Reproduction and fecundity of 3 species of deep-sea fish from the north-east Atlantic Ocean.

By Valérie Allain

ABSTRACT

The reproductive strategies of three benthic species of deep-sea fish from the north east Atlantic were studied : *Helicolenus dactylopterus* distributed between 245 and 800 m in depth, *Coryphaenoïdes rupestris* (400 to 1 500 m depth) and *Alepocephalus bairdii* (650 to 1 700 m depth). A 2-years sampling study (Dec 1995- Dec 1997) allowed us to define the reproductive strategies and fecundity of females of the 3 species. i) *H. dactylopterus* population reproduced from March to June and specimens matured synchronously. Their annual fecundity was indeterminate, but a batch fecundity ranging from 1 212 to 20 504 oocytes per female was measured. ii) The period of reproduction for *C. rupestris* extended from February to November with a maximum from May to November; individuals were asynchronous; annual fecundity was indeterminate, whereas batch fecundity was estimated between 4 078 and 68 780 oocytes per female. iii) We could not determine the precise period of reproduction for *A. bairdii*; however, mature fish were found throughout the year with a major spawning period from January to April and females were not synchronous; the annual fecundity was indeterminate, but a batch fecundity was estimated from 458 to 7 049 oocytes per female. We noted that the deeper the habitat of the species, the longer the reproductive period and the less the females were synchronous during maturation. A long spawning period and asynchronism in maturation could be explained by the lack of pronounced cyclic environmental factors in the deep-sea; but assuming it as a general rule is not possible.

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INTRODUCTION

The exploitation of deep-sea fishes on the slope off the British Isles is recent and began in 1973, but has rapidly risen since the end of eighties. Still little is known on the biology of those species because most of the studies are incomplete. To evaluate the capacity of the deep-sea fishes to renew the stocks, biological studies are needed. In this paper, reproduction is assessed for 3 deep-sea fishes:

• the target fish of the French deep-sea fishery in north east Atlantic: *Coryphaenoïdes rupestris*

• an important by-catch of this fishery: *Alepocephalus bairdii*, one of the most frequently discarded species (Allain & Kergoat, 1997; Connolly & Kelly, 1996)

• another commercial fish: *Helicolenus dactylopterus* that is widely distributed in depth in the Atlantic Ocean and Mediterranean.

Reproductive parameters studied are length and age at sexual maturity, spawning period and fecundity.

MATERIAL AND METHODS

Sampling area and collection

Fish were caught by French semi-industrial trawlers along the western continental slope off the British Isles in deep waters (350 - 1 300 m) between December 1995 and December 1997. They came from 5 fishing zones shown in **Figure 1**. Female ovaries were examined macroscopically and weighed to calculate gonado-somatic index (GSI), and portions of ovaries were sampled for histological examination and to assess fecundity first by establishing oocyte diameter distributions, second by estimating the number of oocytes in chosen samples. The numbers of samples taken for each examination are described in **Table 1**.

Macroscopic examination, age determination and gonado-somatic index (GSI)

The maturity state of ovaries was evaluated macroscopically using a 5-stage scale :

• Stage I : immature, small ovary
• Stage II : maturing, invisible oocytes
• Stage III : maturing, oocytes developed
• Stage IV : mature, oocytes ready to be spawned
• Stage V : spent - resting, empty gonad.

C. rupestris immature females are easily recognised by macroscopic examination and the length at which 50% of females were mature could be determined. However macroscopic criteria are not sufficient to differentiate immature females from resting females for the 2 other species for which microscopic examination was necessary. Females were considered as immature when their ovaries structure was compact, with tightly packed oocytes and as resting mature when ovaries presented a loose structure. Hence, length at which 50% of *A. bairdii* females were mature was determined. But for *H. dactylopterus* this microscopic examination did not allow differentiation of immature from resting mature females. Length at first maturity was then defined as the length of the smallest *H. dactylopterus* female showing microscopic evidence of development (beginning of vitellogenesis).

Age was determined by reading otoliths. *H. dactylopterus* and *C. rupestris* otoliths were embedded in black polyester resin and sliced across the nucleus in 0.5 to 1 mm sections. They were observed, covered with a mixture of alcohol and glycerine, by transmitted light microscopy. Whole *A. bairdii* otoliths were observed in the same mixture but under a transmitted light binocular microscope. Rings on otoliths are considered as annual rings though this has not been validated.

Ovaries and eviscerated fish were weighed with a precision of respectively 0.01g and 1g. The gonado-somatic index was calculated according to the equation below :

$$GSI = \frac{W_O}{W_F} \times 100$$

where W_O is the weight of the 2 ovaries and W_F is the weight of eviscerated fish.

