

International Journal of Agronomy and Agricultural Research

[IJAAR]



ISSN 2223-7054 [Print]

2225-3610 [Online]

IJAAR ©
[Off Print]

VOLUME 9, NUMBER 1, JULY 2016



Copyright © INNSPUB ©

INNSPUB
International Network For Natural Sciences

Website: www.innspub.net

Copyright © INNSPUB 2016



Study of the diet of the common cuttlefish *Sepia officinalis* of the exclusive economic zone (EEZ) of Côte d'Ivoire

Ekumou V. Akesse*¹, Coffi F. Didier Adou², Mamadou Karamoko¹, Jean D. Memel¹, Otchoumou Atcho¹

¹Formation Unit and Research of Sciences of Nature, Nangui Abrogoua University, Abidjan, Cote d'Ivoire

²Department of Sciences and Technology, Higher Teacher Training School, Abidjan, Cote d'Ivoire

Article published on July 31, 2016

Key words: Cephalopods, Diet, *Sepia officinalis*, Stomachs bowl.

Abstract

The diet of the common cuttlefish *Sepia officinalis* was studied from samples collected in the coastal waters of Côte d'Ivoire, for 12 months. According to the qualitative analysis of the stomach contents of all these animals, fish and crustaceans represented respectively, 50.23% and 38.65% of the examined stomachs are the most regularly consumed prey. The monthly evolution of the vacuity coefficient shows that this index varies according to the sexual cycle. Juveniles feed primarily on crustaceans. The stomachs bowl of the adults contains fish but also crustaceans and cephalopods whose frequencies are relatively significant, which would let think that *Sepia officinalis* changes trophic behavior in connection with the evolution of its physiological state and that at the adult state, the animal acquires performances which enable him to apprehend the preys with fast movements in fact the fish.

*Corresponding Author: Ekumou V. Akesse ✉ akessev@yahoo.fr

Introduction

The mollusc cephalopods of the exclusive economic zone (EEZ) of the Côte d'Ivoire are the subject of exploitation as well by the ships trawlers unloading at the fishing port of Abidjan as by some artisanal fishermen. Among them, is the cuttlefish *Sepia officinalis* (Linnaeus, 1758), which is the species most abundantly and regularly unloaded at the fishing port of Abidjan and on some quays paddlers of the capital of Ivory Coast. It is followed *Octopus vulgaris* (Cuvier, 1797) and squid *Loligo vulgaris* (Lemark, 1798). In 2012, approximately 182.631 tons of cuttlefish were recorded in the unloading of the products of sea to the fishing port of Abidjan according to the Management of the Aquaculture and Fishing (DAP). *Sepia officinalis* is a fishery resource worthy of attention and able to compensate for the over fishing of certain species of fish. It is a neritic benthic species which prefers the sandy and muddy bottoms. It feeds mainly on fish, crustaceans, and other molluscs which it captures by projecting its tentacles. Apart from some summary data available on these marine products, some scattered in formations learning about the biology, ecology and cephalopod stock of the EEZ of Ivory Coast, are available. However, the diet of the cuttlefish *Sepia officinalis* is captured in Ivorian waters and landed in Abidjan has not been studied. The diet of the cuttlefish of Senegal coasts, on the other hand, gave places to studies by Bakhayokho (1980). The main aim of this work is to study the trophic behavior of *S. officinalis* and to describe its variability according to the marine seasons and the classes of size of the specimens.

Material and methods

Study area

The maritime frontage of Ivory Coast again called exclusive economic zone (EEZ) of Ivory Coast long of 550Km of coast, constitutes a significant asset for the development of fishing. This maritime frontage located in the gulf of Guinea, receives various fishing units, qualified industrial or artisanal, which help to meet the growing needs of the population in animal protein. The Gulf of Guinea (Fig. 1),

fishing area of Ivorian craftsmen, is located in West Africa, in the large marine ecosystem that represent coastal regions. It is bounded to the north by the West African coast, south of the equator, west of the Cape Palmas (8°W) and in the East by 2°30 E (Pezennec and Bard, 1992). The climate is Guinean and you meet a series of sandy beaches that form a wide arch open to the Atlantic Ocean. Its major feature is the presence of four marine's seasons determined by the temperature variation during the year (Pezennec and Bard, 1992). So, the two cold seasons (a great, from July to October and a small, from January to February) are characterized by a resurgence of cold, salty ocean water (above 35‰ salinity) and a low temperature between 23 and 25°C, hot seasons are also two (a high, from March to June and a small November- December), and are defined by ocean water from the sea with a lower salinity to 35‰ and a high temperature of 28 and 30°C (Golé Bi *et al.*, 2005).

