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Pascal Laffaille, Jean-Claude Lefeuvre, M.-T. Schricke, Eric Feunteun. Feeding ecology of 0-group sea bass *Dicentrarchus labrax* in salt marshes of Mont Saint-Michel bay (France). *Estuaries*, 2001, vol. 24, pp.116-125. 10.2307/1352818 . hal-00736433

HAL Id: hal-00736433

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Submitted on 28 Sep 2012

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Feeding Ecology of 0-Group Sea Bass, *Dicentrarchus labrax*, in Salt Marshes of Mont Saint Michel Bay (France)

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ABSTRACT: 0-group sea bass, *Dicentrarchus labrax*, colonize intertidal marsh creeks of Mont Saint Michel Bay, France, on spring tides (e.g., 43% of the tides) during flood and return to coastal waters during ebb. Most arrived with empty stomachs (33%), and feed actively during their short stay in the creeks (from 1 to 2 h) where they consumed on average a minimum of 8% of their body weight. During flood tide, diet was dominated by mysids, *Neomysis integer*, which feed on marsh detritus. During ebb, when young sea bass left tidal marsh creeks, the majority had full stomachs (more than 98%) and diet was dominated by the most abundant marsh (including vegetated tidal flats and associated marsh creeks) resident amphipod, *Orchestia gammarellus*. Temporal and tidal effects on diet composition were shown to be insignificant. Foraging in vegetated flats occurs very rarely since they are only flooded by about 5% of the tides. It was shown that primary and secondary production of intertidal salt marshes play a fundamental role in the feeding of 0-group sea bass. This suggests that the well known nursery function of estuarine systems, which is usually restricted to subtidal and intertidal flats, ought to be extended to the supratidal, vegetated marshes and mainly to intertidal marsh creeks.

Introduction

North American salt marshes are known to play a nursery role for many fishes and macrocrustaceans, including important fishery species (see Shenker and Dean 1979; Minello and Zimmerman 1983; Boesch and Turner 1984; Kneib 1997). Many of these fishery species depend, for some period of their life cycle, on the intense primary productivity and refuge provided by vascular plants. By comparison, fish communities using European salt marshes are less well studied, although these intertidal habitats are important nursery areas for fish species (i.e., Labourg et al. 1985; Drake and Arias 1991; Cattrijsse et al. 1994; Laffaille et al. 1998, 2000a).

The sea bass *Dicentrarchus labrax* is among the most abundant and exploited fish species of European coasts (see Pickett and Pawson 1994; Pawson and Pickett 1996). As is the case for many species exploited by commercial fisheries, the life cycle of the sea bass is closely associated with coastal environments such as estuaries, lagoons, and tidal flats, which play key nursery functions (i.e., Costa 1988; Kelley 1988; Elie et al. 1990; Feunteun et al. 1999). The nursery ground role of coastal environments is often based on the occurrence of young fish in this habitat, but rarely is it based on examination of factors influencing fish stocks (i.e., Poxton et al. 1983; Smith 1985), such as feeding ecology (Arrhenius 1996). While recent studies on sea

bass focus mainly on conservation, fisheries, and aquaculture (i.e., Pickett and Pawson 1994; Pawson and Pickett 1996), quantitative information on diet is needed to assess the contribution of nurseries such as shallow bays to production of sea bass populations.

The objectives of this paper are to describe feeding ecology of 0-group sea bass in salt marshes of Mont Saint Michel Bay, to quantify the diet, and to assess the nursery role played by salt marshes. We studied the feeding activity in a tidal creek over various time scales (within tides, between tides, monthly, yearly).

Materials and Methods

The Mont Saint Michel Bay (France) is a wide littoral zone situated in the Normano-Breton Gulf (48°40'N, 1°40'W) (Fig. 1). This bay is a macrotidal system with the second highest tidal range in Europe (average: 10–11 m and up to 16 m). The intertidal zone covers 220 km², including 180 km² of mud flats and 40 km² of salt marshes (e.g., supratidal, vegetated marshes and associated intertidal marsh creeks). Salt marshes are incised by a more or less dense creek network where seawater comes in during tidal cycles. Functioning of salt marshes of Mont Saint Michel Bay have been studied since 1979 (Lefeuvre et al. 1994, 1999, 2000). The study site is located in salt marshes dominated by *Atriplex portulacoides* (Bouchard 1996; Bouchard and Lefeuvre 1996). It is situated 2.5 km from the coastline on a 10-m wide creek which drains a 5.7-ha watershed. The water only reaches this canal when the

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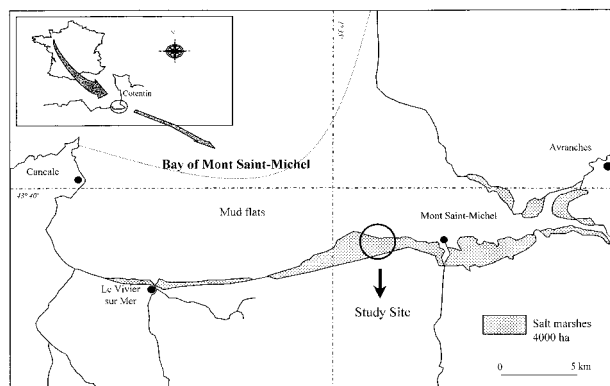


