

REPRODUCTIVE CYCLE OF THE CUTTLEFISH, *SEPIA OFFICINALIS* (L.) IN THE NORTHERN PART OF THE BAY OF BISCAY

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ABSTRACT

The sexual cycle of the cuttlefish, *Sepia officinalis*, from the northern part of the Bay of Biscay was followed over several years (1988 to 1990 and 1992 to 1993). Successive maturity stages are reached at the same time regardless of site in the northern part of the Bay. In this area, the majority of cuttlefish reproduce during their second year of life (group II) whereas the remainder reproduce in their first year (group I). The first visible signs of sexual development concern the testis in males and the genital tract in females. Males mature earlier than females: the first spermatophores appear in July (group II) and October (group I) while mature eggs appear from December (group II) and March (group I). The breeding season lasts from about mid-March to late June (3.5 months).

INTRODUCTION

The cuttlefish, *Sepia officinalis* (Linnaeus, 1758), like most cephalopods, is a short-lived species which reproduces only once over a short period at the end of its life (Mangold, 1987). The main stages of its life are punctuated by important seasonal migrations between shallow waters in summer and wintering areas located in deeper waters. The life cycle of cuttlefish is closely related to environmental factors. Thus, in the northern part of their distribution area (English Channel), they reproduce during the second year of life, during a short breeding season of 2 to 3 months (Boucaud-Camou, Koueta, Boismery & Medhioub, 1991). In contrast, in warmer waters such as those around the Iberian Peninsula, the Mediterranean and the Gulf of Tunis (Coelho & Martins, 1991; Guerra & Castro, 1988; Ezzedine Najaï, 1983; Mangold, 1966), the majority of cuttlefish reproduce at one year old and over a longer period.

In southern Brittany, the length frequency distribution of breeders indicates that cuttlefish are able to reproduce at one or two years of age (Le Goff & Daguzan, 1991). The aim of the present study is to give precise description of sexual maturation and activity of each group.

