



Diel feeding activity of demersal fishes in the Ría de Arousa (Galicia, NW Spain): an area of intense mussel raft culture

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Abstract: A study was carried out on the diel feeding pattern of five species of demersal fishes, *Lesueurigobius friesii* and *Gobius niger* (Gobiidae), *Trisopterus luscus* (Gadidae), *Callionymus lyra* (Callionymidae), and *Symphodus cinereus* (Labridae), in the Ría de Arousa (Galicia, NW Spain), an estuary that supports an intensive raft mussel culture. We have analyzed stomach contents obtained in different habitats (mussel rafts, beach and central channel) over a diel cycle.

Pisidia longicornis is the dominant species of the raft epifauna, and their megalopae made up over 70% of the diet of *L. friesii*, *T. luscus* and *C. lyra* in the middle ría zone, both in the culture areas and in the central channel. In the inner ría raft station the diet of *L. friesii* and *G. niger* was composed mainly of prey from the culture rope epifauna, but no megalopae were present. In the beach zones the diet of *G. niger* and *S. cinereus* was dominated by infaunal prey, mainly polychaetes.

Due to the abundance of food provided by the associated epifauna, mussel culture influences the feeding habits of demersal fishes in the Ría de Arousa. In general, they fed throughout the day without a main period. However, the spring bloom of *P. longicornis* larvae changes the diel feeding activity patterns and diet of the demersal fish community. *S. cinereus* was the only species that showed higher fullness levels during the day in the beach zone, where *P. longicornis* megalopae were not present.

Résumé : L'alimentation quotidienne de cinq espèces de poissons demersaux, *Lesueurigobius friesii* et *Gobius niger* (Gobiidae), *Trisopterus luscus* (Gadidae), *Callionymus lyra* (Callionymidae), *Symphodus cinereus* (Labridae) a été étudiée en détail dans la Ría de Arousa (Galice, NO Espagne), un estuaire d'intense culture de moules en suspension sous radeaux (radeaux de moules, plage et canal central), pendant un cycle de 24 heures.

Pisidia longicornis est l'espèce dominante de l'épifaune des radeaux, et ses mégaloques constituent environ 70 % du régime alimentaire de *L. friesii*, *T. luscus* et *C. lyra*, au milieu de l'estuaire, aussi bien dans les aires de culture que dans le canal central. Au niveau des radeaux de la partie interne de l'estuaire, le régime alimentaire de *L. friesii* et *G. niger* est essentiellement composé de proies provenant de l'épifaune des cordes de culture et les mégaloques sont absentes. Dans les zones de plage, *G. niger* et *S. cinereus* se nourrissent surtout de proies provenant de l'endofaune, principalement de polychètes.

La mytiliculture influence l'alimentation des poissons démersaux de la Ría de Arousa, par les importants apports de nourriture de l'épifaune associée. En général, la prise de nourriture a lieu pendant le jour, sans qu'il apparaisse une période principale. Cependant, la prolifération importante de larves de *P. longicornis* au printemps change le schéma de l'activité alimentaire journalière et le régime alimentaire de ces poissons démersaux. *S. cinereus* est la seule espèce qui montre une réplétion stomacale plus élevée le jour, dans la zone de plage, bien que les mégaloques soient absentes dans cette région.

Keywords: feeding activity, trophic relationships, mussel culture, demersal fishes, Ría de Arousa.

Introduction

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The raft mussel culture which has developed in the Ría de Arousa (Galicia, NW Spain) has brought about major

changes in the ecosystem (Tenore & González, 1975). There are currently around 2200 rafts distributed in polygons, occupying approximately 10% of the ría surface. As far as the benthic system is concerned, the modification of the bottom, with an increase in organic matter levels, has caused a decrease in the infaunal biomass (López-Jamar, 1982), while the epifauna, made up mainly of fishes, crustaceans and echinoderms, has been favourably affected by the increase in the available food supply (Chesney & Iglesias, 1979; Olaso, 1982; Freire, 1993; González-Gurriarán *et al.*, 1995). This is largely due to the fact that fishes and crustaceans have changed their feeding habits in order to utilize the mussels and the epifauna associated with the culture ropes (Chesney & Iglesias, 1979; López-Jamar *et al.*, 1984; Freire, 1993; González-Gurriarán *et al.*, 1995).

To date, there are only preliminary data related to the diet of demersal fishes in the Ría de Arousa (Chesney & Iglesias, 1979; López-Jamar *et al.*, 1984) and there have been no studies done on the influence of mussel raft culture on trophic relationships at the benthic level. An understanding of the daily cycles of feeding activity is important in the analysis of the trophic relationships in marine populations. This paper analyzes the diel pattern of feeding activity and diet composition of the most abundant species of demersal fishes in the Ría de Arousa, as a first step towards understanding the different aspects of their feeding, and to evaluate the effects that the introduction of the culture has had on the diet. The results of this paper will allow the development of a sampling strategy for the study of the feeding of these species.

Material and Methods

Sampling was carried out over a 24-h period (April, 1989) at four stations located in different areas of the Ría de Arousa (Fig. 1). We selected two raft zones, B1 and B5, in the inner and outer ría respectively, and two zones where mussels are not cultured, M2, in the central channel, and P3 which is a typical beach zone. The raft stations, B1 (10 m deep) and B5 (20 m deep) have muddy bottoms, and show an abundance of epibenthic organisms as well as mussels and their epifauna that fall off the culture ropes. The channel station, M2, has a muddy bottom and is 30-40 m deep. The beach zone, P3 (3-5 m deep), has sandy bottoms with abundance of green algae.