Histological examination

Small portions of ovaries were stored in Bouin's fixative, then dehydrated, embedded in paraffin, sliced in 5 µm sections and stained with periodic acid - Schiff (PAS) - haematoxylin for microscopic inspection. Oocytes were classified according to the microscopic 6-stage scale of Le Duff et al. (1996), slightly modified to match the species under study. Post-ovulatory follicles (POF) and atretic oocytes were also recorded.

The relative frequencies of the oocytes stages were established by counting and classifying 100 to 700 oocytes per slide. The females microscopically inspected were classified into 10 maturing state of ovaries characterised by the frequency distribution of oocyte stages, POF and atretic oocytes (Fig. 2).

Oocyte diameter distribution and estimation of fecundity

Portions (0.5 to 145 g) of ovaries were stored in Gilson's fluid for 2-month to 2 year-periods to separate oocytes from ovarian tissue. After dissociation, small oocytes and particles of ovarian tissue were discarded by filtration (80 µm). Remaining oocytes were diluted in water, then separated into 2 parts with a Motoda's tank in a first step (oocytes were too big to be pipetted except for *H. dactylopterus* oocytes). Additional fractionation steps were required to obtain sub-samples of at least 600 oocytes to determine the oocyte-diameter distribution and 350 oocytes to estimate fecundity.

To establish the oocyte-diameter distribution in ovaries, the whole oocytes in a sub-sample were measured and counted. The criteria established by Hunter et al. (1985) and Hunter & Macewicz (1985) were used to define annual fecundity as determinate or indeterminate.

The number of oocytes in the batch exhibiting the most advanced vitellogenesis stage and isolated from the others was determined to assess the absolute and relative batch fecundities defined hereafter:

$$F_A = \frac{C}{\frac{1}{n} \times \frac{1}{2}} \times \frac{W_O}{W_S} \qquad\qquad F_R = F_A \times \frac{100}{W_F}$$

where W_O is the weight of the 2 ovaries, W_S is the weight of the sample stored in Gilson's fluid, W_F is the weight of eviscerated fish, C is the number of oocytes in a sub-sample, n is the number of fractionations and ½ is the dilution factor of Motoda's tank.

RESULTS

First maturity

The length and age at first maturity of the 3 species studied are showed in **Table 2**. Maximum length and age observed in the samples are also given.

Spawning period

Several techniques were used to determine the spawning period of the 3 species.

One of them was the examination of the seasonal patterns of the gonado-somatic index (GSI) during 2 years (**Fig. 1**). The GSI maxima occured:

- in March 1996 and from April to June 1997 for *H. dactylopterus*
- in September - October 1996 and from June to October 1997 for *C. rupestris*
- from February to April 1996 and in January 1997 for *A. bairdii* .

Another technique was the examination of histological slides of ovaries with the aim of determining the maturing state of each female. By examining the time of occurrence of females in the partial-spent stage, the spawning period can be determined (**Table 3**). Using this criterion, spawning took place

- from March to June in 1996 and 1997 for *H. dactylopterus*
- in October - November 1996 and from May to November 1997 for *C. rupestris*
- in October 1996 and June 1997 for *A. bairdii*.

The criterion chosen to determine spawning period is not particularly well suited for the 2 last species because females in the partial-spent stage are scarce.

If *C. rupestris* females in vitellogenesis with hiatus, i.e. the maturing state just prior to the partial spent state, are considered as potentially spawning females, then the spawning period lasts from February to November in 1996 and 1997.

Using the same criteria for *A. bairdii* are not sufficient because females in vitellogenesis with hiatus are also scarce. For this species, females in vitellogenesis without hiatus are observed all year and females are probably able to spawn all year long.

From combined results of the 2 studies, the spawning period was determined :

- from March to June for *H. dactylopterus*; females were synchronous
- from February to November with a maximum from May to November for *C. rupestris*; females were asynchronous
- throughout the year with a maximum from January to April for *A. bairdii*; females were asynchronous

Fecundity

Nature of fecundity of each species was defined by examining the pattern of oocyte-diameter distributions in ovaries of various maturing states (**Fig. 3**). The 3 species show different patterns :

- *H. dactylopterus* : at the beginning of the maturation stage 3-oocytes go into vitellogenesis and this entry is continuous. Just before spawning a batch of oocytes hydrates and is isolated. At the end of spawning period vitellogenic oocytes not spawned become atretic. The number

of batches produced is not known. Annual fecundity of *H. dactylopterus* is indeterminate but a batch fecundity can be estimated just prior spawning.

• *C. rupestris* : the entry of stage-3 oocytes into vitellogenesis is not continuous, they form a batch. The oocytes of this isolated batch grow and just before spawning the batch is divided into several batches which remain isolated from the rest of the oocytes. In some females when a part of the hyaline oocytes are spent (occurrence of post-ovulatory follicles), a new batch of stage-3 oocytes goes into vitellogenesis. The fecundity of *C. rupestris* seems first to be determinate, but the formation of a new batch at the end of spawning shows that annual fecundity is indeterminate, the number of batches produced during the year is not known. However, a batch fecundity can be estimated during early vitellogenesis.