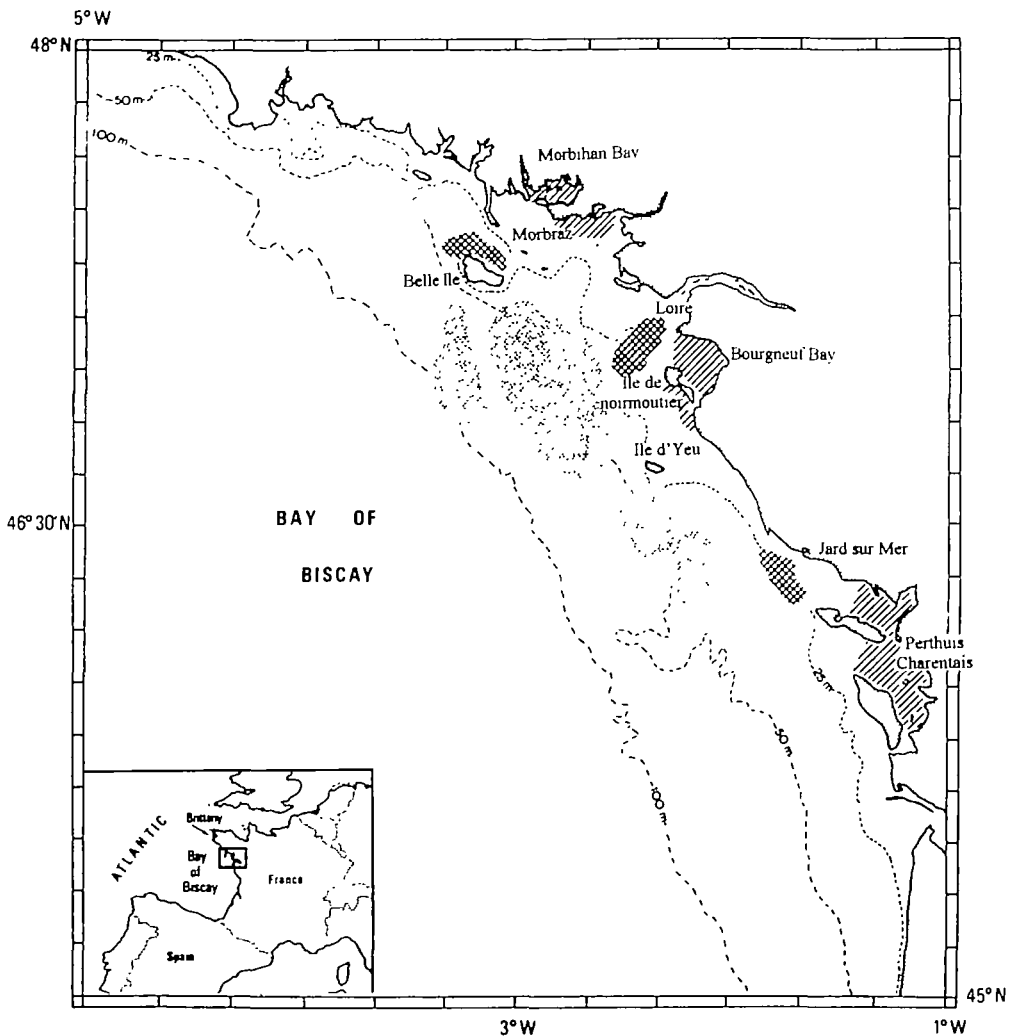
MATERIALS AND METHODS

The material for this study consisted of 1002 cuttlefish collected between June 1988 and June 1990 in southern Brittany. An additional sample of 880 specimens was obtained between November 1992 and December 1993, in order to include information over a longer period and to extend the study area southward in the Bay of Biscay. Animals collected during this second period were divided into two groups according to their origin, to the north or south of the mouth of the Loire River. The cuttlefish were caught by commercial bottom trawlers at depths ranging from 20 to 100 metres, or were trapped during breeding periods in the Golfe du Morbihan or the Bourgneuf Bay (Table 1 and Fig. 1). In all specimens we measured dorsal mantle length (ML), total body wet weight (Wt), fresh gonad and genital tract weight. In females, free ova (mature oocytes > 6 mm) were weighed separately from the remainder of the ovary. The colour of accessory nidamental glands was recorded. In males, spermatophores were extracted from the spermatophoric sac and weighed. Hectocotylus formation was also recorded. Following Mangold (1987) we consider the presence of free ova (mature oocytes > 6 mm) or spermatophores as the criterion of maturity. Maturity stages are expressed as a percentage of total body weight (index) for the following organs:

- in females: ovary (OI), principal (PNI) and accessory (ANI) nidamental gland and oviducal gland (OvI)
- in males: testis (TI), spermatophoric sac without spermatophores (NI) and spermatophores (SI).

Table 1. Origin of the cuttlefish caught in the North and the South of the Loire River.

	North of the Loire	South of the Loire
March	Morbihan Bay and 'Morbraz'	Bourgneuf Bay
April	Morbihan Bay and 'Morbraz'	Bourgneuf Bay
May	Morbihan Bay and 'Morbraz'	Bourgneuf Bay
June	Morbihan Bay and 'Morbraz'	Bourgneuf Bay
July	Morbihan Bay and 'Morbraz'	Bourgneuf Bay
August	Morbihan Bay and 'Morbraz'	Bourgneuf Bay
September	North of Belle Ile	'Jard sur Mer'
October	North of Belle Ile	'Jard sur Mer'
November	North of Belle Ile	North of Noirmoutier
December	South West of 'Belle Ile'	South west of 'Belle Ile'
January	South west of 'Belle Ile'	South west of 'Ile d'Yeu'
February	South west of 'Belle Ile'	South west of 'Belle Ile'

**Figure 1.** Principal sites of cuttlefish captures by the fishermen in the North part of the Bay of Biscay during summer (//), autumn (X) and winter (•).

RESULTS

Life span

Maturity indices show that some cuttlefish are able to mature before they are one year old, whereas others mature during their second year of life. This is in accordance with the observations of Le Goff (1991) in southern Brittany and Gi Jeon (1982) in the Arcachon area. During the breeding season (from mid-March to June), the two generations can be distinguished by their mantle length (Fig. 2). The average ML of group I breeders was 145 mm (140 mm for males and 150 mm for females) and 230 mm in group II breeders (240 mm for males and 220 mm for females). Absence of mature specimens after the spawning season (after July) suggests that the cuttlefish do not survive after spawning. This was also noted by Richard (1971) and Boletzky (1983). Considering that most hatching occurs in July in southern Brittany (Bouchaud, 1991), group I breeders seem to live on average 10 to

13 months and group II breeders, 20 to 23 months (Le Goff, 1991). As abbreviations, we will use GIB for group I breeders and GIIB for group II breeders.

Maturity stages

The maturity indexes are given in Figs 3 to 9. It appears that for females the results are in good agreement from both sampling programmes and both north and south of the mouth of the Loire. Conversely for males there is a shift of about 1 month between the two periods.

