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Food of the European eel *Anguilla anguilla* in the Mauguio lagoon (Mediterranean, France)

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This study deals with temporal variations in eel *Anguilla anguilla* diet, sampled seasonally in the Languedocian Mauguio lagoon (Gulf of Lion), from Autumn 1998 to Summer 1999. Eel mainly feeds on benthic organisms, primarily small Amphipoda, Crustacea (mainly Gammarus gr. locusta), Polychaeta, insect larvae (Chironomidae) and small fish. Based on variations in the eels feeding regime, seasonal influence is illustrated by decreased feeding activity in summer, which progressively increases during the following seasons. The trophic quality available to eels in the Mauguio lagoon depends more on allochtonous inputs from the catchment area than on its own hydrodynamics on which water of marine origin has little influence due to its long distance from the sea. Variations observed during the four seasons illustrate the opportunist type feeding behaviour of eels. They consume the most available benthic preys at a given moment without using a particular feeding strategy like specialisation or generalisation. Eel adapts its diet according to the available resources offered by the ecosystem. Because of this eel, as an amphihaline migrant species, can be characterised as an obvious indirect bioindicator of the trophic capacity and very marked level of confinement in the brackish lagoon ecosystem of Mauguio.

Key words: Gulf of Lion, eel, lagoon, diet, opportunism, bioindicator

INTRODUCTION

The distribution of the European eel *Anguilla anguilla* Linné 1758, extends from Morocco to Scandinavia (BAUCHOT & PRAS, 1980), in the Atlantic ocean and in the Mediterranean sea. This catadromous migrant species is present in brackish and fresh coastal marine waters. Eels are essentially carnivorous, their principal prey being Crustacea, Mollusca, Annelida and insect larvae (LECOMTE-FINIGER, 1983). In the Palavasian lagoon complex (Fig. 1A) from the Gulf of Lion, eel is traditionally the main exploited fish species (LECOMTE-FINIGER & BRUSLÉ, 1984) among sea bass, sea bream, sole, sand smelt and mullets. The European eel is becoming endangered (BRUSLÉ, 1989) and new research on its biology has to be initiated in order to enhance knowledge on the species status, even though its food and feeding characteristics are...
well known. Seasonal variations in the feeding regime of the eel population were studied over a one year period by means of feeding indices in order to obtain a better understanding of the trophic availability and productivity level in the Mauguio lagoon ecosystem with its biological zonation in order to compare it with that in the neighbouring lagoons.

MATERIAL AND METHODS

The sampling site

The fish was sampled in the Mauguio lagoon (Fig. 1B), situated near Carnon City to the south of Montpellier City, that is oriented in an east-west direction to the east of the Prévost lagoon. The lagoon is 11 km long and 2 to 3 km wide, covering a surface area of 31.66 km² and has an average depth of 0.80 m. Inputs of fresh water come from the Salaison, Capouillère and Bérange Rivers with torrential regimes and from four drainage canals and the Rhône River Canal to Sète. City communication with the sea is via a north-south orientated pass, 1.1 km long, 12 m wide and 1.50 m deep. The management of seawater throughout the whole section of the Grau de Carnon (communication with the sea) is by means of a gate, and inputs of fresh water from the Vidourle River have been regulated since March 1981. Salinity varies generally between 8 and 26 g l⁻¹. The hydrodynamics of this vast ecosystem are managed essentially by winds and rainfall.