Fig. 1. Location of the Mont Saint Michel Bay and study site.

water level is > 11.25 m. Salt marsh vegetation is flooded when the water level is > 12.40 m (Troccaz et al. 1994; Laffaille et al. 1998). The salt marshes, including tidal creeks and vegetated tidal flats, can be invaded by fishes only during the spring tides and for a very short period during each tide (about 1 to 2 h). In this study, we compared two flooding events: flooding of tidal creeks (43% of the tides) and flooding of tidal creeks and vegetated tidal flats (5–10% of the tides), in order to assess the contribution of each habitat to the feeding. During the rest of the time, creeks and salt marshes remain unflooded.

Sea bass were caught with a fyke net (4-mm mesh size, 5-m deep, 1.80-m high, 20-m wide) settled across the tidal creek according to methods developed by Laffaille et al. (1998). Sampling was conducted during 99 tides between January 1997 and December 1998. Temporal fluctuations of population abundance and diet was studied at various time scales: seasonally, samples were made monthly; within tide cycles (e.g., series of 10 to 13 successive tides during which water floods the creek at ebb), two tide cycles were sampled in July and November 1997; daily during the tide cycles, morning and evening samplings were conducted; and within tides, during each tide three samples were collected at the beginning, middle, and end of flood and ebb.

Samples were deep frozen (-18°C) until laboratory analyses. Each fish was measured to the nearest 1 mm (fork length, FL) and weighed to the nearest 10 mg (individual fresh body weight, BW). Gut content of sea bass over 20 mm long was analysed. The number of guts containing food was determined (Feeding Index, %FI). Each gut content was weighed to the closest 10 mg (gut content fresh weight, FW). Instantaneous ration (%Ir) was established (Pawson and Pickett 1996): $\%Ir = FW/BW \times 100$. Average %Ir was calculated monthly for flood and ebb in order to assess the minimal quan-

TABLE 1. Seasonal size fluctuations of sea bass caught in salt marsh. FL: fork length (mm). n: number of measured fish.

Year	Month	FL min (mm)	FL max (mm)	FL mean (mm)	n
1997	January	—	—	—	—
	February	—	—	—	—
	March	18	22	21.0	13
	April	22	22	22.0	1
	May	12	21	17.0	5
	June	12	22	17.6	108
	July	12	59	25.9	703
	August	20	78	45.2	469
	September	47	94	68.4	165
	October	59	99	82.5	134
	November	60	112	90.5	66
	December	—	—	—	—
1998	January	—	—	—	—
	February	—	—	—	—
	March	20	22	20.4	11
	April	—	—	—	—
	May	21	21	21.0	1
	June	17	22	18.8	59
	July	17	42	25.1	155
	August	29	67	49.0	140
	September	40	78	59.3	62
	October	43	85	60.0	68
	November	63	104	86.4	38
	December	—	—	—	—

tity of food captured by sea bass during their stay in salt marshes ($= \Delta\%Ir$).

The items in stomachs were determined to species or gender and weighed to the nearest 1 mg (item fresh body weight, IW). For each sample, we calculated the occurrence frequency (%FO), the numeric abundance (%N), and the weight frequency (%B). Each of these indexes have their own meaning and limit (see Berg 1979; Hynes 1950; Hyslop 1980). In order to synthesize these three indexes, we calculated the Main Food Index (MFI), for each food item, accordingly to Zander (1982), Kara and Derbal (1996), and Laffaille et al. (1999b): $MFI_i = [(\%B_i \times (\%N_i + \%FO_i) / 2)^{1/2}] / [\sum(MFI_i)] \times 100$, with $i =$ food item i . The prey are classified according to MFI: primary food ($MFI > 75$), main food ($50 < MFI \leq 75$), secondary food ($25 < MFI \leq 50$), and insignificant food ($MFI \leq 25$).

The standard statistical procedures used in this study are fully described in Sokal and Rohlf (1981). In order to normalize the distribution, an arcsine square root transformation of %Ir was realized. %Ir was analysed by parametric analysis of variance, Tukey's multiple range test, and t -test to determine temporal differences. Temporal variations of diet were analysis by G-test modified by Williams (1976).

Results

A total of 2,220 0-group sea bass were caught and measured (Table 1). None occurred during the

TABLE 2. Food items identified in the stomach contents of sea bass caught during flood and ebb. %N: numeric frequency. %B: biomass frequency. %FO: frequency of occurrence. MFI: main food index. n: number of stomach contents analyzed.

