Feeding behaviour of *Anguilla anguilla* and trophic resources in the Ingril Lagoon (Mediterranean, France)

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Abstract: This study focuses on the diet of the eel *Anguilla anguilla*, sampled during one month of each of the four seasons from autumn 1998 to summer 1999 in the Languedocian Ingril Lagoon (Gulf of Lion). The following feeding indices were calculated based on observations of 11 categories of prey found in the contents of full stomachs: coefficient of vacuity (CV), degree of fullness (DR), occurrence frequency (PP, in %), relative abundance (N, in %) and relative weight (P, in %). A parallel monitoring of the benthic macrofauna was conducted in autumn and spring. The interpretation of the results is based on the degree III of the scale of confinement established by Guélorget & Perthuisot (1983) and on the Costello et al. (1990) method, which combines PP and N. *A. anguilla* mainly feeds on benthic organisms, primarily amphipods crustaceans, polychaetes, insect larvae and small fish. The eel's feeding activity is very low in November and February and usually increases during May. The trophic quality available to the eel population in the Ingril Lagoon depends on its hydro-dynamic variables, which are directly related to its close communication with the sea. Changes observed in the eel's diet over this year long study illustrate an opportunist type of feeding behaviour that reflects the typical composition of the macroinvertebrate species assemblage at a given point in time. Eels consume the type of benthic prey that is most available at a given moment without using a particular feeding strategy (e.g., specialisation or generalisation). The eels adapt by shifting their diet according to the energetic resources available in the ecosystem, which vary depending on hydrological regime. Thus, the facultative catadromous migrant species *Anguilla anguilla* could be used as a bioindicator of changes in the biological zonation and in the available food resources in the brackish ecosystem of Ingril Lagoon during its lagoon-resident ecophase.

Résumé : *Comportement alimentaire de l'anguille européenne* Anguilla anguilla *et disponibilité trophique dans la lagune d'Ingril (Méditerranée, France).* Les anguilles ont été échantillonnées à chacune des quatre saisons de l'automne 1998 à l'été 1999. Les indices alimentaires suivants sont calculés à partir de l'observation de 11 catégories de proies dans les contenus d'estomacs remplis : coefficient de vacuité CV, degré de remplissage DR, pourcentages de présence PP, numérique N et pondéral P. L'interprétation des résultats est fondée sur le degré III de l'échelle de confinement établie par Guélorget & Perthuisot (1983), et sur la méthode de Costello et al. (1990), qui conjugue PP et N. *A. anguilla* se nourrit d'organismes benthiques, principalement de Crustacés Amphipodes, Polychètes, larves d'Insectes et petits Poissons. L'activité alimentaire de l'anguille est très faible en Novembre et Février et augmente en mai. La qualité trophique offerte

à la population d'anguilles par la lagune d'Ingril dépend de son hydrodynamisme variable en raison d'une communication étroite avec la mer. La plus grande partie de la lagune est placée en confinement III de la zonation biologique. Les variations observées dans le régime alimentaire des anguilles montrent un comportement nutritionnel de type opportuniste et reflètent la composition typique de la macrofaune benthique disponible. Les anguilles consomment les proies benthiques les plus disponibles. Elles favorisent momentanément l'importance de la proie sans utiliser de stratégie alimentaire particulière de spécialiste ou de généraliste. L'anguille ajuste son régime alimentaire selon les ressources énergétiques disponibles. L'anguille s'adapte en décalant son régime alimentaire en fonction des ressources disponibles dans l'écosystème, lequel dépend du régime hydrologique. L'espèce migratrice catadrome facultative *A. anguilla* pourrait être utilisée comme un bioindicateur indirect des changements de la zonation biologique et de la disponibilité des resources trophiques dans l'écosystème saumâtre d'Ingril durant son écophase laguno-résidante.

Keywords: Anguilla anguilla ● Mediterranean ● Lagoon ecosystems ● Diet ● Opportunism ● Bioindicator

Introduction

Although the lagoons along the western French Mediterranean coast have the same origin in terms of their formation (Guélorget & Perthuisot, 1983 & 1992), each has its own geomorphological characteristics (e.g., surface area, depth, inputs of fresh or marine water, catchment area, and the nature of sediment). These characteristics influence the physico-chemical factors of the ecosystem, such as salinity, temperature, and water renewal, which in turn depend on climatic conditions. Fluctuations in these factors during the various seasons cause significant variability in the biological populations present, which in turn affects the fish populations (Bouchereau, 1994 & 1995; Zamora, 1999; Bouchereau et al., 1991 & 2000; Bouchereau & Chaves, 2003; Chaves & Bouchereau, 2004; Garnerot et al., 2004).

High primary production is one characteristic of lagoon environments. Because of this, numerous allochthonous species of marine origin, especially fish, penetrate the lagoon either by passive migration during their planktonic stage when an entrance is available or actively as soon as swimming against the current is possible. In the Mediterranean area, migration into lagoons usually is related to feeding (Frisoni et al., 1984; Quignard, 1984; Frisoni & Guélorget, 1986) and development rather than to breeding (Joyeux et al., 1991a & 1992; Bouchereau et al., 1991; Bouchereau, 1994 & 1995; Bouchereau & Guélorget, 1999; Pampoulie et al., 1999a). However, sedentary species, which can be considered to be bioindicators of the environmental conditions, can also be found in lagoons (Tomasini et al., 1991; Bouchereau & Guélorget, 1998; Pampoulie et al., 1999b).

The most commercially important fish species and those most harvested by artisanal fisheries in the lagoons of the Mediterranean are the sea bass *Dicentrarchus labrax* Linnaeus 1758, the sea bream *Sparus auratus* Linnaeus 1758, the sole *Solea vulgaris* Quensel 1806, the European eel *Anguilla anguilla* Linnaeus 1758, the atherine or silverside *Atherina boyeri* Risso 1810 and the mullets *Liza sp.* and *Mugil cephalus* Linnaeus 1758. Among these, the facultative catadromous migrant eel *A. anguilla* is the lagoon-resident species that occurs most frequently in space and time in the Languedocian lagoons.