Females

The growth of the ovary (Fig. 3) becomes perceptible in the most precocious individuals from late September in GIIB and late December in GIB. So, there is a gap of 3 months between the two generations. No decrease in GI could be found for the two generations during the breeding season, in spite of the free

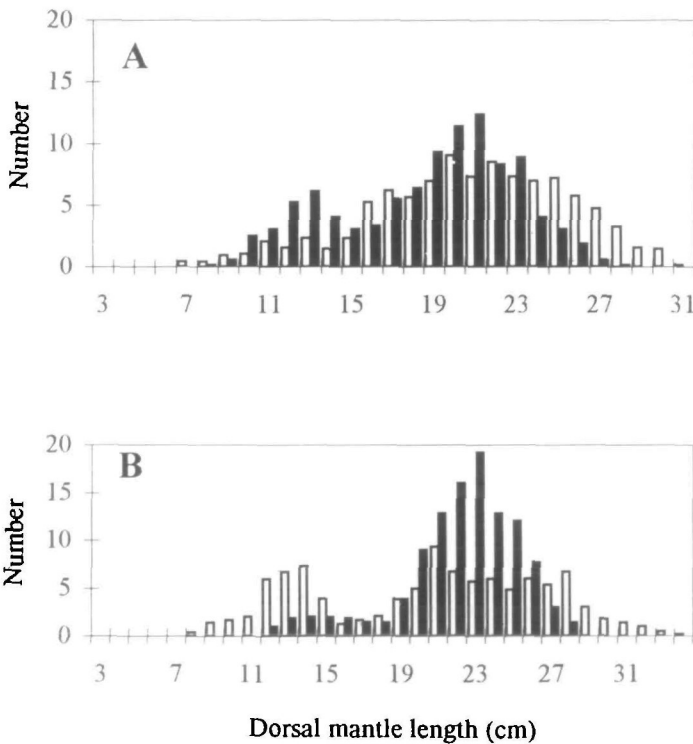


Figure 2. Length frequency distribution of male (white) and female (black) cuttlefish in the course of reproduction. Animals were caught in the Morbihan Bay and the Bourgneuf Bay during the breeding season 1992 (A) and in the Morbihan Bay during the 1989 breeding season (B).

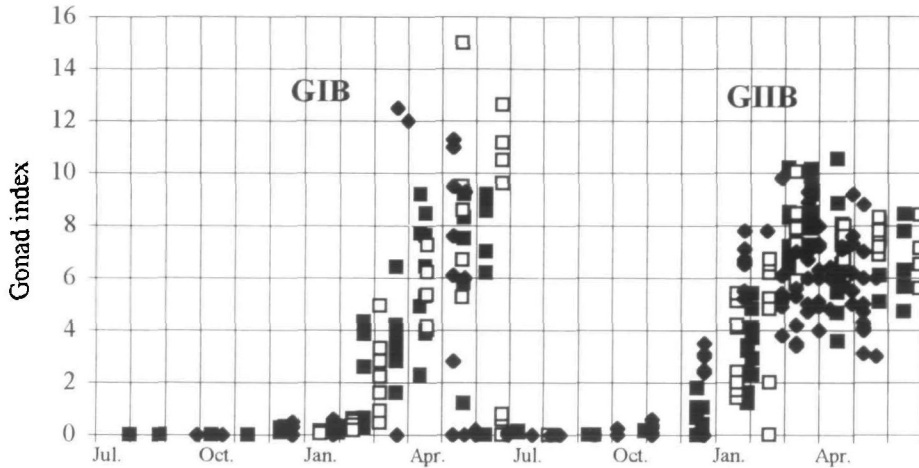


Figure 3. *Sepia officinalis* females. Gonad index (OI 5 gonad weight/body weight) of group I (GIB) and II (GIIB) breeders collected in the North of the Loire from 1988 to 1990 (◆) and 1991 to 1992 (■) and in the South of the Loire from 1991 to 1992 (□).

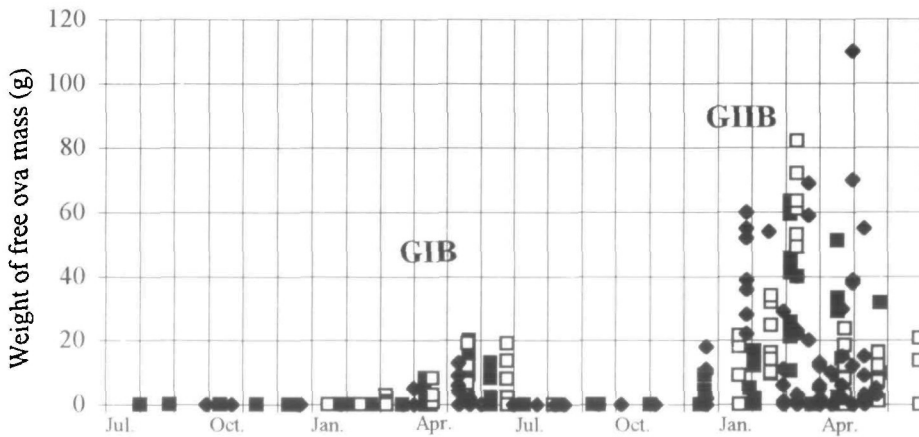


Figure 4. *Sepia officinalis* females. Weight of free ova mass (oocytes . 6 mm) of group I (GIB) and II (GIIB) breeders collected in the North of the Loire from 1988 to 1990 (◆) and 1991 to 1992 (■) and in the South of the Loire from 1991 to 1992 (□).