• *A. bairdii* : the entrance into vitellogenesis of stage-3 oocytes is continuous. Several batches are produced at the same time, but only one develops to spawning by increasing in diameter. When the isolated batch is spawned, then the next evolves. The number of batches produced is not known and annual fecundity of *A. bairdii* is indeterminate, but a batch fecundity can be estimated during late vitellogenesis.

Absolute and relative batch fecundities (F_A, F_R) were estimated for the 3 species and relationships between F_A and length, weight and age were calculated (**Table 4**).

DISCUSSION

Helicolenus dactylopterus

First maturity
The smallest mature specimen observed during this study was 13 cm long and 7 years old. This fish was exceptionally old for its length. The Von Bertalanffy growth curve established for this species predicts an age of 3-4 years, which is the age at first maturity defined for the same species off coasts of Morocco by Boutière (1958).

Spawning period
Wheeler (1968) reports a difference in the time of spawning, which may occur in November-December in the South of Europe and later in the North. In fact, the spawning period was determined to be at the end of autumn and beginning of winter in Mediterranean by Djabali *et al.* (1993), Bini (1969) and Dieuzeide *et al.* (1954); in November-December off West of Celtic Sea by Quéro & Vayne (1997); and from March to June off West of British Isles in the present study.

Coryphaenoïdes rupestris

First maturity
First maturity was determined at 50 cm of total length (≈13 cm pre-anal length -Lpa-), 11 cm (Lpa) - 10 years, and between 9 and 11 years old respectively by Gordon & Hunter (1994); Bergstad (1990) and Kelly *et al.* (1996) although it was determined at 11.5 cm (Lpa) and 14 years old in this study.

Spawning period
The numerous studies done on the reproduction of *C. rupestris* have often produced contradictory results because they are incomplete. Kelly *et al.* (1996); Magnusson & Magnusson (1995); Gordon & Hunter (1994) and Bergstad, (1990) established, as in the

present study, that the spawning period of this species is widespread throughout the year, but a major spawning occurs in autumn. In contrast Geistdoerfer (1979) reports a short spawning period in spring.

Fecundity

Fecundity was estimated to be between 9 000 and 64 000 oocytes per females by Kelly et al. (1996), Gordon & Hunter (1994), and Alekseyev et al. (1992). These values correspond to the data of this study. However, the nature of fecundity was defined only by Kelly et al. (1996), who established that fecundity was determinate. In the present study, it is assumed that annual fecundity is indeterminate because a new vitellogenesis beginning at the end of the previous one was observed in some females. Thus several cycles of vitellogenesis can occur during a spawning period unless, as suggests Alekseyev (1995), C. rupestris has a biannual reproductive cycle.

Alepocephalus bairdii

Oocytes development and first maturity

During the present study no large females in resting were recorded. This fact was also mentioned by Nazarov (1983). He showed that, in A. bairdii, no resting females were encountered among individuals of 75 cm or more, the « repeat spawners »; the females below this length were ready for their first spawning. In the present study 95 females (48 - 73 cm) were resting. Nine other individuals (58 - 68 cm) were in early vitellogenesis. The lack of large females in resting and early vitellogenesis could be explained by either a geographical or bathimetric segregation between females in different maturing states or by assuming that only the smallest females, less than 73 cm S.L., would undergo a resting period during their first sexual cycles whereas the longest ones would spawn several times per year, each year without resting.

Spawning period

Golovan & Pakhorukov (1975) have suggested that spawning of A. bairdii living in the central east Atlantic Ocean takes place in winter. According to Nazarov (1983) it may extend over a longer period in the north east Atlantic. In the present study, the author did not observe a well-defined spawning period, females seem to spawn throughout the year with a maximum from January to April.

Fecundity

In 1983 Nazarov estimated the batch fecundity of 12 females of A. bairdii to be from 2 477 to 8 664 oocytes per female; these values were similar to those observed by Golovan & Pakhorukov (1975; 1980) and in the present study. Nazarov (1983) assumed A. bairdii to be a batch spawner, but his analysis led him to conclude to an « only once a year » spawn.