In the Palavasian lagoon complex (Fig. 1A) of the Gulf of Lion, eel was traditionally the main exploited fish species (Lecomte-Finiger & Bruslé, 1983) among eel, sea bass, sea bream, sole, sand smelt, and mullets. Due to its massive decline (recruitment, yield, stock), the European eel is becoming critically endangered (Bruslé, 1989; Freyhof & Kottelat, 2008), and new research focused on its ecology is necessary to enhance the species' status, even though much already is known about its biology, feeding behaviour, and habitat choice of fresh water resident eels (Frost, 1946; Keast & Webb, 1966; Ezzat & El Seraffy, 1977; Charlon & Blanc, 1983; Lammens et al., 1985; Elie & Rigaud, 1987; Lammens & Visser, 1989; Mann & Blackburn, 1991; Barak & Mason, 1992; Costa et al., 1992; Proman & Reynolds, 2000; Cullen & McCarthy, 2007; Heinsbroek et al., 2007).

Because *A. anguilla* forms an individual group among the ten functional groups of lagoon fish in Languedoc Roussillon (Dumay et al., 2004), it can be used as a functional unit to simplify the study of the complex lagoon ecosystem and its interactions. In this study, the year-round feeding behaviour of *A. anguilla* was described by means of feeding indices to obtain a better understanding of the trophic availability and biological productivity level of the Ingril Lagoon ecosystem in light of its biological zonation. We then compared the results of this study with those of two others conducted at the same time and under the same conditions in the neighbouring Prévost (Bouchereau et al., 2006) and Mauguio (Bouchereau et al., submitted) Lagoons
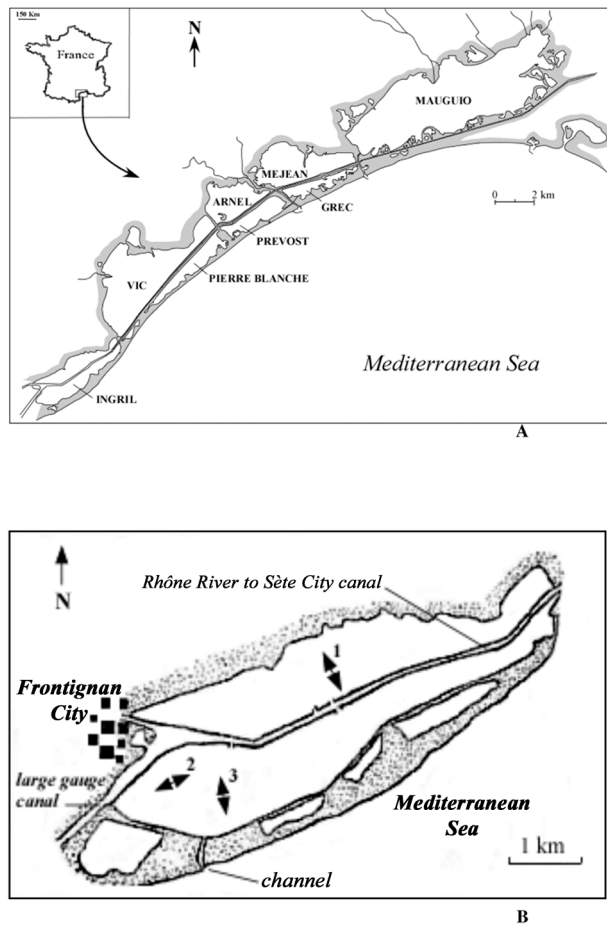
Figure 1. *Anguilla Anguilla*. **A.** Location of the Palavasian lagoons in the Languedoc Province, France (Golfe du Lion). **B.** The Ingril lagoon and the three sampling sites (arrows).

Figure 1. *Anguilla Anguilla*. **A.** Emplacement du complexe lagunaire palavasien dans la région du Languedoc, France (Golfe du Lion). **B.** La lagune d'Ingril et les trois sites d'échantillonnage (flèches).

to point out similarities and differences. Together, these studies contribute to our knowledge about eel feeding behaviour and the effects of benthic fauna on fish resources of closely related lagoons.

Ingril Lagoon (Fig. 1B) is located in the Gulf of Lion and stretches out parallel to the coast between Frontignan City to the southeast and Vic Lake further east (Bouchereau & Vergne, 1999). It is divided into two parts by the Rhône River Canal to Sète City and is 4.8 km long and 1.2 km wide with a surface area of 5.76 km² (Bouchereau & Vergne, 1999). It communicates with the sea via a stabilised passage, which ensures satisfactory renewal with seawater. Because permanent exchanges with the marine domain are favoured, Ingril Lagoon is not very confined. Hydrodynamic processes

are active due to the action of winds and tides (although these remain limited in microtidal-type environments in the Mediterranean).

The whole southern central region of the lagoon (Fig. 1B) is regularly influenced by incoming seawater. According to the F.O.G.E.M. (2006), the mean salinity is between 24 and 32 (min: 3.6; max: 52.4) and the mean dissolved oxygen content is ~ 10 mg.L^{-1} (min = 0.8, max > 20). The sea floor is colonised by beds of *Cymodocea nodosa* and *Zostera noltii* and by small marine-type phanerogamina and benthic and nectobenthic macrofauna, thus providing wide biodiversity. The fauna is represented in particular by the pelecypods *Ruditapes decussatus* (Linnaeus, 1758), *R. aureus*, *Gastrana fragilis* (Linnaeus, 1758), *Scrobicularia plana* (da Costa, 1778), *Loripes lacteus* (Linnaeus, 1758), *Mactra glauca* (Born, 1778), *Tellina tenuis* (da Costa, 1778), *Donax trunculus* (Linnaeus, 1767), and *D. semistriatus* Poli, 1795, the polychaetes *Owenia fusiformis* (Delle Chiaje, 1841), *Glycera convoluta* Keferstein, 1862 and *Nephtys hombergii* Savigny, 1818 and the crustaceans *Corophium volutator* (Pallas, 1766), *Idothea viridis* Slabber, 1775, *I. baltica* (Pallas), *Carcinus mediterraneus* Czerniavsky, 1884 and *Upogebia littoralis* Makarov, 1938. This region is situated in zone III of the scale of confinement established by Guélorget & Perthuisot (1983 & 1992).