ova weight decrease related to egg laying that occurred in April in GIIB and June in GIB (Fig. 4). It can be concluded that the growth of immature oocytes compensates for the emission of free ova during the laying period. The first free ova appear in December in GIIB and in March in GIB, when the two generations are still in the wintering area. Free ova become visible 4 months before the migration for reproduction in GIB and only one month before migration in GIIB. The number of free

ova is closely linked to the cuttlefish length as has already been noted by Mangold (1987) and Boletzky (1983). The biggest free ova mass was 110 g, which is approximately of 650 free ova ready to be laid. It was found in a female of 260 mm ML in early May 1990.

The development of the principal nidamental gland begins in July in GIIB and in October, in GIB (Fig. 5). In both groups the maturation of the nidamental gland starts 2 months before that of ovaries, that is

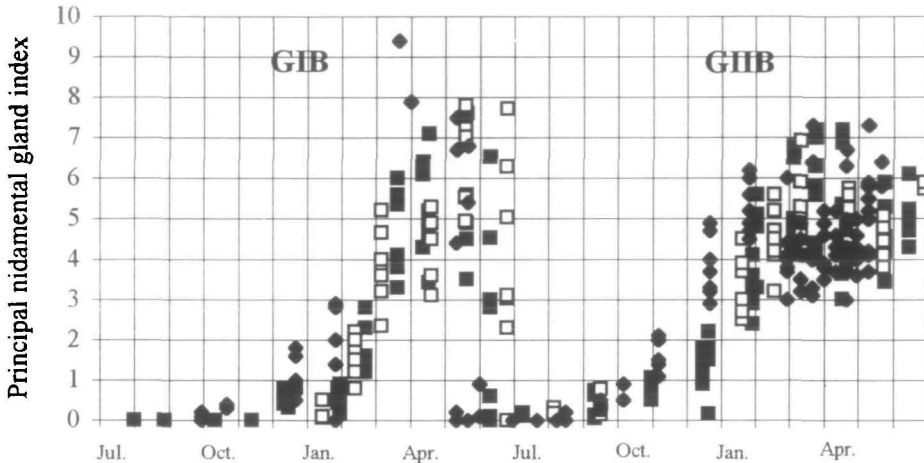


Figure 5. *Sepia officinalis* females. Principal nidamental gland index (PNI = principal nidamental gland weight/body weight) of group I (GIB) and II (GIIB) breeders collected in the North of the Loire from 1988 to 1990 (◆) and 1991 to 1992 (■) and in the South of the Loire from 1991 to 1992 (□).

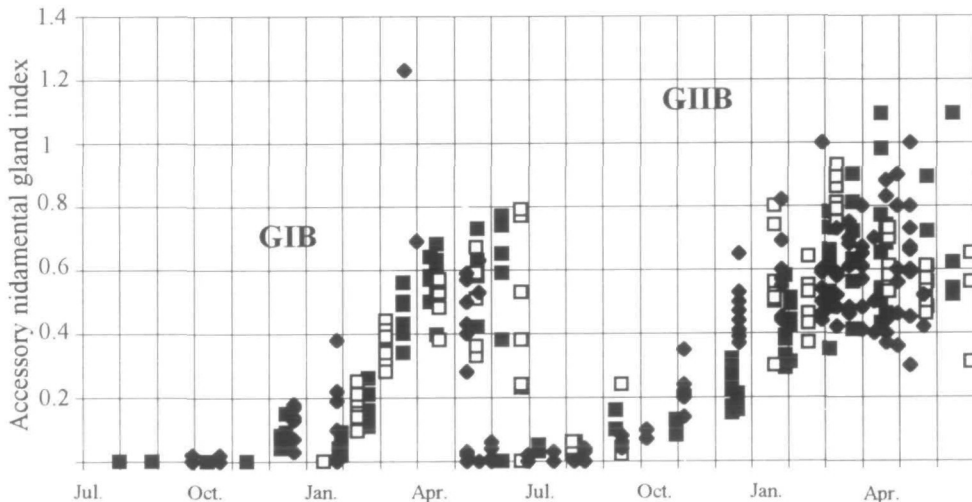


Figure 6. *Sepia officinalis* females. Accessory nidamental gland index (ANI = accessory nidamental gland weight/body weight) of group I (GIB) and II (GIIB) breeders collected in the North of the Loire from 1988 to 1990 (◆) and 1991 to 1992 (■) and in the South of the Loire from 1991 to 1992 (□).