Taxon	Flood (n = 328)				Eb (n = 781)			
	%N	%B	%FO	MFI	%N	%B	%FO	MFI
Fishes								
<i>Pomatoschistus</i> sp.	0.24	1.04	5.00	1.50	0.03	0.06	0.37	0.10
Insects	0.10	0.06	0.65	0.14	0.46	0.12	1.58	0.32
Arachnids	0.05	0.16	0.73	0.23	0.27	0.44	1.43	0.56
Crustacean								
Decapods								
<i>Crangon crangon</i>	0.02	0.20	0.33	0.17	0.09	0.52	0.37	0.32
<i>Palaemonetes varians</i>	0.09	1.31	1.69	0.98	0.32	1.43	2.96	1.40
<i>Carcinus maenas</i>	0.22	0.54	0.93	0.51	0.40	1.45	2.36	1.29
Amphipods								
<i>Orchestia gammarella</i>	19.20	23.05	28.62	21.28	58.24	72.93	78.85	63.93
<i>Corophium volutator</i>	2.95	1.63	8.57	2.78	6.32	1.57	16.10	3.84
<i>Bathyporeia</i> sp.	—	—	—	—	0.39	0.14	0.21	0.19
Isopods								
<i>Sphaeroma rugicauda</i>	0.01	0.11	0.09	0.07	0.26	0.78	0.66	0.55
<i>Eurydice pulchra</i>	4.72	2.97	14.25	4.81	8.47	2.30	12.05	4.44
Mysids								
<i>Neomysis integer</i>	45.60	46.30	64.47	45.77	14.21	7.98	28.52	11.94
Copepodites	26.14	18.11	17.20	17.91	8.56	7.72	7.16	4.23
Undetermined	—	—	—	—	0.04	0.05	0.28	0.08
Mollusca								
Lamellibranchia								
Tellinidae	0.22	0.21	0.93	0.32	0.01	0.01	0.24	0.03
<i>Cardium</i> spp.	0.10	2.20	2.50	1.53	0.01	0.06	0.09	0.05
Cephalopoda								
<i>Sepiolo</i> sp.	0.02	0.12	0.33	0.13	—	—	—	—
Polychaetes								
<i>Hediste diversicolor</i>	0.22	1.83	2.63	1.46	1.89	7.29	11.90	6.48
Vegetable	0.08	0.19	1.64	0.37	0.12	0.14	1.06	0.26

winter samples which suggests that they do not colonize salt marshes during the cold season. They appeared between March and July, sizes ranging between 12 and 22 mm (average 21 mm), which suggests a long recruitment period. After June, the average sizes increased, showing a high growth rate of nearly 1.2% d⁻¹. In October 1998, part of the cohort (largest sizes) did not occur. The young of the year stop invading the marsh in November at sizes ranging between 63 and 112 mm (average 89 mm).

Of 1,279 guts analysed, 487 (303 in 1997 and 184 in 1998) were from fish caught at flood and 792 (592 in 1997 and 200 in 1998) were caught at ebb. %Ir increase considerably and significantly (*t*-test, *t* = 27.2, *p* < 0.001) from 4.8% ± 2.8 to 12.9% ± 3.4 between flood and ebb, respectively. At each tide, sea bass ingested an average weight of food equivalent at least to 8.1% of their body weight. %FI followed the same trend. At flood, about 67.4% of the fish had stomachs that contained at

least one food item, whereas %FI drops to 98.6% at ebb.

During flood, diet was composed of 17 taxa (Table 2). The main prey were *Neomysis integer* (MFI = 45.8%), which occur in 64.5% of the stomachs. This mysid was a secondary food. It dominated the diet in numbers (%N = 45.6%) and in weight (%B = 46.3%). *Orchestia gammarellus* occurred but MFI is 21.3% because it was only present in 28.6% of the stomachs and copepodites represented 26.1% of the preys and had a MFI = 18.0%. Except *N. integer*, all the other species contributed little to the diet (MFI, %N, %B, and %FO < 25%).

During ebb, the diet was composed of 18 taxa (Table 2). Even if the species were similar to the flood diet, two new items appeared (*Bathyporeia* sp. and an undetermined crustacean) and one (*Sepiolo* sp.) disappeared resulting in a significantly different diet composition (G test, G_{adj} = 47.2, *p* < 0.005). During ebb, the main food item was *O. gammarellus* (MFI = 63.9%), which occurred in

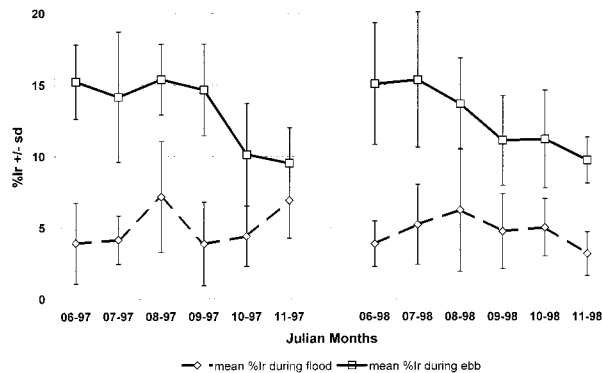


Fig. 2. Seasonal fluctuation of average instantaneous ration (%Ir) budgets between ebb and flood.

75.9% of the stomachs. This amphipod dominated the prey community (%N = 58.2%, %B = 72.9%). All the other prey were of lesser importance (individual MFI < 25%), although mysids occurred in 28.5% of the stomach contents.