The physico-chemical conditions in Ingril Lagoon are relatively unstable and thus regularly create a critical situation, like dystrophic crisis, for the aquatic fauna (F.O.G.E.M., 2006). There is much less renewal with sea water and a much more marked level of confinement in the northern region parallel to the Rhône Canal to Sète City and in the two extremities of the lagoon (Fig. 1B). These areas belong to the paralic zone and the populations there consist entirely of strictly paralic species such as the molluscs *Cerastoderma glaucum* (Poiret, 1789), *Abra ovata* (Philippi, 1836), *Hydrobia ulvae* (Pennant, 1777), *H. acuta* (Draparnaud, 1805), *H. ventrosa* (Montagu, 1803) and *Bittium reticulatum* (da Costa, 1778), the polychaete *Nereis diversicolor* Linnaeus,1758, and the amphipod *Gammarus gr. locusta*. These regions are positioned in zones IV and V of the scale of confinement established by Guelorget & Perthuisot (1983 & 1992).

Material and Methods

Sampling

Seasonal sampling was conducted during one period of 5 consecutive days during each of the four seasons from autumn 1998 to summer 1999. A passive fishing gear called the *capéchade* (Bouchereau et al., 1989) was used for

fishing. This system involves a *paradière*, which is a netting that acts as a barrier, and a tower or triangle towards which fish are directed and are thus trapped in the pot or fyke net. Three sampling sites were chosen (Fig. 1B) in zone III. The *capéchades* were brought up daily at 10 a.m. after 24 hours of fishing during the following periods: 1-5 November 1998, 22-26 February 1999, 10-14 May 1999, and 6-10 September 1999. The eels caught were immediately placed in a cooler filled with ice and transported to the laboratory, where the digestive tracts of 144 specimens (the total for the whole study) were extracted and preserved in 10% formaldehyde for our study of stomach contents (Bouchereau & Vergne, 1999). It should be noted that some specimens might have digested their food during their time inside the net. Because of this, empty stomachs were not taken into account when calculating the indices (except for the coefficient of vacuity).

To study the benthic macrofauna, we used the standardized method of the *Agence de l'Eau*. One sample of sediment representing a surface area of 0.1 m² was collected at each of three sites (Fig. 1A) with an Eckman-Birge grab (a type bottom sampler) during the November and May sampling periods. All macrofauna present was picked out of the sediment, preserved, sorted, and identified to the lowest possible taxon. Mean densities (number of individuals in one item per 0.1 m²) of macrofauna were calculated from the three sites.

Laboratory observations

The total length of eels was measured to the inferior millimetre. From January to April 2000, the digestive tract of each of the 144 specimens was examined under a binocular microscope to identify and count prey ingested and present in the stomach contents. The macrofauna from the sediment samples were also processed at this time. The degree of taxonomic determination is a function of the time required for digestion of the bolus (Joyeux et al., 1991b). Categories of prey and benthic macrofauna were identified to the family level and, when possible, to the species level (Perrier, 1929; Tregouboff & Rose, 1978), and they were then grouped into larger taxonomic categories. When prey such as fish had been badly preserved, the number of specimens present was defined by counting cephalic parts and bone pieces.

Data processing

The feeding regime of *A. anguilla* was studied in each season by calculating 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):

$$CV = 100 \times (Nv/Nt) \dots\dots\dots\dots\dots\dots\dots\dots(1)$$

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 $N_1 = 25\%$, $N_2 = 75\%$, and $N_3 = 100\%$ of the total volume of the digestive tube:

$$DR_{(1, 2, 3)} = 100 \times (N_{(1, 2, 3)}/Nt) \dots\dots\dots\dots\dots(2)$$

$N_{(1, 2, 3)}$ represents the number of digestive tubes divided according to the three levels of fullness and Nt 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):

$$PP = 100 \, (Nti/Np) \dots\dots\dots\dots\dots\dots\dots\dots(3)$$

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

$$N = 100 \, (Ni/Npt) \dots\dots\dots\dots\dots\dots\dots\dots(4)$$

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:

$$P = 100 \, (Pi/total \, points) \dots\dots\dots\dots\dots\dots(5)$$

To calculate percentages in points (P), the numeric method of points (Hynes, 1950; Pillay, 1952) modified and adapted by Joyeux et al. (1991b) and Pampoulie & 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 without being digested. This method enables a better evaluation of the original food intake based on digested

Table 1. *Anguilla Anguilla*. Points attributed to prey items, adapted from Joyeux et al. (1991b) and Pampoulie & Bouchereau (1996).

Tableau 1. *Anguilla Anguilla*. Points attribués aux catégories de proies, adapté de Joyeux et al. (1991b) et de Pampoulie & Bouchereau (1996).

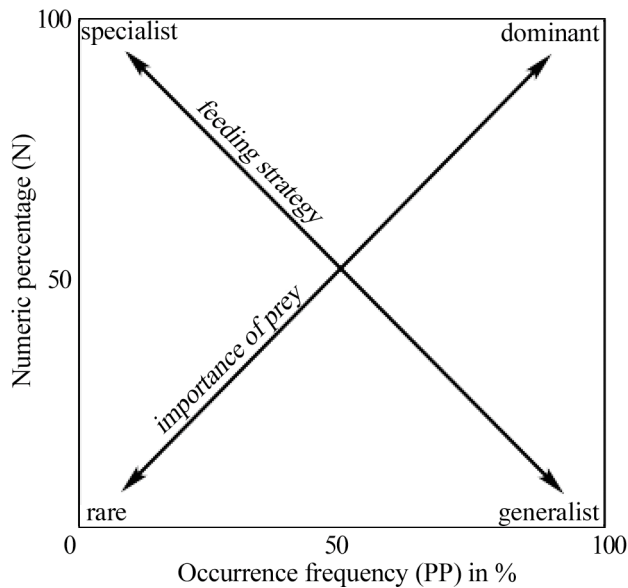| Categories of prey	Points	Categories of prey	Points
Fish	100.0	*Gammarus gr. locusta*	10.0
Polychaeta	40.0	*Corophium insidiosum*	5.0
Nematoda	40.0	Insects	5.0
Decapoda	25.0	Mollusca	1.0
Crustacea	15.0	Scales	1.0
Isopoda	10.0	Ostracoda	0.5
Amphipoda	10.0	Copepoda	0.5

Figure 2. *Anguilla Anguilla*. Diagram explaining the Costello et al. (1990) method according to the feeding strategy: specialist or generalist and the importance of prey: dominant or rare (Amundsen et al., 1996).