CONCLUSION

Results of our study on the reproductive parameters of the 3 species, indicated that the deeper the habitat of the species, the longer the reproductive period: 4, 10 and 12 months respectively for H. dactylopterus, C. rupestris and A. bairdii. This would indicate a relationship between depth and reproductive period length. But assuming it as a general rule is not possible, e.g. Hoplostethus atlanticus (living in 1 000-m bathymetric zone) is a counter-example with a

1-month spawning period in February off West of British Isles (Berréhar and Du Buit 1998 ; personal communication). The lack of synchronisation in individual gonad maturation and/or individual spawning in the 2 deepest populations studied was also notable. Long spawning periods and asynchronism in maturation could be explained by the lack of pronounced cyclic environmental factors in the deep-sea

Reproduction can be estimated by several factors that are all subject to uncertainty, therefore more studies are necessary to accuratly estimate reproductive parameters :
- Length at first maturity can be determined, but age at first maturity is dependant on age determination, which is still neither validated nor calibrated among readers.
- When females are synchronous, the spawning period can be determined, but when they are not, the definition of spawning period becomes imprecise and needs to be calibrated.
- Fecundity is often estimated and assumed as annual regardless of its determinate or indeterminate nature. The establishment of the pattern of fecundity is necessary before it can be estimated. In the case of indeterminate annual fecundity, even if a batch fecundity can be estimated, the number a batches produced are often not known and annual fecundity can't be assessed.

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Table 1 : Number of samples taken to characterise reproduction of the 3 species.

	Macroscopic examination	Gonado-somatic index (GSI)	Histological examination	Assessment of fecundity (oocyte-diameter distribution; estimation of fecundity)
Helicolenus dactylopterus	1 258	565	529	61 (17 ;8)
Coryphaenoïdes rupestris	1 247	507	506	154 (16 ;62)
Alepocephalus bairdii	972	349	372	145 (15 ;54)

Table 2 : Length and age at first maturity and maximum length and age for the 3 species.

	Length at first maturity (cm)	Age at first maturity (years)	Maximum length observed (cm)	Maximum age determined (years)
Helicolenus dactylopterus	13 (Standard length)	7	32.5	43
Coryphaenoïdes rupestris	11.5 (Pre-anal length)	14	29.5	54
Alepocephalus bairdii	55 (Standard length)	15	93	38

Table 3 : Monthly distribution of the maturing states of ovaries of the 3 species recorded from December 1995 to December 1997.

Helicolenus dactylopterus

Date	Maturing state of ovaries							Total
	1	2	3	5	6	7	8	
Dec 95	9	2						11
Jan 96								0
Feb 96	11	1						12
Mar 96			9	6		1		15
Apr 96	1		2	1		4	11	19
May 96	11							11
Jun 96				4		5	9	18
Jul 96	15						1	16
Aug 96	15						4	19
Sep 96	21							21
Oct 96	31							31
Nov 96	9							9
Dec 96	15	1						16
Jan 97	18	2	1					21
Feb 97	6	7	6					19
Mar 97	11	8	14	1				34
Apr 97	18	1	3	7	1		2	32
May 97	6			1		11	11	29
Jun 97	20		2	10		4	2	38
Jul 97	31							31
Aug 97	39							39
Sep 97	24							24
Oct 97	15							15
Nov 97	27	2						29
Dec 97	8	12						20
Total	361	36	37	29	1	25	40	529

Alepocephalus bairdii

Date	Maturing state of ovaries						Total
	1	2	3	4	6	9	
Dec 95	6		5				11
Jan 96	3		4				7
Feb 96	2		8	1			11
Mar 96		1	10	2		1	14
Apr 96				2		3	5
May 96	1	1	10			2	14
Jun 96	2		14	1			17
Jul 96	4		13	1		1	19
Aug 96	1	1	8			1	11
Sep 96	5	1	15	2		1	24
Oct 96	7		6		1		14
Nov 96	4		7	1		1	13
Dec 96	6	1	21	1			29
Jan 97	1		1				2
Feb 97							
Mar 97	1	1	2				4
Apr 97	3		17	2		4	26
May 97	10		4			4	18
Jun 97	9		15	2	1	13	40
Jul 97	9		14				23
Aug 97	11		17	1		1	30
Sep 97	2		1				3
Oct 97	1	1	7				9
Nov 97	6	2	17			1	26
Dec 97	1		1				2
Total	95	9	217	16	2	33	372

Coryphaenoïdes rupestris

Date	Maturing state of ovaries								Total
	1	2	3	4	6	8	9	10	
Dec 95	2	8	2						12
Jan 96		4	2			1	2	1	10
Feb 96	8	3	4	3				3	21
Mar 96	7			5					12
Apr 96	5	5	3	2					15
May 96	5	1		6					12
Jun 96	5	2		7			1		15
Jul 96	12	1		6					19
Aug 96	3	8	2	7		1			21
Sep 96	10	5		9			2		26
Oct 96	3	10	1	6	1	6	2		29
Nov 96	4	8		2	2	1			17
Dec 96	12	11	1			3	1		28
Jan 97	6	8	1						15
Feb 97	8	7	1	3					19
Mar 97	4	4	7	6					21
Apr 97	4	4	2	9					19
May 97	12	3		13	2		2		32
Jun 97	2	2	2	25	1				32
Jul 97	7	6		13	1		2		29
Aug 97	1	3		16					20
Sep 97	6	5		5		2	2		20
Oct 97	2	1		14	1	1			19
Nov 97	8	14	4	4	1	5	4		40
Dec 97	1	2							3
Total	137	125	32	161	9	13	15	14	506