TEMPORAL VARIATIONS

In 1997 and 1998, %Ir was always significantly lower at flood than at ebb (*t*-test, *t* = 24.3 and 15.4, respectively, both *p* < 0.001). This difference of 8.2% in 1997 and 8.0% in 1998 showed a very low interannual diversity of the minimal ingested food quantity.

During flood, in 1998 a total of 76.2% of the sea bass had at least one prey item in their stomachs whereas there were only 58.5% in 1997. During both years, there was no significant difference between the diets (*G* test, *G*_{adj} = 18.8, *p* > 0.5). *N. integer* was the main prey both in 1997 and in 1998 (MFI = 45.6% and 46.4%, respectively).

During ebb, %FI is equivalently high in 1997 and 1998 (%FI = 98.9% and 98.3%, respectively). The diet is statistically similar in both years with respect to flood (*G* test, *G*_{adj} = 11.2, *p* > 0.75). In 1997 and 1998, *O. gammarellus* was the main food item (MFI = 64.2% and 65.6%, respectively).

During each monthly sample, %Ir was always significantly lower during flood (*t*-test, all *p* < 0.01). This suggests that sea bass forage actively as they invade the salt marsh (Fig. 2). The food consumed was heterogeneous across months: Δ%Ir peaks between June and September in 1997 (8.2% < Δ%Ir < 11.3%) and between June and August in 1998 (7.4% < Δ%Ir < 11.2%). Minimum values were observed in November 1997 (Δ%Ir = 2.6%). During the whole study period, the feeding index was always lower at flood than at ebb (Fig. 3). The highest %FI occurred in August (%FI = 86.9% and 94.5% in 1997 and 1998, respectively) and October (%FI = 87.5% and 87.23% in 1997 and 1998, respectively). At ebb, %FI was often close to 100.

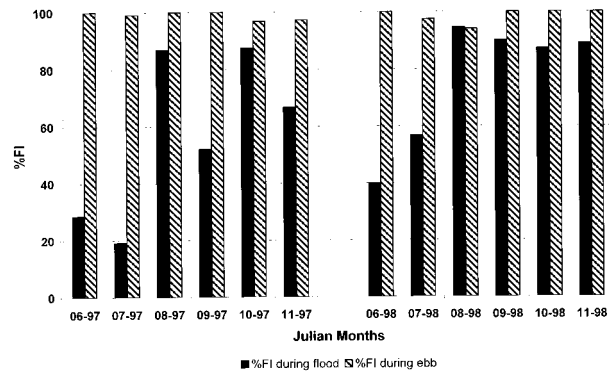


Fig. 3. Seasonal fluctuation of feeding index (%FI) during flood and ebb.

During flood in 1997 and 1998 (Fig. 2), a significant monthly trend was observed (*F* = 6.763, *p* < 0.001 in 1997 and *F* = 2.617, *p* = 0.026 in 1998). The diet composition showed similar trends in both years (Fig. 4). At the beginning of the season, copepods were the main prey (MFI = 73.4% and 62.1% in 1997 and 1998, respectively) but they were progressively replaced by mysids from August to October (MFI from 44.1% to 75.5%). After August, *O. gammarellus* appeared in the diet and became the dominant prey in November (MFI = 95.2% and 82.8% in 1997 and 1998, respectively). In both years, other prey contributed little to the diet.

During ebb in 1997 and 1998 (Fig. 2), the trends of %Ir were heterogeneous (*F* = 23.384 and 11.081 in 1997 and 1998, respectively, both *p* < 0.001). %Ir was highest during summer (15.5%) and dropped during autumn (9.5%). Whatever the month, *O. gammarellus* appeared to be the main prey for the young sea bass, MFI ranging between 47.5% and 91.6%, except in September 1997 and July 1998 (Fig. 5). In June 1997 and 1998 only

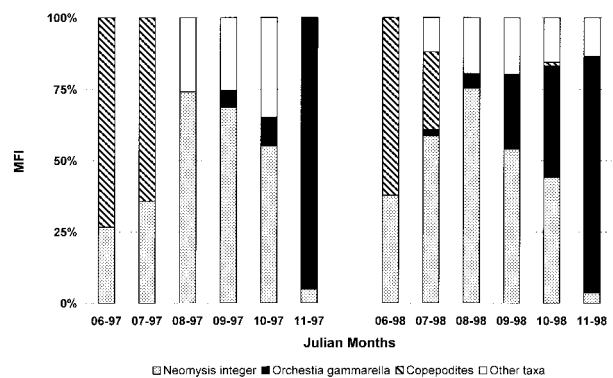


Fig. 4. Seasonal fluctuations of *Orchestia gammarellus*, *Neomysis integer*, copepodites, and other food items identified in the stomach contents of sea bass caught during flood. MFI = main food index.