Figure 2. *Anguilla Anguilla*. Diagramme explicatif de la méthode de Costello et al. (1990) selon la stratégie alimentaire de spécialiste ou de généraliste, et l'importance de la proie dominante ou rare (Amundsen et al., 1996) avec les pourcentages de présence (PP) et numérique (N).

remains. The number of points assigned in this case, therefore, reflects the level of satiety at the moment when prey were swallowed (Bouchereau & Guélorget, 1999).

The indices CV and DR were calculated by season. 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 type and its numeric importance during the season. Each PP, N, and P value was tested between two sampling period running by the Spearman unilateral non-parametric statistical correlation test (r_s). This was the most appropriate test to use considering the various

characteristics of the samples (e.g., variables did not exhibit normality). Values are expressed in percentages. This test was applied to the PP, N, and P indices to study possible qualitative and quantitative temporal changes in the feeding regime of *A. anguilla*. Values of r_s were compared with critical values (Tomassone et al., 1995). The null hypothesis Ho: Series 1 = Series 2 was tested; if the calculated value was greater than the critical value (p < 0.05), Ho could not be accepted and the two series of data were considered to be different.

To facilitate the interpretation of results, we used the Costello et al. (1990) method, which graphically combines the percentage of presence (PP) with the numeric or catch percentage (N) of each prey type (Fig. 2). Costello et al. (1990) suggested 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 around 100% of presence and 1% of abundance indicate that predators have a specialized feeding regime.

Results

Eel samples

From September 1998 to August 1999, 144 eels were harvested. Extreme seasonal abundance values were observed, with a minimum of 3 collected in November and a maximum of 70 in September; 9 and 62 were collected in February and May, respectively.

General feeding spectrum

Anguilla anguilla has a very generalistic feeding regime, as 11 different categories of prey were counted (Table 2); the main components were the amphipod *Gammarus gr. locusta*, fish, chironoma larvae of insects, and polychaetes. The number of categories present gradually increased from November (0) to February (3), reached a maximum in May (10), and then decreased in September (8).

Table 2. *Anguilla Anguilla*. Relative occurrence (in % classes) of different prey items observed in the stomach contents, in the Ingril lagoon.

Tableau 2. *Anguilla Anguilla*. Présence relative (en classes de %) des différentes catégories de proies observées dans les contenus stomacaux des individus de la lagune d'Ingril.

0.01-1.00%	1.01-3.00%	6.01-12.00%	12.01-24.00%	24.01-48.00%
Mollusca Isopoda Amphipoda Ostracoda	Decapoda Crustacea (other) Fish	Annelida Polychaeta	Chironomidae Scales	*Gammarus gr. locusta*

Coefficient of vacuity CV

Out of the 144 eels harvested, 3 in November (29.8 ≤ TL (cm) ≤ 54.7), 9 in February (18.0 ≤ TL (cm) ≤ 68.0), 62 in May (21.2 ≤ TL (cm) ≤ 49.8), 70 in September (18.5 ≤ TL (cm) ≤ 65.6), 80 had empty stomachs (Table 3) and 64 (18.0 ≤ TL (cm) ≤ 65.6) had full stomachs. The stomachs of three eels harvested in November were empty, so we were unable to calculate feeding indices for this season. In February, May and September, respectively, 7 (35.2 ≤ LT (cm) ≤ 40.6), 22 (22.5 ≤ LT (cm) ≤ 39.5), and 35 (18.5 ≤ LT (cm) ≤ 65.6) stomachs were full. The vacuity (Fig. 3) reached a minimum (22.2%) in February and a maximum (100%) in November.

Degree of fullness DR

Stomachs were the fullest in February (25.0 ≤ DR3 ≤ 28.6; 40.0 ≤ DR1 ≤ 57.1) and empty in November (Fig. 3). In May and September, the pattern of CV and the different DR classes were nearly the same (65.7 ≤ DR1 ≤ 68.2; 22.7 ≤ DR2 ≤ 22.9; 9.1 ≤ DR3 ≤ 11.4).

Temporal changes in feeding index PP, N, and P

Based on the occurrence frequency (PP), the most common prey present in the stomach contents during the three sampling periods were fish species and insects larvae (Table 3). Polychaetes and *Gammarus gr. locusta* were present in May and September among 10 and 8 categories respectively. However, the occurrence frequency of these prey types varied inversely in the two cases. Polychaetes were more frequent in September (24.2%) and *Gammarus gr. locusta* in May (56.3%).
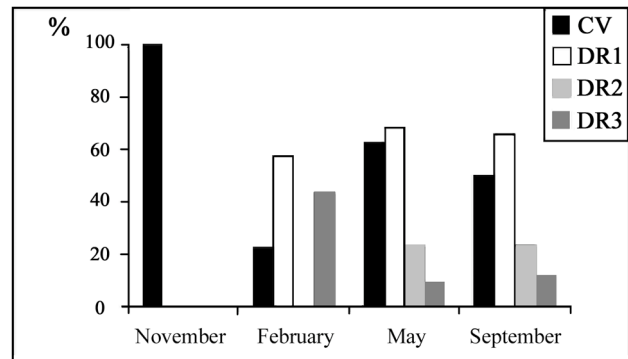

Figure 3. *Anguilla Anguilla*. Variation of the vacuity index CV and stomach filling index DR1, DR2 and DR3 (in %) in the Ingril lagoon versus the sampling period.
Figure 3. *Anguilla Anguilla*. Variation du coefficient de vacuité CV et des indices de remplissage DR1, DR2 et DR3 (en %) des estomacs dans la lagune d'Ingril selon la période d'échantillonnage.

The number of prey (N) was generally maximal for insects larvae and *Gammarus gr. locusta* (Table 3). However insects larvae had a maximum N in February (50.0%), the season during which eels did not capture *Gammarus gr. locusta*, but did consume a significant number of decapods (40%). Polychaetes were most consumed in September (25.4%), and eels ate the most of *Gammarus gr. locusta* (82.1%) in May.