1: Sexual resting
2: Beginning of vitellogenesis
3: Vitellogenesis without hiatus
4: Vitellogenesis with hiatus
5: Partial spent without hiatus
6: Partial spent with hiatus
7: End of spawning without hiatus
8 End of spawning with hiatus
9: Recovery of vitellogenesis at the end of spawning
10: Recovery before vitellogenesis

Table 4 : Absolute and relative batch fecundities of the 3 species. (r :correlation factor ; p : probability of acceptance of Pearson's correlation test ; NS : non significant correlation ; S : significant correlation)

|	Number of females examined and their length range	Absolute batch fecundity (number of oocytes per female)	Relations between absolute batch fecundity (F_A) and length (Lst - standard length or Lpa), weight and age	Relative batch fecundity (number of oocytes per 100g of eviscerated fish)
Helicolenus dactylopterus	8 females 19-25 cm Lst	range 1 212 - 20 504 mean ± 95% confidence limit 7 729 ± 4 598	F_A=2 146.9Lst-39 234 (r=0.71, p=0.05, NS) F_A=49.28Weight-7 024 (r=0.81, p=0.01, S) F_A=1 444.5age-7 979.8 (r=0.93, p=0.001, S)	range 421 - 4 836 mean ± 95% confidence limit 2 376 ± 1 093