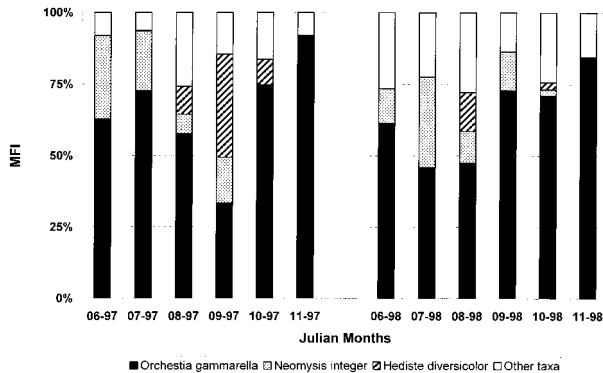


Fig. 5. Seasonal fluctuations of *Orchestia gammarellus*, *Neomysis integer*, *Hediste diversicolor*, and other food items identified in the stomach contents of sea bass caught during ebb. MFI = main food index.

three items were identified; *O. gammarellus* (MFI = 62.8% and 61.4% in 1997 and 1998, respectively) remained the main prey, followed by mysids (MFI = 29.1% and 12.11%, respectively) and copepods (MFI = 8.1% and 26.5%, respectively). In July 1998, two prey dominated: *O. gammarellus* (MFI = 45.8%) and *N. integer* (MFI = 31.7%). In September 1998, two other prey dominated: *Hediste diversicolor* (MFI = 36.1%) and *O. gammarellus* (33.3%). During the other months, diet was composed of 5 to 13 taxa. Except for *O. gammarellus*, MFI were always below 25% and these species were considered nonsignificant prey.

BETWEEN TIDE VARIATIONS

When the salt marsh is flooded, two cases are distinguished: either the creeks are flooded alone and vegetated tidal flats are not flooded (case nf) with water levels < 12.40 m, or creeks and vegetated tidal flats are both flooded (case f) with levels > 12.40 m.

In July 1997, %Ir (%Ir for nf = 14.6% ± 4.2, n = 133; %Ir for f = 14.0% ± 4.0, n = 223) observed during these two types of events was not significantly different (*t*-test, *t* = -1.344, *p* = 0.180). Nearly all the sea bass had a full stomach as they left the salt marsh (%FI = 100% and 98.7% for nf and f, respectively). There was no significant difference between diets observed in both cases (G-test, $G_{adj} = 10.22$, *p* > 0.25). *O. gammarellus* was always the main food item for nf (MFI = 69.8%) and for f (MFI = 54.1%). *N. integer* was the second most important prey, it was secondary for f (MFI = 37.4%) and insignificant for nf (MFI = 20.8%). All the other species were insignificant prey.

In November 1997, %Ir was not significantly different (*t*-test, *t* = 0.692, *p* = 0.492) between tides (water level < 12.40 m) that did not flood salt marshes (%Ir = 8.4% ± 4.1, n = 31) and tides

(water level > 12.40 m) that flooded vegetation (%Ir = 9.3% ± 3.6, n = 32). Nearly all the sea bass had a full stomach as they left the salt marsh (%FI = 93.6% and 96.9% for nf and f, respectively). In spite of statistically significant differences between diets for n and nf (G-test, $G_{adj} = 24.55$, *p* < 0.005), *O. gammarellus* was always the main food item (MFI = 82.5% and 87.4% for nf and f, respectively). This difference was due to insignificant prey mainly from marine origin in nf cases (*N. integer*, *Erydice pulchra*, *Palaemonetes varians*, and *Tellinidae*) and mainly vegetated tidal flats residents for f cases (*Corophium volutator*, Arachnids, and plant detritus).

In conclusion, very little differences of diet were observed according to the tidal amplitude. This suggests that the feeding activity of 0-group sea bass does not depend upon the submersion of the vegetated tidal flats. The tidal creeks seem to act as a drainage area where the secondary production of the whole salt marsh gets concentrated.

Two events were considered and compared: morning tides (high tides during morning sampling) and evening tides (high tides during evening sampling). In July 1997, no significant %Ir differences (*t*-test, *t* = 1.403, *p* = 0.124) were observed between morning (%Ir = 14.7% ± 4.0, n = 133) and evening tides (%Ir = 14.2% ± 4.6, n = 224). Feeding index also had little difference (%FI = 99.3% and 99.1%, respectively). There was no significant difference between diets observed in both cases (G-test, $G_{adj} = 11.81$, *p* > 0.25). Even if *O. gammarellus* was always the principal food item (MFI = 72.7% and 48.6% during morning and evening tides, respectively), mysids had a stronger contribution to the diet at evening tides (MFI = 20.8% and 38.8% during morning and evening tides, respectively). All the other species were insignificant prey.

In November 1997, no significant %Ir differences (*t*-test, *t* = -1.278, *p* = 0.207) were observed between morning (%Ir = 9.5% ± 3.5, n = 36) and evening tides (%Ir = 7.9% ± 4.2, n = 27). %FI was similar (%FI = 92.6 and 97.2%, respectively). November diet was significantly different (G-test, $G_{adj} = 20.0$, *p* < 0.05). Even if *O. gammarellus* was always the principal food item (MFI = 91.6% and 83.0% during morning and evening tides, respectively), mysids had a stronger contribution during evening tides diet (MFI = 10.1% and 0.5%, respectively) and *N. integer* is replaced by other insignificant species during morning tides.