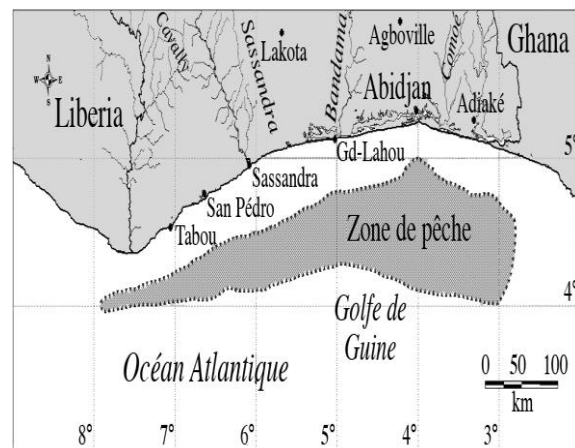


Fig. 1. Fishing zone of Ivory Coast artisanal fisheries.

Strategy of sampling and analysis of the stomachs contents

Sampling was carried out monthly (July 2014 at June 2015) at the fishing port of Abidjan at the time of the unloading of the trawlers and at the quay paddler of Vridi-canal. The pelagic trawl was the machine used for the capture of the individuals unloaded at the fishing port and the local jig was used for those unloaded at Vridi-canal. For the trawlers, the tide was estimated at 8 days on average while that of the paddlers lasted only a few hours.

Each month, a case and a basin of *S. officinalis* are sampled in a random way, respectively at the fishing port of Abidjan and the quay paddler of vridi-canal. Taken biometric measurements are: the dorsal mantle length (DML) in centimetre, total weight (W) and eviscerate weight (We) in gram. After having determined the sex and the various stages of maturation of each individual (juveniles (<18cm) and adult (≥18cm)), certain stomachs were analyzed on the spot in a fresh state, and for other animals, the part of the digestive tract lain between the oesophagus and the stomach, was detached and preserved in a formol solution at 5% to be examined later on. At the laboratory the stomachs were dissected and the contents rinsed with water on a series of sieve of meshes 1000 μm, 500 μm and 250 μm, before being examined with the naked eye or the binocular magnifying glass according to the size of the individuals preys. The various preys were sorted, counted, weighed and identified. The preys are given as far as possible using the identification keys of Fischer *et al.* (1987a; 1987b), but generally, they are in a stage of advanced degradation and in this case, only the solid parts, enabled us to reach the systematic class of the prey. Principal indices already used by several authors (Hyslop, 1980; Castro and Guerra, 1990; Collins *et al.*, 1994; Coelho *et al.*, 1997) were applied in order to determine quantitatively (Cv) and qualitatively (F, Cn, W) the introduced preys.

Vacuity Coefficient,

$$VC\% = \frac{\text{anumberofemptystomachs}}{\text{anumberofexaminedstomachs}} \times 100$$

Frequency of occurrence, (F)

$$F\% = \frac{\text{a number of stomach containing item i}}{\text{a number of examined full stomachs}} \times 100$$

Percentage in a number of the preys, (Cn)

$$Cn\% = \frac{\text{Total number of the item i}}{\text{Total number of allitems}} \times 100$$

Percentage in weight of the preys,

$$W\% = \frac{\text{Weightoftheitemi}}{\text{Total weight of thepreys}} \times 100$$

The index of relative importance of item (IRI) (Pinkas *et al.*, 1971) and the food coefficient (Q) (Hureau, 1970), were used to have a more significant approach of the diet of *S. officinalis*:

Index of relative importance, $IRI = F\%(Cn\% + W\%)$

The expression expressed as a percentage is form:

$$IRI\% = \frac{IRI}{\sum IRI} \times 100$$

Food coefficient, $Q = W\% \times Cn\%$

This classification takes account at the same time of abundance and the importance in mass of the species-preys. The classification of the species preys or groups of species-preys is made according to values of Q. If ($Q > 200$), the preys are qualified the preferential ones; if ($20 < Q < 200$), the preys are secondary, and if ($Q < 20$), the preys are additional.