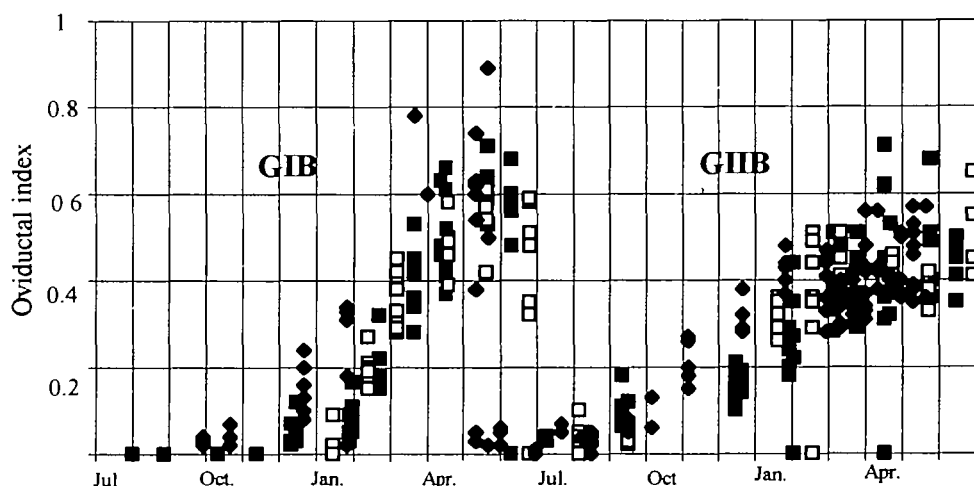
July–August in GIIB and November in GIB. The nidamental index reaches its maximum from April in GIIB and during February to April in GIB. This gland can weigh more than 100 g, i.e. up to 9% of total body weight in precocious females. In GIIB, it represents 0.3 to 0.65%.

The accessory nidamental gland follows the

same pattern as the principal gland (Fig. 6). In GIB growth begins in August and weight levels off during the following March. It then represents about 0.6% of total body weight. Growth begins in November in GIB and becomes stabilized from April, the accessory gland then represents nearly 0.5% of total body weight of the animal.

Table 2. Monthly changes in the colour of the accessory nidamental gland in group I (GIB) and II (GIIB) females.

glands Date	Colour of accessory nidamental	
	GIB	GIIB
June to October	translucent	translucent
November	translucent	translucent/pink
December	translucent	translucent/pink
January	translucent	
translucent/coral		
February	translucent	pink/coral
March	translucent	orange/coral
April	translucent	coral
May	translucent	coral
June	translucent	coral
July	translucent/pink	
August	translucent/pink	
September	pink/orange	
October	orange/coral	
November to May	coral	

**Figure 7.** *Sepia officinalis* females. Oviducal index (Ovi = oviducal gland weight/body weight) of group I (GIB) and II (GIIB) breeders collected in the North of the Loire from 1988 to 1990 (◆) and 1991 to 1992 (■) and in the South of the Loire from 1991 to 1992 (◻).

The accessory nidamental gland takes on a pink tinge from November in the most precocious females of GIB (nearly 5.5 months old, Table 2). In contrast, in the less precocious individuals, this occurs 2 to 2.5 months later, i.e. in February. Accessory glands remain translucent and very poorly developed in GIB, until June–August (approximate age: 12 months). All GIIB glands become coral-red coloured from November. The coloration of these glands is visible 7 to 8 months before the

breeding season in GIIB and 3 to 5 months before the breeding season in GIB.

Development of the oviducal gland is synchronous with development of the principal nidamental gland and occurs from August to May of the next year in GIIB and from October to May–June in GIB (Fig. 7). The synchronism between the oviducal and nidamental glands could be partly explained by their similar structure, as observed by Richard (1971) and Boismery (1988).

Males

The gonad index (Fig. 8) increases from mid-August in the most precocious GIB of the 1988 cohort and 1.5 month later, from late September, in the 1992 cohort (approximately 2 and 3 months old). Such a gap is not visible in GIIB, in which testis development occurs from June to July (at the age of 11 to 12 months old). Testis weight reaches a maximum (3% of total body weight) in April to May in GIB and from February in GIIB (2% of total body weight). No decrease in testis weight occurs in the following months.

Spermatophoric sac development begins at the same time as testis development, that is from mid-August in 1988 GIB, from late September in 1992 GIB and on average June–July in GIIB. The maximal values of the spermatophoric sac index (on average 1.2%) are reached in February (GIIB) and in March (GIB).

The first spermatophores (Fig. 9) appear from mid-October in all GIB (nearly 4 months old) and 2.5 months earlier, i.e. from mid-July in GIIB (nearly 12 months old). Their weight represents at the most 0.9% (GIB) and 0.5% (GIIB) of total body weight. After reproduction, from March to July in GIB and from February to July in GIIB, the weight of spermatophores as a percentage of total weight decreases drastically.