Very little differences of diet were observed according to the nyctemeral variations. This suggests that the feeding activity of 0-group sea bass does not depend upon the time of the day.

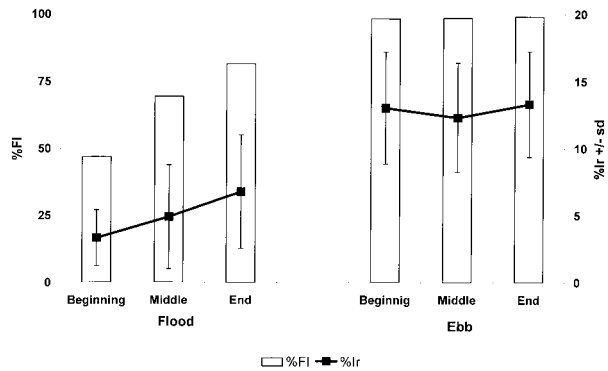


Fig. 6. Variation of %FI and %Ir during the tide cycle from flood to ebb (beginning, middle, and end).

WITHIN TIDES VARIATIONS

During flood the feeding index increased from 46.9% to 69.4% and 81.5% (Fig. 6), and %Ir increased significantly ($F = 33.352$, $p < 0.001$; Tukey's multiple range test, all $p \leq 0.001$) between the beginning (%Ir = $3.3\% \pm 2.1$, $n = 144$), the middle (%Ir = $4.9\% \pm 3.9$, $n = 158$), and the end of flood (%Ir = $6.8\% \pm 4.2$, $n = 185$). Sea bass foraged actively in the salt marsh during flood. The diet composition also evolved significantly during the beginning and middle of flood (G-test, $G_{adj} = 35.97$, $p < 0.005$) and between the beginning and end of flood (G-test, $G_{adj} = 32.73$, $p < 0.005$). Even if the main food items were mysids (Fig. 7) whose contribution increases in the diet during flood (MFI = 42.9% at the beginning, 62.0% at the middle, and 72.8% at the end of flood); other items were insignificant prey during flood (individual MFI < 12%). No significant between-year difference occurred, either from the quantitative, (t -test, all $p > 0.05$) or qualitative point of view (G-test, all $p > 0.05$). It is suggested that a yearly reproducible phenomenon is described.

During ebb, feeding is much more stable (Fig. 6). A significant temporal evolution of %Ir was observed ($F = 3.464$, $p = 0.032$). It was due (Tukey's multiple range test, $p = 0.011$) to the slightly lowest mean occurring during the middle of the ebb (on average, %Ir = $12.9\% \pm 3.4$). But %FI remains > 98% and therefore we considered it stable. This steadiness also concerned the diet composition (G-test, all $p > 0.9$), *O. gammarellus* being the main food item (Fig. 7) at the beginning (MFI = 58.0%), the middle (MFI = 66.1%) and the end of ebb (MFI = 65.6%). All other prey were insignificant food items (individual MFI < 13%). The diversity of food items increased from 14 to 18 during ebb and was higher than that observed during flood (from 10 to 11 items).

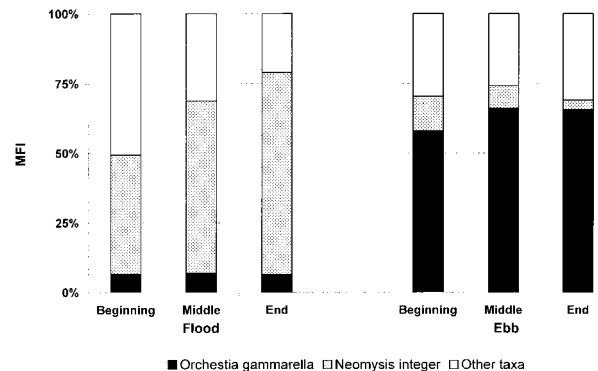


Fig. 7. Variation of *Orchestia gammarellus*, *Neomysis integer*, and other food items identified in the stomach contents of sea bass caught between flood and ebb (beginning, middle, and end). MFI = main food index.