Index of Schoener: The comparisons of the diet between the two biological stages and the seasons were made using the index of Schoener. It made it possible to evaluate the degree of similarity between the stages of maturity and the seasons.

$$\alpha = 1 - 0,5 \left(\sum_{k=0}^n |pxi - pyil| \right)$$

Pxi = proportion of a prey i consumed by a stage of maturity or individuals of one season (X),

Pyi = proportion of a prey i consumed by a stage of maturity or individuals of one season (y).

The diets are considered significantly similar when the value of α is higher than 0,6 ($\alpha > 0.6$).

Statistical analysis

Using the program Statistica version 7.1, the coefficient of correlation of the rows of Spearman was used to see whether there is or not a relation between the diets (probability criticizes retained: $p < 0.05$). The computed values on the basis of index of relative importance (IRI) made it possible to check the bond between the diets of the classes of sizes and the marine seasons.

Results

Monthly variation of the coefficient of vacuity

A total of 528 stomachs were examined during the study period from July 2014 to June 2015 and 121 were empty. The coefficient of vacuity calculated for this purpose is 22.91%. Its graph (Fig.2) shows the highest percentages in the months of September and February respectively 28.60% and 26.02%.

The lowest vacuity coefficients were registered the months of April (18.06%) and May (18.1%).

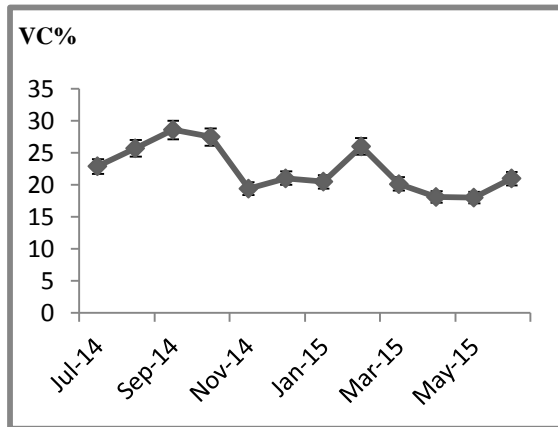


Fig. 2. Monthly evolution of the coefficient of vacuity at *Sepia officinalis*.

Variation of the coefficient of vacuity according to the marine seasons

Fig. 3 gives the evolution of the coefficient of vacuity of *S. officinalis* according to the marine seasons in the exclusive economic zone of Ivory Coast. The specimens fished during the cold seasons recorded the highest percentages of vacuity coefficient (Great season (26.19%) and small season (23.26%)). The smallest percentage of vacuity was recorded during the great hot season (19.59%).

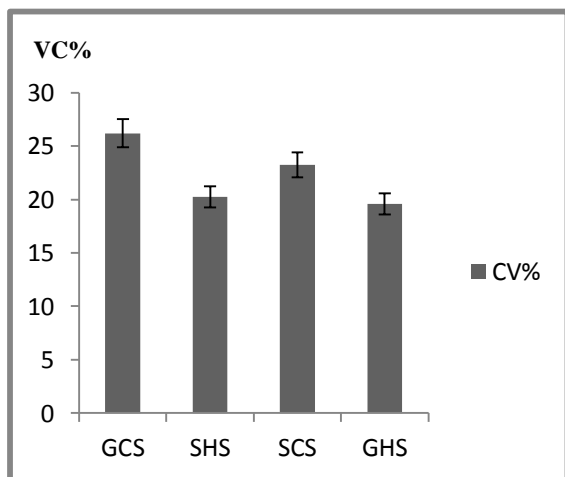


Fig. 3. Seasonal evolution of the coefficient of vacuity of *Sepia officinalis*.

GCSF (great cold season); SHS (small hot season); SCS (small cold season); GHS (great hot season).

Variation of the coefficient of vacuity according to the size

The graphical representation of vacuity coefficient according to the two classes of size shows that the coefficient of vacuity in the adults (24.21%) is higher than that of juveniles (16.03%) (Fig. 4).