The hectocotylized arm is always completely formed before the appearance of the first

spermatophores (Table 3), although its formation begins nearly one month after the onset of testis growth.

A gap of nearly one month appears between the testis (or spermatophoric sac) development recorded in GIB during the two periods (1988 to 1990 and 1992 to 1993, Figs 8 and 9). It seems that the 1988 cohort was more precocious than the 1992 cohort. Development of testis, spermatophoric sac and spermatophores is otherwise similar in the samples collected north or south of the mouth of the Loire.

DISCUSSION

Observations from the same landing site indicate a notable coincidence of maturity stages, especially in females. This conclusion relies mainly on observation of accessory nidamental glands (in females), the hectocotylus arm and the presence (or absence) of spermatophores (in males) seen in a great number of specimens, some of which were collected for dissection. The onset of maturation follows the 'all or nothing' rule in accordance with Richard (1967) who emphasized neuroendocrine control of the optic gland in maturation, as first described by Wells and Wells (1972) for *Octopus vulgaris*. In *Sepia officinalis*, a minimal period of darkness of 12 hours per day is necessary to trigger growth of the ovary in females (Richard, 1971). That corresponds to the photoperiod we have from September

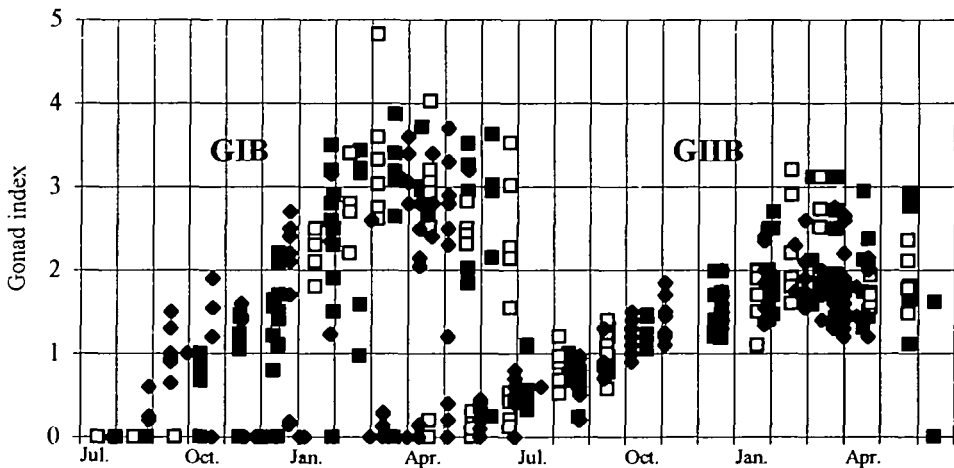


Figure 8. *Sepia officinalis* males. Gonad index (TI = testis weight/body weight) of group I (GIB) and II (GIIB) breeders collected in the North of the Loire from 1988 to 1990 (◆) and 1991 to 1992 (■) and in the South of the Loire from 1991 to 1992 (□).

Table 3. Seasonal formation of the hectocotylosed arm and of appearance of spermatophores. +: presence of completely formed hectocotylus and presence of spermatophores; + -: beginning of the hectocotylus formation; + -: in process of formation.

Dates	Group II Breeders		Group I Breeders	
	Hectocotylus arm	Spermatophores	Hectocotylus arm	Spermatophores
June	-	-	-	-
July	-	-	-	-
August	-	-	-/+ -	-
September	-	-	-/+	-/+
October	-	-	-/+	-/+
November	-	-	-/+	-/+
December	-	-	-/+	-/+
January	-	-	+	+
February	-	-	+	+
March	-	-	+	+
April	-	-	+	+
May	-/+ - -	-	+	+
June	-/+ - -	-	+	+
July	-/+	-/+		
August	+ -/+	-/+		
September	+	-/+		
October to May	+	+		