Ten-minute tows were taken using a beam trawl with a 10 mm mesh net having an effective opening of 4 m (Iglesias, 1982; González-Gurriarán *et al.*, 1995). Each station was sampled every 6 hours (4 times per station during the 24-h cycle), and 3-4 tows were taken each time. Specimens were immediately fixed in 4% neutralized formaldehyde, which had also been previously injected in the abdominal cavity. After 48-h they were stored in alcohol 70%.

The following species were studied: *Lesueurigobius friesii* (Malm) (Gobiidae) and *Trisopterus luscus* (Linnaeus) (Gadidae) at stations B1, B5 and M2; *Gobius niger* Linnaeus (Gobiidae) at P3 and B1; *Callionymus lyra* Linnaeus (Callionymidae) at B5 and *Symphodus cinereus* (Bonnaterre) (Labridae) at P3. A subsample of 50 individuals from each species, station, and time was taken (1274 individuals in total) for the fullness and stomach contents analyses (in the case of smaller captures all the specimens were analyzed). As the food was well macerated (in a state of disintegration), handling these small-sized particles was difficult and it was hardly feasible to completely separate the different types of prey, in order to weigh them individually. So, in cases where more than one diet component per stomach was found, dry weight per prey was estimated from the total dry weight of the contents, which was determined by heating at 60°C for 48 hours, and relative importance of each component according to the point method. This method gives us a visual estimate of the relative importance of each prey, determined at the lowest possible taxonomic level, compared to total food volume (Hyslop, 1980).

Stomach fullness for each sample was estimated using two indices: percentage of stomachs containing food, and fullness index (FI) based on percentage of body dry weight ($FI = (\text{food dry weight/body dry weight}) * 100$). Dry weight of the specimens analyzed was calculated using conversion factors from wet weight previously estimated by Iglesias (1982). Diet composition was expressed as FI per type of prey (FI_j):

$$FI_j = \frac{\sum_{i=1}^n FI_{ji}}{\sum_{i=1}^n FI_i}$$

where FI_{ji} is the weight percentage of prey j in the stomach i , FI_i is the body weight percentage of the food for specimen i , and n is the number of stomachs analyzed.

Diet diversity was obtained using the Shannon index (H' , in \log_2) with data in %bdw for each species, station and time. A covariance analysis (ANCOVA) was used to study the variations in fullness level (food dry weight), throughout the diel cycle as well as between stations, with body dry weight as the covariate (Jenkins & Green, 1977). Differences in consumption of the most important prey between hours for each species and station were analyzed using analysis of variance (ANOVA). For *G. niger* and *L. friesii*, which were the most abundant species and appeared in the greatest number of stations, a cluster analysis of diet composition was done using the samples for each station and time. This was carried out by means of the trophic similarity percentage and the cluster algorithm UPGMA. A factorial correspondence analysis was done in order to extract the main factors that determined diet variation, using data on diet composition for the different species in each station and at each time.

