accommodated. The bootstrap technique applied to daily ration estimates by Boisclair and Leggett (1986) seems adequate but is not widely available.

Whatever the true daily ration may have been in either year it was clearly at least four times lower in 1985 than in

1986. Extrapolating food consumption as measured in a single 24-h cycle to longer time periods can therefore lead to considerable over- or underestimates. Many different hypotheses, that cannot be falsified on the basis of the present field results, where many biotic and abiotic factors known and unknown may have influenced feeding intensity, can be proposed to account for this finding. Part of the explanation for the higher daily ration in 1986 may be the effect of day length. Fonds (1979) observed that growth rate and food consumption in plaice and sole, kept in the laboratory at constant temperatures but with a natural daylight cycle, were correlated to day length, thus being maximal in June and minimal in December. However, between early August and late September this would only account for a relatively small difference in feeding intensity. For example, in *P. microps* from a tideless environment Antholz *et al.* (1991) observed little difference in stomach fullness between July and September.

Evans (1984) measured a daily ration of 5–12% of body dry weight for *Pomatoschistus minutus*. A 1% of body ADW consumption, as estimated for 1985, seems to be a very low daily ration for fast-growing tiny fish. Therefore, gobies were possibly food-limited in September 1985 and not in August 1986. Without data on the time trajectory of food availability in the area it is impossible to verify this. From the stomach analyses (Fig. 5) it is clear that the items taken most frequently were largely the same in both years. Only the cypris larvae of Cirripedia showed a similar time trajectory in both years, being mostly taken around low tide.

The food-limitation hypothesis is not incompatible with the hypothesis that feeding intensity was related to the spring–neap cycle, as prey abundance may be determined by the same cycle (e.g. Morgan, 1990). There is an obvious selective advantage for barnacle larvae, which have to settle in the upper part of the intertidal zone, to make use of the spring–neap cycle. The observation that the goby otoliths exhibited a strongly-banded pattern (Fig. 6) with 14 rings within each band suggests that a semilunar rhythm in growth and food consumption may be present. Such semilunar banding has been observed in many fish species but is as yet unexplained (Campana and Neilson, 1985). A semilunar rhythm is expected in benthic-feeding animals such as plaice (Gibson, pers. comm.) that exploit the richness of intertidal flats during high tide or in fishes that are exclusively intertidal (e.g. Northcott, 1991). Its significance is rather less obvious in zooplankton-feeding subtidal fishes such as the 25–29 mm *P. lozanoi* in the present study. However, though preliminary counts in relation to the known spawning time of *P. lozanoi* suggest the rings are daily (Arellano, unpublished); validation of the daily nature of the rings has yet to be accomplished and the suggested correspondence to the spring–neap cycle, i.e. wider rings deposited around spring tide and thinner rings deposited around neap tide, also requires confirmation.

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