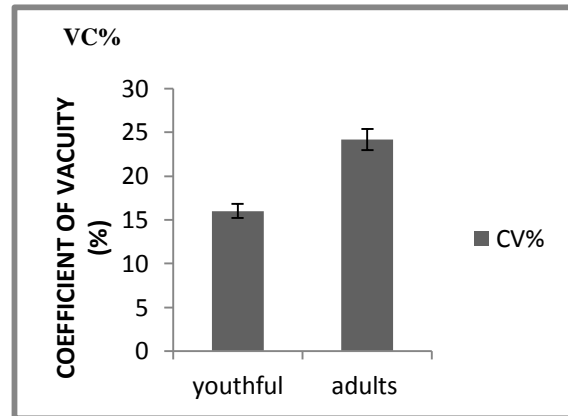


Fig. 4. Evolution of the coefficient of vacuity according to the sizes of *Sepia officinalis*.

General profile of the diet

Of all the 528 stomachs of *S. officinalis* from the trawler and artisanal fisheries examined, 407 contained food. Eight food categories divided into five groups were identified (Table I). These fish, crustaceans, cephalopods, polychaetes and plant debris. The group of fish is constituted of fish not identified because of their very advanced stage of digestion and two families (Clupeidae and Polynemidae) in which are respectively, agenus and a species. The group of crustaceans is constituted of the shrimp *Penaeus notialis* and the brachyoures (crab). A single species of cephalopod was found in the food bowl of *S. officinalis*. It's about *Sepia officinalis* itself. According to classification with the food coefficient (Table 1), fish and crustaceans are the preferential preys with respective coefficients $Q=1069.4$ and $Q=680.7$ ($Q>200$). Cephalopods ($Q=8.5$), plants debris (5.08) and Polychaetes ($Q=1.65$) constituted additional preys. The analysis of the index of relative importance indicates that fish are the preferential preys (IRI=54.37%) followed crustaceans (IRI=43.87%). This analysis reveals that of all the categories of consumed preys, the shrimp *Penaeus notialis* is most significant (IRI=30.08%), it is followed unspecified fish (IRI=22.62),

genus *Sardinella* (IRI=17.38), and species *Galoidès decadactylus* (IRI=14.37). Cephalopod (IRI=0.83), plants debris (IRI=0.56) and polychaetes (IRI=0.37), are regarded as accidental preys.

Variation of the diet according to the marine seasons.

The diet was analyzed according to four marine seasons which are: the great cold season, the small hot season, the small cold season and the great hot season (Fig.5). In great cold season, fish (50.2%) and crustaceans (48.76%) constituted the preferential preys. Cephalopods (1.04) are additional preys, while the other groups were not indexed during this season. During the small hot season crustaceans (85.31%) become the preferential preys and fish (14.69%) constitute the secondary preys.

As for the other groups, they do not appear among the preys identified during this season. In small cold season, the diet is focused on the fish (61.01%) which constituted the principal preys, crustaceans (38.99%) are certainly significant in the food bowl, but constituted secondary preys compared to fish.

During the great hot season, consumption is dominated considerably by fish (77.81) which constitutes the main preys. Crustaceans (15.5%) are secondary prey, while cephalopods (6.45%), polychaetes (0.16 %) and plant debris (0.08%) are prey accessories (IRI<10 %). The index of Schoener ($\alpha = 0.58$) calculated on the basis of numerical percentage (Cn), shows that the diet is significantly different between the small hot season and the great hot season. It shows no significant difference, between the great hot season and the great cold season ($\alpha = 0.81$), and between the great cold season and the small cold season ($\alpha = 0.93$).

This index ($\alpha = 0.84$) does not show variation of diet between the small hot season and the small cold season. The coefficient of correlation of the rows of Spearman, calculated on the basis of indicial percentage of food consumed during the four seasons, indicates a significant correlation between the great cold season and the small hot season ($N=8; RS=0.79; p < 0.05$),

between the great cold season and the small cold season ($N=8 RS=0.88; p < 0.05$) and between the small hot season and the small cold season ($N=8 RS=0.82; p < 0.05$). It is concluded for this purpose a similarity between the diets those seasons taken in pairs. This coefficient is not significant between the great hot season and the small hot season ($N=8; RS=0.46; p < 0.05$) and between the great hot season and the small cold season ($N=8; RS=0.43; p < 0.05$). It brings out a variation of the diet between these last seasons.

Change in diet depending on the size of Sepia officinalis

The collected specimens have dorsal mantle length (DLM) ranging between 10 cm and 30 cm. Two classes of sizes were established according to the size of the first sexual maturity (L50).