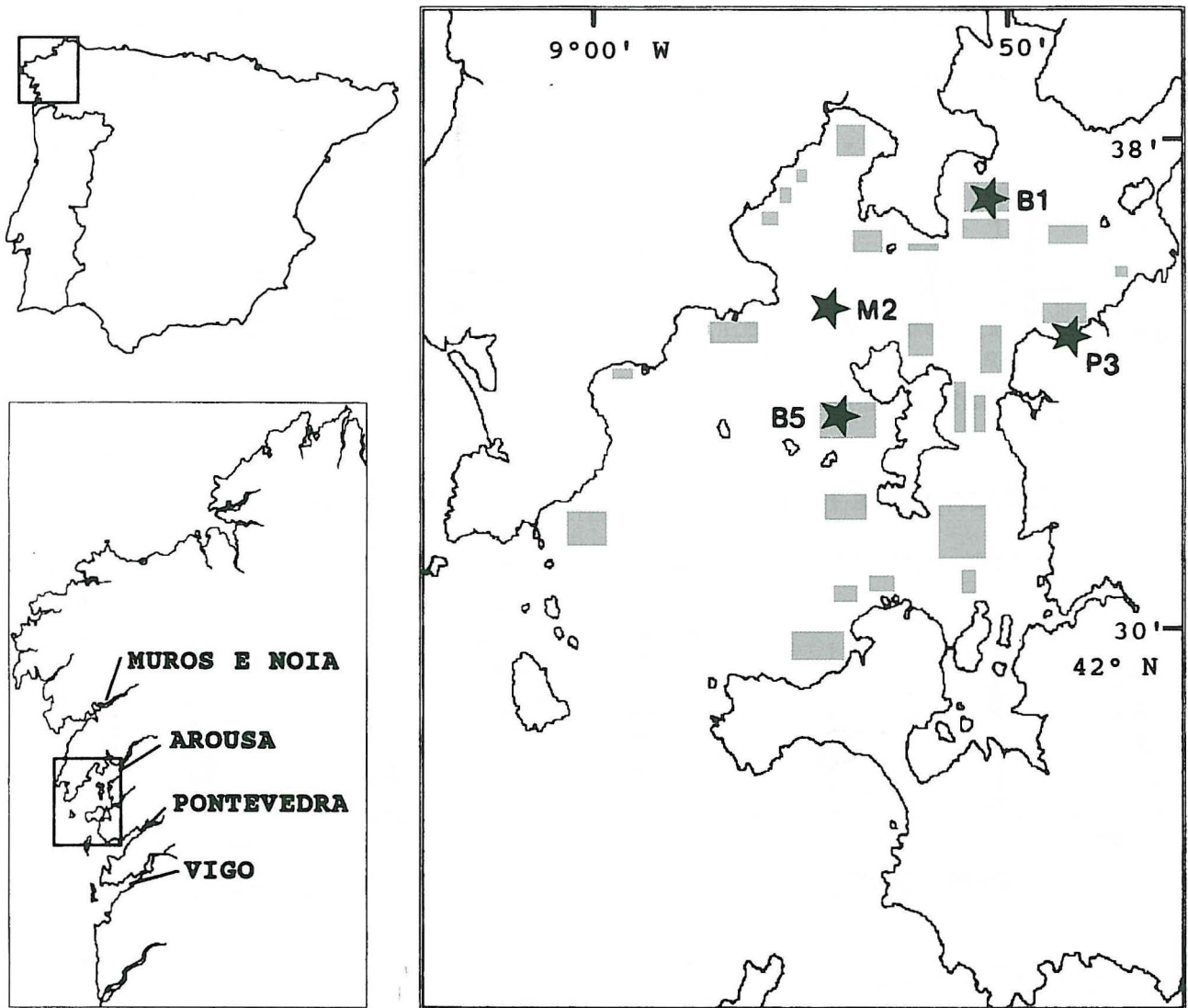


Figure 1. Rías Baixas de Galicia (NW Spain). Location of raft polygons (dotted areas) and sampling stations (stars) in the Ría de Arousa. B1 and B5: raft stations; M2: channel station without rafts; P3: beach station.

Figure 1. Rías Baixas de Galice (NO Espagne). Localisation des aires à radeaux (aires en pointillé) et des stations d'échantillonnage (étoiles) dans la Ría de Arousa. B1 et B5: stations à radeaux; M2: station du canal sans radeaux; P3: station de plage.

Results

Feeding activity

Lesueurigobius friesii showed a different feeding pattern at the two raft stations (Fig. 2). Although fullness index values were higher at dusk at B1, which is the shallower, there were no significant differences throughout the diel cycle (ANCOVA, $P=0.171$) (Table 1). The opposite is true at B5, where night fullness was significantly lower than the values found in the other samples ($P<0.001$). As at B5, at station M2 there were significant differences in FI depending on the time of day ($P<0.001$). The day samples had

maximum fullness values, as compared to the dusk and particularly the night samples.

Mean stomach fullness level (as FI) was significantly different ($p<0.05$) in the raft stations (0.63 ± 0.034 in B1 and 0.74 ± 0.031 in B5) (Table 1). In both cases it was lower than in the central channel station, M2 (1.03 ± 0.046), where the mean size of specimens analyzed (84 mm) was larger than in the raft stations (75 mm). *L. friesii* showed a high percentage of stomachs containing food in all stations, with mean values around 90%, and there were no important variations throughout the day.