Sampling

From September 1998 to August 1999, 183 eels (15.6 ≤ LT (cm) ≤ 72.0; 5.3 ≤ M (g) ≤ 830.0) were harvested during the four seasons in the Mauguio lagoon: 9 in autumn, 18 in winter, 26 in spring and 130 in summer. Sampling was carried out at a rate of five consecutive days per season. Fishing gear used for sampling consisted in a fixed net: the “capéchade” (BOUCHEREAU et al., 1989). This system (Fig. 2) involves a “paradière”, a net acting as a barrier and a tower or triangle towards which fish are directed and are thus trapped in the pot or fyke net. One sampling site was chosen (Fig. 1B) in zone IV of confinement, after the biological zonation proposed by GUÉLORGET & PERTHUISOT (1983, 1992). The Mauguio lagoon (Fig. 1B) has a very restricted rate of sea water renewal throughout the year and thus confinement is very marked over almost all the basin. Except for a very limited region at the mouth of the small canal opening into the lagoon (zone III) the whole ecosystem is positioned in zones IV, V and VI of the paralic domain according to the scale devised by GUÉLORGET & PERTHUISOT (1983, 1992). The “capéchades” are generally brought up daily after 24 hours of fishing effort. It should be noted that certain specimens caught could have digested their feed during captivity in the
Because of this empty stomachs have not been taken into account in calculating indices. The unit of sampling effort is the same for each day and therefore for each season.

Stomachs of 183 specimens were extracted and preserved in 10% formaldehyde with a view to studying stomach contents (BOUCHEREAU & VERGNE, 1999). Laboratory observations

Stomachs of each specimen were examined under a binocular microscope to identify and count prey ingested. The degree of taxonomic determination is a function of the time required for digestion of the bolus (JOYEUX et al., 1991). Categories of prey were defined into large taxonomic groups and if possible up to genus level (TREGOUBOFF & ROSE, 1978). Where prey had been badly preserved the numbers of specimens present were defined by counting cephalic parts and bone pieces where fish were concerned.

Data processing

The feeding regime of *A. anguilla* was studied in each seasonal sampling by means of the five following indices described by BOUCHEREAU & GUÉLORGET (1999):

- The coefficient of vacuity (CV): the percentage of empty stomachs (Nv) in relation to the total number of stomachs examined (Nt)

\[
CV = 100 \left( \frac{N_v}{N_t} \right) \quad (1)
\]

- The degree of fullness of the digestive tube (DR): this represents the subjective evaluation of the degree of fullness of the digestive tube, consisting of three levels corresponding to N1 = 25%, N2 = 75% et N3 = 100%, of total volume of the digestive tube

\[
DR_{(1, 2, 3)} = 100 \left( \frac{N_{(1,2,3)}}{N_t} \right) \quad (2)
\]

where \(N_{(1, 2, 3)}\) represents the number of digestive tubes divided according to the three levels of fullness and \(N_t\) represents the total number of digestive tubes analysed. Interpretation of this index depends on the evaluation made by the researcher at the moment of observation.

- The occurrence frequency (PP) of prey in stomach contents: the percentage of stomachs examined containing the category of prey i (Nti) in relation to the number of stomachs containing prey (Np)

\[
PP = 100 \left( \frac{N_{ti}}{N_p} \right) \quad (3)
\]

- The numeric percentage (N): the percentage of prey counted in one category i (Ni) in relation to the total number of prey counted (Npt)

\[
N = 100 \left( \frac{N_i}{N_{pt}} \right) \quad (4)
\]

- The percentage in points (P): the percentage of prey ingested in the category i (Pi) in relation to the total number of points for all prey ingested

\[
P = 100 \left( \frac{P_i}{Total \ points} \right) \quad (5)
\]

To calculate percentages in points (P), the numeric method of points (HYNES, 1950; PILLAY, 1952) modified and adapted by JOYEUX et al. (1991) and PAMPOLIE & BOUCHEREAU (1996) (Table 1) was used. This method assigns a certain number of points as a function of the state
of satiety of the predator’s stomach and of the mass of prey observed during digestion. In this approach, a certain number of points is given to each zoological group in proportion to the average size (mass) of these animals had they not been ingested. This method enables a better evaluation to be made of feed intake based on digested remains. The number of points assigned in this case therefore reflects the level of satiety at the moment when prey were swallowed (BOUCHEREAU & GUELORGET, 1999).

The indices PP, N and P were calculated by season and by category of prey. Indices PP and N illustrate the presence or absence of a given prey and its numeric importance during the season.