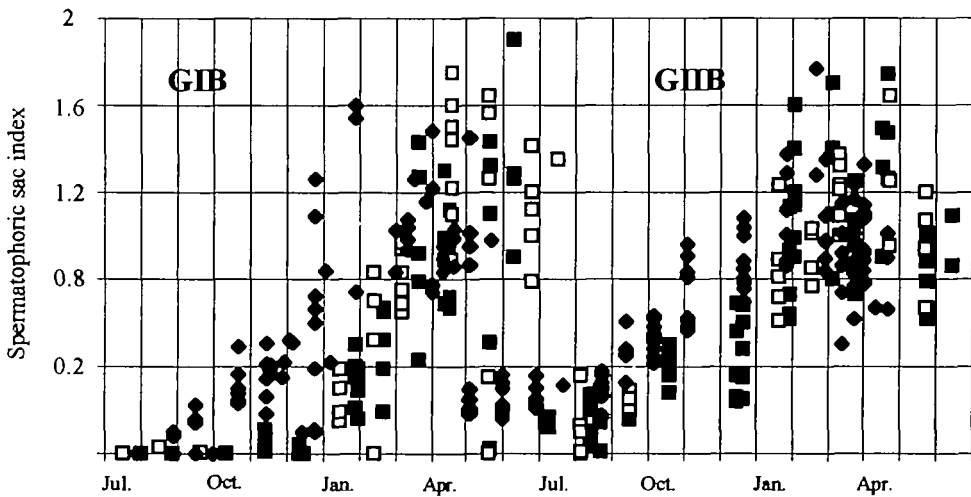


Figure 9. *Sepia officinalis* males. Spermatophoric sac index (NI = spermatophoric sac without spermatophores weight/body weight) of group I (GIB) and II (GIIB) breeders collected in the North of the Loire from 1988 to 1990 (◆) and in the South of the Loire from 1991 to 1992 (□).

when GIIB ovaries begin to grow. Moreover, sexual development is enhanced by the scotophase (length of night per day) in both sexes, these photostimulation processes become evident only at a given size (the somatic threshold). Obviously, the size limit beyond which animals begin to mature is

smaller in males (the first signs of maturation that we could observe was form 60 mm in males and 100 mm in females). Based on our observations, it appears that synchronism of maturity stages could be explained by close links between the endogeneous processes of maturation and external factors. However, the

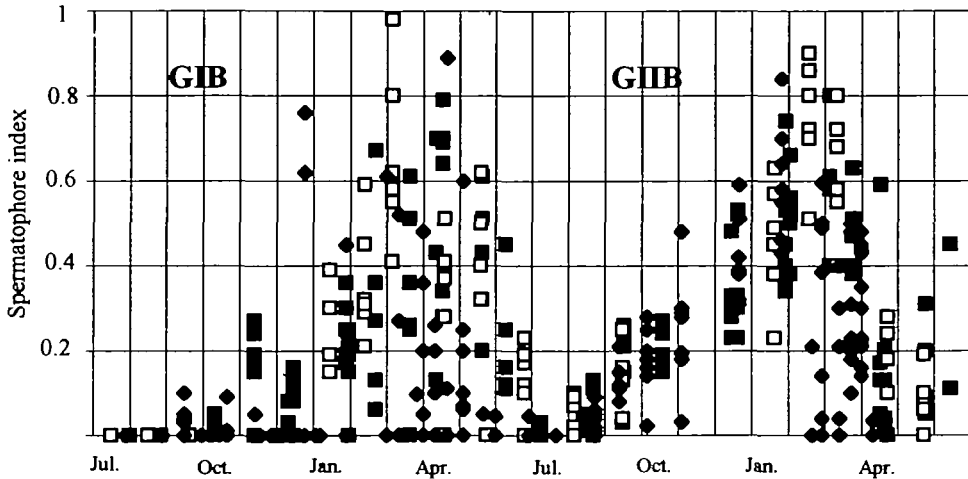


Figure 10. *Sepia officinalis* males. Spermatophore index (SI = spermatophores weight/body weight) of group I (GIB) and II (GIIB) breeders collected in the North of the Loire from 1988 to 1990 (◆) and 1991 to 1992 (■) and in the South of the Loire from 1991 to 1992 (□).

fact that testis growth begins during long days in GIIB would mean that the photoperiod control is less important for males as pointed out by Richard (1971) and Koueta *et al.* (1995). This could also explain the greater sexual precocity of males in comparison with females.

Synchronism of sexual organ growth, observed at different geographical sites, would mean that ecological factors (temperature, light, food), acting in each zone are not different enough to generate visible differences in the triggering of sexual cycles from one zone to another. We know in *Sepia officinalis* that vertical migrations coincide with gonad maturation (Boletzky, 1989). In the area studied, it has also been noted that females start laying eggs as soon as they reach shallow waters (Bouchaud, 1991). Furthermore, the fact that the first breeders arrived at the same time (they are caught by fishermen around mid-March) in the three main reproductive areas of the North of the Bay of Biscay (Morbihan Bay, Bourgneuf Bay and Pertuis Charentais) supports our conclusion concerning the synchronism of maturity stages at the level of the population.

Two age groups of breeders live in the north of the Bay of Biscay. A majority of individuals reproduce during their second year of life (GIIB) whereas others reproduce in their first year (GIB). The proportion of each group varies from one year to another and is quite different between males and females. The percentage of GIB, derived from samples of about

one hundred specimens of the same cohort, was 47% for males and 30% for females in December 1992, the following year it was 41% and 11% for males and females respectively. The higher proportion of precocious breeders in males could reflect a higher flexibility between endogenous processes of maturation and ecological factors.