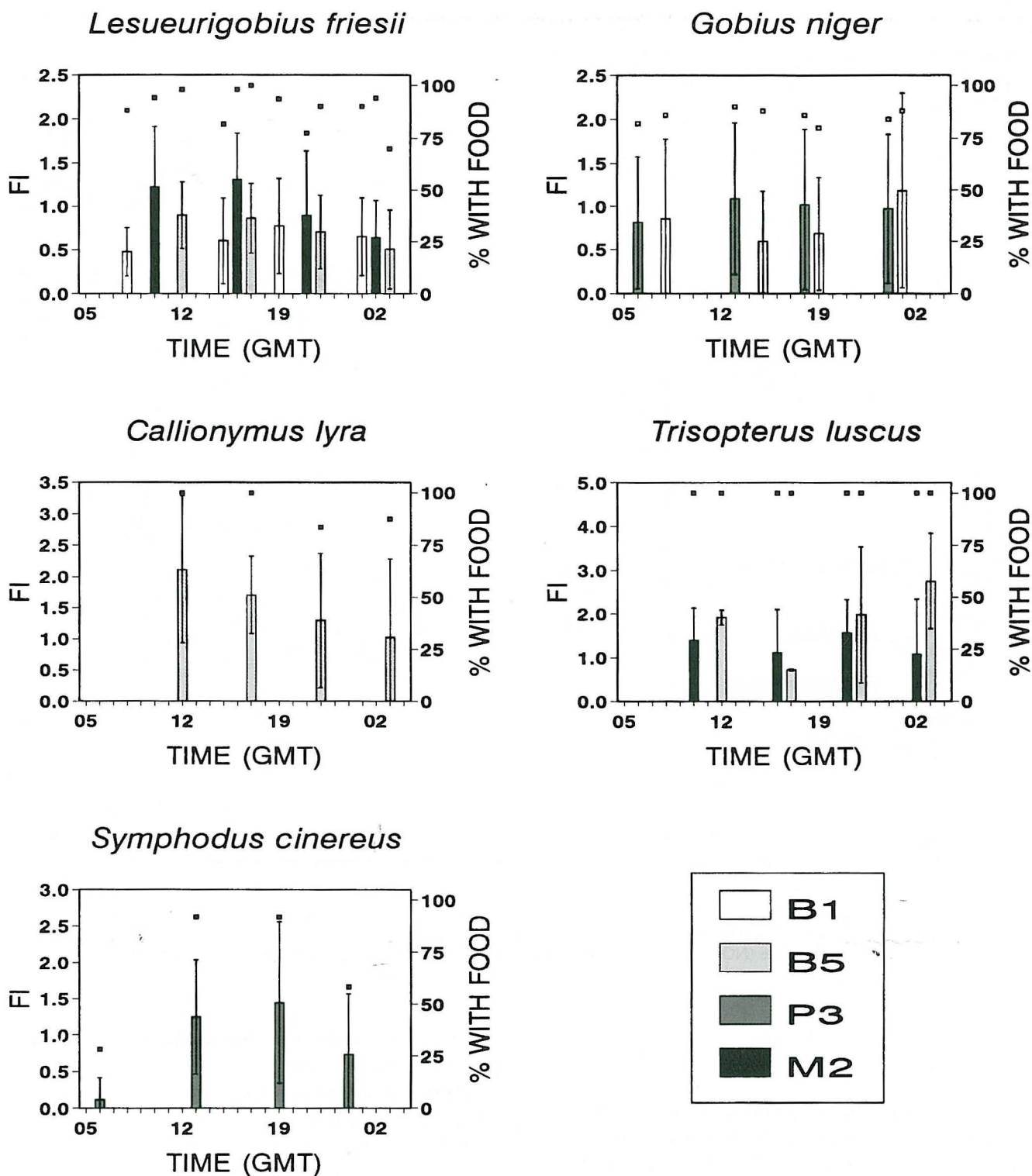


Figure 2. Daily evolution of stomach fullness (measured as FI \pm standard deviation) and percentage of stomachs with food (dots) for the different species and stations sampled. Data of *T. luscus* in B1 were not included because of the low number of individuals captured.

Figure 2. Évolution journalière de la réplétion stomacale (mesurée comme FI \pm écart type) et pourcentage d'estomacs avec nourriture (points) pour les différentes espèces et stations échantillonnées. Les données de *T. luscus* à B1 ne sont pas indiquées en raison du petit nombre d'individus récoltés.

Table 1. ANCOVA results comparing stomach fullness (food dry weight) in the different species of demersal fishes between stations, and times in each station. The *F*-statistic value and its probability *P* (in brackets) are shown. Where there is a significant difference ($P < 0.05$), an *a posteriori* comparison was carried out between times and stations in pairs. The underlined samples were not found to be significantly different from each other ($P > 0.05$). In all cases, except for *C. lyra*, data were logarithmically transformed to obtain variance homogeneity (Bartlett test, $P > 0.05$). N=number of individuals analyzed.

Tableau 1. Résultats de l'ANCOVA effectuée pour comparer la réplétion stomacale (poids sec de nourriture) chez différentes espèces de poissons démersaux, entre stations, et entre heures de prélèvement dans chaque station. La valeur du test-*F* et sa probabilité *P* (entre parenthèse) sont indiquées. Lorsque les différences sont significatives ($P < 0.05$), des comparaisons *a posteriori* ont été faites entre paires d'heures et de stations. Les échantillons soulignés ne sont pas significativement différents entre eux ($P > 0.05$). Dans tous les cas, sauf chez *C. lyra*, les données ont été transformées logarithmiquement pour obtenir l'homogénéité des variances (test de Bartlett, $P > 0.05$). N = nombre d'individus analysés.

		SUM OF STATIONS	B1	B5	M2	P3
<i>Lesueurigobius friesii</i>	N	564	183	200	181	----
	Food dry weight	13.902 (0.000)	1.691 (0.171)	13.511 (0.000)	8.429 (0.000)	----
	Covariate	147.998 (0.000)	12.927 (0.000)	72.713 (0.000)	50.263 (0.000)	----
		M2 B5 B1		<u>12 17</u> 22 03	<u>16 10 21 02</u>	
<i>Gobius niger</i>	N	400	200	----	----	200
	Food dry weight	4.417 (0.013)	1.600 (0.191)	----	----	1.982 (0.118)
	Covariate	13.681 (0.000)	0.212 (0.646)	----	----	1.146 (0.236)
		P3 B1				
<i>Trisopterus luscus</i>	N	87	11	29	47	----
	Food dry weight	7.128 (0.001)	5.031 (0.055)	4.061 (0.019)	0.910 (0.446)	----
	Covariate	24.887 (0.000)	5.262 (0.051)	9.026 (0.006)	17.395 (0.000)	----
		B1 B5 M2		<u>03 12 22 17</u>		
<i>Callionymus lyra</i>	N	----	----	49	----	----
	Food dry weight	----	----	1.806 (0.161)	----	----
	Covariate	----	----	64.909 (0.000)	----	----
<i>Symphodus cinereus</i>	N	----	----	----	----	174
	Food dry weight	----	----	----	----	45.481 (0.000)
	Covariate	----	----	----	----	36.100 (0.000)
						<u>13 19</u> 06 24

Gobius niger followed a similar feeding pattern in stations B1 and P3 (Fig. 2). Neither zone showed significant differences in fullness level throughout the day (ANCOVA, $P > 0.05$) (Table 1), although the night samples from B1 had higher values. Mean fullness was greater in P3 (0.97 ± 0.059) than in B1 (0.83 ± 0.062) ($P = 0.013$), and mean body size was smaller in the beach station than in the raft station (106 mm in B1 and 82 mm in P3). Therefore in the ANCOVA results we observed that body weight did not have a significant effect if each station was analyzed individually; however, body weight was significant in the analysis of the total data. On the other hand, the percentage of stomachs containing food as well as FI varied very little throughout the day (around 85%).