Coryphaenoïdes rupestris	62 females 13-27 cm Lpa	range 2 489 - 68 780 mean ± 95% confidence limit 23 189 ± 4 066	$Log_{10}(F_A)$=3.4Log_{10}(Lpa) -0.089 (r=0.78, p=0.000, S) F_A=28.54Weight-2 187.3 (r=0.79, p=0.000, S) F_A=618.6age+4 760 (r=0.26, p=0.048, S)	range 465 - 5 945 mean ± 95% confidence limit 2 532 ± 255
Alepocephalus bairdii	54 females 63-88 cm Lst	range 458 - 7 049 mean ± 95% confidence limit 3 371 ± 365	F_A=74.35Lst-2 081 (r=0.34, p=0.013, S) F_A=0.56Weight+1 794 (r=0.34, p=0.011, S) F_A=-17.29age+3 735 (r=-0.05, p=0.723, NS)	range 10 - 219 mean ± 95% confidence limit 125 ± 12
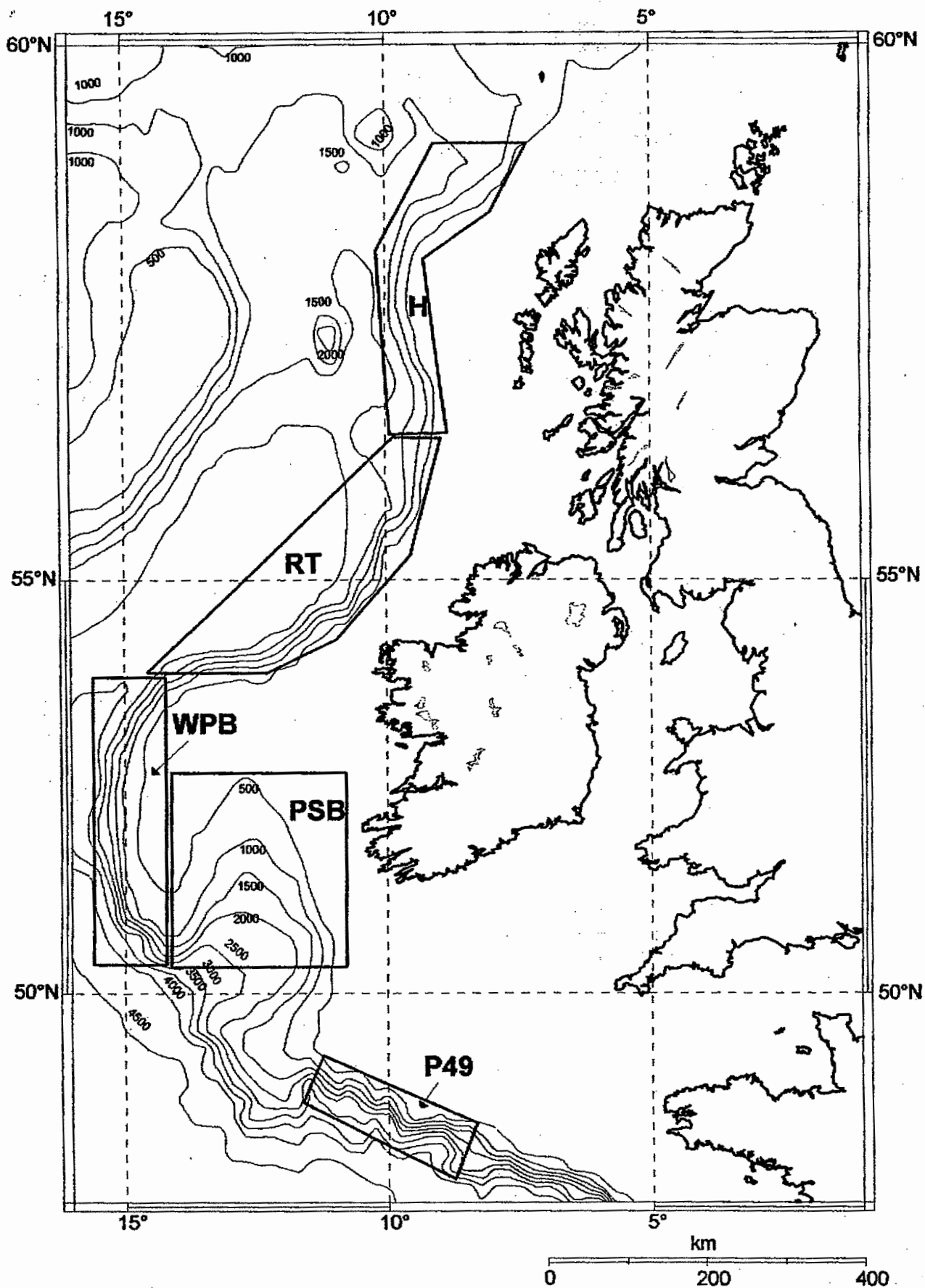
Fig. 1: Sampling areas, H: Hebridean Terrace (56°N-59°N), RT: Rockall Trough (53°40'N-56°N), WPB: West Porcupine Bank (50°30'N-53°40'N and 14°W-16°W), PSB: Porcupine Sea Bight (50°N-52°30'N and 11°W-14°W) and P49: Pointe 49 (49°N-49°40'N).
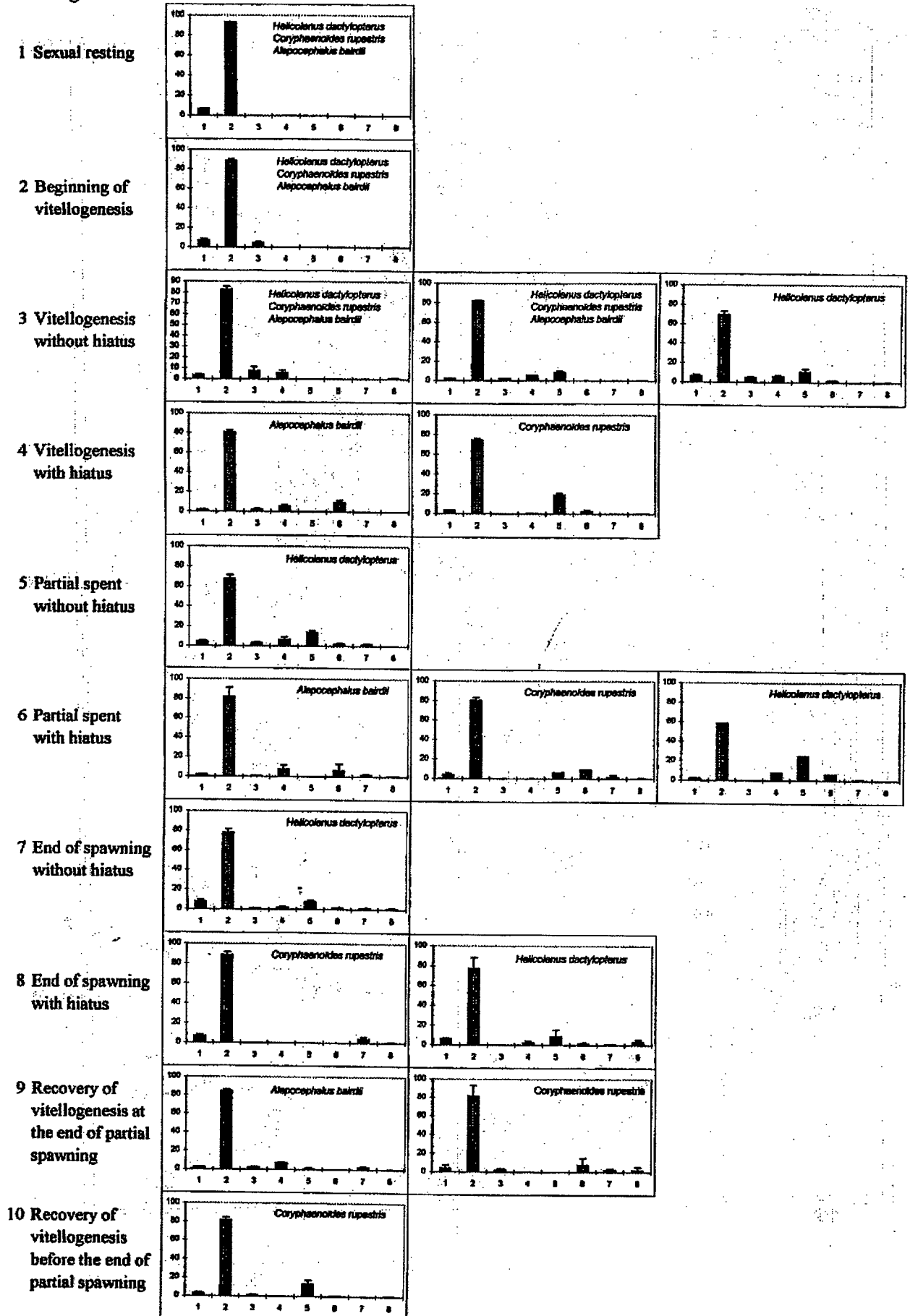
Maturing state of ovaries