Specimens of small size ($10 \leq DLM < 18$ cm) constituted the group of juveniles and those of big size ($18 \leq DLM < 30$ cm), the group of adults. Fig. 6 indicates the index of relative importance of juveniles and the adults. For the juveniles ones, the crustaceans constituted the preys mainly consumed (% IRI=96.56).

Among those, the shrimp *Penaeus notialis*, is the principal one (% IRI = 92.99). The incidentally consumed food, are fish (% IRI=2.71), polychaetes (0.63) and plants debris (0.1). Cephalopod miss stomachs contents. Regarding adults, consumption is mostly dominated by fish (IRI=73.35%), crustaceans (IRI=24.76%) being considered secondary prey. Other foods represented by cephalopods (% IRI=1.49), plant debris (% IRI=0.27) and polychaetes (% IRI=0.13) are ingested incidentally.

The index of Schoener calculated on the basis of numerical percentage between these two groups ($\alpha = 0.43 < 0.6$) shows a significant change of the diet between juveniles ones and adults. The correlation coefficient of Spearman calculated from the percentages of index relative importance of juveniles and adults was not significant ($N=8; RS=0.25; p < 0.05$). This reflects a change in the diet between the two groups.

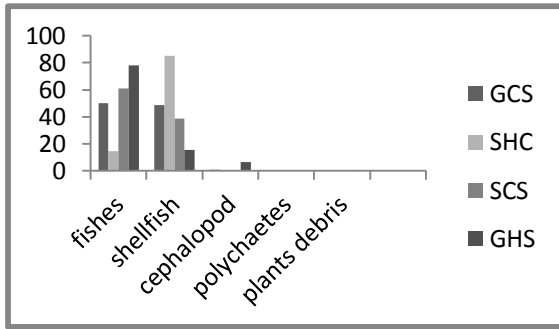


Fig. 5. Composition of the diet of *Sepia officinalis* according to the marine seasons.

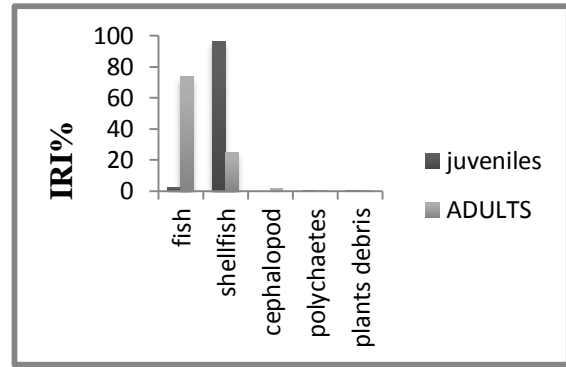


Fig. 6. Composition of the diet of *Sepia officinalis* according to the sizes.

Note: GCS (great cold season);SHS (small hot season);SCS (small cold season);GHS (great hot season).

Table 1. Composition of the diet of *Sepia officinalis* of the EEZ of Ivory Coast and percentages of the corresponding food indices.

Preys	Cn(%)	W(%)	F(%)	%IRI	Q
fish					
Unspecified fish	19,03	28,94	17,36	22,62	550,73
<i>Sardinella sp.</i>	15,49	14,7	18,98	17,38	227,7
<i>Galoidès decadactylus</i>	17,35	16,77	13,89	14,37	290,96
Crustacean					
Macroures					
<i>Panaeus notialis.</i>	22,39	21,36	22,68	30,08	478,25
Brachyours					
Crabs	13,8	14,67	15,97	13,79	202,45
Cephalopod					
<i>Sépia officinalis</i>	4,29	1,92	4,4	0,83	8,24
Polychaetes	2,99	0,55	3,48	0,37	1,64
Plants debris	4,66	1,09	3,24	0,56	5,07
TOTAL					
FISH	51,87	60,41	50,23	54,37	1069,4
CRUSTACEANS	36,19	36,03	38,65	43,87	680,7
CEPHALOPODS	4,29	1,92	4,4	0,83	8,24
POLYCHAETES	2,99	0,55	3,48	0,37	1,65
PLANTS DEBRIS	4,66	1,09	3,24	0,56	5,08

Note: Cn%: numerical percentage; W%: percentage by weight; %F: percentage of occurrence; IRI: percentage of index of relative importance; Q:food coefficient.