In the case of *Trisopterus luscus*, the highest fullness values in the raft stations were always found at night (ANCOVA, $P = 0.055$ in B1 and $P = 0.019$ in B5) (Fig. 2, Table 1), although in both cases a small number of individuals was captured ($n = 11$ and $n = 29$, respectively). In station M2 ($n = 47$), there were no significant differences in fullness levels at the different times of day ($P > 0.05$).

In general, this species was found to have higher fullness values than the others, with maximums FI of 2.41 and 2.75 in B1 and B5 respectively. All the specimens examined contained food. Mean fullness throughout the day was significantly greater in the raft stations than in M2 (Table 1), where the mean size of the individuals caught was larger (144 mm, as compared to 136 mm in B5 and 134 mm in B1).

Symphodus cinereus exhibited a well-defined feeding pattern in the beach station (ANCOVA, $P < 0.001$) (Table 1), with peaks in fullness level and percentage of stomachs containing food found in the day samples (a maximum FI value of 1.45 at 19 hours and a minimum of 0.12 at 06 hours) (Fig. 2). No relationship was found between feeding activity and tides in this shallow water area, as maximum fullness values appeared at both high and low tides.

Callionymus lyra showed a very high percentage of stomachs containing food, reaching 100% in the day samples (Fig. 2). Maximum fullness values were obtained during the day, although there were no significant differences (ANCOVA, $P > 0.05$) (Table 1). This was partly due to the small number of specimens analyzed.

Diel changes in diet composition

Lesueurigobius friesii: The diet composition of this species was highly variable, mainly because of the *Pisidia longicornis* megalopae. In stations B5 and M2 this prey made up 73 and 96% of the diet, respectively, whereas in the inner zone, B1, where this species is less abundant (Corral & Alvarez-Ossorio, 1978; Fernández *et al.*, 1990), it did not appear in the stomach contents (Fig. 3a). In B1 this species fed mainly on polychaetes (30%) and non-decapod crustaceans, generally amphipods, caprellids (20%), mainly *Phthisica marina* and *Pseudoprotella phasma*, and gammarids (16%), largely *Jassa falcata*.

There was a major variation in the diet during the diel cycle: the consumption of the dominant prey in each station differed significantly according to the time of day (ANOVA, $P < 0.05$) (Table 2). In B1, the consumption of polychaetes decreased at dawn (Fig. 3a). In B5 and M2 the megalopae appeared to a greater extent during daylight hours, although only B5 showed great fluctuations (from 95.2% at 12:04 hours to 23.9% at 03:26 hours). In this station other prey were consumed more heavily at night, due to a decrease in the consumption of megalopae.

The results of the cluster analysis coincided with those mentioned earlier (Fig. 3a). First, B1 samples differed from those in B5 and M2. In these areas, the samples with the megalopae as the dominant component constituted a group of very high similarity (greater than 90%).

Gobius niger: In the two stations analyzed, B1 and P3, polychaetes were the dominant prey in the diet (30% in B1 and 47% in P3) (Fig. 3b). In B1, fish and adult specimens of *P. Longicornis* were also important prey in stomach contents, whereas in P3 the diet was also composed of gammarids, decapods and molluscs, but with much lesser importance.

The cluster analysis grouped the diet of this species in terms of habitat (Fig. 3b), and temporal variations were much less important. There were no variations in the diet composition of this species throughout the day with the sole

exception of the polychaetes in B1 ($P < 0.05$) (Table 2), which appeared in greater quantities at night (particularly at 19 hours).

Callionymus lyra: In station B5 it fed mainly on *P. longicornis*, both megalopae and adults, making up over 70% of the diet (Fig. 3c). Temporal changes were found to influence the consumption of *P. longicornis* megalopae (Table 2), which were more abundant in daytime samples.

Trisopterus luscus: This species fed mainly on crustaceans and other fishes (Fig. 3d). *P. longicornis* appeared as the dominant prey both in the megalopa stage (in M2 and to a lesser extent in B5) and in the adult stage (all stations). In B1 other important prey were fish and the caprellid *Pseudoprotella phasma*, while in B5 and M2 fish and *Natantia* along with *P. longicornis* made up over 90% of the diet.

As happens with *L. friesii*, the temporal variations were basically determined by the megalopae (Table 2), which were consumed to a greater extent during the daytime.

Symphodus cinereus: This species consumed mostly foraminiferans (23%) and polychaetes (35%, mainly *Platynereis dumerilii* and others nereids), and to a lesser extent, non-decapod crustaceans (largely gammarids) (Fig. 3e). Temporal changes affected both foraminiferans and polychaetes (Table 2). Foraminiferans appeared mostly at night and at dusk whereas the polychaetes were more abundant in the diet of this species at 13 and 19 hours.

The diet of demersal fish did not show great fluctuations in diversity values throughout the diel cycle, except for *L. friesii* in station B5, where the consumption of megalopae decreased at night, causing an increase in diet diversity (Fig. 4). Differences in diversity values were important between species, and particularly between stations. There was a group of samples with high diversity values (generally $H' > 3$), corresponding to stations P3 and B1, and another group with low diversities (less than 0.5) whose diet was dominated by megalopae.

The correspondence analysis showed that habitat was a determining factor in the diet composition of demersal fish (Fig. 5). In fact it was more important than the interspecific differences within each zone or than the diel cycle variations. The first axis (29.7% of the variance) differentiates the samples where *P. longicornis* megalopae were the dominant prey compared to the rest of the samples, grouping the outer ría stations B5 and M2 and the inner ría stations, B1 and P3. The second axis, however, (19.7% of the variance) shows the diet variability in demersal fish in zones where megalopae were absent, and where predation was strongest on fishes, *P. longicornis* adults, *Natantia* or caprellids in B1 or on foraminiferans, polychaetes and plant components in P3.