1 Sexual resting

2 Beginning of vitellogenesis

3 Vitellogenesis without hiatus

4 Vitellogenesis with hiatus

5 Partial spent without hiatus

6 Partial spent with hiatus

7 End of spawning without hiatus

8 End of spawning with hiatus

9 Recovery of vitellogenesis at the end of partial spawning

10 Recovery of vitellogenesis before the end of partial spawning

Fig.2: Maturing states of ovaries illustrated by different oocyte frequency distributions observed in the 3 species.
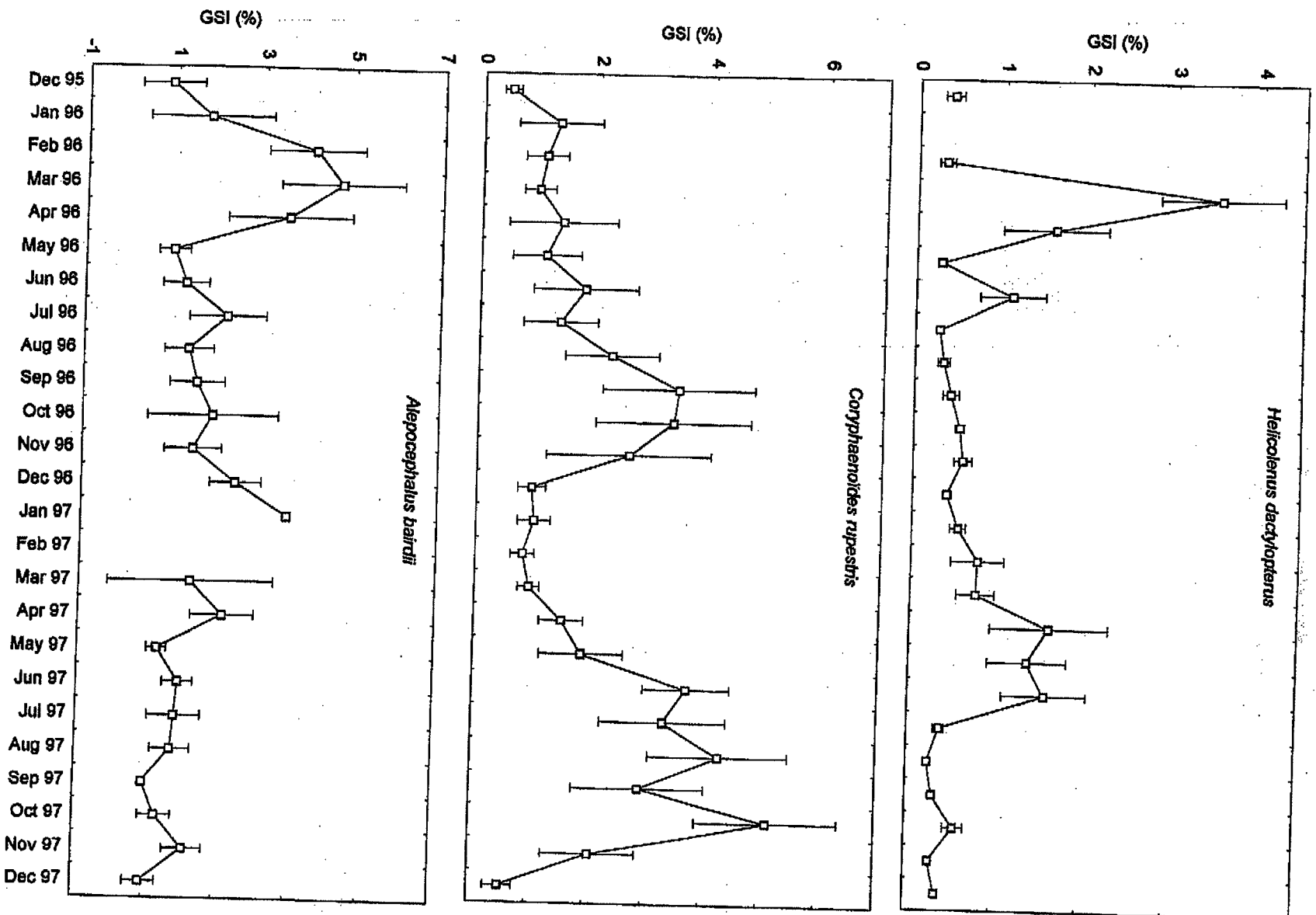
12