In conclusion, the north of the Bay of Biscay appears to be a transition area, between the English Channel where precocious breeders are absent (Medhioub, 1986) and southern waters where precocious breeders seem to be in the majority (Guerra & Castro, 1988; Ezzedine Najafi, 1983; Mangold, 1966).

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REFERENCES

- BOISMERY, J. 1988. Structure et développement de la glande de l'oviducte de la seiche, *Sepia officinalis* L. *Haliotis*, 18: 75-84.
- BOLETZKY, S.V. 1983. *Sepia officinalis*. In: *Cephalopod life cycles*, vol. 1: *Species Account* (P.R. Boyle ed.), 31-52. Academic Press, London.

- BOLETZKY, S.V., 1989. Réflexion sur les facteurs du déterminisme des migrations chez les céphalopodes. *Océanis*, **15**: 115-120.
- BOUCAUD-CAMOU, E., KOUETA, N., BOISMERY, J. & MEDHIOUB, A. 1991. The sexual cycle of *Sepia officinalis* from the Bay of Seine. In: *La seiche* (E. Boucaud-Camou, ed.), 141-142. Acta of the first international symposium on the cuttlefish *Sepia*, Centre de Publications de l'Université de Caen.
- BOUCHAUD, O. 1991. Etude de la reproduction de la seiche commune *Sepia officinalis* dans le Golfe du Morbihan: premiers résultats. In: *La seiche* (E. Boucaud-Camou, ed.), 153-166. Acta of the first international symposium on the cuttlefish *Sepia*, Centre de Publications de l'Université de Caen.
- COELHO, M.L. & MARTINS, M.C. 1991. Preliminary observations on the biology of *Sepia officinalis* in Ria Formosa, Portugal. In: *La Seiche* (E. Boucaud-Camou, ed.), 131-140. Acta of the first international symposium on the cuttlefish *Sepia*, Centre de Publications de l'Université de Caen.
- EZZEDINE NAJAI, S. 1983. Contribution à l'étude de la biologie des pêches des Céphalopodes de Tunisie. Application à l'espèce *Sepia officinalis*. Thèse 3^o cycle, Faculté des Sciences de Tunis, 229 p.
- GI JEON 1982. Etude des populations de seiche (*Sepia officinalis* L.) du Golfe de Gascogne. Thèse 3^o cycle, Université de Nantes, 272 p.
- GUERRA, A. & CASTRO, B.G. 1988. On the life-cycle of *Sepia officinalis* in the Ria de Vigo. *Cahiers de Biologie Marine*, **29**: 395-405.
- KOUETA, N., BOUCAUD-CAMOU, E., & RENOU, A.M. 1995. Gonadotropic mitogenic activity of the optic gland of the cuttlefish, *Sepia officinalis*, during sexual maturation. *Journal of the Marine Biological Association of the U.K.*, **75**: 405-411.
- LE GOFF, R. 1991. *Biologie et migrations de la Sepia officinalis L. (Mollusque Céphalopode Sepiidae) dans le secteur Morbraz-Golfe du Morbihan (Sud Bretagne)*. Thèse d'Université, Rennes I, 233 p.
- LE GOFF, R. & DAGUZAN, J. 1991. Growth and life cycle of the cuttlefish *Sepia officinalis* L. (Mollusca: Cephalopoda) in South Brittany (France). *Bulletin of Marine Sciences*, **49**: 341-348.
- MANGOLD, K. 1966. *Sepia officinalis* de la Mer Catalane. *Vie et Milieu*, **17**: 961-1012.
- MANGOLD, K. 1987. Reproduction. In: *Cephalopod life cycles, vol. 2: Species Accounts* (P.R. Boyle, ed.), 157-200. Academic Press, London.
- RICHARD, A. 1967. Rôle de la photopériode dans le déterminisme de la maturation génitale femelle de *Sepia officinalis*. *Comptes Rendus d'Académie des Sciences de Paris*, **264** (D): 1315-1318.
- RICHARD, A. 1971. Contribution à l'étude expérimentale de la croissance et de la maturation sexuelle chez le Céphalopode *Sepia officinalis* L. (Mollusque, Céphalopode). Thèse Doctorat d'Etat, Université de Lille, 264 p.
- WELLS, M.J. & WELLS, J. 1959. Hormonal control of sexual maturity in Octopus. *Journal of Experimental Biology*, **36**: 1-33.
- WELLS, M.J. & WELLS, J. 1972. Optic gland and the state of the testes in *Octopus*. *Marine Behaviour and Physiology*, **1**: 71-83.