According to biomass expressed as a percentage in points (P), the principal prey type constituting the bolus differed by sampling period (Table 3). In February, fish (44.4%) and decapods (44.4%) were well represented. In

Table 3. *Anguilla Anguilla*. Seasonal variations of the diet index in the Ingril lagoon; PP: Occurrence frequency in %; N: numerical frequency in %; P: Points frequency in % of prey items.
Tableau 3. *Anguilla Anguilla*. Variations saisonnières des indices alimentaires dans la lagune d'Ingril; PP : Pourcentage de présence ; N : Pourcentage numérique ; P : Pourcentage de points des diverses catégories de proies.

| Categories of preys	Occurrence PP			Numeric N			Points P		
	Feb.	May	Sep.	Feb.	May	Sep.	Feb.	May	Sep.
Polychaeta	-	9.38	24.24	-	2.24	25.37	-	7.22	52.17
Mollusks	-	3.13	3.03	-	0.75	1.49	-	0.06	0.08
Ostracods	-	3.13	-	-	0.75	-	-	0.03	-
Isopoda	-	6.25	-	-	1.49	-	-	1.20	-
Gammarus gr. l.	-	56.25	6.06	-	82.09	13.43	-	66.17	6.90
Amphipoda (other)	-	3.13	3.03	-	0.75	2.99	-	0.60	1.53
Decapoda	44.44	9.38	-	40.00	8.96	-	44.44	18.05	-
Crustacea (other)	-	-	9.09	-	-	13.43	-	-	17.26
Chironomidae	44.44	3.13	27.27	50.00	1.49	22.39	11.11	0.60	5.75
Fish	11.11	3.13	6.06	10.00	0.75	2.99	44.44	6.02	15.34
Scales	-	3.13	21.21	-	0.75	17.91	-	0.60	5.75
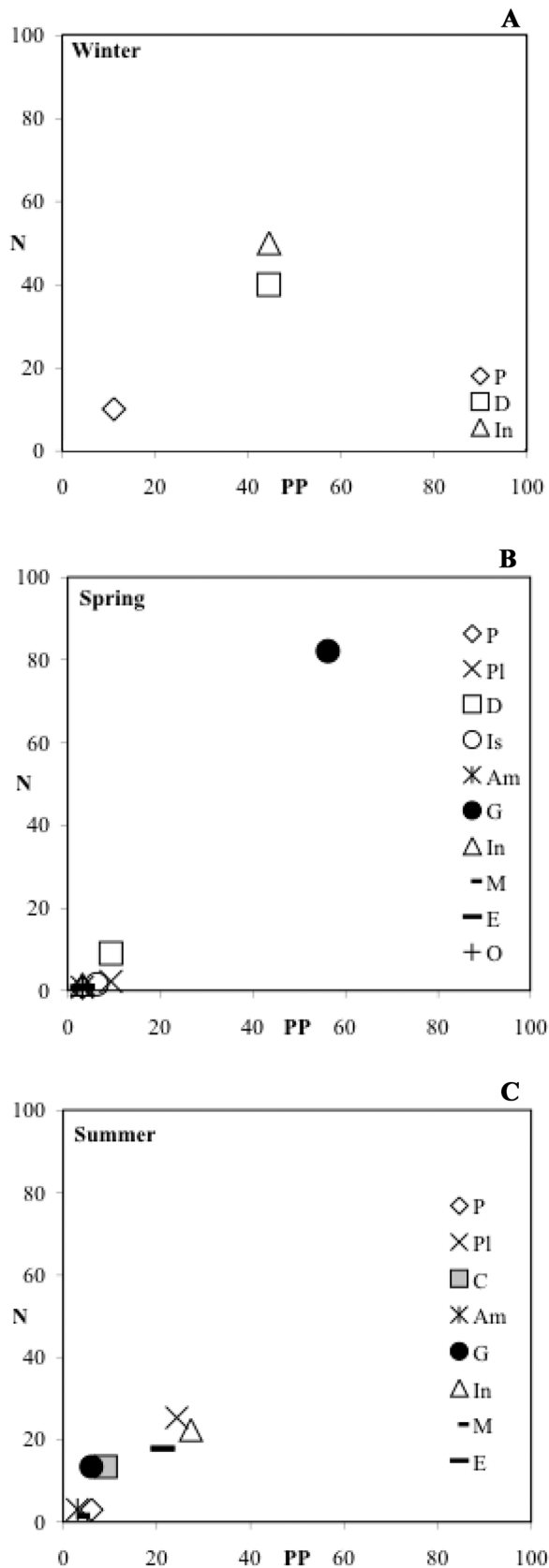
Figure 4. *Anguilla Anguilla*. Relationship, according to Costello et al. (1990), between the Numerical Index N, Occurrence Index PP of prey items in the Ingril lagoon during the 1998/1999 sampling periods. **A.** February**. B**. May. **C.** September. Am: Amphipoda; C: Crustacea; D: Decapoda; E: Scales; G: *Gammarus gr. locusta*; In: Insects; Is: Isopoda; M: Mollusca; O: Copepoda; P: Fish; Pl: Polychaeta.

Figure 4. *Anguilla Anguilla*. Relations, selon Costello et al. (1990), entre indices numérique N et de présence PP des caté- gories de proies dans la lagune d'Ingril aux trois campagnes d'échantillonnages 1998/99. **A.** Février. **B.** Mai. **C.** Septembre. A : Amphipodes ; C : Crustacés ; D : Décapodes ; E : Écailles ; G : *Gammarus gr. Locusta* ; In : Insectes (*Chironomidae*) ; Is : Isopodes ; M : Mollusques ; P : Poissons ; Pl : Polychètes.

May, *Gammarus gr. locusta* (66.2%) constituted the largest part of the ingested biomass. In September, polychaetes were the main prey type (52.2%).

The Spearman correlation test (Table 4) revealed that no significant differences existed between sampling periods for PP, N, or P. Seasonal data for the combination of PP and N frequencies (Fig. 4) illustrate the importance of prey rather than the eel's feeding strategy. The feeding strategy seems to be between specialist and generalist. It was in February that decapods and insects (Fig. 4A) were the main and common prey types and in May that *Gammarus gr. locusta* (Fig. 4B) was of outstanding importance and abundance. During September (Fig. 4C), all of the prey types were at the same level of importance; no single prey type was of outstanding importance at this time, and eels fed on a higher variety of prey items.