Seasonal evolution was tested by the Spearman unilateral non-parametric statistical correlation test (rs). This test is the most appropriate considering the various characteristics of samples. Values are expressed in percentages and variables do not follow Normal laws. This test is applied to the three indices PP, N and P in order to study possible qualitative and quantitative changes in the feeding regime of A. anguilla.

Values rs were compared with critical values for probability levels P = 0.05 and 0.01 (TOMASON, 1995). The null hypothesis Ho: Series 1 = Series 2 is considered; if the calculated value is > than the critical value (P>0.05 or 0.01), Ho cannot be accepted and the two series of data are considered to be different.

To facilitate the interpretation of results, the COSTELLO et al. (1990) method was used. This graphically combines the percentage of presence (PP) with the numeric or abundance percentage (N) of each prey (Fig. 3).

COSTELLO et al. (1990) suggest that the two diagonals represent, respectively, the importance of prey (dominant, rare) and the predator’s feeding strategy (specialist, generalist). The points close to 100% of presence and 100% of abundance represent dominant prey. Points who are around 100% of presence and 1% of abundance indicate that predators have a specialized feeding regime.

### RESULTS

Anguilla anguilla has a very generalistic feeding regime as 13 different categories of prey were counted (Table 2) and were distributed principally between small fish, Polychaeta Annelids, Amphipoda Crustacea, and larvae of insects Chironoma. This number gradually increased from autumn (5) to winter (6) and spring (8) and reaching a maximum (10) in summer.

Of 183 eels harvested, 76 were observed to have empty stomachs (Fig. 4) and 107 presented

<table>
<thead>
<tr>
<th>Categories of prey</th>
<th>Points</th>
<th>Categories of prey</th>
<th>Points</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fish</td>
<td>100.0</td>
<td>Gammarus gr. locusta</td>
<td>10.0</td>
</tr>
<tr>
<td>Polychaeta</td>
<td>40.0</td>
<td>Corophium insidiosum</td>
<td>5.0</td>
</tr>
<tr>
<td>Nematoda</td>
<td>40.0</td>
<td>Insects</td>
<td>5.0</td>
</tr>
<tr>
<td>Decapoda</td>
<td>25.0</td>
<td>Mollusca</td>
<td>1.0</td>
</tr>
<tr>
<td>Crustacea</td>
<td>15.0</td>
<td>Scales</td>
<td>1.0</td>
</tr>
<tr>
<td>Isopoda</td>
<td>10.0</td>
<td>Ostracoda</td>
<td>0.5</td>
</tr>
<tr>
<td>Amphipoda</td>
<td>10.0</td>
<td>Copepoda</td>
<td>0.5</td>
</tr>
</tbody>
</table>
filled stomachs \((21 \leq L_T (cm) \leq 51)\), i.e. a CV of 41.5\% (Fig. 4). The vacuity reached a minimum (36.2\%) in summer and a maximum (100\%) in winter.

Stomachs were fullest (Fig. 4) in winter \((DR_3 = 28.6\%)\) and spring \((DR_3 = 25.0\%)\), half full \((40.0\% \leq DR_2 \leq 57.1\%)\) and quarter full during each season \((41.7\% \leq DR_1 \leq 68.7\%)\) except winter \((DR_1 = 14.3\%)\). No stomach was completely full in autumn \((DR_3 = 0\%)\) and only a few in summer \((DR_3 = 3.61\%)\).

Based on the occurrence frequency PP, present prey in the stomach contents (Table 3) were *Gammarus gr. locusta* \((9.1 < PP < 33.3)\) larvae of *Chironoma* insects \((9.1 < PP < 16.7)\) and Polychaeta \((9.1 < PP < 43.9)\), regardless of the season. Fish had a high occurrence in autumn \((16.7\%)\) and in spring \((27.3\%)\) but were absent in winter and summer. The occurrence frequency PP of *Gammarus gr. locusta* decreased with the season. It reached a maximum in autumn (33.3\%) – winter (17.7\%) and a minimum in spring (9.1\%) – summer (10.0\%). There exists a significant difference \((p \geq 0.05)\) between summer and autumn. New prey appear in winter (Isopoda) spring (other Crustacea) and summer (Nematoda, Corophium, other Amphipoda and Decapoda).