Fig.3: Seasonal patterns of GSI (mean + 95% confidence limits) from December 1995 to December 1997 of *H. dactylopterus, C. rupestris* and *A. bairdii.*

Helicolenus dactylopterus   _Coryphaenoïdes rupestris_   _Alepocephalus bairdii_
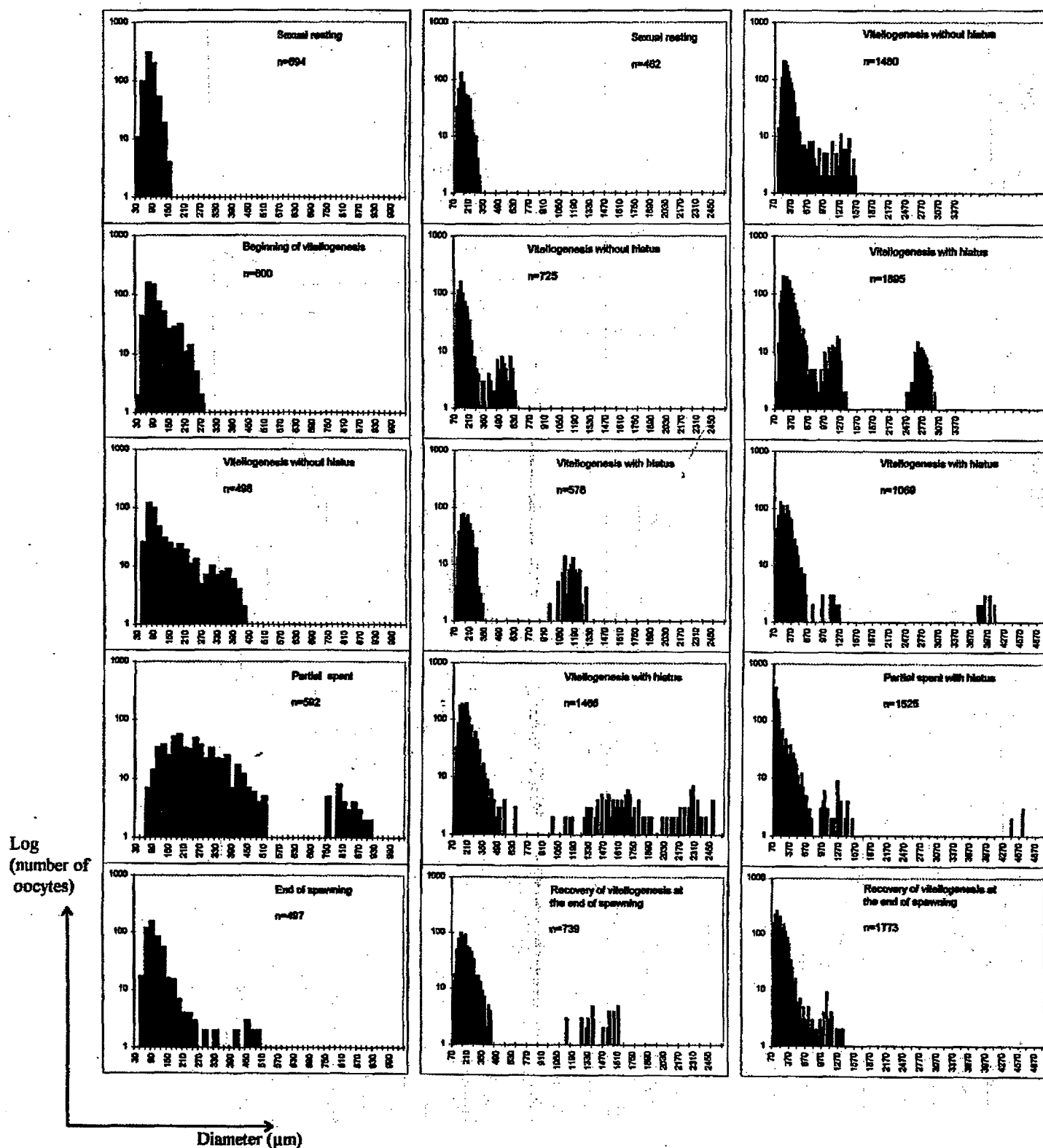

Fig. 4: Oocyte-diameter distributions of the 3 species in ovaries in different maturing states.