The benthic macrofauna

The total species richness SR was 63, with 23 in November and 42 in May (Tables 5 & 6). Polychaetes (28), molluscs (11), and amphipods (12) were the most numerous species. The highest mean densities for both sampling periods were observed for isopods (129.0 ind 0.1 m^{-2}), molluscs (64.8 ind 0.1 m^{-2}), and polychaetes (43.8 ind 0.1 m^{-2}). Amphipods were scarce. Mean densities did not vary between November and May, but values for molluscs, polychaetes, and crustaceans decreased from November to May, where the value for isopods increased.

Discussion

We used the Costello et al. method (1990) and applied Guélorget & Perthuisot's confinement concept (1983) to interpret our results and to connect the adaptive responses of eels with the availability of food in the Ingril Lagoon

Table 4. *Anguilla Anguilla.* Conclusion of the statistical test of Spearman between two successive periods with the index: PP: Occurrence frequency in %; N: numerical frequency in %; P: Points frequency in % of prey items, in the Ingril lagoon; ns: non significant.

Tableau 4. *Anguilla Anguilla.* Résultats du test statistique de Spearman entre deux périodes successives avec les indices PP : Pourcentage de présence ; N : Pourcentage numérique ; P : Pourcentage de points des diverses catégories de proies dans la lagune d'Ingril ; ns : non significatif.

Ingril lagoon	PP		N		P	
	r_s	0.05	r_s	0.05	r_s	0.05
February / May	0.26	ns	0.39	ns	0.44	ns
May / September	-0.07	ns	0.12	ns	0.14	ns

ecosystem. The feeding regime of *A. anguilla* residing in Ingril Lagoon essentially is based on the benthic organisms that can be grouped together into 11 important categories. These consist mainly of amphipods, decapods, chironoma larvae, small fish, and polychaetes (Table 3). This spectrum resembles that observed by Lecomte-Finiger (1983) in three lagoons from the neighbouring Roussillon Province and enables *A. anguilla* to be given the status of a second-order carnivorous species. Schneider et al. (1987) also described very similar feeding spectra in the Mediterranean and Black Seas. However, in our study echinoderms were not observed in the stomachs of *A. anguilla*, as they occur in this type of lagoon, which is not very confined according to Guélorget & Perthuisot (1983 & 1992). Two species of echinoderms were observed in the sediment (Table 5); according to Guelorget & Perthuisot (1983), the presence of sea urchins is limited to the mouth of estuaries and in zones under permanent marine influence (zone II). *A. anguilla* is more active in the warm season than in the cold season; its catchability by passive fishing gear is higher in May–September than in other parts of the year.

The temporal pattern of the coefficient of vacuity in the stomachs of *A. anguilla* reveals either a variation in food uptake or in feeding choice. Eels are known to feed less in February, and they are less active and thus harder to capture (and catch levels are reduced) during this time of year. This could explain why the catches in November and February were small and why the stomach contents were missing or their numbers were weak when stomachs were full. The percentage of empty stomachs is negatively correlated with temperature (Barak & Mason, 1992), which is why few filled stomachs were found in November and February. In the Adour Basin area (France), first feeding begins when the water temperature is higher than 10 °C (Charlon & Blanc, 1983). From 10 °C and below, growth is inhibited and individual activity and food intake are very low or non-

existent (Elie & Daguzan, 1976). This pattern seemed to be evident in Ingril Lagoon and in the Languedoc-Roussillon, where the average daily temperature per month is below 10°C from November to March (Ifremer, 2007). At temperatures above 30°C, *A. anguilla* stops feeding in the lagoons in this region (Lecomte-Finiger, 1983).

In Ingril Lagoon, maximum prey diversity (10–8 items) was observed in May and September (Table 3). The prey consisted of isopods, amphipods, decapods, other crustaceans, and fish. This enlargement of the feeding spectrum could be related to the warming up of water in the lagoon, which in turn influences the reproductive cycle of these species: An increase in temperature accelerates the larval development phase, leading to the appearance of these species in the environment (Duperchy, 1998). Reduction in the diversity of prey, which was observed in November and February, was followed by an increase in the number of available prey in the sediment during those periods.

In February, the eel's feeding spectrum was reduced to three items, of which decapods and insects were the most consumed items. Insects were the most numerically important prey and fish and decapods constituted the major part of the biomass. Physico-chemical changes in the lagoon ecosystem due to climate during this period could have caused differences in the availability of prey species. To compensate for this, the eel likely reduced its diet to what was available during this period; this is in contrast to the scenario in the Prévost Lagoon, where the eel enlarged its feeding spectrum in February (Bouchereau et al., 2006).

In May, *Gammarus gr. locusta*, the most represented prey, have a fundamental role in eel diets (Table 3 & Fig. 4). Nevertheless a predominantly relatively low level of stomachs fullness was observed during this period, in this lagoon.

In September, polychaetes and insects were the most consumed prey, with polychaetes constituting both larger numbers and biomass. Effluents from the neighbouring industrial zone at Sète City during this period seemed to favour the appearance of detritivorous prey (such as polychaetes and chironoma larvae consumed mainly by the dominant yellow eel) adapted to more confined zones. Despite a different feeding regime characterized by many items (8/11), eels digested their prey more rapidly in September (Table 3 & Fig. 4), with the majority of stomachs relatively empty, because their metabolism was increased by high temperature.

In November, the small number (3) of eel specimens caught (and with 100% of vacuity) is insufficient to allow us to draw conclusions for this season. However, Bouchereau et al. (2006) caught 31 individuals during the same period in the Prévost lagoon, and they exhibited 49% CV and 81% DR1 fullness.

Table 5. Benthic macrofauna from the Ingril lagoon grouped according to items observed in November 1998 and May 1999; +: present; -: absent; Insects, Fish, scales are missing or not taken into account.

Tableau 5. Macrofaune benthique de la lagune d'Ingril regroupée selon les items observés en novembre 1998 et mai 1999 ; + : présence; -: absence ; Insectes, Poissons, écailles sont absents ou non pris en compte.