Discussion

On the Britain Atlantic coast, sea bass spawn between February and April (Boulineau-Costanea 1969). Young of the year migrate towards coastal marine waters such as estuaries (Claridge and Potter 1983; Costa 1988; Kelley 1988) and bays (Elie et al. 1990; Feunteun and Laffaille 1997). In Mont Saint Michel Bay, sea bass colonize macrotidal salt marshes between March and November, but juveniles occur during the whole year in tidal mud flats (Lam Hoi 1969; Laffaille et al. 1999a). The utilization of these coastal environments as nurseries has been mainly attributed to their high productivity (McLusky 1981; Boesch and Turner 1984). Other factors are also important (Blaber and Blaber 1980) such as reduced salinity (Bœuf and Lasserre 1978; Alliot and Pastoureaud 1979; Dendrinou and Thorpe 1985) and shelter (see Boesch and Turner 1984). Their presence in salt marshes appears to last longer than in other sites such as marshes of Arcachon Bay (France) where they occur from May to September (Labourg et al. 1985) or marshes of Westerschelde estuary (Netherlands) (Cattrijsse et al. 1994). Sea bass were found mainly at 0+ stages, although 1+ fish occurred in small numbers (Laffaille et al. 1998, 2000a). Very young fishes most often drifted passively by the currents into salt marshes (Shenker and Dean 1979; Fortier and Legett 1982) and/or by selective tidal transport (Arnold 1981; Dame and Allen 1996). This is the case of 0-group sea bass that only stay, on average, during 1 to 2 h in the creeks during spring tides (about 43% of the tides). During winter, sea bass probably go back offshore where the temperature is higher than in the salt marsh as has been shown in other littoral nurseries (i.e., Claridge and Potter 1983; Aprahamian and Barr 1985; Labourg et al. 1985).

0-group sea bass colonize salt marsh creeks to

forage, regardless of the season, tide amplitude, time of the day, and time of the tide. This study confirms a general assumption that juveniles of transient nekton invade intertidal creeks during flood to feed (i.e., Helfman et al. 1983; Kleypas and Dean 1983; Rountree and Able 1992; Szeldmayer and Able 1993). Diet does not vary significantly according to tidal range and time of the day. On average, they consume the equivalent of a minimum 8% of their body weight. Two stages are observed according to the time of tide. During flood, 55% of fishes have empty stomachs and %Ir is 3%. The tide drifts high densities of mysids (especially *N. integer*) from coastal marine waters (Zagursky and Feller 1985; Cattrijsse et al. 1994), which then become highly accessible for young sea bass during flood. At the end of flood, only about 20% of sea bass had empty stomachs and %Ir had increased to 7%. During ebb, sea bass continue to forage and return seawards with less than 1% not having eaten (mean %Ir = 13%). The main food item is the amphipod *O. gammarellus*, which is one of the most abundant species of salt marsh creeks and vegetated areas in Mont Saint Michel Bay (Fouillet 1986; Créach et al. 1997). This species mainly feeds on salt marsh macrodetritus and diatoms (Créach et al. 1997) and becomes available for bass during spring tides each time the creeks and/or the vegetated marshes are flooded (> 43% of the tides). 0-group sea bass appear to have an opportunistic feeding behavior as has already been shown for most nekton species in marshes (e.g., Barry et al. 1996; Kneib 1997). The low vacuity and the important food quantity consumed during the very short period of submersion of the salt marsh creeks and/or vegetated areas show the voracity of this species (e.g., Labourg and Stéquent 1973; Hervé 1978; Ferrari and Chierigato 1981; Roblin and Bruslé 1984; Pickett and Pawson 1994; Pawson and Pickett 1996; Laffaille et al. 2000b).

A rapid food intake and maintenance of a constant stomach content during digestion favors a high assimilation of food (Godin 1981), and may cause the %Ir observed in the salt marsh for 0-group sea bass to be underestimated. Most of the mysids found at flood are absent from the stomach content at ebb. They are assumed to be assimilated quickly as *O. gammarellus* are ingested in the salt marsh. Because $\Delta\%Ir$ is often $\geq 10\%$ (in June, July, and September), we suggest that young sea bass food uptake is $> 10\%$ in the tidal salt marsh.

After October, the water temperature decreases rapidly in Mont Saint Michel Bay and is $< 10^\circ\text{C}$ in November. As in most fish species, temperature has a major influence on growth and food intake of 0-group sea bass (Alliot et al. 1983; Russell et al. 1996). In experimental conditions, the food intake

of juvenile sea bass decreased rapidly at temperatures $< 10^\circ\text{C}$ and stops for temperatures $< 7^\circ\text{C}$ (Tesseyre 1979; Lancaster 1991; Russell et al. 1996). The decrease of sea bass densities and of their feeding activity in autumn and in winter appears to be due to colder temperatures.

Apart from Labourg and Stéquent (1973) who found important quantities of insects in the diet, most authors (i.e., Aprahamian and Barr 1985; Ferrari and Chierigato 1981; Pickett and Pawson 1994; Pawson and Pickett 1996) show that the diet of young sea bass is largely dominated by small crustaceans (copepods, mysids, amphipods, isopods). During the present study, 17 and 18 taxa were found in the stomach content at flood and ebb, respectively. All the items described in other studies were found, but the main food item was the mysids *N. integer* at flood and the amphipod *O. gammarellus* at ebb. Other prey were only considered as accessory except, at ebb, the polychaete *H. diversicolor* which was abundant in September 1997, during the major recruitment period of this species (Gillet 1986) which makes it easily accessible to demersal predators such as sea bass and sand gobies (Laffaille et al. 1999b, 2000b; this study). This result confirms that polychaetes may constitute an important food item for young sea bass, as shown by a number of authors (Kennedy and Fitzmaurice 1972; Léauté 1984; Kara and Derbal 1996).