The maximum numbers of prey (Table 3) are found in summer with fish in spring (62.50%),

![Fig. 4. Seasonal variation of the A. anguilla vacuity index CV and stomachs filling indices DR1, DR2 and DR3 (in %) in the Mauguio lagoon](image-url)
Gammarus gr. locusta (50.0%) in autumn, Gammarus gr. locusta, insects (28.8%) in winter, fish scales (28.6%) in autumn, and Polychaeta in winter (20.3%) and summer (20.2%). The number of prey N of Gammarus gr. locusta decreased from autumn (50%) – winter (28.8%) to spring (3.1%) – summer (6.7%). The opposite variation was observed in insect larvae, with a maximal N in winter (28.8%). Eels consumed fish all year round except in winter when a new prey was observed - Isopoda (5.9%).

Expressed as a percentage of points P, biomass ingested by A. anguilla (Table 3) in autumn consisted of Polychaeta (45.7%) and Gammarus gr. locusta (32%). Between autumn and winter an increase in the biomass of Polychaeta (45.6 to 62.3%) was observed and a reduction in the importance of Gammarus gr. locusta (32.0 to 22.1%). In spring, fish made up the major part of biomass ingested (96.2%) whereas Polychaeta comprised the major part of biomass in the eels stomach contents sampled in summer (83.6%).

Tests on the indices P and N illustrated significant differences between autumn and summer (p<0.05).

DISCUSSION

The work reported herein focuses more on the seasonal change in the diet of the eel population rather than simply being a new study describing the sex, age, size or ecophase of eel individuals. In using the method of Costello et al. (1990) and Guélorget & Perthuisot’s (1983) confinement concept, results are interpreted and related to the adaptive responses of eels with the trophic availability as a possible characteristic of this particular Mauguio lagoon ecosystem.

The feeding regime of eels residing in the Mauguio lagoon is essentially based on benthic organisms, grouping together 13 important categories of different prey. These consist mainly of Amphipoda and Decapoda Crustacea, Polychaeta Annelida and Chironomidae larvae supplemented relatively alternately according to the season by small fish and molluscs. This spectrum essentially confirms that observed by Lecomte-Finiğer (1983), and enables eels to be given the status of a second order carnivorous species. Fisher et al. (1987) and Schneider et al. (1987) also describe very similar feeding spectra. Echinodermata, which are exclusively associated with zone II of the biological zone, were not observed in the stomachs of eels. This confirms that eels occur in rather more confined parts, and the sampling site chosen was situated in zone IV in the sense according to Guélorget & Perthuisot (1983, 1992). The presence of sea urchins is limited to the mouth of estuaries and in zones under permanent marine influence. Eel is more active during the warm season than the cold season. Its catch ability by passive fishing gear is higher in spring-summer.

The seasonal evolution of the coefficient of vacuity reveals a variation in feed uptake or in feeding choice of eel. Do eels feed more in winter, a period during which fewer are harvested or more in summer when more are harvested? Or should the influence of temperature on digestion time, which is longer in the cold season than in the warm season, be considered? This could explain why in winter stomachs are fuller with biomass containing a lower diversity of prey because of a lesser choice offered. In the Mauguio lagoon maximal diversity is observed in prey in spring and summer (8-10 items). Only fish and Isopoda are absent in summer when Nematoda, Decapoda and other Amphipoda become apparent. This enlarging of the feeding spectrum could be related to the warming of water which in turn influences the biological cycle of these species susceptible to favoring a particular ecophase in the lagoon: an increase in temperature accelerates the larval development phase leading to the presence of these species in the environment (Duperchy, 1998). Reduction in the diversity of prey observed in the stomach contents in autumn and winter is followed by an increase in the number of available prey consumed during those periods.