Discussion

The coefficient of vacuity of the common cuttlefish *Sepia officinalis* is higher during the cold seasons than during the hot seasons, reflecting a trophic activity significantly greater during recent seasons. That would mean that the trophic activity of these animals increases considerably in certain months of the hot seasons, particularly at the time of pre-reproduction.

The food needs to be linked to the breeding season. In fact, for the period of breeding, the males like the mature females, feed little. According to Richard (1971), adults in reproduction stop feeding because the genitals compress the digestive system, which can partly explain the rise in the coefficient of vacuity of these animals in the economic zone of Ivory Coast during cold seasons.

This same report was made by Hatanaka (1979), Sanchez and Obarti (1993) on the octopus *Octopus vulgaris* which is a species of Cephalopod showing similarities with the common cuttlefish, nutritionally and reproductively. These authors think that the common octopus feeds more in hot season than cold season. Vacuity coefficient is higher in mature specimens than juveniles, this shows that, feeding activity in juveniles is much higher compared to adults. Our results corroborate those described by Mangold (1982) in the Gulf of Morbihan.

He estimates that the coefficient of vacuity increases with the age of the cuttlefish, for juveniles, high nutrition allows rapid growth after hatching. The classification of the items according to the two methods (the index of relative importance: IRI and the food coefficient: Q) makes it possible to affirm that *S. officinalis* nourishes mainly fish and crustaceans.

This is in conformity so that found others authors in the Gulf of Tunis (Najäi et Ktari, 1979), in Ria de Vigo (Guerra, 1985), and out of bay of Rance (Le Mao, 1985). Many fish species could not be positively identified because of their very advanced state of digestion; however, from fish bone, scales and other solid parts, one could argue that it is teleost small sizes.

The observation we made is that *S. officinalis*, feeds on prey whose size is less than the predator it is. Richard (1971) indicates also the existence of a relationship between the size of the preys and the size of the cuttlefish what agrees with our remarks on the fact that the introduced preys are always lower than the predator. The very advanced state of digestion of stomach bowl could be explained by the fact that the digestion of the cuttlefish is very fast. The concept of rapid digestion was elucidated by Altman and Nixon (1970).

According to these authors, Cephalopods secrete, starting from posterior salivary glands a "powerful enzyme" which acts on the attachment of the muscles of the preys.

External digestion is followed of a very fast internal digestion; it is practically accomplished in less than four to six hours (Wells, quoted by Soufia NAJAI and Mohamed Hédi KTARI, 1974). In addition to finding pieces of flesh or arm, we identified the beaks of *S. officinalis* in some examined stomachs.

This allows us to confirm the cannibal character of cuttlefish. However he has not been given to us to find the remains of food (remains of cephalopods) in the stomachs of juveniles, cannibalism is related to the size of these animals.

This phenomenon has been noted by Richard (1971), he believes that this occurs when the animals are under nutrition status; the weakest are always the victims. *S. officinalis* diet's does not vary considerably according to the marine seasons, we could say that the cuttlefish of the exclusive economic zone of the Ivory Coast selects its prey and it is not nourished by the availability of prey resources.

The bolus of juveniles consists mainly of crustaceans, while the adult is mainly dominated by fish. The food of the cuttlefish is in connection with the physiological state of the animal. That would like to say that in a juvenile's state, the cuttlefish not being able to capture faster preys, it simply feeding animals easier to capture. Castro and Guerra (1990), noted that during his life, the importance of crustaceans as prey decreases the benefit of fish.

Conclusion

The food preferendum of the common cuttlefish *Sepia officinalis* of the exclusive economic zone of Ivory Coast is primarily consisted two great zoological groups, the fish and the crustacean's decapods.

The other categories of preys, Cephalopods (cannibalism), polychètes and plants debris are introduced incidentally. The diet does not vary considerably according to the marine seasons.

However, this cephalopod food differs depending on the size of the specimens. Indeed, as the size increases, the individuals of this species acquire the aptitude to catch increasingly large preys.

Acknowledgement

I wish to thank my professor, director of the pole of research livestock productions, of university NANGUI ABROGOUA, which directed me towards the study of the Cephalopods. I express my gratitude in Phd of our laboratory, which helped me to correct this manuscript. Finally, I would like to thank all the authors of this paper.