PHYLLUM **Class or Order** Family	*Genus species*	Nov.			May		
		1	**2**	**3**	**1**	**2**	**3**
CNIDARIA							
Anthozoa							
Actinaria	Unidentified sp.	+	+	+	+	+	+
TURBELLARIA	Unidentified sp.	-	-	-	-	-	+
NEMERTINI	Unidentified sp.	-	-	-	-	-	+
ANNELIDA							
Polychaeta							
Aphroditidae	*Aphrodites* sp.	-	+	-	-	-	-
Canalipalpata	*Aphelochaeta sp*	-	-	-	-	-	+
Capitellidae	*Capitella capitata* (Fabricius, 1870)	+	-	-	-	+	+
Cirratulida	*Heteromastus filiformis* (Claparède, 1864)	-	-	-	+	+	+
	Notomastus latericius Sars, 1851	+	-	+	-	-	+
	Chaetozone sp	-	-	-	-	-	+
	Cirriformia tentaculata (Montagu, 1808)	-	-	-	-	-	+
Eunicidae	*Eunicide* sp.	+	-	-	-	-	-
Glyceridae	*Glycera unicornis* Savigny, 1818	-	-	-	-	-	+
Lumbrineridae	*Lumbrineris latreilli* Audouin & Milne Edwards, 1834	-	-	-	-	-	+
	Neanthes caudata (Delle Chiaje, 1828)	-	-	-	+	+	+
Nereidae	*Nereis* sp.	+	+	+	-	-	-
	Platynereis sp.	+	+	-	-	-	-
	Platynereis piriformis Canning, Lai & Lie,1974	+	+	-	-	-	-
	Nereis caudata (Delle Chiaje, 1841)	+	+	+	-	-	-
	Platynereis dumerilii (Audouin & Milne Edwards, 1833)	-	-	-	+	-	-
	Scolelepis fuliginosa (Claparède, 1868)	+	-	-	-	-	-
Onuphidae	*Onuphis emerita* Audouin & Milne-Edwards, 1833	-	+	-	-	-	-
Ophelidae	*Armandia cirrhosa* Filippi, 1861	-	-	-	-	+	+
Phoronidae	*Phoronis psammofila* Cori, 1889	-	-	-	-	-	+
Serpulidae	*Hydroides elegans* (Haswell, 1883)	-	-	-	-	-	+
Spionidae	*Aonides oxicephala* (Sars, 1862)	-	-	-	-	-	+
	Malacoceros fuliginosus (Claparède, 1868)	-	-	-	+	+	+
	Nerine foliosa (Audouin & Milne Edwards, 1833)	-	+	-	-	-	-
	Nerine sp.	-	+	-	-	-	-
	Pseudomalacoceros tridentata (Southern, 1914)	-	-	-	-	-	+
	Polydora caeca (Oersted, 1843)	-	-	-	-	+	+
Terebellidae	*Amphitritides gracilis* (Grube, 1860)	-	-	-	+	-	-
Oligochaeta	Unidentified sp	-	-	-	-	-	+
MOLLUSCA							
Bivalvia							
Cardidae	*Cerastoderma glaucum* (Poiret, 1789)	-	+	-	-	+	-
	Parvicardium exiguum (Gmelin, 1791)	-	-	-	-	+	-
Mytilidae	*Musculista senhousia* (Benson, 1842) ?	-	-	-	-	+	-
Scrobiculariidae	*Scrobicularia cottardi* (Payraudeau, 1826)	-	-	-	-	+	+
Semelidae	*Abra ovata* (Philippi, 1836)	-	+	-	-	-	-
Veneridae	*Tapes decussatus* (Linné,1758)	+	+	-	-	-	+
	Venerupis aurea (Gmelin, 1791)	-	-	-	-	+	+
	Loripes lacteus (Linné,1758)	-	+	-	-	-	-
Gastropoda							
Nassaridae	*Cyclope neritea* (Linné, 1758)	-	-	-	-	+	-
Scaphandridae	*Roxania utriculus* (Brocchi, 1814)	-	-	-	-	+	-

Opistobranchiae	*Acteon* sp.	-	+	-	-	-	-
CRUSTACEA							
Amphipoda							
Aoridae	*Microdeutopus anomalus* (Rathke, 1843)	-	+	+	-	-	-
Caprellidae	*Phtisica marina* Slabber, 1769	-	-	+	-	-	-
Dexaminidae	*Dexamine spinosa* (Montagu, 1813)	-	+	+	-	-	-
Gammaridea	*Gammarus crinicornis* Stock, 1966	-	+	+	-	-	-
	Unidentified sp. 1	-	-	-	+	+	+
	Unidentified sp. 2	-	-	-	+	+	+
	Unidentified sp. 3	-	-	-	+	+	+
	Unidentified sp. 4	-	-	-	-	+	+
	Unidentified sp. 5	-	-	-	-	+	-
	Unidentified sp. 6	-	-	-	-	-	+
Peracaridae	*Eurystheus* sp.	-	+	+	-	-	-
Isopoda							
Cyathridae	*Cyathura arinata* (Krøyer 1847)	-	-	-	-	+	-
Idoteidae	*Idotea chelipes* (Pallas, 1766)	-	-	-	-	+	+
Idoteidae	*Idotea viridis* Slabber, 1775	-	+	-	-	-	-
Mysidacea							
Mysidae	*Siriella clausii* Sars, 1876	-	-	-	-	+	-
Bodotriidae	*Iphinoe* sp.	-	-	-	-	+	-
Portunidae	*Carcinus maenas* (Linnaeus, 1758)	-	+	-	-	-	-
ECHINODERMATA							
Asteroida							
Asterinidae	*Asterina gibbosa* Pennant, 1777	-	-	-	+	-	-
Ophiurida							
Ophiuridae	Unidentified	-	+	-	-	-	-

In Ingril Lagoon, the dominant prey types varied greatly with the sampling period (Fig. 4): In February, decapods and insects were dominant (Fig. 4A); in May *Gammarus gr. locusta* dominated (Fig. 4B), and in September polychaetes and insects were dominant (Fig. 4C). The eels showed a large variation in CV. They consumed almost completely different prey during the three sampling periods in which full stomachs were found. High CV (100% in November) and DRI (always greater than 57%) values suggest that feeding for *A. anguilla* is not easy. Thus, it is possible that

Table 6. *Anguilla Anguilla*. Mean species richness SR of the benthic macrofauna present in the Ingril lagoon, and mean density D (ind.0.1m^{-2}) in each item, in November and May; s: standard deviation.