In autumn and winter, Gammarus and Chironomidae are the most numerically important prey even if Gammarus and fish make up the major part of biomass. Polychaetae and scales are more consumed in spring and even more so in summer than in other seasons. Physico-
chemical changes in the ecosystem due to seasonal climate could cause differences in trophic availability. Thus to compensate for this, the eel reduces its diet to the available prey during this period contrary to the Prévost lagoon were the eel enlarges its feeding spectrum (BOUCHEREAU et al., 2006) by targeting its feeding towards the taxonomic category present such as small sedentary lagoon fish species, in particular Pomatoschistus sp. belonging to the Gobiidae family. Eels consume these species in lagoons in east Corsica (CASABIANCA & KIENER, 1969).

No determination can be made if the observed scales are the remains of fish digestion or are prey removed from fish by the eels. In the latter case it is a question of lepidophagus species (BLABER, 2000). Scale prey has been observed with fish in autumn and spring and also in larger quantities in summer without observation of fish in the contents. Perhaps A anguilla extracts scales from juvenile Mugil cephalus, Sparus aurata or Dicentrarchus labrax as do numerous estuarine fish, which are known to remove scales for feeding purposes, such as Arius felis in the Gulf of Mexico which remove the scales of Mugil cephalus (HOESE, 1966). Eel feeding activity depends on temperature, decreasing between 28 and 30°C and stopping under 10°C, and that silver eels, mainly present in autumn and winter seasons, reduce or stop their feeding activity (LECOMTE-FİNİGER, 1983). This might explain why abundance was low in our autumn and winter fixed net samples and why a majority of stomachs were empty. The same phenomenon has been observed (BOUCHEREAU et al., 2006) under the same fish sampling conditions in the neighbouring Prévost lagoon (Fig. 1A), with a minimum of 13 specimens caught in winter, all with empty stomachs.

In spring, small fish species, certainly newly recruited, enter into the lagoon for a trophic ecophase (M. cephalus, S. aurata, D. labrax, Solea vulgaris and Platicthys flesus), and in summer Polychaeta and scales are favourite prey. These play a fundamental role in eel diets (Table 3; Fig. 5), in addition to Gammarus gr. locusta which curiously is not as predominant in the eels diet during this period of the year as in autumn. However, in this lagoon the level of fullness observed only in summer, decreases significantly compared to the winter-spring period.

No observations of year-long dominant prey were made in the feeding regime of eel in this lagoon. They vary significantly with the season (Fig. 5) in favour of Gammarus gr. locusta and scales in autumn, though not in winter, except for a group comprising Gammarus gr. locusta, Polychaeta insects and mollusca, fish in spring and scales and Polychaeta in summer.

In spite of the wide diversity in the feeding spectrum of eels, the Mauguio lagoon does not appear to be as productive in benthic populations as it was up to the middle of the 1980s (BOUCHEREAU et al., 1990; BOUCHEREAU, 1994). The variation amplitude of eel stomachs vacuity is low, between 37 and 61%. Few eels feed well throughout the whole year. Only a part of them fed well in winter and spring.

In addition, eels consume completely different prey during the four seasons which leads to the assumption that if eels do not always consume their favourite prey, it is because it is not sufficiently available in permanence in the Mauguio lagoon. For this reason, it can be said that eels living in the Mauguio lagoon ecosystem have a trophic status of generalist-opportunist and thus enlarge their spectrum in accordance with availability offered by the lagoon and the species requirements. According to COSTELLO et al. (1990) diagrams presentation (Fig. 5) A. anguilla expresses high adaptive capacities via its either generalist or opportunist status depending on the season and thus confirms the hypothesis previously espoused of possible changes in the species feeding choice and intake of prey. Gammarus and Polychaeta in autumn-winter alternate with fish in spring-summer, the second remaining rather weak in number and weight. They also show that the lagoon does not provide such a varied and constant supply of prey all through the year due to its own characteristics and the variability of local climate.

In a temperate climate, ecosystems such as the Mediterranean lagoons, biological potential (especially benthic and nectobenthic densities and biomass) is high in spring (period of recruit-
ment and growth) and in summer if the lagoon environment is not affected by dystrophic conditions. In autumn, this potential is also high as specimens recruited during the spring season have reached adult size and it is possible that the new recruitment of juveniles of numerous species can happen again (QUIGNARD, 1984). Winter is the only season where there is a relatively low potential linked to drastic conditions (especially temperature) in the shallow laminar milieu causing massive mortality even among endogenous species.