Discussion

The Ría de Arousa is dominated by small gobies and other species of limited mobility, although species such as

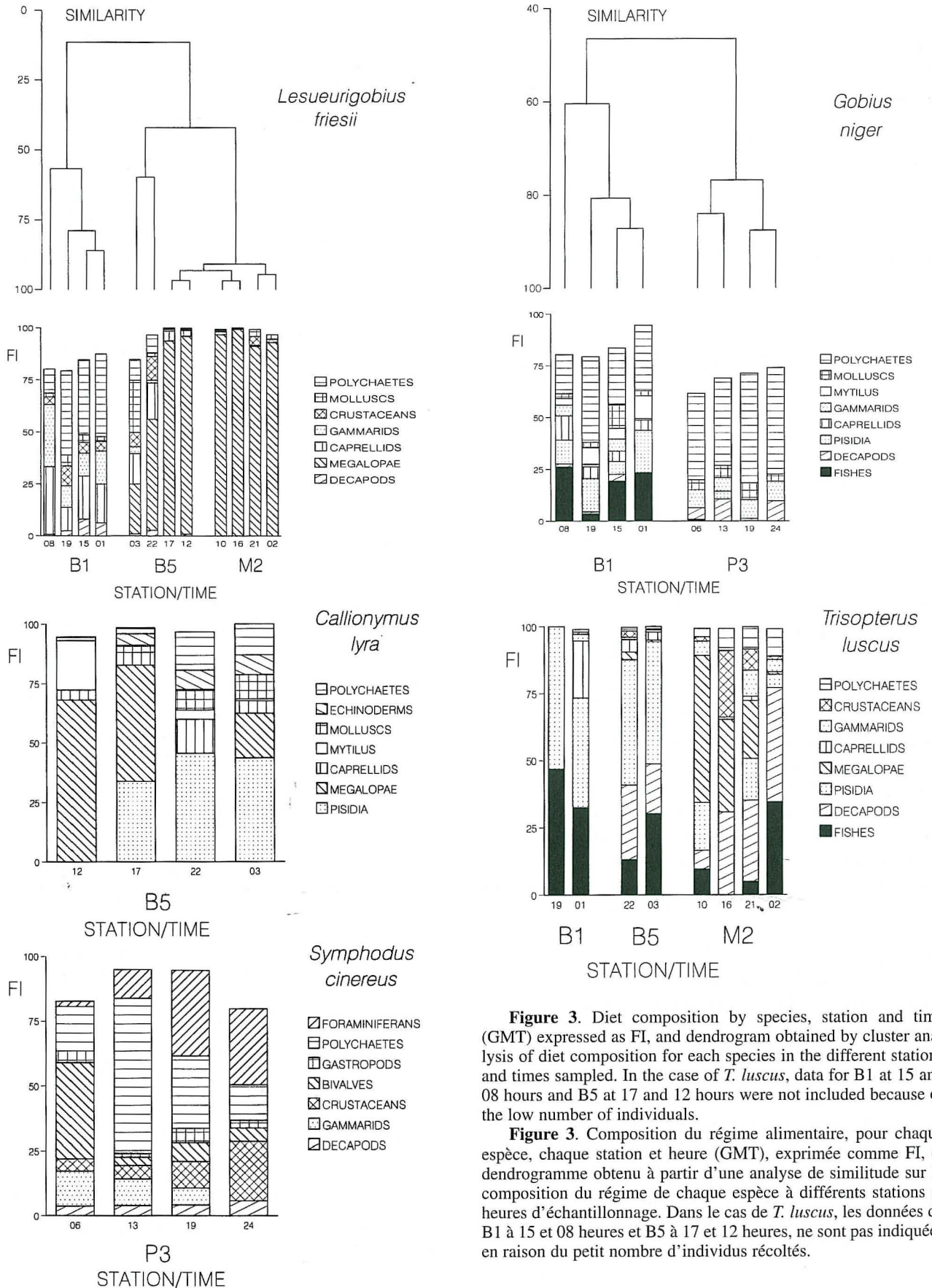


Figure 3. Diet composition by species, station and time (GMT) expressed as FI, and dendrogram obtained by cluster analysis of diet composition for each species in the different stations and times sampled. In the case of *T. luscus*, data for B1 at 15 and 08 hours and B5 at 17 and 12 hours were not included because of the low number of individuals.

Figure 3. Composition du régime alimentaire, pour chaque espèce, chaque station et heure (GMT), exprimée comme FI, et dendrogramme obtenu à partir d'une analyse de similitude sur la composition du régime de chaque espèce à différentes stations et heures d'échantillonnage. Dans le cas de *T. luscus*, les données de B1 à 15 et 08 heures et B5 à 17 et 12 heures, ne sont pas indiquées en raison du petit nombre d'individus récoltés.

Table 2. ANOVA results comparing dominant prey consumption (as FI) throughout the diel cycle for each species and station (only prey having significant differences, $P < 0.05$ are shown). The results of the Student-Newman-Keuls (S-N-K) test comparing the different times in pairs are also given (the underlined samples are not significantly different, $P > 0.05$). Data were logarithmically transformed to homogenize the variances.