References

- Altman S, Nixon M.** 1970. Use of the beaks and radula by *Octopus vulgaris* in feeding. *Journal Zoologique London* **161**, 25-38.
- Bakhayokho M.** 1980. Pêche et biologie des céphalopodes exploités sur les côtes du Sénégal (12°20N-16°03N). Thèse de spécialité (3ème cycle), Mention biologie, Université de Bretagne Occidentale, Brest 119 p.
- Castro B, Guerra A.** 1990. The diet of *Sepia officinalis* (Linnaeus, 1758) and *Sepia elegans* (D'Orbigny, 1835) (Cephalopoda, Sepioidea) from the Ria de Vigo (NW Spain). *Scientia Marina* **54**, 375-388.
- Coelho M, Domingues P, Balguerias E, Fernandez M, Andrade JP.** 1997. A comparative study of diet of *Loligo vulgaris* (Lamarck, 1799) (Mollusca: Cephalopoda) from the south coast of Portugal and the Saharan Bank (Central-East Atlantic). *Fisheries Research*, **29**, 245-255.
- Collins MA, De Grave S, Lordan C, Burnell GM, Rodhouse PG.** 1994. Diet of the squid *Loligo forbesi* Steenstrup (Cephalopoda: Loliginidae) in Irish waters. *ICES Journal of Marine Science* **51**, 337-344.
- Direction de l'aquaculture et des pêches DAP.** 2012. Annuaire des statistiques des pêches et de l'aquaculture 25p.
- Fischer W, Bauchot ML, Schneider M.** 1987a. Méditerranée et Mer Noire. Invertébrés. Fiches d'identification des espèces pour les besoins de la pêche. Rome **I**, 1-760.
- Fischer W, Bauchot ML, Schneider M.** 1987b. Méditerranée et Mer Noire. Vertébrés. Fiches d'identification des espèces pour les besoins de la pêche. Rome **II**, 761-1530.
- Gole Bi GG, Koffi KJD, Dadi SG.** 2005. Contribution socio-économique de la pêche artisanale en Côte d'Ivoire. DFID, Programme pour des Moyens d'Existence Durables dans la Pêche (PMEDP) en Afrique de l'Ouest (GCP/INT/735/UK).
- GUERRA A,** 1985. Food of the cuttlefish *Sepia officinalis* and *Sepia esculentain* the Ria de Vigo (N.W. Spain) (Mollusca: Cephalopoda). *Jool. Ser A.GBR* **207(4)**, 511-519.
- Hatanaka H.** 1979. Studies on the fisheries biology of common *Octopus* off the north-west coast of Africa. *Bull Far Seas Fish Res Lab* **17**, 13-124.
- Hureau JC,** 1970. Biologie comparée de quelques poissons antarctiques (Nototheniidae). *Bull. Inst. Océanogr. Monaco* **68(1391)**, 1-245.
- Hyslop EJ.** 1980. Stomach contents analysis. A review of methods and their application. *Journal Fish Biological* **17**, 411-429.
- LE MAO P.** 1985. Place de la seiche *Sepia officinalis* (Mollusque Céphalopode) dans les chaînes alimentaires du Golfe Normando-Breton. *Cahier Biologie Marine* **XXVI** 331-340.
- Mangold K.** 1982. Quelques aspects de la croissance des céphalopodes. *Océanis* **8**, 533-549.
- NAJAI S, KTARI M.** 1974. Etude du régime alimentaire de la seiche commune *Sepia officinalis* Linné, 1758 (Mollusque, Céphalopode) du golfe de Tunis. *Bulletin Institut National Scientifique Technique Océanographique. Pêche Salammbô* **6(1-4)**, 53-61.
- Pezennec O, Bard FX.** 1992. Importance écologique de la petite saison d'upwelling ivoiro-ghanéenne et changements dans la pêcherie de *Sardinella aurita*. *Aquaculture Living resource* **5**, 249-259.
- Pinkas L, Oliphant MS, Iverson LK.** 1971. Food habits of albacore, blue fin tuna and bonito in Californian waters. *Calif. Fish. Game* **152**, 1-105.

RICHARD A. 1971. Contribution à l'étude expérimentale de la croissance et de la maturation sexuelle de la seiche *Sepia officinalis* L. (Mollusque: Céphalopode). Thèse de Doctorat d'Etat, Université de Lille, n° **2453**, 264P.

Schoener TW. 1970. "Non-synchronous spatial of lizards in patchy habitats," Ecology, vol. **51**, pp. 408.