Seasonal changes observed in the eel diet, summarised as winter: fish, Decapoda, insect larvae, spring: Amphipoda from benthic meiofauna, summer: Polychaeta, should be related to the specific characteristics of the Mauguio lagoon: trophic productivity and hydrodynamics. In the Mauguio lagoon, A. anguilla’s diet is not fundamentally different from that of A. anguilla in the Roussillon lagoons situated further West. The feeding regime is, in fact, carnivorous and based on benthic prey (Gammarus gr. locusta, Polychaeta, insect larvae and small fish). Variations observed during the four seasons illustrate opportunist type feeding behaviour already observed (LECOMTE-FINIGER, 1983; BOUCHEREAU et al., 2006, 2009) in elver and
small eel in the Roussillon Province. These eels consume the most available benthic prey, preferring temporarily the importance of prey without using any feeding strategy focusing on either specialisation or generalisation. Such behaviour demonstrates the high capacity of eel to adapt to the Mauguio biotope. A certain selection of prey can take place as a function of its activity and accessibility. If however a seasonal influence does exist in the Mauguio lagoon with decreased feeding activity in summer, and which is reversed and increases progressively with the following seasons, this ecosystem is individualised due to the trophic quality it can offer to eels and certainly because of its particular hydrodynamic characteristics (CHAVES & BOUCHEREAU, 2004; GARNEROT et al., 2004; CABERTY et al., 2004).

It must be pointed out that the Mauguio lagoon is regularly affected by dystrophic crises during the summer season, which more or less destroy all in situ populations. Trophic resources in this basin appear to vary greatly between a good (spring) and bad (summer) season (FRISONI et al., 1984) from the nutritional point of view for eels. In addition to its weak hydrodynamics, the ecosystem is very much under the influence of increasing environmental and human pressure. This study confirms the adaptive capacity of Anguilla anguilla and reveals characteristics showing it to be a bioindicator of the available resources that the lagoon offers and a more and more threatened species in lagoon ecosystems.

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Prehrana jegulje *Anguilla anguilla* u laguni Mauguio 
(Sredozemno more, Francuska)

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**SAŽETAK**

U ovom radu se raspravlja o vremenskim kolebanjima u prehrani jegulje *Anguilla anguilla*, koja je uzorkovana sezonski u laguni Mauguio pokrajine Languedoc u Lionskom zaljevu, od jeseni 1998. do ljeta 1999. Jegulja se hrani bentoskim pridnenim organizmima, i to pretežit o manjim 
rakušcima (poglavito *Gammarus gr. locusta*), mnogočetinašima, larvama insekata (Chironomidae) 
i manjim ribama. Temeljem varijacija u prehrambenom režimu jegulje sezonski utjecaj pokazuje 
da hranidbena aktivnost opada u ljeto, dok progresivno raste u ostalim godišnjim dobima. Trofička 
kvaliteta dostupna jeguljama u laguni Mauguio ovisi više o alohtonom unosu iz slivnog područja 
ega o vlastitoj hidrodinamici na koju morska voda ima malo utjecaja zbog njenog dugog miješanja s 
morem. Zapažena kolebanja tijekom četiri godišnja doba ukazuju na oportunistički tip prehrambenog 
ponašanja jegulje. Ona se hrani najdostupnjim bentoskim organizmima u datom trenutku bez ikakve 
prehrambene strategije kao što je su to specijalizirana ili generalizirana prehrambena strategija. 
Jegulje prilagodavaju svoju prehranu prema dostupnoj hrani unutar ekosustava. Stoga se jegulja kao 
migracijska vrsta može biti okarakterizirana kao očiti indirektni bioindikator trofičkog kapaciteta i 
vrlo značajnog nivoa ograničenja u ekosustavu bočate lagune Mauguio.

**Ključne riječi:** jegulja, prehrana, laguna, oportunizam, bioindikator