Tableau 2. Résultats de l'ANOVA réalisée pour comparer la consommation des proies prédominantes (exprimée comme FI) pendant le cycle journalier, pour chaque espèce et chaque station (seules les proies pour lesquelles des différences significatives ont été trouvées, $P < 0.05$, sont indiquées). Les résultats du test de Student-Newman-Keuls (S-N-K) réalisé pour comparer les différentes paires d'heures sont aussi présentés (les échantillons soulignés ne sont pas significativement différents, $P > 0.05$). Les données ont été transformées logarithmiquement pour obtenir l'homogénéité des variances.

SPECIES	STATION	PREY	F	P	S-N-K tests
<i>Lesueurigobius friesii</i>	B1	Polychaetes	3.948	(0.010)	19 01 14 08
	B5	Megalopae	40.200	(0.000)	12 17 22 03
		Other crustaceans	8.230	(0.000)	22 03 17 12
		Other bivalves	5.640	(0.001)	03 22 12 17
		Other gastropods	6.770	(0.000)	03 22 12 17
		Polychaetes	4.820	(0.003)	03 22 12 17
	M2	Megalopae	15.870	(0.000)	16 10 02 21
		Gammarids	8.620	(0.000)	16 21 02 10
<i>Gobius niger</i>	B1	Polychaetes	3.985	(0.009)	19 01 14 08
<i>Trisopterus luscus</i>	B1	Pisidia	5.815	(0.039)	19 08
	B5	Megalopae	7.130	(0.001)	17 12 22 03
	M2	Megalopae	10.450	(0.000)	10 16 21 02
		Gammarids	3.945	(0.016)	21 10 02 16
		Other crustaceans	4.265	(0.011)	16 21 02 10
<i>Callionymus lyra</i>	B5	Natantia	6.047	(0.002)	12 17 22 03
		Megalopae	13.580	(0.000)	12 17 03 22
<i>Symphodus cinereus</i>	P3	Mytilus	12.660	(0.000)	06 13 19 24
		Polychaetes	10.970	(0.000)	13 19 24 06
		Foraminiferans	8.514	(0.022)	19 24 13 06

Trisopterus luscus, which is larger in size and has a wider foraging range, are also abundant (Chesney & Iglesias, 1979; Iglesias, 1982). Mussel culture has modified both the structure and abundance of the epibenthic community, by changing the feeding habits of the different species. Raft epifaunal organisms, mainly *P. longicornis* and amphipods, in addition to the mussel itself, are important elements in the food web of the ría for demersal fish (López-Jamar *et al.*, 1984; this paper) as well as for decapod crustaceans (González-Gurriarán *et al.*, 1995; Freire, 1993).

Several studies indicate that the main groups of prey consumed by the different species are similar in different geographical areas. *T. luscus* feeds mainly on crustaceans (Van der Broek, 1978; Armstrong, 1982; Puente, 1986; Robin & Marchand, 1986; Dauvin, 1988; Santos, 1989;) and *G. niger* consumes polychaetes and amphipods (Vass *et al.*, 1975; Fabi & Frogli, 1983; Vessey & Langford, 1985). *C. lyra* has a variable diet in different areas, with preference for crustaceans and polychaetes (Dauvin, 1988; this paper), or echinoderms and polychaetes (Van der Veer *et al.*, 1990). The diet of *L. friesii* is the most highly variable (Gibson & Ezzi, 1978) even in zones within the Ría de Arousa.

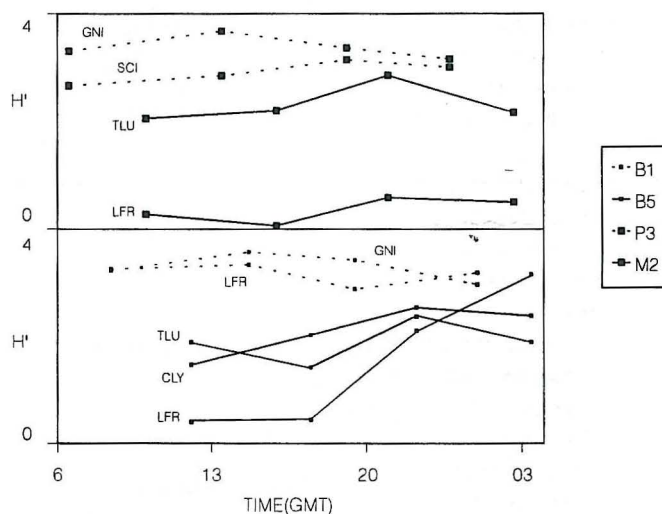


Figure 4. Daily evolution of diversity (H') in the diet of demersal fish in each station. LFR= *L. friesii*, GNI= *G. niger*, TLU= *T. luscus*, CLY= *C. lyra*, SCI= *S. cinereus*.

Figure 4. Évolution journalière de la diversité (H') du régime alimentaire des poissons démersaux à chaque station. LFR = *L. friesii*, GNI = *G. niger*, TLU = *T. luscus*, CLY = *C. lyra*, SCI = *S. cinereus*.