A significant monthly growth of 0-group sea bass was shown; the diet therefore changes, size of items increasing with the size of the predator. In June and July, copepodites were the main food item at flood as they are very small benthic prey attractive for the smallest stages of sea bass. During the season, the size of the prey increased. Small copepodites disappeared from the diet as larger prey (*Sphaeroma rugicauda*) appeared. The size of consumed *O. gammarellus* also increased during the season.

The present study shows that the diet of the young sea bass is directly related to their demersal behavior and mostly to the availability of prey items in the environments they colonize, although terrestrial items, such as arachnids and insects, which occur in vegetated salt marshes (Fouillet 1986), were not abundant in the diet. Diets were similar whether vegetated salt marshes were flooded or not, as *O. gammarellus* was always the main food item, suggesting that terrestrial prey accidentally fall in the creeks. Foraging in vegetated flats might occur but very rarely as it is only possible when they are flooded (about 5% of the tides). This suggests that, during their short stay in the salt marsh system, young sea bass did not often colonize the vegetated tidal flats and that they foraged in the

tidal marsh creeks or riparian zone where food was available.

THE SALT MARSH-SEA BASS ECOLOGICAL RELATIONSHIP

O. gammarellus is a resident species of Mont Saint Michel Bay salt marshes, including marsh creeks and vegetated flats (Fouillet 1986; Créach et al. 1997). This amphipod, which mainly feeds on halophyte plant detritus and benthic diatoms produced by the whole salt marsh (Créach et al. 1997), represents a major food item for sea bass. However, it is only available when the tidal creeks and/or the vegetated salt marshes are flooded. *N. integer* is a marine-estuarine crustacean. Dense aggregations of the detrital material inside the tidal marsh creeks may attract this animal to enter the creeks to feed (Zagursky and Feller 1985; Cattrijsse et al. 1994). The mysids play a major role in the detrital food chain of coastal marine and estuarine waters (Mees and Hamerlynck 1992). The mysid is a primary food item during the flood, before sea bass invade the creeks. Young sea bass exploit the secondary production and, indirectly, the important primary production of the macrotidal salt marshes. The latter therefore appears to play an essential nursery role for sea bass and sustains the productivity of this highly valuable commercial fish species, in the Mont Saint Michel Bay and many adjacent coastal waters.

For several technical reasons (ease of capture, diet analysis, etc.), we only analyzed fish > 20 mm. Smaller fish are abundant from March to June. During this period, maximum $\Delta\%I_r$ were observed. Therefore sea bass between 12 and 20 mm FL could be even more dependent upon productivity of salt marshes.

Similar conclusions have been made for fish such as gobies (*Pomatoschistus* spp.) and mullets (*Liza* spp.). Sand gobies, *P. minutus* and *P. lozanoi*, have very similar diets to young sea bass and also exploit secondary production of the salt marsh (Laffaille et al. 1999b). These species are among the most abundant in western Europe. They represent important basic prey for a range of fish, aquatic birds, and mammals (Hamerlynck et al. 1993; Hamerlynck and Cattrijsse 1994). Mulletts consume at least 10% of their body weight in a mixture of silt and organic matter (mainly composed of benthic diatoms) as they invade the tidal creeks, and therefore they directly exploit the primary productivity of the salt marshes (Laffaille et al. 1998). These fish species play key roles in the littoral food web and in transfers of organic matter between tidal marshes and coastal marine waters (Laffaille et al. 1998; Lefeuvre et al. 1999).

O. gammarellus is not the only resident species of

these salt marsh creeks and vegetated flats. In the halophile vegetation, insects and arachnids are also very abundant (Fouillet 1986) and occur as accessory prey in the diet of sea bass. Decapods (*Carcinus maenas*), amphipods (*C. volutator*), isopods (*Sphaeroma rugicauda* and *E. pulchra*), bivalves (*Tellinidae* and *Cardium* spp.), and polychaetes (*H. diversicolor*) are also major components of the invertebrate community of the tidal salt marsh creeks (Créach et al. 1997). It is known that tidal salt marshes support high densities of benthic invertebrates (Kneib 1984; Wenner and Beatty 1993; Covi and Kneib 1995) that are usually important in the diet of many species that exploit tidal marshes (Barry et al. 1996). In Mont Saint Michel Bay, together with *O. gammarellus*, these species represent 76% of the numbers and more than 86% of the biomass of food ingested in the salt marsh by young sea bass in the tidal creeks of the salt marsh.

In order to improve our knowledge on the relations between fish (such as sea bass) and coastal wetlands (such as salt marshes), it seems important to develop future research on the extent to which food ingested in the salt marsh creeks and vegetated flats contributes to the growth of fish species exploiting resources and the extent to which salt marshes contribute to the sustainability of the population and the stock caught in local and regional fisheries.

ACKNOWLEDGMENTS

This study was funded by the Environment and Climate European Programme (DG XII) European Salt Marshes Modelling no. ENV4-CT97-0436. Thanks to A. Radureau, A. Baisez, Calou, Tintin, and two anonymous referees for their comments and corrections on an earlier version of this manuscript. We are also grateful for the help provided by many students and colleagues during the field work.

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