Tableau 6. *Anguilla Anguilla*. Richesse spécifique SR moyenne de la macrofaune benthique présente dans la lagune d'Ingril et densité moyenne D (ind.0,1m^{-2}) dans chaque item, en Novembre et Mai ; s : écart-type.

Categories of preys	November			May			Total		
	SR	D	s	SR	D	s	SR	D	s
Cnidaria	1	27.00	15.87	1	24.00	39.84	1	25.50	27.17
Turbellaria	0	0.00	0.00	1	0.67	1.15	1	0.33	0.82
Nemertini	0	0.00	0.00	1	0.33	0.58	1	0.17	0.41
Polychaeta	12	53.67	7.02	18	34.00	26.51	28	43.83	20.42
Oligochaeta	0	0.00	0.00	1	0.67	1.15	1	0.33	0.82
Mollusks	5	96.00	165.41	8	33.67	39.40	11	64.83	112.83
Isopoda	1	50.00	62.45	2	208.00	48.54	3	129.00	99.96
Gammaridae	1	0.00	0.00	7	2.00	3.46	8	1.00	2.45
Amphipoda (other)	4	1.33	2.31	0	1.00	1.00	4	1.17	1.60
Decapoda	1	0.33	0.58	0	0.00	0.00	1	0.17	0.41
Crustacea (other)	0	38.00	43.21	2	0.00	0.00	2	19.00	34.35
Echinodermata	1	0.33	0.58	1	0.67	1.15	2	0.50	0.84
TOTAL	23	22.22	53.29	42	25.42	60.38	63	23.82	56.57

the eel has widened its feeding spectrum to include decapods and polychaetes, which in Ingril Lagoon play a very important role in the nutrition of this species. According to Costello et al.'s diagrams (Fig. 4), *A. anguilla* exhibits a high adaptive capacity via its either generalist or opportunist status (depending on the season); this finding confirms the hypothesis of possible changes in the species' feeding choice and intake of prey. Eels are rather opportunist in Ingril Lagoon.

It should be noted that because the November and February sampling sizes were very low and all stomachs containing food were used for analysis, the Costello et al. (1990) method presents disadvantages. This method is very susceptible to low sample sizes. Moreover, nearly empty stomachs should not be used, as digestion might lead to an overestimation of slowly digested organisms (Admunsen et al., 1996). However, eels with filled stomachs could have been caught in the net just before the sampling, whatever the date. The diagrams also show that the lagoon does not provide a varied and constant supply of prey throughout the year due to its own characteristics and the variability of local climate. This result is based on the parallel monitoring of the benthic macrofauna conducted within the lagoon in November and May.

February is the period during which the least benthic and nectobenthic resources are present due to harsh hydrological conditions in the laminar ecosystem. May is the period when juvenile eels are recruited and September is the period of important growth for the recently settled individuals. In the absence of dystrophic conditions, which completely destroy all populations, November would appear to be the period during which the most important resources are available, as new recruitment adds to the populations of the numerous species already settled.

Modification of prey consumed by eels during the different sampling periods reflected the availability of resources: February: fish, decapods, and insect larvae; May: amphipods from the benthic meiofauna; September: polychaetes. These results are related to the trophic qualities of the lagoon and its ability to produce energy in synergy with its hydrodynamics (confinement) and the life cycle of benthic micro- and macrofaunal species and small sedentary lagoon fish (e.g., Gobiidae and Atherinidae).

The diet of *A. anguilla*, which was dominated by chironomids, isopods, amphipods, and small fish, reflected the typical composition of the macroinvertebrate species assemblage of Ingril Lagoon. The eel's preference for the gammarids was better represented by the various feeding indices based on stomach contents than by the data from the sediment samples.

In Ingril 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 carnivorous and based on benthic prey (*Gammarus gr. locusta*, polychaetes, insect larvae, small fish). Variations observed during the three sampling periods illustrate an opportunist feeding behaviour for this eel, which previously was observed by Lecomte-Finiger (1983) in elver and small eels in the Roussillon Province and by Bouchereau et al. (2006) in the Prévost Lagoon in Languedoc Province. These eels consume the most available benthic prey without using a specialised or generalised feeding strategy. Behaviour such as this demonstrates the eel's high capacity to adapt to the Ingril Lagoon biotope. A certain selection of prey can take place in function of prey's activity and accessibility. If, however, a seasonal influence does exist in Ingril Lagoon-with decreased feeding activity in September, which then reverses and increases progressively in February and May-then this ecosystem is individualised due to its trophic quality and its particular hydrodynamic characteristics. As previously described, the biological organisation of the lagoon according to confinement is well defined from the point of communication with the sea. The basin is only very slightly confined throughout most of its total area and is mostly characterised by zones II and III. The three sampling sites were located in zone III. Only the zones the furthest away from the pass and therefore from the principal currents of marine origin exhibit marked confinement (zones IV and V). Lammens et al. (1985) showed that in Lake Tjeukemeer, The Netherlands, that because of hydrological regime the stock of the young planktivorous fish is determined to a great extent by the immigration of allochthonous larval smelt and varies markedly without changing the stability of the bream and eel populations, which can switch from a planktivorous to a benthivorous diet (bream) and from chironomid larvae to a mollusc diet (eels). Lammens & Visser (1989) observed that among eels, proportions of chironomid feeders and fish feeders differed between years, lakes, and seasons and changed in response to changing feeding conditions.

Trophic resources in this basin appear to vary greatly between good (May) and medium (September) from the nutritional point of view for eels. In addition to its weak hydrodynamics, this lagoon ecosystem is under the influence of environmental and human pressure with the increasing urbanisation. In contrast to most lagoons in Languedoc, the fishing area of the Ingril Lagoon has a limited surface area. It also does not receive any individualised fresh water tributaries, thus continental inputs are limited essentially to rainfall. The area surrounding the lagoon is wooded and covered by dense vegetation, which limits the occurrence of leaching of soil constituents. This phenomenon happens during heavy rainfall of the Mediterranean type, which is brief and infrequent during the year. Human pressure therefore remains relatively low throughout the year.

This study of the feeding habits of *A. anguilla* confirmed this species' adaptive capacity and showed it to be a bioindicator species that can be used to understand the functioning of lagoon ecosystems.

Acknowledgements

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