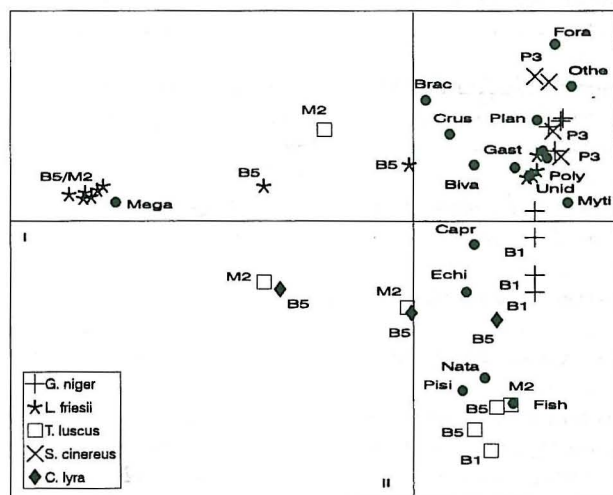


Figure 5. Correspondence analysis: distribution of samples of the different species for each station and time and diet components on axes I and II. Biva = Bivalves, Brac = Brachyurans, Capr = Caprellids, Echi = Echinoderms, Fish = Fishes, Fora = Foraminiferans, Gast = Gastropods, Myti = *Mytilus galloprovincialis*, Nata = Natantia, Crus = Other crustaceans, Mega = *Pisidia longicornis* megalopae, Othe = Others, Pisi = *Pisidia longicornis* adults, Plan = Plants, Poly = Polychaetes, Unid = Unidentified.

Figure 5. Analyse des correspondances: distribution sur les axes I et II des échantillons des différentes espèces pour chaque station, chaque heure et composants du régime alimentaire. Biva = Bivalves, Brac = Brachyours, Capr = Caprelliens, Echi = Echinodermes, Fish = Poissons, Fora = Foraminifères, Gast = Gastéropodes, Myti = *Mytilus galloprovincialis*, Nata = Natantia, Crus = Autres crustacés, Mega = Megalopes de *Pisidia longicornis*, Othe = Autres, Pisi = Adultes de *Pisidia longicornis*, Plan = Végétaux, Poly = Polychètes, Unid = Non identifiés.

There are more important differences in the specific composition of the diet, reflecting the structure of the prey communities in each habitat. In the case of the Ría de Arousa, this depends largely on mussel culture, and is evidenced by the differences found in the diet composition between stations. However, because of their mobility, demersal fish from nearby areas have access to the raft zones, where they go in search of food (López-Jamar *et al.*, 1984).

Our findings indicate that diet variability on a temporal and spatial as well as interspecific level, is closely related to the consumption of *P. longicornis*, in particular its megalopae. The feeding rhythms observed are associated with diets made up largely of megalopae. The daily vertical migrations of *P. longicornis* megalopae (Alvarez-Ossorio, pers. com.) may cause variations in its availability to different predators throughout the day. However, the predation on *P. Longicornis* megalopae should be considered a seasonal phenomenon and cannot be extrapolated to other times of the year. The reproductive cycle of *P. longicornis* (unpu-

blished data) is seasonal, giving rise to blooms of larvae in spring which comprise over 90% of the zooplankton (Corral & Alvarez-Ossorio, 1978).

For *L. friesii* the difference in fullness levels between stations seems to suggest that the appearance of megalopae causes a functional response with an increase in consumption rate, as compared to situations where this food source is not available (this was seen in B1 or in the B5 night samples, when they did not consume many megalopae). This was confirmed by the relationship between size and fullness level compared to the others species. While the FI decreases with mean size in all stations for *G. niger* and *T. luscus*, *L. friesii* showed the opposite pattern with a higher fullness level in areas where megalopae were consumed, in spite of the fact that they were larger in size than in other zones.

In general, the diel feeding patterns have been discussed in terms of environmental factors (Nash, 1982; Robin & Marchand, 1986; Van der Veer *et al.*, 1990), especially light and tides in estuarine zones. This may be the case of *S. cinereus* which showed greater daytime activity and consumed prey having little or no mobility.

Although environmental factors may be the primary cause, they may act indirectly, giving rise to cyclical changes in the activity of potential prey, which would modify their catchability by the different predators. An example is the feeding rhythm observed in *L. friesii* related to vertical migrations of *P. longicornis* megalopae in the channel zone of the ria, where they attain high densities (Corral & Alvarez-Ossorio, 1978). The existence of a feeding rhythm in this species was observed in others areas such as the west coast of Scotland, with diurnal maximum activity (Nash, 1982). However, in the inner part of the Ría de Arousa, where *P. longicornis* larvae are not abundant and *L. friesii* consumes mainly polychaetes and epifaunal amphipods, no variations in feeding rhythm through the day were found, as occurred in others areas where this species presents a similar diet (Gibson & Ezzi, 1978).

T. luscus, on the other hand, had a greater activity at night in the raft areas. Other studies suggest that the daily rhythm of this species is related more to the modification of the type of prey throughout the day rather than the fullness level, due to the daily variations in the activity patterns of its dominant prey, particularly the crustaceans *Crangon*, (Robin & Marchand, 1986) and *Processa* (Puente, 1986). In the Ría de Arousa *T. luscus* showed a very high percentage of stomachs with food, as occurred in others areas (Labarta, 1976; Puente, 1986; Costa, 1988; Dauvin, 1988).

Another important factor related to activity rhythms would be the behavioral adaptation to biological interactions, such as the modification of activity patterns in terms of predation risk by the fish (Magnhagen, 1988; Lima & Dill, 1990), although it is difficult to evaluate.

The feeding activity in fish populations have usually been studied through the analysis of stomach contents over diel cycles (Jenkins & Green, 1977). These studies should be analyzed with caution, as the type of diet (prey with or without calcified parts) and duration of gastric evacuation do not make stomach content analysis the most suitable method for the study of feeding activity (Eggers, 1977; Walsh & Fitzgerald, 1984; Freire, 1993; González-Gurriarán *et al.*, 1995). Nonetheless, the picture presented by the feeding pattern is generally quite accurate (Eggers, 1977), and provides information to make food consumption estimates.

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